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TABLE OF CONTENTS

Volume 101

INDEX TO NEW TAXA

VOLUME 101

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

Mammalia

PLANTAE

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
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A NEW SUBSPECIES OF *LEIOCEPHALUS PERSONATUS* (SAURIA: IGUANIDAE) FROM HAITI

Frank Gali, Albert Schwartz, and Alejandro Suarez

Abstract.—A new isolated subspecies of *Leiocephalus personatus* is described from near the southern coast of the Haitian Tiburon Peninsula. Comparisons are made with its most closely related geographical congener, *L. p. personatus.*

Schwartz (1967) recorded one female *Leiocephalus personatus* Cope from the town of Aquin, Département du Sud, Haiti, which he questionably assigned to the subspecies *L. p. personatus.* Aquin lies on the southern coast of the Haitian Tiburon Peninsula, and the locality is separated from the nearest population of *L. personatus* by the intervening Massif de la Hotte. Much additional material, collected by Richard Thomas, from the Aquin area allows us to clarify the status of the population of Aquin *L. personatus,* which is distinct from *L. p. personatus,* and for which we propose the name.

Leiocephalus personatus elattoprosopon, new subspecies

Holotype.—USNM 197370, adult male, ca. 1 km inland, basal portion of the Morne Dubois "peninsula," Dépt. de Sud, Haiti, one of series collected 20 Jul 1971 by native collectors; original number ASFS V26037.

Paratypes.—(All from Haiti, Dépt. du Sud): ASFS V26036, same data as holotype; CM 83051–60, MCZ 156222–31, MNHNSD 221–30, USNM 197383–91, Aquin, 12–13 Jul 1971, native collectors; ASFS V25793, ca. 11 km SE Vieux Bourg d'Aquin, 14 Jul 1971, native collectors; ASFS V26030–31, beach area at base of Morne Dubois "peninsula," 20 Jul 1971, R. Thomas; ASFS V26051–621, basal area at the base of the Morne Dubois "peninsula," 21 Jul 1971, native collectors.

Associated specimen.—ASFS V25728, Grosse Caye, south of Aquin, Dépt. du Sud, Haiti.

Diagnosis.—A subspecies of *Leiocephalus personatus* characterized by pale gray middorsal region with pale buff lateral stripes; ventral color pale green with very pale green (nearly white) spotting; mask present but restricted and usually dorsal to ear opening; chin and anterior throat dark gray rather than black; sides red with pale gray-green centers to scales; median dorsal scales between occiput and vent 40–63 ($\bar{x}$ = 50.1 ± 1.7 = twice standard error of mean), median rows of dorsal scales 19–40 (28.6 ± 1.6).

Distribution.—Département du Sud, Haiti, from the vicinity of Vieux Bourg d'Aquin northward to Aquin and onto the Morne Dubois "peninsula"; presumably also Grosse Caye off this southern coast.

Description of holotype.—Adult male with following measurements and counts (all measurements in millimeters): SVL (snout–vent length) 80, tail length 105; dorsal crest scales occiput-axilla 16, dorsal crest scales on trunk 26; one-half midbody scales 22; subdigital fourth toe tricarinate scales 22/22; loreals 4; 4 prefrontal scales, row incomplete; 7/8 supraocular scales; supraorbital semicircles incomplete; parietal scales in contact.

Dorsal ground color pale gray, dorsolateral stripes pale buff in life but faded in preserved specimen; sides red with pale gray-green centers to scales, becoming greener on lower sides, with gray to pale stripes which may be very indistinct; mask dark brown with dark gray in loreal region, mask restricted and ending dorsal to ear opening; top of head brown with gray supraocular scales; upper surface of hindlimbs dark green with pale green spotting, forelimbs pale gray-green with pale green spotting; chin and anterior throat dark gray rather than black, followed by pale gray scales randomly smudging balance of throat; ventral ground color pale green (gray-green laterally) with very pale green (nearly white) spotting; tail brown above and light brown below.

Variation.—The series of 55 specimens of *L. p. elattoprosopon* has the following scale counts: dorsal crest scales occiput-vent 40–63 ($\bar{x}$ = 49.8 ± 1.7); dorsal crest scales occiput-axilla 16–27 (21.4); dorsal crest scales on trunk 19–40 (28.6 ± 1.6); tricarinate scales 15–26 (21.4); loreals 4–17 (5.7); supraoculars 6/6 (30 specimens), 6/5 (1), 5/5 (2), 7/6 (10), 7/7 (6), 7/8 (4), 6/8 (2); semicircles more often complete (95%), and parietals usually in contact (91%). The prefrontal row varies between 3 and 5 scales (Mo = 3), the median head shields are 4–8 (Mo = 5), and the frontoparietal row is more often complete than not (49 of 55 specimens). The largest male has a SVL of 83 and is a topotype, and the largest females measure 60 SVL and are from Aquin.

The series of specimens was described in life as follows. Males have a dorsal pale gray ground color; some adult males have pale buff dorsolateral stripes obvious, others lack this feature. All males have 2 to 4 dark brown nuchal bars, more obvious in some than in others. Sides have red scales with other pale scales gray-green centered, the scales becoming greener on the lower sides, and limited ventrolaterally by gray to pale stripes which may be very indistinct. Mask dark brown with dark gray in loreal region; mask present but restricted and usually dorsal to ear opening. In some specimens the mask extends further posteriorly than in others. The ventral ground color is pale green (gray-green laterally) with very pale green (nearly white) spotting. The throats are green and ventrals are 40–64 ($\bar{x}$ = 50.1 ± 1.7), and median dorsal trunk scales are 19–40 (28.6 ± 1.6). In *L. p. personatus* these counts are 47–61 (53.5 ± 1.0) and 24–40 (32.4 ± 1.0), respectively.

Remarks.—*Leiocephalus p. elattoprosopon* is similar to *L. p. personatus* in having a head scutellation formula of 3-5-4 (prefrontals-medians-frontoparietals). Both subspecies have masks, but they differ in that the mask in *L. p. elattoprosopon* usually is restricted dorsal to the ear opening, unlike that of *L. p. personatus* in which the mask extends half way to the forelimb insertion, including the eyes and the loreal region, and as far anteriorly as the tip of the snout.

The distribution of *L. p. elattoprosopon* as currently known is restricted to the Morne Dubois "peninsula," and north to Aquin and Vieux Bourg d'Aquin, a distance of about 0.7 km.

It is intriguing that *Ameiva chrysolaema evulsa* Schwartz (1973) and *L. p. elattoprosopon* occur in much the same general area, although the former species occurs (as far as known) only on Grosse Caye, whereas *L. p. elattoprosopon* occurs on the adjacent mainland, as well as on Grosse Caye. Both lizards represent southern outlier populations of species that are limited, on the Tiburon Peninsula, to the northern coast (*Leiocephalus*; 25 km) or extend only a short distance along the coast west of Port-au-Prince (*Ameiva*; 85 km). Intervening areas, which have been intensively sampled, seem not to harbor populations of either lizard. It seems that the Aquin-Morne Dubois "peninsula" region has a peculiar relictual fauna that was once more widespread, or continuous with relatives farther to the east and north.

Etymology.—The name *elattoprosopon* is from the Greek elatton (less) and prosopon (face, mask), in reference to the reduced dark mask in this subspecies in contrast to that in *L. p. personatus.* The name is used as an appositional noun.

Specimens examined.—(Other than *L. p. elattoprosopon*; all are *L. p. personatus* from Haiti): Dépt. du Sud, Jérémie (MCZ 3615, two syntypes); Les Roseaux (MCZ 74626–39); 16 km E Baradères (USNM 80773–66); Grand Boucan (USNM 80774–87); Presqu'île de Baradères, vicinity of Grand Boucan (ASFS V26282–338); Petit Trou de Nippes (USNM 80788–98); 1.7 km SE Anse à Veau (ASFS V42829); 2.7 km S Anse à Veau, 46 m (ASFS V43187–88); Ti Anse, ca. 9.5 km NW Miragoâne (ASFS V26212–17); 9.7 km SW Miragoâne (MCZ 25433); Dépt. de l'Ouest: Léogâne (MCZ 13834–37); 3.2 km SW, less than 1.6 km E Léogâne, ±122 m (ASFS V8317–22); Bayeux (USNM 75906); L'Acul (USNM 72607–12); just W Grand-Goâve (ASFS V36552–68, ASFS V45471, ASFS V45513, ASFS V45528).

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SYNONYMY OF THE GENUS *NECTONEANTHES* IMAJIMA, 1972, WITH *NEANTHES* KINBERG, 1866 (POLYCHAETA: NEREIDIDAE)

Robin S. Wilson

Abstract.—*Nectoneanthes oxypoda* (Marenzeller, 1879) and *N. alatopalpis* (Wesenberg-Lund, 1949) are synonymized with *Neanthes succinea* Leuckart, 1847. *Nectoneanthes* Imajima, 1972, with type species *Nereis* (*Alitta*) *oxypoda* Marenzeller, thus becomes a junior synonym of *Neanthes* Kinberg, 1866. An undescribed species of *Neanthes* is recognized. *Nectoneanthes ijimai* (Izuka, 1912) is once more referred to *Neanthes,* and *Nectoneanthes latipoda* Paik, 1973 and *N. multignatha* Wu, Sun & Yang, 1981 are referred to *Neanthes* for the first time.

The genus *Nectoneanthes* was erected by Imajima (1972) for two species of *Neanthes* Kinberg, 1866, which lack falcigers in all neuropodia: *N. oxypoda* (Marenzeller, 1879) (type species by original designation) and *N. ijimai* (Izuka, 1912). Three additional species have subsequently been placed in the genus: *Nectoneanthes latipoda* Paik, 1973; *N. multignatha* Wu, Sun & Yang, 1981; and *N. alatopalpis* (Wesenberg-Lund, 1949) which was transferred from *Neanthes* to *Nectoneanthes* by Wu, Sun & Yang, 1981.

In a previous paper (Wilson 1984) I examined all Australian material of *N. oxypoda* and synonymized these records with *Neanthes succinea* (Leuckart, 1847). I have now been able to examine type material of *Nereis* (*Alitta*) *oxypoda* Marenzeller and *Nereis alatopalpis* Wesenberg-Lund, which are here shown to be junior synonyms of *Neanthes succinea. Nectoneanthes* Imajima, 1972 thus falls into synonymy with *Neanthes* Kinberg, 1866.

Loss and breakage of atokous setae occurs prior to metamorphosis in epitokous nereidids (Clark 1961), hence absence or apparent absence of neuropodial falcigers should not be accepted as a valid taxonomic character unless undamaged specimens encompassing a wide size range and thus age are available for study. The specimens examined in this study and all literature records represent large specimens with expanded parapodial lobes which are probably approaching epitoky.

The three remaining species that have been referred to the genus *Nectoneanthes* and an undescribed form previously confused with *N. oxypoda* appear to be valid species and are here referred to the genus *Neanthes.* This determination can only be confirmed when atokous material of these species becomes available for study; however, it has not been possible to obtain material of these three oriental species. These taxa are discussed below.

All species discussed here are adequately figured in the original descriptions or in subsequent publications; these figures are referred to in the relevant descriptions below and no new figures are presented here.

The specimens examined in this paper are deposited in the following institutions: British Museum (Natural History), London (BMNH); National Science Museum, Tokyo (NSMT); Zoological Museum, Copenhagan (ZMK); Naturhistorisches Museum, Vienna (ZMV) and National Museum of Natural History, Smithsonian Institution, Washington (USNM).

Neanthes Kinberg, 1866

Neanthes Kinberg, 1866. Type species: *N. vaalii* Kinberg, 1866 (designated by Hartman, 1959:249).—Hartman, 1940:219 (generic definition emended); 1959:249 (for additional synonymies).

Nectoneanthes Imajima, 1972. Type species: *Nereis (Alitta) oxypoda* Marenzeller, 1879 (by original designation). New synonymy.

Definition.—Eversible pharynx with conical paragnaths on both rings. Four pairs of tentacular cirri. Parapodia biramous. Notosetae homogomph spinigers; neurosetae including homogomph and heterogomph spinigers (emended after Fauchald 1977:89).

Remarks.—As a consequence of the new synonymies made in this paper, several species previously placed in *Nectoneanthes* Imajima have been referred to *Neanthes* Kinberg. These species are not presently known to possess neuropodial falcigers and thus violate the widely used definition of *Neanthes* provided by Fauchald (1977). Wilson (1984:221) however noted that three species of *Neanthes* belonging to Group I in Fauchald's (1972) subdivision of the genus are already known to lack neuropodial falcigers: *N. agnesiae* (Augener, 1918); *N. chingrighattensis* (Fauvel, 1932) and *N. mexicana* Fauchald, 1972. In view of the incomplete material presently available of these species, and the loss and replacement of setae which is known to occur in ageing nereidids, the presence of neuropodial falcigers should no longer be included in the generic definition of *Neanthes* and the generic definition of Fauchald (above) is emended accordingly.

Additional comments on the synonymy of *Nectoneanthes* with *Neanthes* are included in the *Neanthes succinea* Remarks section (below).

Neanthes succinea (Leuckart, 1847)

Nereis succinea Leuckart, 1847:154, pl. 2, figs. 9, 11.

Nereis (Alitta) oxypoda Marenzeller, 1879: 120–122, pl. 2, fig. 3. New synonymy.

Nereis oxypoda.—Monro, 1934:362–363 (in part, specimen collected by Chen).

Nereis (Neanthes) oxypoda.—Ibáñez, 1972: 24–26, fig. 1.

Nereis alatopalpis Wesenberg-Lund, 1949: 281–283, figs. 15–17. New synonymy.

Nectoneanthes alatopalpis.—Wu, Sun & Yang, 1981:152–153, fig. 94A–F; 1985: 168–170, fig. 94A–F.

Neanthes succinea.—Wilson, 1984:218–221, fig. 4A–F (includes additional synonymies).

Material examined.—JAPAN: ("wahrscheinlich bei Yokohama" Marenzeller, 1879:122) coll. Roretz 1876, 2 syntypes of *Nereis oxypoda,* ZMV 2140. Tokyo Bay, coll. Döderlein, 1 specimen of *Nereis oxypoda,* ZMV 781.

CHINA: Amoy, coll. T. Y. Chen, No. 27, 1 specimen of *Nereis oxypoda,* BMNH ZK 1933.3.2.40.

IRAN: Gulf of Oman, Sta 72C, 12 km von Yask, coll. G. Thorson, 20.4.1937, holotype (by monotypy) of *Nereis alatopalpis,* ZMK.

Description.—Two syntypes of *Nereis oxypoda*: larger syntype with pharynx partly extended, consisting of anterior fragment of 169 setigers, about 260 mm long, 9 mm wide anteriorly (excluding parapodia), decreasing to 7 mm wide in middle setigers and 3.5 mm wide in posteriormost setigers; smaller syntype with pharynx fully everted, consisting of anterior fragment of 103 setigers, about 100 mm long, 5 mm wide anteriorly decreasing to 2.5 mm wide in posteriormost setigers. Color pale yellow. Prostomium dorsoventrally flattened, with 1 pair of triangular palps with very small palpostyles, 1 pair of antennae about ¼ as long as prostomium. Four pairs of tentacular cirri, longest extending back 3–4 setigers, with cylindrical cirrophores basally; cirrophores of 2 dorsal pairs longer than ventral pairs, forming ⅓–¼ of length of cirrus. Jaws amber, with 11–12 small lateral teeth on smaller syntype; larger syntype with darker, stouter jaws with indistinct teeth. Pharynx with pale amber paragnaths, pointed cones on area VI, low domes on all other areas. Larger syntype with many maxillary ring paragnaths indistinct or lost, area I = 0; II = 3–4; III = 4; IV = about 6; V = 0; VI = 10 in circular group on left, 0 on right side; VII–VIII = about 50 small paragnaths in 2 irregular rows. Smaller syntype with I = 0; II = 14/16; III = 5; IV = 14/17; V = 1; VI = 10, 10; VII–VIII = 56 in 2 irregular rows. Notopodia and neuropodia each with 3 triangular lobes throughout, posterior parapodia with dorsal notopodial lobe becoming greatly expanded and enclosing dorsal cirrus in large notch (Marenzeller 1879: pl. 2, fig. 3). Dorsal and ventral cirri approximately equal to length of neuropodial lobes throughout. Both syntypes with most setae shed or broken; few notopodial homogomph spinigers present and homogomph and heterogomph setae with appendages missing remain in many neuropodia.

Specimen from Japan (ZMV 781) consisting of anterior fragment of 81 setigers, about 100 mm long, 6 mm wide anteriorly; only 25 anterior setigers in good condition. Agrees with description of syntypes except as follows: pharynx everted, area I = 4 in longitudinal series; II = 19/21; III = 6; IV = 16/17; V = 3; VI = 11/12; VII–VIII = 77 in 2–3 rows, including single evenly spaced anterior row of larger cones. Setae of anterior setigers mostly intact, homogomph spinigers in notopodia, homogomph and heterogomph spinigers in both neuropodial fascicles.

Specimen from China (BMNH ZK 1933.3.2.40) immature female epitoke with coelomic gametes, entire but regenerating posteriorly, 80 setigers, about 75 mm long, 5 mm wide (part of material examined by Monro 1934 and Wilson 1984). This specimen also agrees with the above descriptions and apparently lacks neuropodial falcigers.

Holotype of *Nereis alatopalpis* (ZMK) incomplete posteriorly, broken into 3 pieces: an anterior fragment with pharynx everted, 46 setigers, 25 mm long, 2.5 mm wide; fragment of 16 setigers, 7 mm long and fragment of 10 setigers, 4 mm long. Prostomium strongly flattened, triangular, with small palpostyles, antennae ¼ as long as prostomium; 4 pairs of tentacular cirri, longest extending back 4 setigers, 2 dorsal pairs with cirrophores accounting for about ⅕ of length of cirri. Jaws translucent amber, smooth distally, with 5–6 indistinct teeth basally. Paragnaths pale amber domes, arranged as follows: area I = 1; II = 11/9; III = 0; IV = 8/9; V = 0; VI = 8/11 in circular groups; VII–VIII = about 32 in 2 widely spaced irregular rows. Notopodia and neuropodia each with 3 acutely triangular lobes, dorsal and ventral cirri about as long as parapodial lobes. Dorsal notopodial lobe greatly expanded posteriorly, enclosing dorsal cirrus in large notch (Wesenberg-Lund 1949:fig. 16a–d). Notosetae homogomph spinigers, neurosetae homogomph and heterogomph spinigers in both fascicles.

Remarks.—Marenzeller's original description of *Nereis oxypoda* was very detailed and agrees with that of the two syntypes re-examined in this study. There are no significant differences in the form of the paragnaths and parapodia between this material and epitokes and sub-epitokes of *Neanthes succinea* (Leuckart) as described by Pettibone (1963:165) and Wilson (1984: 218). *Nereis alatopalpis* Wesenberg-Lund was also found to be identical to previous descriptions of *N. succinea. Nereis oxypoda* and *N. alatopalpis* are thus formally synonymized with *Neanthes succinea* and *Nectoneanthes* Imajima, 1972 (of which *N. oxypoda* is the type species) becomes a junior synonym of *Neanthes* Kinberg, 1866.

Imajima (1972) gave absence of neuropodial falcigers and expansion of the dorsal notopodial lobe as distinguishing characters of *Nectoneanthes*; however, these are characters associated with the development of epitoky. All material previously referred to *Nectoneanthes* represents large (100–300 mm long) specimens and it is probable that even the "atokes" described by Izuka (1912) and Imajima (1972) are in fact epitokes at varying stages of development. Several smaller specimens of *N. succinea* and the holotype of *N. alatopalpis* examined here apparently lack neuropodial falcigers; however, in the absence of a detailed study of the ontogeny of *N. succinea* this character alone is insufficient to form the basis of a new taxon.

Other nereidid species can apparently achieve sexual maturity in either their second or third year (e.g., *Hediste diversicolor* (Müller) and *Nereis pelagica* Linnaeus as indicated by Olive & Garwood (1981), Mettam et al. (1982), and Möller (1985)), hence sexual maturity and epitokal modifications may also occur in *N. succinea* at different sizes and ages. It is possible that different populations differ in this respect: e.g., Reish (1977) noted that a population of *N. succinea* introduced into the Salton Sea, California, differed from nearby natural populations only in reaching a larger size.

This paper does not address the possibility that sibling species may be present within what is now known as *Neanthes succinea.* Examples already exist of widely distributed nereidid species complexes which are morphologically similar but exhibit distinct reproductive patterns (reviewed by Smith 1958): *Hediste*[1] *diversicolor* (Müller)/*Neanthes japonica* (Izuka)/*N. limnicola* (Johnston) and *Platynereis dumerilii* (Audouin & Milne Edwards)/*P. megalops* (Verrill)/*P. massiliensis* (Moquin-Tandon). *Neanthes succinea* may also be shown to represent such a complex; however, large numbers of specimens and knowledge of life histories of populations from widespread localities will be needed to detect sibling species if they exist.

The present study shows that the taxa *Nectoneanthes, N. oxypoda,* and *N. alatopalpis* (recorded only from within the range of *Neanthes succinea*) can no longer be retained.

Distribution.—*Neanthes succinea* is widely distributed in the Northern and Southern Hemispheres (Pettibone 1963, Day 1967). It is likely that some of the more recent records are the result of introductions by humans, both intentional and accidental (Smith 1963, Reish 1977, Proskurina 1979).

Neanthes sp.

Nereis oxypoda.—Okuda, 1933:247, pl. 13, figs. f–h (not Marenzeller 1879).

Nereis oxypoda var.—Monro, 1934:362–363 (in part, 2 specimens collected by Ping) (not Marenzeller 1879).

Nereis (*Neanthes*) *oxypoda.*—Treadwell, 1936:268 (not Marenzeller 1879).

Nectoneanthes oxypoda.—Imajima, 1972: 113–117, figs. 35–37.—Paik, 1972:135, fig. 4a–h; 1973:82, figs. 1k, l, 2, table 1 (not Marenzeller 1879).

Neanthes (*Nectoneanthes*) *oxypoda* var.—Wilson, 1984:220–221 (not Marenzeller 1879).

Material examined.—JAPAN: Kojima Bay, Okayama Prefecture, coll. K. Izuka, 17 Dec 1906, 3 specimens labelled *Nectoneanthes oxypoda,* NSMT 5290–5292.

CHINA: Amoy, Outer Harbour, coll. Prof. C. Ping, 6 Apr 1923, No. 3, 2 specimens identified by Monro, 1934 as *Nereis oxypoda* var., BMNH ZK 1926.4.27.22–23. Amoy, No. 27, coll. T. Y. Chen, 1 gravid female identified as *Nereis* (*Neanthes*) *oxypoda* by Treadwell, 1936, USNM 22240.

Description.—Six specimens: smallest 104 setigers, 80 mm long, 4.5 mm wide (anterior fragment); largest 160 setigers, 260 mm long, 6 mm wide (complete). Prostomium flattened, wider than long, 1 pair of triangular palps with small palpostyles, 1 pair of an-

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[1] *Hediste* is currently held to be a monotypic genus (Hartmann-Schröder 1971, Fauchald 1977); a review of this group is required since obviously closely related species are presently placed in separate genera.

tennae about ¼ as long as prostomium. Four pairs of tentacular cirri, longest extending back to setiger 3, 2 dorsal pairs with short indistinct cirrophores. Two pairs of dark red subdermal eyes. Jaws translucent amber with 6–12 distinct lateral teeth. Paragnaths amber, consisting of pointed cones on areas VI and maxillary ring, low domes elsewhere, arranged as follows: area I = 2–4 in longitudinal series; II = 16–30; III = 4–15 in triangular patch; IV = 24–32; VI = 8–13 in circular group; V–VIII = continuous band of 100–200 paragnaths, 6–8 rows deep dorsally and ventrally, tapering to 2–3 rows deep laterally (Imajima 1972:fig. 35b, c). Notopodia and neuropodia each with 3 acutely triangular lobes throughout and with dorsal and ventral cirri of about equal length to that of each parapodial lobe. Parapodial lobes of similar proportions throughout, excepting dorsal notopodial lobe greatly expanded posteriorly, enclosing dorsal cirrus in large notch (Imajima 1972:fig. 35d–h). Notosetae homogomph spinigers, neurosetae homogomph and heterogomph spinigers in dorsal and ventral fascicles. Anal cirri extending back over posteriormost 12–13 setigers.

Remarks.—Imajima (1972) apparently did not examine the syntypes of *Nereis* (*Alitta*) *oxypoda* Marenzeller, 1879, in designating that species as the type species of *Nectoneanthes.* Imajima's detailed description of new material from several Japanese localities agrees with that given above for *Neanthes* sp. but differs significantly from *Neanthes succinea* in the arrangement of paragnaths on the oral ring: *N. succinea* has a ventral band of up to about 80 paragnaths tapering to a narrower band laterally and absent dorsally; *Neanthes* sp. has 100–200 oral ring paragnaths forming a continuous band 6–8 rows deep dorsally and ventrally and tapering to 2–3 rows laterally, exactly as figured by Imajima (1972:fig. 35b, c). In all other respects these specimens agree with the description of large specimens of *N. succinea* but in view of the substantial differences noted above this material is here considered to represent a separate species. *Neanthes* sp. is not formally described and named here since all specimens examined are large and lack neuropodial falcigers; as with *N. succinea* (see above), smaller specimens of this form may be found to possess neuropodial falcigers but in any case it is desirable that a formal description of this taxon be based on a wider size range of material than is currently available.

The above discussion shows that Imajima (1972) misidentified his specimens as *Nereis* (*Alitta*) *oxypoda* Marenzeller, 1879, when designating that species as the type species of *Nectoneanthes.* Under Article 70 (b) of the International Code of Zoological Nomenclature (3rd edition), the case must then be referred to the International Commission on Zoological Nomenclature to designate a type species for the genus *Nectoneanthes*; in the interest of stability I shall be proposing to the Commission that *Nereis (Alitta) oxypoda* Marenzeller, 1879, be so designated.

Distribution.—Recorded from China, Japan and Korea.

Neanthes ijimai (Izuka, 1912)

Nereis ijimai Izuka, 1912:174–176, pl. 2, fig. 1, pl. 19, figs. 1–9.

Neanthes ijimai.—Imajima and Hartman, 1964:144–145.

Nectoneanthes ijimai.—Imajima, 1972: 117.—Wu, Sun & Yang 1981:146–148, fig. 90A–H; 1985:161–163, fig. 90A–H.—Srinivasa Rao & Sarma, 1982:447, figs. 6, 7.

Nectoneanthes imajimai (sic.).—Wilson, 1984:220 (demonic typographical error for *Nectoneanthes ijimai*).

Remarks.—Izuka's original description referred to a very large specimen (390 mm long for 215 segments); however, the only subsequent reports of new material relate to smaller specimens (40 mm long by Srinivasa Rao & Sarma 1982; up to 12 mm long, 3.5 mm wide for 25 anterior setigers by Wu et al. 1981). These smaller specimens were reported to lack neuropodial falcigers; however, as noted above in the *Neanthes succinea* Remarks section, this character alone should not form the basis of a new genus. *Neanthes ijimai* is distinguished from other similar species discussed here by the absence of paragnaths on areas I, III and V of the pharynx.

Distribution.—Recorded from China, Japan and India.

Neanthes latipoda (Paik, 1973), new combination

Nectoneanthes latipoda Paik, 1973:81–84, figs. 1, 2.

Remarks.—The description of *Neanthes latipoda* by Paik (1973) was apparently based on larger specimens (163 mm long for 127 segments, 15 mm wide). As with the species of *Nectoneanthes* discussed above, the distinguishing characters of *N. latipoda* can probably be attributed to the large size and approaching epitoky of the specimens examined. The description and figures by Paik show that *N. latipoda* is very similar to epitokes of *N. succinea* but differs in the arrangement of paragnaths: the band of paragnaths of the maxillary ring are continuous through the dorsal region as a single scattered band. As noted above, the maxillary ring band is not continuous dorsally in *N. succinea. Neanthes latipoda* appears to be intermediate between *Neanthes* sp. (above) and *Neanthes succinea* and is retained here as a separate species.

Distribution.—Korea.

Neanthes multignatha (Wu, Sun & Yang, 1981), new combination

Nectoneanthes multignatha Wu, Sun & Yang, 1981:148–149, fig. 91A–H; 1985: 163–164, fig. 91A–H.

Remarks.—The figures of *N. multignatha* in the original description by Wu, Sun & Yang 1981 indicate that this species is very close to *N. succinea,* perhaps differing in the reduced numbers of paragnaths on areas III and IV of the pharynx.

Distribution.—China.

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LIMNODRILOIDES FAXATUS AND *DOLIODRILUS PUERTORICENSIS*, NEW LIMNODRILOIDINAE (OLIGOCHAETA: TUBIFICIDAE) FROM PUERTO RICO

Christer Erséus and Michael R. Milligan

Abstract.—*Limnodriloides faxatus,* new species, with long, heavily muscular atrial ducts, dorsal spermathecal pores and torch-shaped sperm bundles in the spermathecal ampullae, and *Doliodrilus puertoricensis,* new species, with atrial ducts that are only moderately modified (by comparison with its congeners) and minute spermathecae, are described from the west coast of Puerto Rico.

A few marine Tubificidae (subfamilies Rhyacodrilinae, Phallodrilinae, and Tubificinae) were recently described from Aguadilla and Mayagüez Bays in Puerto Rico by Milligan (1986) from material collected by Dr. A. Stoner for the Center for Energy and Environmental Research, University of Puerto Rico. A new member of the Limnodriloidinae from the same collection, *Limnodriloides faxatus,* is described in the present paper together with *Doliodrilus puertoricensis,* another new species from the west coast of Puerto Rico. The material of the latter, which was placed at the first author's disposal by Dr. M. L. Jones at the National Museum of Natural History (USNM), Washington, D.C., originates from a benthic community study in Laguna Joyuda (near Mayagüez) conducted by Mr. R. L. Castro at the Department of Marine Sciences, University of Puerto Rico.

The anterior end of one of the specimens of *D. puertoricensis* was sectioned and stained in Heidenhain's hematoxylin and eosin; the remaining material was stained in paracarmine or Grenacher's alcohol borax carmine and mounted whole in Canada balsam. The types series are deposited at the USNM.

Limnodriloides faxatus, new species
Fig. 1

Holotype.—USNM 101460, whole-mounted specimen.

Type locality.—Mayagüez Bay, 1 mile offshore, 18°15′48″N, 67°12′05″W, 11.5 m, silt and clay with pockets of detritus (coll. A. Stoner, 14 May 1985).

Paratypes.—USNM 101461, 2 specimens from Aguadilla Bay, 18°29′03″N, 67°10′44″W, 16 m, mud and shell fragments (coll. A. Stoner, 18 Apr 1985).

Other material examined (authors' collection).—Six specimens: 1 from type locality, 4 from locality of paratypes, and 1 from another station in Aguadilla Bay, 38 m, coarse sand and shell (coll. A. Stoner, 18 Apr 1985).

Description.—Length (only 1 complete specimen) 7.1 mm, 52 segments. Width at XI (compressed, whole-mounted worms), 0.17–0.26 mm. Clitellum extending over XI–XII in 1 paratype, poorly developed in other specimens. Setae (Fig. 1A) bifid, 35–50 μm long, 1.5–2 μm thick, with upper tooth slightly thinner and shorter than lower. Setae 2–3 per bundle anteriorly, absent from X–XI, 2 per bundle in postclitellar seg-

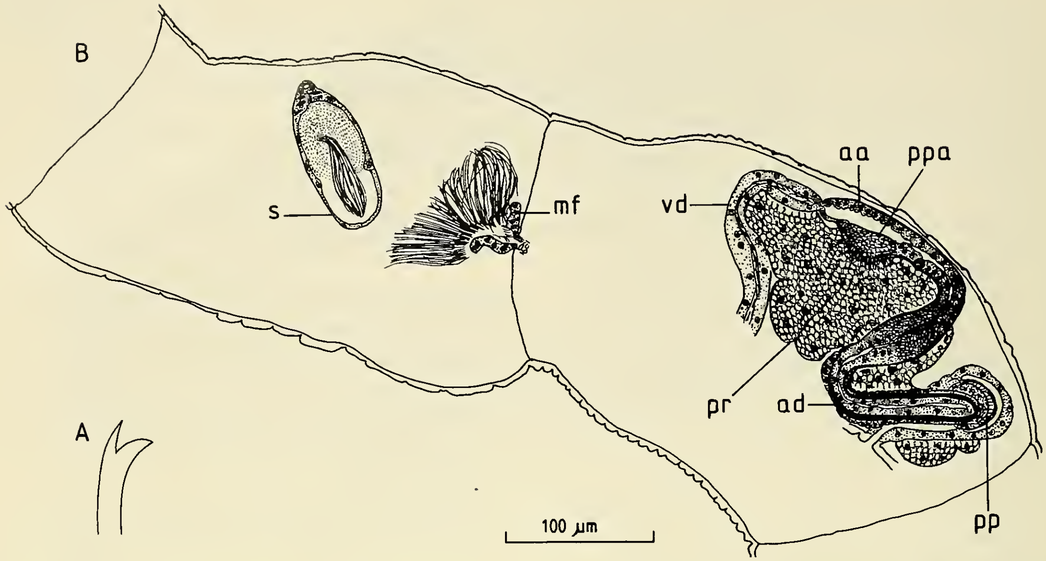

Fig. 1. *Limnodriloides faxatus*: A, Free-hand drawing of seta; B, Lateral view of genitalia in segments X–XI. (aa = atrial ampulla, ad = atrial duct, mf = male funnel, pp = pseudopenial papilla, ppa = prostatic pad, pr = prostate gland, s = spermatheca, vd = vas deferens.)

ments. Male pores paired in line with ventral setae in posterior part of XI. Spermathecal pores in line with dorsal setae in middle of X.

Pharyngeal glands in IV–V. Pair of slender oesophageal diverticula present anteriorly in IX. Male genitalia (Fig. 1B) paired. Vas deferens 16–22 μm wide, probably somewhat longer than atrium (not observed in its full length in available material), entering atrium apically. Atrial ampulla 40–75 μm long, 28–50 μm wide, ventrally bearing conspicuous prostatic pad; latter causing wall of ampulla to bulge considerably. Prostate gland large and lobed. Atrial duct slender (about 280 μm long in holotype), entally narrow and without granulation, in middle part with granulated inner epithelium and thin outer lining, ectally without granulation but with up to 10 μm thick muscular lining. Atrial duct terminating in large papilla at inner end of voluminous copulatory sac. Spermathecae (Fig. 1B, s) oblong, 100–145 μm long, 35–55 μm wide, with short (sometimes indistinct) ducts and thin-walled ampullae. In postcopulatory individuals, each ampulla with 1–2 torch-shaped, very characteristic bundles of sperm, latter partly embedded in amorphous mass of secretion.

Remarks.—The dorsal spermathecae, the long atrial ducts, and the absence of spermathecal setae render *L. faxatus* a member of the *agnes*-group within *Limnodriloides* (cf. Erséus 1982). The new species is easily distinguished from the other forms within this group by its wide and heavily muscular atrial ducts (ducts narrow and with thin muscular lining in the other species), and the characteristic shape of the sperm bundles in the spermathecae.

Etymology.—The name *faxatus* means 'with torch,' or 'flame,' and refers to the appearance of the sperm bundles in the spermathecae.

Distribution and habitat.—Known only from the west coast of Puerto Rico. Subtidal, muddy or shelly sediments, 11.5–38 m depth.

Doliodrilus puertoricensis, new species
Fig. 2

Holotype.—USNM 101462, whole-mounted specimen.

Type locality.—Laguna Joyuda, an en-

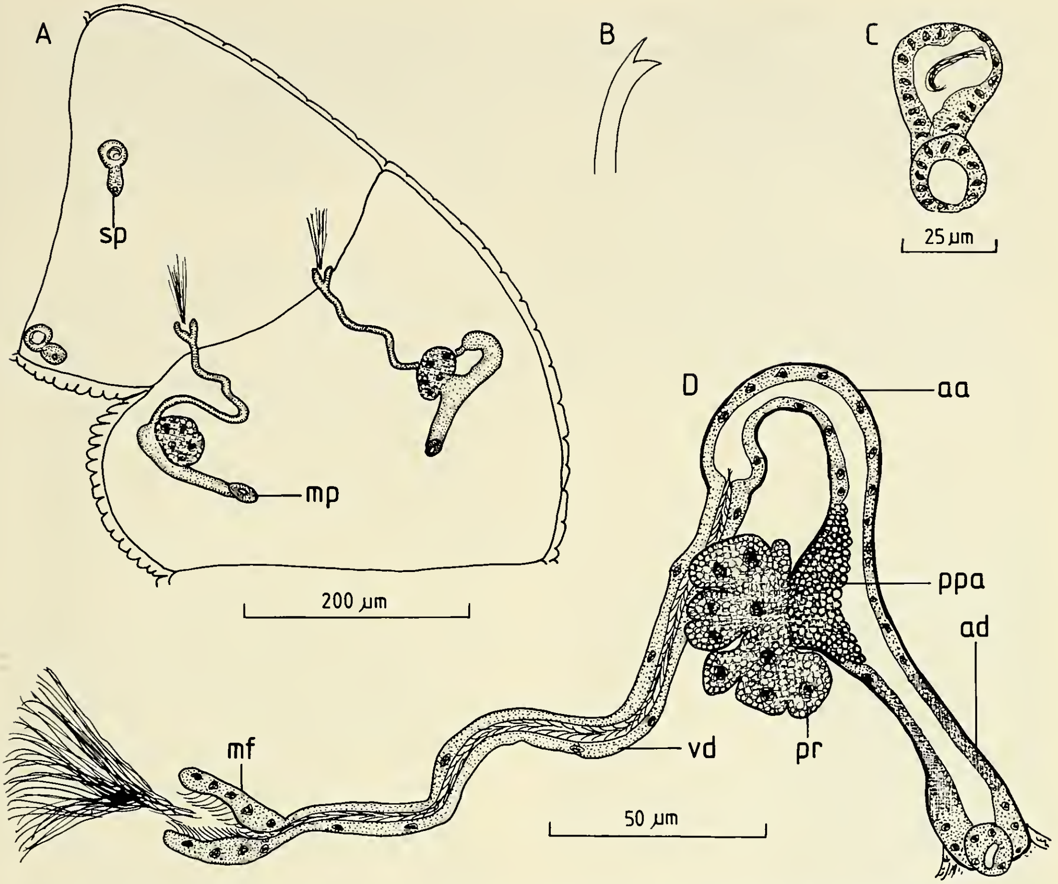

Fig. 2. *Doliodrilus puertoricensis*: A, Ventral view of segments X–XI, showing size and location of spermathecae and male ducts; B, Free-hand drawing of seta; C, Spermatheca; D, Male efferent duct. (mp = male pore, sp = spermathecal pore; other abbreviations as in Fig. 1.)

closed brackish-water lagoon (salinities fluctuating between 8 and 44‰) located 9 km S of Mayagüez, W Puerto Rico, 1–2.5 m, mud (material coll. R. L. Castro on several occasions between 9 Nov 1978 and 10 Jul 1979, holotype on 10 Jan 1979).

Paratypes.—USNM 101463–101468, 1 sectioned and 5 whole-mounted specimens from type locality.

Other material.—USNM 101469–101485, 17 whole-mounted specimens, including immature and partially mature worms, from type locality.

Description.—Length (fixed specimens) 6.1–10.7 mm, 44–65 segments. Diameter at XI (whole-mounted, somewhat compressed worms) 0.32–0.44 mm. Clitellum extending over XI–XII. Setae (Fig. 2B) bifid, with upper tooth thinner than, but about as long as, lower. Bifids 40–60 µm long. 1.5–2.5 µm thick, (1)2–4 per bundle anteriorly, (1)2–3 per bundle in postclitellar segments. Ventral setae absent from XI. Male pores (Fig. 2A, mp) paired in line with ventral setae, posterior to middle of XI. Spermathecal pores (Fig. 2A, sp) paired in line with ventral setae, anteriorly in X.

Pharyngeal glands in III–V. Oesophagus dilated, thick-walled and with reticulate blood-plexus, in whole length of IX. Male ducts and spermathecae small in relation to body size (cf. Fig. 2A). Male genitalia (Fig. 2D) paired. Vas deferens 7–10 µm wide, about as long as atrium, joining apical end of latter. Atrium slender, tubular, about 165 μm long, with thin but distinct outer lining of muscles. Both ental part of atrial ampulla and ectal duct narrow (10–19 μm wide), with thin inner epithelium; middle part of atrium (ectal part of ampulla) conspicuously wider (about 25 μm), containing cone-shaped prostatic pad. Atrial duct shorter than ampulla, somewhat granulated in its middle part, ectally slightly dilated and opening to exterior through simple pore. Prostate gland small, lobed. Spermathecae (Fig. 2C) very small, with 24–27 μm long, 18–19 μm wide, ducts, and more or less spherical, 20–30 μm wide ampullae; ducts ectally dilated in fully mature specimens. Sperm as a small, curved bundle in each spermathecal ampulla.

Remarks.—This is the third species in the genus *Doliodrilus* Erséus, 1984, which accommodates limnodriloidines with (1) modified oesophagus in IX (but without proper anteroventral diverticula in this segment), (2) slender atria with a distinct prostatic pad in most ectal part of each atrial ampulla, (3) simple atrial ducts terminating in simple male pores, although the most ectal part of the ducts may be dilated, sharply bent, or modified into a posteriorly directed blind sac, and (4) a similar dilation of the most ectal part of the spermathecal ducts; cf. definition of genus given by Erséus (1985).

Doliodrilus puertoricensis is with regard to the atrial ducts the least modified species of the genus; in *D. tener* Erséus, 1984 (from Hong Kong) there is an abrupt bend about two-thirds down the length of the atrial ducts and in *D. diverticulatus* Erséus, 1985 (from Saudi Arabia) this 'bend' is further elaborated into a blind sac. The new species is further distinguished from the other two by its very small, roundish spermathecal ampullae, and its fewer setae (up to 5 or 6, occasionally even 7, setae per bundle anteriorly in the others), and from *D. diverticulatus* by its lack of an unpaired, dorsal oesophageal diverticulum in segment IX.

Distribution and habitat.—Known only from the type locality, west coast of Puerto Rico. Subtidal muds, subject to fluctuating salinities, 1–2.5 m depth. The species cooccurs with *Thalassodrilides gurwitschi* (Hrabě) and *T. belli* (Cook); cf. Erséus (1981).

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PENNELLA MAKAIRA, NEW SPECIES (COPEPODA: PENNELLIDAE) FROM THE ATLANTIC BLUE MARLIN, *MAKAIRA NIGRICANS,* IN THE CARIBBEAN SEA

W. E. Hogans

Abstract.—A new species of pennellid copepod, *Pennella makaira,* is described. Collected from the flesh of *Makaira nigricans* off Puerto Rico, *P. makaira* belongs to the group of species in the genus *Pennella* which are less than 50 mm in total length. It differs from its congeners in the size and arrangement of cephalothoracic papillae, and the structure and segmentation of the first and second antennae.

During an examination of the parasitic copepod genus *Pennella* Oken, 1815, in the collection of the United States National Museum of Natural History, three specimens of a previously undescribed species were discovered. This new species, *P. makaira* is described and illustrated herein.

Methods

The cephalothorax of each specimen was cleaned with 20% warm NaOH. After cleaning, one each of the first and second antennae and swimming legs were removed from the cephalothorax of two specimens and cleared in 85% lactic acid to reveal structural details. Figures were drawn with the aid of a camera lucida or drawing tube under phase-contrast microscopy (Photozeiss).

Pennella makaira, new species
Figs. 1–6

Description (based on 3 specimens).—Pennellidae: cephalothorax (Fig. 2a, b) subspherical, with rounded anterior end slightly excavate at center in dorsal view. Surface of anterior end completely covered by papillae (antennary processes). Papillae large, clavate to clublike, branched at margins; becoming smaller and spherical to knoblike at center. Junction of posterior end of cephalothorax and anterior of neck with 2 lateral horn holdfasts. Holdfast horns cylindrical, unbranched. Neck short, stout, cylindrical, expanded at junction with trunk. Trunk cylindrical, slightly transversely ridged, three-quarters total length, curved slightly ventrally in all specimens. Oviducts on ventral surface at junction of posterior end of trunk and anterior of abdomen. Abdomen dorsoventrally compressed, posterior extremity bifid, rounded. Ventral surface of abdomen covered by 2 rows of plumelike processes; plumes single or secondarily branched (Fig. 3). Egg strings (Fig. 4) incomplete, portions remaining cylindrical, filiform. Eggs uniseriate. Mean total length of specimens 28 mm (27–29 mm). First antennae (Fig. 5) 3-segmented, setose. Basal segment subquadrangular. Second segment cylindrical, with at least 22 setae (some probably missing in all specimens). Terminal segment three-quarters length of second segment, with apical armature of 12 setae; 9 long, flagelliform; 3 short, spiniform. First antennae on dorsal surface of cephalothorax, near anterior margin. Second antennae (Fig. 6) immediately anterior to first, 2 segmented, chelate, with large recurved claw closing on triangular spur on distal margin. Single, stout seta at base of

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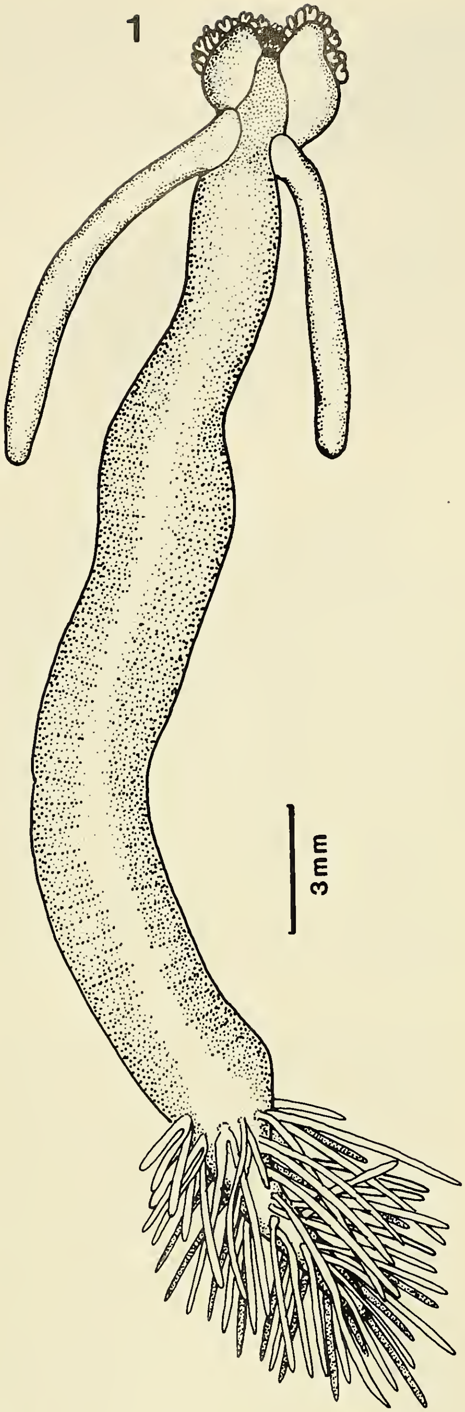


Fig. 1. *Pennella makaira*: trunk, lateral; cephalothorax, dorsal (holotype).

claw. Basal segment subquadrangular. Coxa of second antennae attached to subquadrangular scleritorized plate with single triangular pigment spot. Mouth pennellid, buried between papillae on anterior end of cephalothorax. Maxillae, maxillipeds not discernible. Four pairs of swimming legs on ventral surface close to posterior margin of cephalothorax. First 2 pairs biramous, third and fourth pairs uniramous.

Armament formula as follows:

	Endopod		Exopod	
	1	2	1	2
Leg 1	1-0	7	1-1	5,11
Leg 2	1-0	7	1-1	5,1
Leg 3	—	—	0-0	?,?
Leg 4	—	—	0-0	4,1

Male and pre-metamorphosis female unknown.

Host.—*Makaira nigricans* Lacépède (Atlantic blue marlin).

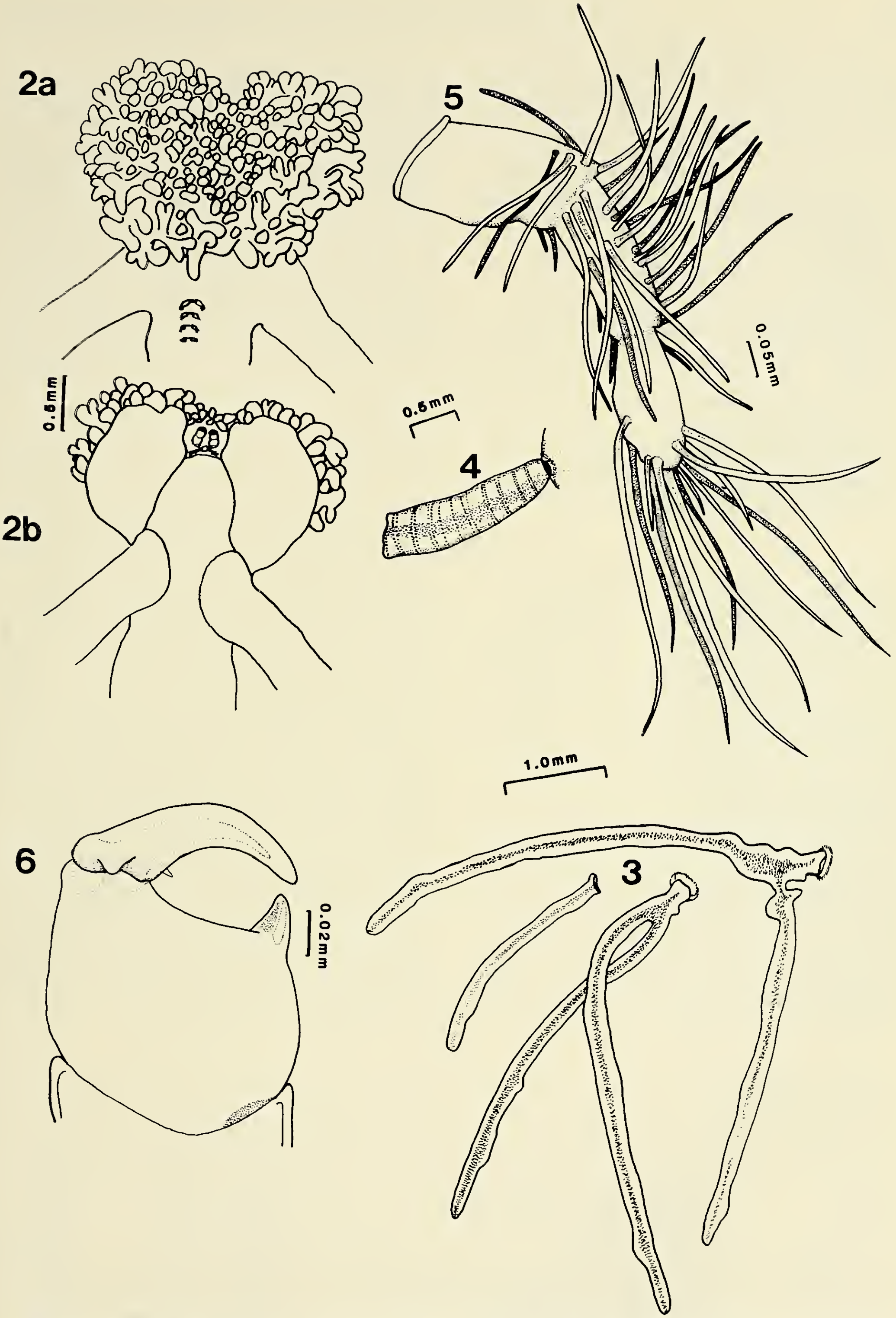
Site of infestation.—Branchiostigeal area: cephalothorax, lateral horns and neck of parasite embedded in flesh.

Locality.—San Juan Canyon, Puerto Rico.

Holotype.—USNM 111554.

Paratype.—USNM 222997.

Discussion.—During the examination of more than 200 specimens of *Pennella* in the USNM, three features were found which could be used for separating species of the genus: 1) Overall size of the mature female. Wilson (1917) used total length of the parasite (excluding egg strings) to separate the known species into two groups, those longer than 100 mm and those less than 50 mm. This is, from my examinations, a valid character for general sorting of species; *P. makaira* is in the less-than-50 mm category. 2) The number of segments of the first and second antennae and the structure of the terminal segment of the second antennae is consistent for each species. 3) In small species, the size, shape and arrangement of cephalothoracic papillae is similar among



Figs. 2–6. *Pennella makaira*: 2a, Anterior end of paratype, ventral; 2b, Same, dorsal; 3, Plumules from abdominal brush; 4, Egg string (incomplete); 5, First antenna, dorsal; 6, Terminal segment of second antenna, dorsal.

Table 1.—Comparisons of antennae structure of *Pennella makaira* to similar species in the genus *Pennella.*

Species	First antennae number of segments	Second antennae number of segments
P. biloboa	*	3
P. elegans	*	3
P. exocoeti	4[a]	2
P. longicauda	5	3
P. makaira n. sp.	3	2
P. platycephalus	*	*
P. robusta	3	3
P. sagitta	3[b]	2

* No available information.

[a] Based on two specimens identified by C. B. Wilson from *Exocoetus volitans* (USNM 112252).

[b] Based on one specimen identified by the author from *Histrio histrio* (BMNH 1985, 471).

specimens collected from the same host species or individuals of host species.

Pennella makaira is the smallest species of *Pennella* yet recorded from a scombroid fish. One other slightly larger species from scombrids, *P. biloboa* Kirtisinghe, 1932, was reported from the sailfish, *Istiophorous brevirostris* collected off Sri Lanka. The inadequate description of this species precludes any detailed comparisons. I have been unable to obtain the single type specimen for comparative purposes. From the limited figures in the original description, *P. biloboa* appears to be a slimmer, more delicate parasite than *P. makaira.* Gnanamuthu (1957) described four species of *Pennella* from flyingfishes off the coast of India. None of the species are adequately described. I have not been able to secure type material for any of these species: *P. elegans, P. longicauda, P. platycephalus,* and *P. robusta.* They could, judging from the limited figures, be specimens of a single species differing only in age. All four species have total lengths less than *P. makaira.* Two other small species, *P. exocoeti* (Holten, 1802), and *P. sagitta* (Linnaeus) appear to be valid. They have been well described previously and figured and can be distinguished from the new species as follows: *P. exocoeti* is found only on flyingfishes of genus *Exocoetus.* It has a 4-segmented first antenna, whereas the first antenna of *P. makaira* has only three segments. In addition, the distal spur of the terminal segment of the second antenna of *P. exocoeti* is much larger and more sharply pointed than in *P. makaira. Pennella sagitta* is found only on the sargassum fish *Histrio histrio*; it is a very delicate parasite with no spherical cephalothoracic papillae. One species which approaches *P. makaira* in total length, *P. diodontis* Oken, Chamisso, & Eysenhardt, 1821, is found, supposedly, only on diodontid porcupine fishes. The validity of the species has been questioned frequently (see Wilson 1917). It has never been adequately described. Although most of the above-listed species are of uncertain validity, a comparison of antenna structure and papillae form for each (compiled from the original descriptions) with those exhibited by *P. makaira* is shown in Tables 1 and 2, respectively.

Table 2.—Comparison of the structure of papillae of the cephalothorax of *Pennella makaira* to similar species in the genus *Pennella.*

Species	Papillae shape	Papillae arrangement	Papillae size
P. biloboa	spherical to clavate, unbranched	partially covering	variable
P. elegans	spherical to clavate, unbranched	partially covering	similar
P. exocoeti	club-like to spherical, unbranched	partially covering	variable
P. longicauda	clavate, unbranched	partially covering	variable
P. makaira n. sp.	tubiform to spherical, bifid irregular branching	completely covering	variable
P. platycephalus	spherical clavate to spherical, branching	partially covering	similar
P. robusta	clavate to spherical, branching	completely covering	variable
P. sagitta	tubiform, irregular branching	completely covering	similar

Acknowledgments

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THE PARASITIC ISOPOD *HOLOPHRYXUS ACANTHEPHYRAE* STEPHENSEN (EPICARIDEA: DAJIDAE) FROM THE SUBANTARCTIC SOUTH PACIFIC, WITH NOTES ON ITS SYNONYMY AND HOST

Robert A. Wasmer

Abstract.—The dajid isopod *Holophryxus acanthephyrae* Stephensen, 1912a, is newly reported from the subantarctic South Pacific. A female of the species, and the male recovered from her marsupium, collected attached to the carapace of a specimen of the oplophorid shrimp *Acanthephyra pelagica* (Risso) are described. It is concluded that *Isophryxus concavus* Schultz, 1977, the type species of the genus *Isophryxus,* recorded from the antarctic and subantarctic South Pacific, is a junior synonym of *Holophryxus acanthephyrae.* The three other known species of *Isophryxus, I. quadratohumerale* Schultz, 1978, *I. polyandrus* Schultz, 1978, and *I. septapodus* Schultz, 1978, are transferred to *Holophryxus.* Physical damage caused to the host shrimp by *H. acanthephyrae* is discussed. A list of the known species of *Holophryxus,* their distributions, and known host species is presented.

During a study of the pelagic caridean shrimps belonging to the family Oplophoridae collected by the USNS *Eltanin* from the antarctic and subantarctic South Pacific during the U.S. Antarctic Research Program (Wasmer 1986), I found an ovigerous female dajid isopod loose among specimens of the oplophorid *Acanthephyra pelagica* (Risso) collected at station 1723 of *Eltanin* cruise 24. A note in the sample bottle indicated that the isopod was collected attached to one of the shrimps in the sample, and a male specimen of *A. pelagica* in the bottle was found to have marks on the dorsal surface of its carapace which appeared to have been made by the mandibles and pereopods of the isopod. An additional male specimen of *A. pelagica* from *Eltanin* cruise 19, station 1480 was noted to have marks on its carapace similar to those on the shrimp from station 1723 of cruise 24, although no isopod was present in the sample bottle when it was obtained from the Smithsonian Oceanographic Sorting Center (SOSC).

I tentatively identified the female isopod (and the male found enclosed in her marsupium) from station 1723 as a member of the genus *Holophryxus* Richardson, based on the redescription by Butler (1964) of *H. alaskensis* Richardson, 1905 (the type species of the genus) and my examination, 1966, of the type specimens of *H. californiensis* Richardson, 1908 (synonymized with *H. alaskensis* by Butler in 1964) and of *H. giardi* Richardson, 1908. The examination of the types of these latter two species was made in conjunction with the identification of several dajids from shrimps collected off the coast of Oregon by oceanographic vessels of Oregon State University.

Of the five previously recognized species of *Holophryxus,* only one has been recorded from an oplophorid shrimp. Stephensen (1912a) described *H. acanthephyrae* based on a mature female collected off Greenland attached to the carapace on an oplophorid he identified as *Acanthephyra purpurea,* but which he later concluded (1912b) was *A. multispina,* a synonym of *A. pelagica* (see Wasmer 1986). The recent redescription of the female and the first description of the male of *H. acanthephyrae* by Jones & Smaldon (1986), published while the current work was in an early draft stage, strengthened my conclusion that the female and male isopod from *Eltanin* station 1723 are *H. acanthephyrae* Stephensen.

The dajid genus *Isophryxus* was established by Schultz (1977), with the type species *I. concavus.* The description was based on the holotype female and the allotype male found enclosed in her marsupium collected by a midwater trawl at station 1480 of *Eltanin* cruise 19. Eight additional specimens (six females and two males) of the species were recorded (Schultz 1977) from six midwater trawl stations occupied by the *Eltanin* during cruises 11, 15, and 19 in the antarctic and subantarctic South Pacific. The host species of none of these specimens was known to Schultz. Schultz pointed out that *I. concavus* is similar to the type species of the genus *Holophryxus,* from which it otherwise differs by having the pereonal segments indicated on the dorsal surface of the female. Schultz (1978) subsequently described three additional species of *Isophryxus* (*I. quadratohumerale, I. polyandrus,* and *I. septapodus*) from specimens collected by midwater trawls during *Eltanin* cruises 24, 25, and 35 in the antarctic and subantarctic South Pacific. Again, the host species is not known for these three species.

The purpose of this paper is to describe the female and male *Holophryxus acanthephyrae* from *Eltanin* station 1723, and to propose, based on examination of the pertinent types, that *Isophryxus concavus* Schultz is a synonym of *Holophryxus acanthephyrae* Stephensen. Evidence of physical damage caused to the host shrimp by *H. acanthephyrae* is also discussed. Lastly, a list of the known species of *Holophryxus,* their distributions, and known host species is presented.

Suborder Epicaridea
Family Dajidae
Holophryxus acanthephyrae Stephensen
Fig. 1A–D

Holophryxus acanthephyrae Stephensen, 1912a:112, figs. 13, 15–21.—Jones & Smaldon, 1986:303, figs. 1–6.

Isophryxus concavus Schultz, 1977:93, figs. 17A–17I, 18A–18H, 18O, 18P.

Material.—Ovigerous female (22.7 mm long and 10.7 mm wide), and male (2.3 mm long, 1.1 mm wide) from marsupium of female, collected attached to a male specimen of the oplophorid shrimp *Acanthephyra pelagica* (Risso), cl. 26.0 mm, from USNS *Eltanin* cruise 24, sta 1723 (18 Jul 1966, 40°01′S, 149°57′W to 40°05′S, 149°55′W, 880 m), USNM 233550.

Description.—Adult female: Body symmetrical, oblong-ovate, dorsal surface convex, ventral surface strongly concave anteriorly. Color in alcohol light yellow.

Dorsal prominence of cephalon slightly bilobed, not visible from below. Cephalic ridge narrow in dorsal view, anterior margin sinuous. Eyes absent.

True segmentation of pereon evident only in lateral view, indicated by posterior 4 pairs of 5 coxal plates; first pair of coxal plates fused with cephalic ridge, forming anterior boundary of oral area; fifth pair small, separated from fourth by distinct space. Dorsal surface of pereon with 3 shallow transverse furrows in integument behind rounded prominence of cephalon.

Pleon continuous with but narrower than pereon, tapering posteriorly to rounded extremity, unsegmented, lacking pleopods and uropods. Dorsal surface of pleon deeply excavated on both sides of midline near junction with pereon.

Oral area bounded anteriorly and laterally by flattened flange-like cephalic ridge.

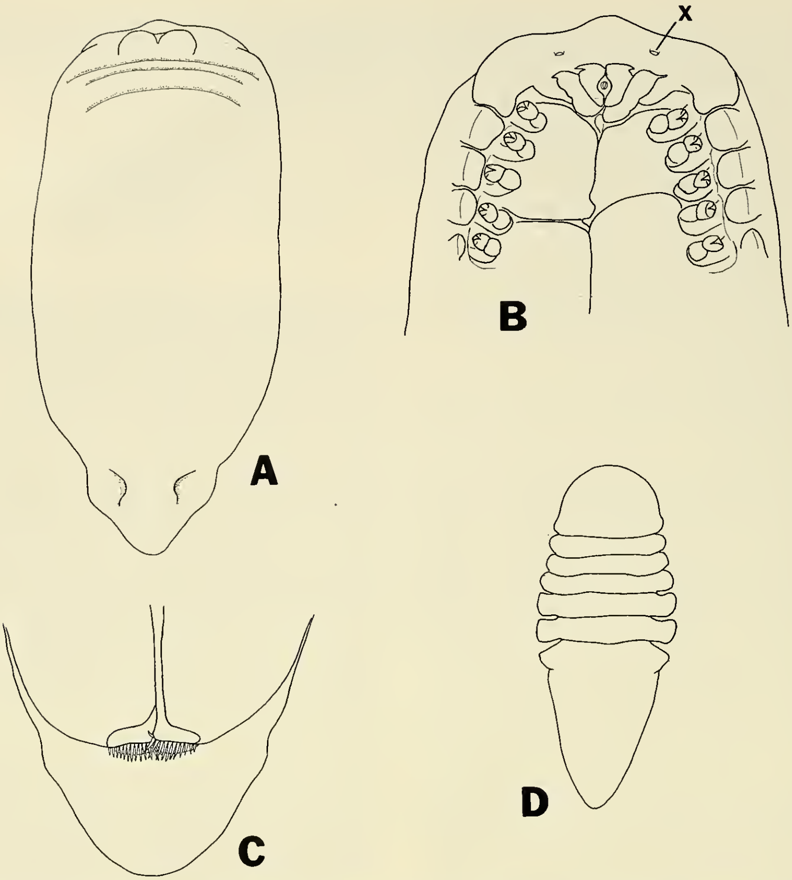

Fig. 1. *Holophryxus acanthephyrae, Eltanin* station 1723: A, Dorsal view, mature female; B, Ventral view, anterior part of pereon, mature female, x = pit organ; C, Ventral view, posterior part of pereon and pleon, mature female; D, Dorsal view, male.

Cephalic ridge with pair of narrow, slit-like pores or pit organs (Fig. 1B, x) about halfway from midline to lateral edge. First and second pairs of antennae unsegmented and flattened, with elongate lobe-like peduncles surrounding oral area. Tips of mandibles styliform, visible in central part of oral area; remaining mouthparts not visible without dissection. Five pairs of short pereopods present (pereopods 6 & 7 lacking), posterior 4 pairs arising from bases near separate coxal plates. Pereopods prehensile, all of similar size and shape, with dactyls strongly recurved and clawlike.

Five pairs of incubatory plates (oostegites) arising from bases of pereopods; only first and fifth pairs visible, covering other 3 pairs. Fifth pair of plates largest, extending to posterior end of pleon and forming largest part of marsupium, medial edges overlapping slightly; posterior margin of each ending in flattened crest just before pleon, each fringed with long spines (12 on left, 13 on right) above posterior end of marsupium.

Male: Elongate, symmetrical, dorsal surface slightly convex, ventral surface concave. Color in alcohol yellowish white.

Cephalon large, rounded anteriorly, completely fused with pereonite 1, lateral margin slightly indented posteriorly, indicating anterior limit of first pereonite. Eyes absent. First antennae short, composed of 3 articles;

second antennae somewhat longer (composed of 3 articles?), directed posteriorly; neither pair visible in dorsal view. Mandible tips projecting from oral area.

Pereonites 2–6 distinctly separated from each other, pereonite 7 almost completely fused with pleon; lateral margins of second through sixth rounded, lateral margins of seventh conical. Seven pairs of prehensile pereopods present.

Pleon conical, slightly longer than pereonites 1–6 combined, longer than wide, unsegmented, tapering posteriorly to narrowly rounded extremity. Pleopods and uropods absent.

Remarks.—Based on my comparison of the female and male dajid specimens and their host (*Acanthephyra pelagica*) from *Eltanin* station 1723 with the female holotype of *Holophryxus acanthephyrae* Stephensen, and its type host (*Acanthephyra pelagica*) obtained on loan from the Universitetets Zoologiske Museum in Copenhagen, as well as the description of the species given by Jones & Smaldon (1986), it is concluded that these specimens are identical with *H. acanthephyrae.*

There appear to be no significant differences between the holotype of *H. acanthephyrae* and the specimen from the *Eltanin* oplophorid. Both specimens are ovigerous females of comparable size and shape. The morphological details visible in dorsal, ventral, and lateral views of the two specimens are in very good agreement, although there is a minor difference in the number of spines on the posterior marginal crests of the fifth incubatory plates of the two specimens (14 on each in the case of the holotype, but only 12 and 13 on the specimen from the *Eltanin*).

The female described here is also in essential agreement with the female *H. acanthephyrae* redescribed and illustrated by Jones & Smaldon (1986), although that specimen is smaller and somewhat more deformed. The cephalic pores, first pointed out by Jones & Smaldon (1986), are also easily seen on the female described here. I was unable to see the pores on the holotype of *H. acanthephyrae* or on other members of the genus examined in the course of this study; perhaps the opening to the pore, which may be a sense organ of some type, can be contracted or closed off by the isopod so that it would be especially hard to see on some preserved specimens.

It is unfortunate that Stephensen did not have a male specimen of *H. acanthephyrae* with which the present male specimen can be compared. It is very likely that his holotype female has a male in her marsupium; several of the previously recorded males of other *Holophryxus* species have been taken from ovigerous females on which the medial margins of the fifth incubatory plates are close together or from females which have recently emptied marsupia (Rustad 1935, Butler 1964, Jones & Smaldon 1986).

The male described here is very similar to the male described by Jones & Smaldon (1986). The shape of the lateral margins of the seventh pereonites differ in the two specimens, being more conical in the present specimen. However, as pointed out by Jones & Smaldon (1986), there are few diagnostic characters separating the males known for the different species of *Holophryxus,* as well as evidence of some variation in body form between males of the same species.

The fact that the holotype of *H. acanthephyrae* and one of the four specimens of the species reported by Jones & Smaldon (1986), as well as the present female, were collected on specimens of the oplophorid shrimp *Acanthephyra pelagica* is strong evidence that the dajid from the *Eltanin* material is *Holophryxus acanthephyrae.* Each of the five species of *Holophryxus* for which the host is known occurs on only a single species of pelagic decapod shrimp (see below).

Holophryxus acanthephyrae has been recorded previously from the type locality in Davis Strait west of Greenland (60°07′N, 48°26′W) and from the Western Approaches and Bay of Biscay (Stephensen

1912a, Jones & Smaldon 1986). The present record from the subantarctic South Pacific thus considerably extends the known distribution of the species. This new record is not totally unexpected when the wide distribution of its host in the North Atlantic from about 13°N northward, the Mediterranean, the South Atlantic from 24°S southward, and the Indo-Pacific between 32°S and 57°S (Wasmer 1986) is considered.

Discussion

Notes on synonymy.—Comparison of the holotype and allotype of *Isophryxus concavus* Schultz in the National Museum of Natural History with the holotype of *Holophryxus acanthephyrae* and with the female and male dajids from *Eltanin* station 1723 identified herein as *H. acanthephyrae,* has convinced me that Schultz (1977) mistakenly separated *Isophryxus* from *Holophryxus* and that *Isophryxus concavus* and *Holophryxus acanthephyrae* are in fact the same species. By the rule of priority, *Isophryxus concavus* should therefore be considered a junior synonym of *Holophryxus acanthephyrae* and *Isophryxus* becomes a junior synonym of *Holophryxus.*

Schultz (1977) appears to have overlooked Butler's 1964 redescription of *Holophryxus alaskensis* Richardson, 1905, the type species of the genus. Butler pointed out that folds in the dorsal integument of the pereon of several specimens of that species give the impression of segmentation, but that the folds are not related to segmentation. Richardson did not mention well defined transverse folds in her description or show them in her figures of *H. alaskensis*; however, the specimens were apparently somewhat stout and irregularly shaped when preserved (Butler 1964), and for that reason the folds are probably not so evident. Folds or furrows are also present on the dorsal integument of the pereon of *Hypodajus georgiensis* Nierstrasz & Brender à Brandis (1931:212, figs. 106–108), synonymized with *Holophryxus alaskensis* by Butler (1964). Anterior dorsal integumentary furrows of the pereon are present to some extent on all other known species of *Holophryxus* and have been noted in descriptions or are visible on figures of those species, as indicated in the following citations: *H. giardi* Richardson, 1908:fig. 1; *H. richardi,* Stephensen, 1912a:fig. 11; Rustad, 1935:16, fig. 4; *H. acanthephyrae* Stephensen, 1912a:113, fig. 15; Jones & Smaldon, 1986:309, fig. 2A and 2B; and *H. fusiformis* Shiino, 1937:188, fig. 1A and 1B.

The flattened posterior marginal crests armed with long fringing spines on the fifth incubatory plates of the holotype and paratype females of *I. concavus* (not mentioned in Schultz's description of the species but visible in his figs. 17A and 18B) also indicate that these specimens belong to the genus *Holophryxus.* Such crests are apparently present on mature females of the other species of the genus. Although Richardson (1905) does not specifically mention the crests and spines in her diagnosis of the genus or in her description of *H. alaskensis,* her fig. 8c seems to indicate the presence of spines on the posterior part of the fifth incubatory plates. Butler (1964), in his redescription of *H. alaskensis,* mentions the presence of such fringed crests on the fifth incubatory plates on mature females of the species, although his fig. 1c curiously does not show them. The crests are also drawn and described by Nierstrasz & Brender à Brandis (1931:212, fig. 108) in their description of *Hypodajus georgiensis.* Richardson (1908) does not mention the fringed crests in her description of *Holophryxus giardi* and they do not show on her fig. 1, but in my examination of the syntypes I found that they are in fact present on the mature female but folded downward and under the posterior edge of the fifth incubatory plates so as to be hidden from view; this is the result of the specimen being somewhat deformed when preserved. For the other species in the genus, the following citations show the pres-

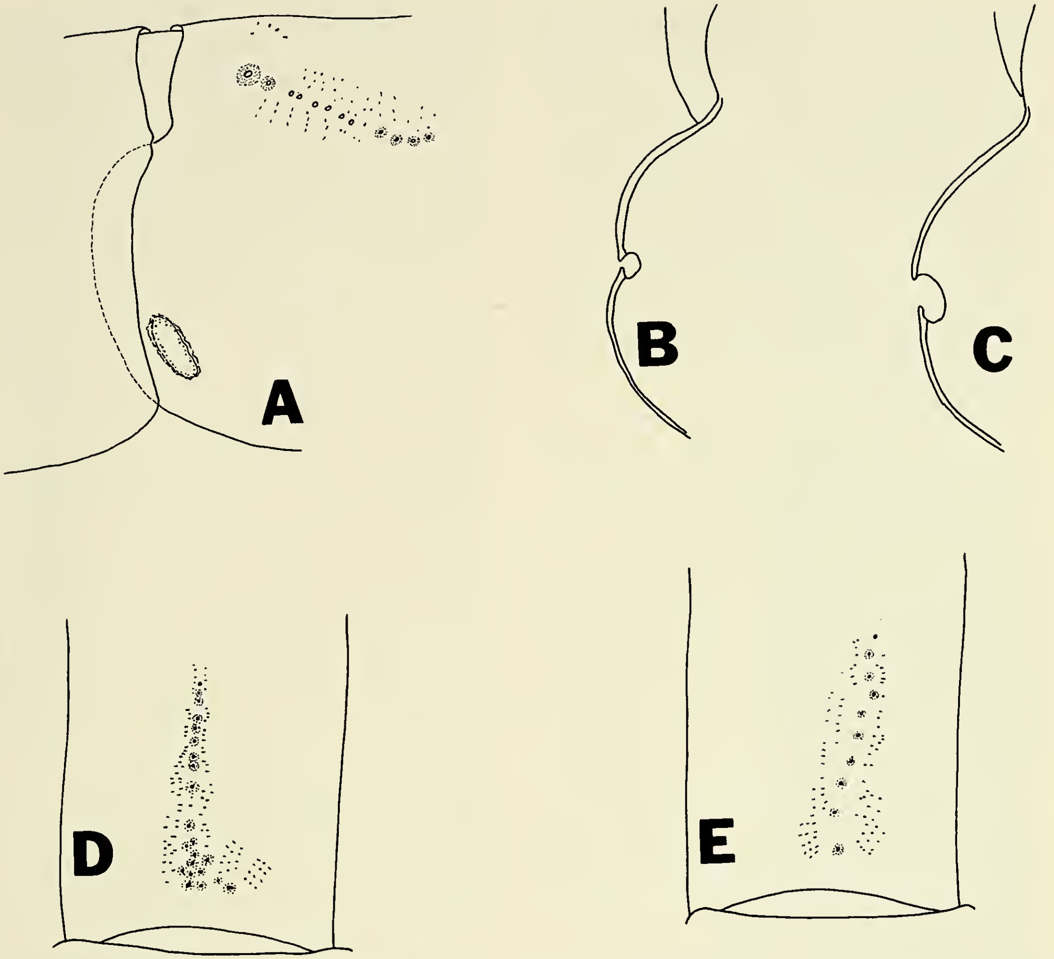

Fig. 2. *Acanthephyra pelagica*: A, Type host to *Holophryxus acanthephyrae* Stephensen, from *Tjalfe* station 322, view of posterior right carapace; B, Posterior right carapace edge of specimen from *Eltanin* station 1723; C, Posterior right carapace edge of specimen from *Eltanin* station 1480; D, Posterior dorsal surface of carapace of specimen from *Eltanin* station 1480, showing marks caused by mandibles and pereopods of isopod; E, Posterior dorsal surface of carapace of specimen from *Eltanin* station 1723, showing marks caused by mandibles and pereopods of isopod.

ence of this morphological feature: *H. richardi,* Stephensen, 1912a:109, 110, figs. 9, 11; Rustad, 1935:26, fig. 14; *H. acanthephyrae* Stephensen, 1912a:115, figs. 15, 17; Jones & Smaldon, 1986:309, figs. 2C and 2D; and *H. fusiformis* Shiino, 1937:190, figs. 1B, C.

The allotype male and other males recovered by Schultz (1977) from females of *I. concavus* show no apparent morphological differences between the male *H. acanthephyrae* described here and that described by Jones and Smaldon (1986).

The host of *Isophryxus concavus* was unknown to Schultz (1977) because the isopods apparently fell off the hosts at the time of collection. The presence of a male specimen of the oplophorid *Acanthephyra pelagica* (carapace length 26.5 mm), USNM 233552, from *Eltanin* station 1480 (the type locality station for *I. concavus*) with marks from the pereopods and mandibles of an isopod on the posterior dorsal surface of its carapace (Wasmer 1986), strongly suggests that this shrimp may have been the host of the holotype of *I. concavus.* The marks on the shrimp (Fig. 2D) are similar to those described and illustrated by Stephensen (1912a) on the type host of *Holophryxus acanthephyrae* and to those on the specimen of *A. pelagica* (Fig. 2E) which was the host of the dajid identified as *H. acanthephyrae* from *Eltanin* station 1723; this latter shrimp is on deposit in the National Museum (USNM 233551).

Although it is difficult to gauge accurately the size of the isopod responsible for the marks on the shrimp from *Eltanin* station 1480, the marks are not inconsistent with an isopod 21.6 mm long (the length of the holotype of *I. concavus*). The holotype of *H. acanthephyrae* is 22 mm long (Stephensen 1912a), and the specimen from *Eltanin* station 1723 is 22.7 mm long; the marks on the carapaces of these latter two specimens are in the same size range as those on the presumed host specimen of *I. concavus.*

An attempt was made to identify additional host specimens of *A. pelagica* from the six *Eltanin* stations listed by Schultz (1977) where the paratypes of *I. concavus* were collected. This attempt was not successful; none of the 14 specimens of *A. pelagica* from five of the stations have any marks indicating they served as hosts to isopods, and no specimens of *A. pelagica* were reported from the sixth station. However, if the specimen of *A. pelagica* from *Eltanin* station 1480 is assumed to be the type host of *I. concavus,* then the evidence becomes stronger that the specimens described as *I. concavus* are in reality *H. acanthephyrae.*

In addition to the undue significance attached by Schultz (1977) to the presence of the dorsal integumentary folds on the pereon of the genus *Isophryxus,* several other, more minor, erroneous interpretations of morphology are present in his diagnosis of the genus and in the description of *I. concavus.* These misinterpretations involve the supposed absence of both pairs of antennae in the females, the presence of "flattened mouthparts," and the misnumbering of the lateral edges of the pereonites (coxal plates).

The two pairs of antennae on females of the genus *Holophryxus* have presented difficulties of interpretation for most previous investigators, probably due to the rather unusual appearance of these appendages and to the lack of sufficient numbers of specimens for adequate dissection. Nierstrasz & Brender à Brandis (1931) and Shiino (1937) incorrectly considered both pairs of antennae to be entirely absent and interpreted them as the maxillipeds. Richardson (1905) considered both antennae to be rudimentary and articulated. Butler (1964) considered them to be rudimentary and flattened, with the first pair being questionably articulated; he also called a part of the peduncle of the second antennae the maxilliped, an error pointed out by Coyle & Mueller (1981). Stephensen (1912a) considered both pairs of antennae to be present but questionably articulated. Rustad (1935), with access to a number of specimens of *H. richardi,* was able to carry out detailed dissections and preparations with hot sodium hydroxide and pyrogallic acid stain to investigate the structure of the two pairs of antennae, as well as the mouthparts. Of the mouthparts, only the tips of the mandibles and part of the maxillipeds were normally visible without dissection. The two pairs of antennae were described by Rustad as being more or less deformed and "cushiony," and encircling the oral cone; even though they occasionally appeared to be articulated, the special preparative techniques used showed them to be unjointed.

Comparison of Schultz's (1977) fig. 17B of the anterior ventral part of *I. concavus* with fig. 16 of Stephensen (1912a) and figs. 2 and 7 of Rustad (1935) leads to the conclusion that what Schultz refers to as flattened mouthparts on his specimens represent the first and second pairs of antennae of Stephensen and Rustad.

In at least several (and perhaps all) of the species of *Holophryxus,* the first pair of coxal plates on adult females is coalesced with the cephalic ridge and the posterior four pairs of coxal plates are generally separate and evident as rounded or acute projections lateral to pereopods 2–5 (see Richardson 1908: 690, fig. 1, for *H. giardi*; Rustad 1935:9, fig. 2, for *H. richardi*; Shiino 1937:188, fig. 1B, C, for *H. fusiformis*; Stephensen 1912a:113, 11r, fig. 16, and Jones & Smaldon 1986: 309, fig. 2C for *H. acanthephyrae*). Figure 1B herein, showing the anterior ventral region of the specimen of *H. acanthephyrae* from *Eltanin* station 1723, is in general agreement with fig. 16 of Stephensen (1912a) and fig. 2C of Jones & Smaldon (1986) and shows the first coxal plates to be fused with the cephalic ridge, with the first pereopods arising from near the posterolateral part of the ridge. The lateral edges of pereonal segments I–IV of Schultz (1977) should therefore more correctly be referred to as coxal plates II–V.

The three additional species of *Isophryxus* (*I. quadratohumerale, I. polyandrus,* and *I. septapodus* described by Schultz (1978) from *Eltanin* cruises 11, 15, and 19 need to be briefly considered here. The presence of weak anterior furrows or folds suggesting segmentation of the pereon, the presence of fringing spines on the posterior margin of the fifth oostegites, and the form of the males clearly indicate that *I. quadratohumerale* and *I. polyandrus* represent species of *Holophryxus.* The situation with *I. septapodus* is perhaps less clear-cut than that with the other described species of *Isophryxus.*

Rustad (1935), Butler (1964), and especially Coyle & Mueller (1981) have shown that the development of the juvenile female stage into the mature *Holophryxus* female involves loss of pleopods, uropods, abdominal segmentation, a change in the mandibles from the sagittate form of the cryptoniscid to a rasplike organ capable of drilling into the carapace, and a reduction of pereopod 7 (with only its coxal plate remaining); in the final changes to the adult form, coxal plate 7 is lost, oostegites 1–5 are formed, the body region between pereopods 5 and 6 lengthens, and pereopod 6 is finally lost and its coxal plate reduced to a small bump or papilla which may persist at the posterior part of the pereon (as illustrated in Nierstrasz & Brender à Brandis 1913, Shiino 1937, and Butler 1964). Breeding does not occur until the marsupium is formed (Coyle & Mueller 1981), a condition that is probably not complete until the fringing spines are present on the posterior margins of the fifth oostegites.

Contrary to Schultz's statement (1978:83) about the absence of spines on the posterior margin of the marsupium of *I. septapodus,* my examination of the holotype of this species showed them to be present. Based on the above information, I suggest that the gravid female holotype of *I. septapodus* is a specimen of *Holophryxus* on which the fringing spines are present on the posterior marsupial margin, but which still has vestiges of the seventh pereopods and the corresponding seventh coxal plates, represented by the posterior two pairs of processes on the posterior ventral part of the pereon (see Schultz 1978:fig. 11A), as well as jointed sixth pereopods and the corresponding sixth coxal plates, represented by the more anterior two pairs of processes on the posterior ventral part of the pereon.

Whether these posterior appendages are retained much beyond maturity in *H. septapodus* (Schultz) can be determined only when additional mature specimens come to hand. Rustad (1935:16–17, figs. 3, 6) has shown that at least in *H. richardi* there is some individual variation in regard to the stage of development at which the sixth pereopods finally disappear (being absent on a specimen of 11.2 mm total length, but still present on another of about 12.9 mm total length); in both these cases, fringing spines are already present on the fifth oostegites. He also suggests (Rustad 1935:12) that the entire genus *Holophryxus* is possibly exceptional among the Dajidae in having the oostegites developed before the sixth pereopods have completely disappeared.

It is significant to note that Schultz (1978) considered the first pereonal segment to be completely fused with the cephalon in the latter three *Isophryxus* species.

Damage to host.—The holotype of *H. acanthephyrae* was collected and photographed attached to the posterior surface of the carapace of its host, with its cephalon directed posteriorly (Stephensen 1912a:fig. 13); one of the four specimens of the species reported by Jones & Smaldon (1986:fig. 1) was collected attached to its host in the same position. Three other species of *Holophryxus* (*H. alaskensis, H. giardi,* and *H. richardi*) have been found similarly attached to their hosts (Richardson 1908:figs. 2, 4; Stephensen 1912a:fig. 13; Rustad 1935; Butler 1964, 1980:fig. 7B). The pereopods and mandibles of the isopod leave marks on the carapace of the host as the isopod grows, moves, and feeds (Stephensen 1912a: figs. 14, 18). The mandibles perforate the carapace to the epithelial and connective tissues underneath, but the clawlike dactyls of the pereopods do not completely perforate the carapace (Rustad 1935).

Figure 2E shows the marks made by the pereopods and mandibles of the specimen of *H. acanthephyrae* collected attached to the specimen of *Acanthephyra pelagica* from *Eltanin* station 1723; Fig. 2D shows similar marks on the specimen of *A. pelagica* from *Eltanin* station 1480, the presumed host to *I. concavus.* The holes left by the mandibles tend to be larger than those of the pereopods and surrounded by a large ring of darkly stained tissue. The marks present on both shrimps indicate that the isopods progressively moved posteriorly on the carapaces as the isopods increased in size.

Coyle & Mueller (1981) provided complete descriptions of the larval and juvenile stages of *Holophryxus alaskensis.* The epicarid stage of *H. alaskensis* uses stage V of the copepod *Euchaeta elongata* as an intermediate host, on which it metamorphoses through the microniscid stage to the cryptoniscid stage, which then seeks out the shrimp final host (*Pasiphaea pacifica*). The cryptoniscid crawls beneath the carapace of the shrimp and attaches to the body wall in the branchial chamber above the gills, where it metamorphoses to the juvenile stage. It then moves out of the branchial chamber, up the side of the first abdominal somite and onto the dorsal surface of the carapace, where it attaches and assumes the mature adult form.

Few details of the life cycle of *H. acanthephyrae* are known, although Stephensen (1912a) described an epicarid larval stage from the marsupium of the holotype. From marks and damage (described below) to the carapaces of the two host specimens of *A. pelagica* at hand, and to the type host of *H. acanthephyrae* (which accompanied the holotype when it was obtained on loan from the Universitetets Zoologiske Museum), I suggest that the cryptoniscid stage of *H. acanthephyrae* also attaches inside the branchial chamber of the host. The juvenile female then apparently burrows through the branchial region of the carapace and gains access directly to the outer surface of the carapace, from whence it moves dorsally, begins to feed, and develops into the mature female.

While I was examining the type host of *H. acanthephyrae,* I noticed an oblong, depressed scar on the posterior part of the right branchial region of the shrimp (Fig. 2A). The same area is visible in Stephensen's (1912a:fig. 13) photograph as a darkened area, although over the years the darkened color has apparently become much less evident. The two *Eltanin* specimens of *A. pelagica* which served as hosts for *H. acanthephyrae* show evidence of damage to the right branchial region of their carapaces (Fig. 2B, C), as if something ate or burrowed through at these locations. The damage is contiguous with the posterior edge of the carapaces of these specimens and the edges of the wounds are rounded and partly healed, as if they are of some age.

A small male specimen of *A. pelagica*, carapace length 11.5 mm, from station 1204 of *Eltanin* cruise 14 has two relatively fresh, unhealed holes in the left branchial region of its carapace. Schultz (1977) recorded two small (2.2 and 2.5 mm long) female dajids from the same *Eltanin* station; the specimens were not given a formal species name at the time, but were identified simply as dajid species. Since the specimens bear some resemblance to the immature female of *H. giardi* described and illustrated by Richardson (1908), I suggest that these small dajids may represent a species of *Holophryxus*, and that it is probable, based on the damage to the specimen of *A. pelagica* from station 1204, that they represent juvenile females of *H. acanthephyrae* which had only recently burrowed from the branchial chamber of the host shrimp to the outside of the carapace, from where they were dislodged upon collection or subsequent handling.

Distributions and hosts of Holophryxus *species.*—Eight species of *Holophryxus* are currently recognized. The final host species is known for only five of the eight, and the intermediate host is known for only one of these five. Each of the five species for which the final host is known apparently uses a single species of pelagic decapod shrimp as a host. It is expected that the distributions of the various *Holophryxus* species would therefore be limited to those of their single host shrimps. The currently recognized *Holophryxus* species, their distributions, and known hosts are as follows (in chronological order);

1. *H. alaskensis* Richardson, 1905. Northeastern North Pacific, Santa Barbara Channel, California to Prince William Sound, Alaska. Intermediate host, stage V of the copepod *Euchaeta elongata*; final host *Pasiphaea pacifica* Rathbun.
2. *H. giardi* Richardson, 1908. Northwestern North Pacific, off Bering Island (54°48′N, 164°54′E). Final host, *Bentheogennema borealis* (Rathbun).
3. *H. richardi* Koehler, 1911. Central North Atlantic (33°41′N, 36°55′W) north to Davis Strait west of Greenland (66°21′N, 57°04′W), in Denmark Strait between Iceland and Greenland, south of Iceland, to west coast of Norway, and to south of England. Final host, *Sergestes arcticus* Krøyer.
4. *H. acanthephyrae* Stephensen, 1912a. North Atlantic from Davis Strait (60°07′N, 48°26′W) west of Greenland and to south of England, and subantarctic and antarctic waters of South Pacific. Final host, *Acanthephyra pelagica* (Risso).
5. *H. fusiformis* Shiino, 1937. Northwestern North Pacific off east coast of Japan. Final host, *Sergia prehensilis* (Bate).
6. *H. quadratohumerale* (Schultz, 1978). Subantarctic waters of southeastern South Pacific. Final host not known.
7. *H. polyandrus* (Schultz, 1978). Subantarctic waters of southeastern South Pacific. Final host not known.
8. *H. septapodus* (Schultz, 1978). Subantarctic waters of southeastern South Pacific. Final host not known.

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COPEPODA (CRUSTACEA) FROM A SEASONALLY FLOODED MARSH IN ROCK CREEK STREAM VALLEY PARK, MARYLAND

Janet W. Reid

Abstract.—Species of Copepoda (Crustacea) collected from a seasonally flooded marsh in Rock Creek Stream Valley Park, Maryland, included the cyclopoids *Acanthocyclops vernalis* (Fischer), *Diacyclops bicuspidatus thomasi* (S. A. Forbes), and *Diacyclops palustris,* new species, and the harpacticoid *Attheyella* (*Mrazekiella*) *americana* (Herrick). The female of *D. palustris* is described; the species seems most closely related to *D. haueri* (Kiefer). *Diacyclops clandestinus* Yeatman is renamed *D. yeatmani.* A key to North American species of *Diacyclops* is presented. Some specimens of *A. americana* differ slightly from extant descriptions in details of the anal operculum and setation of the third swimming leg.

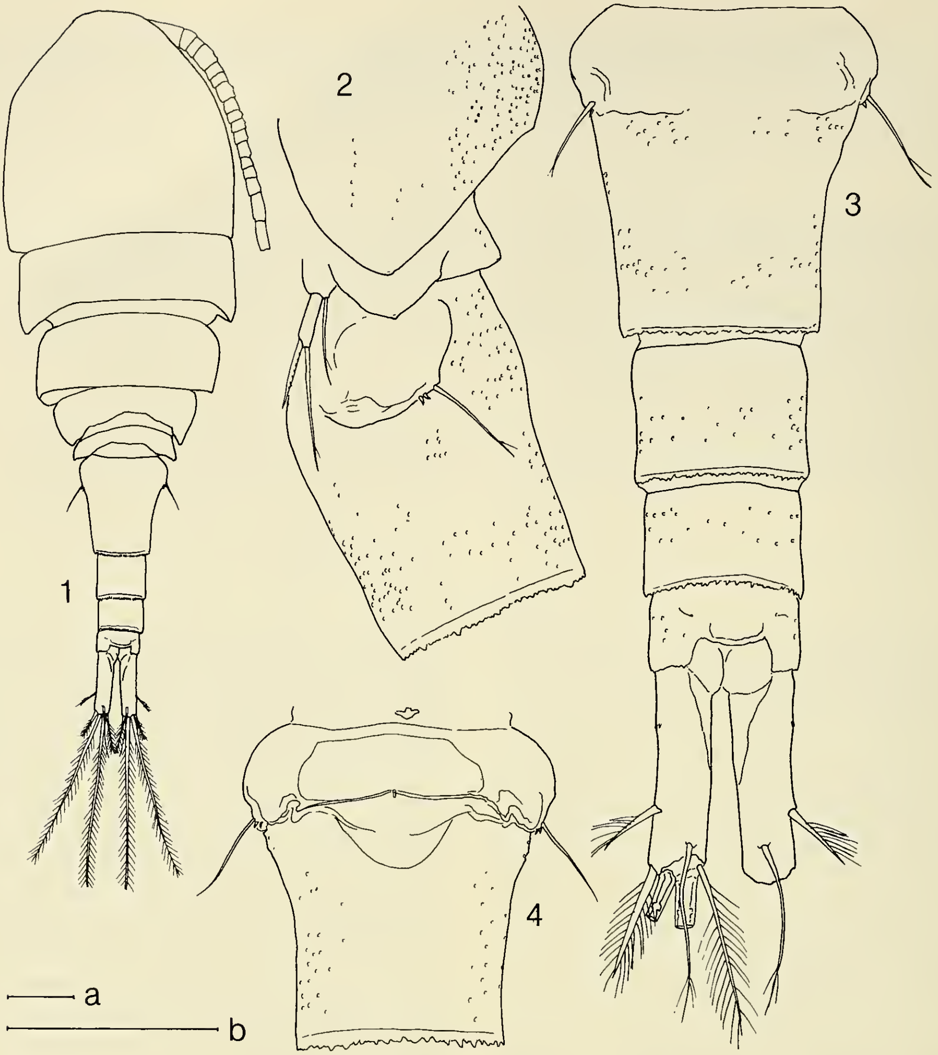
Mr. William B. Yeaman of the National Park Service brought a sample of water and detritus from a marsh in Rock Creek Stream Valley Park, Maryland, to Dr. Thomas E. Bowman of the Department of Invertebrate Zoology for identification of the aquatic fauna. The sample contained four species of Copepoda: *Acanthocyclops vernalis* (Fischer, 1853), 23 ♀♀, 3 ♂♂, 2 copepodites; *Diacyclops bicuspidatus thomasi* (S. A. Forbes, 1882), 1 ♂; *Attheyella* (*Mrazekiella*) *americana* (Herrick, 1884), 7 ♀♀, 1 ♂; and 2 ♀♀ of a previously undescribed species of *Diacyclops.* This species is described below as *D. palustris.* Variations of the population of *A. americana* from extant descriptions are also noted below.

The collection was made on 23 Aug 1986 in a small marsh located in Rock Creek Stream Valley Park, Unit 3, Montgomery County, Maryland, on the west side of the park opposite Puller Drive, Kensington; about 39°01′41″N, 77°05′27″W. The marsh is shaded by broad-leaved deciduous hardwood trees such as red maple (*Acer rubrum*) and black willow (*Salix nigra*). The area is in the floodplain of Rock Creek; surface water usually persists from November through May during years of normal or above normal rainfall. Standing water disappears in summer and early fall, although soils remain saturated. Any heavy rain which occurs during this period will briefly return the area to its standing water conditions. The first heavy rains following autumn leaf drop typically refill the wetland. The marsh is classified as a Palustrine System, Class FO (forested), Subclass 1 (broad-leaved deciduous), Water Regime E (seasonally flooded, saturated) (National Wetlands Inventory, Fish and Wildlife Service, U.S. Department of the Interior; Cowardin et al. 1979). During the unusually dry summer of 1986, standing water was absent for long periods, though soils remained saturated; the collection was made after a rain.

Family Cyclopidae Sars, 1913
Diacyclops palustris, new species
Figs. 1–19

Material examined.—1 ♀, holotype, dissected on 1 slide, National Museum of Natural History—USNM 232186. 1 ♀, paratype, dissected on 1 slide, USNM 232187.

Female.—Length of holotype (excluding



Figs. 1–4. *Diacyclops palustris,* new species, female holotype: 1, Habitus, dorsal, omitting pores on somites (both next innermost terminal setae on caudal rami broken); 2, Posterior 2 pedigers and genital segment, left lateral; 3, Urosome, dorsal; 4, Genital segment, ventral. Scale a, Fig. 1; Scale b, Figs. 2–4; scales = 100 μm.

caudal setae) 1140 μm; length of paratype 1130 μm. Posterior 2 pedigers (Figs. 1, 2) not markedly expanded laterally, each with small tubercle on posterolateral margin; posterior margins of urosomites with serrate hyaline membranes, except anal somite which has fine spinules along posteroventral margin. All somites (Figs. 2–4) with tiny pits; pattern of these pits different in holotype and paratype. Genital segment (Figs. 2–4) expanded anteriorly, slightly longer than broad; seminal receptacle with posterior part little expanded. Caudal ramus (Fig. 3) 4.5–6× longer than broad, with lateral row of 5 spinules about ¼ distance from base of ramus. Lateral seta of ramus inserted at distance from base of ramus equal to about 65% of length of ramus. Both longest apical setae of holotype broken; lengths of setae of paratype as follows: lateral 40

Figs. 5–14. *Diacyclops palustris,* new species, female holotype: 5, Antennule, ventral; 6, Antennule, articles 1 and 2, dorsal; 7, Antenna, anterior; 8, Antenna, article 1, posterior; 9, Labrum; 10, Mandible; 11, Maxillula; 12, Maxilla; 13, Maxilliped, posterior; 14, Maxilliped, anterior. Scale = 100 μm.

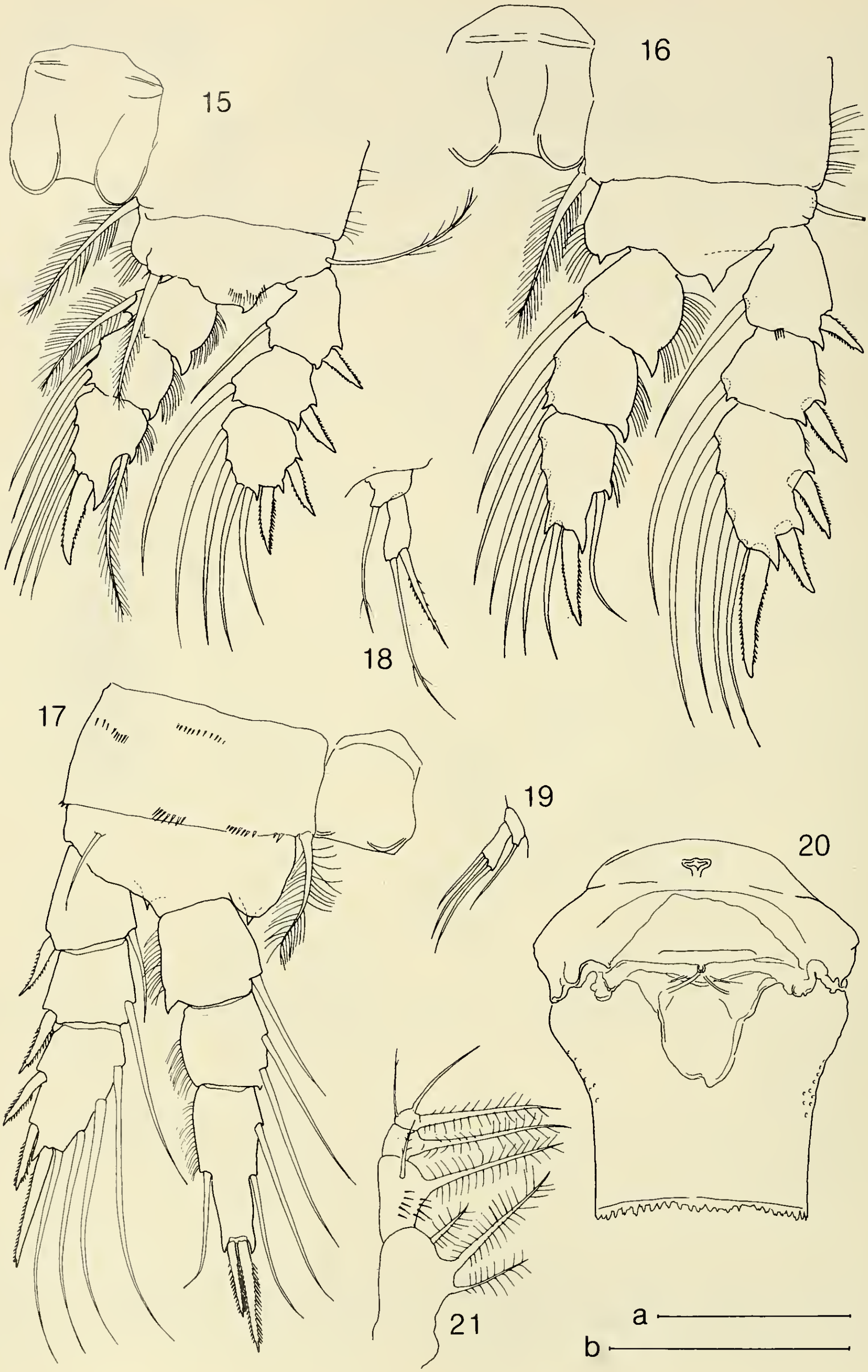

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Table 1.—Proportions of some structures of *Diacyclops palustris,* new species, compared to those of *D. haueri* (Kiefer, 1931a). Abbreviations: CR, caudal ramus; P4 enp3, article 3 of endopod of leg 4; P5, leg 5.

Structure	*D. palustris*	*D. haueri*
CR, ratio of length : breadth	4.5–6:1	8–10:1
CR, ratio of length of next outermost terminal seta to length of outermost terminal seta	5.0:1	5.81:1
CR, ratio of next innermost terminal seta to length of outermost terminal seta	8.1:1	9.66:1
P4 enp3, ratio of length : breadth	2.26:1	2.53–3.0:1
P4 enp3, ratio of length of endopod to length of inner terminal spine	1.34:1	1.86:1
P5, ratio of length of terminal spine to length of article 2	1.7:1	1.2:1

μm; dorsal 63 μm; innermost to outermost apical setae 65, 420, 260 and 52 μm respectively; thus innermost apical seta about 1.25× longer than outermost apical seta. All caudal setae finely plumose.

Antennule (Figs. 5, 6) of 17 articles, reaching midlength of prosomite 2; with slender esthetascs on articles 12, 16 and 17; few small pits on dorsal surface of article 1; and 2 terminal articles with narrow, smooth hyaline membrane. Antenna article 1 (Figs. 7, 8) with 3 groups of spinules on posterior surface, 1 group of 4 spinules on anterior surface, and 3 spinules near base on lateral margin; paratype with some pits on anterior surface of articles 3 and 4. Labrum and remaining mouthparts as in Figs. 9–14. Swimming legs 1–4 (Figs. 15–17) with rami of 3 articles and spine formula 2,3,3,3. Leg 1, seta on medial expansion of basipod 2 reaching distal margin of endopod article 2. Legs 2 and 3 essentially similar. Basal lamellae of all legs without armament, but with smooth protrusions each side, those of leg 1 most and those of leg 4 least developed. Terminal article of endopod of leg 4 2.26 × longer than broad; inner terminal spine 1.40× longer than outer terminal spine.

Leg 5 (Fig. 18) of 2 free articles, inner spine of article 2 1.7× longer than article, outer seta nearly 3× longer than article. Left leg 5 of paratype (Fig. 19) with 3 subequal setae; right leg 5 as in holotype. Leg 6 (Figs. 2–4) consisting of 2 spinules and 1 seta.

Etymology.—Named for the marsh habitat.

Remarks.—Among North American species of *Diacyclops, D. palustris* most resembles *D. haueri,* with which it shares a slender leg 4 terminal endopod article having the inner terminal spine longer than the outer. However, comparison of the Rock Creek specimens with the original descriptions of *D. haueri* (Kiefer, 1931a, b) and with specimens from a pond in Wooster, Ohio, collected by Mr. Andrew Weaver on 23 Feb 1948 and lent by Dr. Harry C. Yeatman, revealed several differences. The caudal rami of *D. palustris* are relatively short, and there exist other differences in proportion between the two species (Table 1). The posterior expansion of the seminal receptacle of *D. palustris* is less developed than in *D. haueri* (Fig. 20). The anal operculum of *D. haueri* is unusually convex and strongly thickened (Kiefer 1931b:fig. 23). Setules of the maxilliped of *D. palustris* (Fig. 13) are sparse, while most setae of the maxilliped

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Figs. 15–21. 15–18, *Diacyclops palustris,* new species, female holotype: 15, Leg 1; 16, Leg 2; 17, Leg 4 (setules of most setae of swimming legs omitted for clarity); 18, Leg 5. Fig. 19, *D. palustris,* female paratype, left leg 5. Figs. 20–21, *Diacyclops haueri* (Kiefer, 1931a), females from Wooster, Ohio: 20, genital segment, ventral; 21, maxilliped. Scale a, Figs. 19, 20; Scale b, Figs. 15–18, 21; scales = 100 μm.

of *D. haueri* bear many, closely set setules (Fig. 21). The seta on the medial expansion of the basipod 2 of leg 1 of *D. haueri* reaches the apex of endopod article 3. The inner terminal spine of endopod article 3 of leg 4 of *D. palustris* is straight, while that of *D. haueri* is bent outwards at midlength.

Diacyclops palustris is the fifteenth species and subspecies of the genus recorded from North America (Dussart & Defaye 1985). Since the widely used keys of Yeatman (1958) and of Pennak (1978) include only 11 and 10 species respectively, it seems useful to include an updated key. The formulation of this key owes much to the extensive discussions of variations within North American populations of several members of the genus *Diacyclops* by Yeatman (1944).

Dussart and Defaye (1985) suggested that in order to avoid confusion with *D. languidoides clandestinus* (Kiefer, 1926), *D. clandestinus* Yeatman, 1964 be renamed. I concur and propose the new name *D. yeatmani,* used below. The name of course honors Dr. Harry C. Yeatman for his many contributions to copepod systematics.

Key to Females of Species of *Diacyclops* Recorded from North America

1\. Antennule with 11 articles 2
– Antennule with 12 articles 4
– Antennule with 16 or 17 articles 5
2\. Lateral seta of caudal ramus inserted at about midlength of ramus .... *D. nanus* (G. O. Sars, 1863)
– Lateral seta of caudal ramus inserted at distal ⅔ to ¾ of ramus 3
3\. Leg 4 endopod 3 with outer terminal spine and inner terminal seta ... *D. jeanneli putei* (Yeatman, 1943)
– Leg 4 endopod 3 with 2 terminal spines .... *D. languidoides* (Lilljeborg, 1901)
4\. Caudal rami 4–5× longer than broad .... *D. crassicaudis* (G. O. Sars, 1863)
– Caudal rami 3.1–3.6× longer than broad .... *D. crassicaudis brachycercus* (Kiefer, 1927)
5\. Antennule of 17 articles 6
– Antennule of 16 articles .... *D. languidus* (G. O. Sars, 1863)
6\. Leg 4 endopod 3, outer terminal spine longer than inner terminal spine or seta 7
– Leg 4 endopod 3, inner terminal spine or seta longer than outer terminal spine 9
7\. Seta of article 2 of leg 5 about 2× length of spine 8
– Seta and spine of article 2 of leg 5 subequal .. *D. navus* (Herrick, 1882)
8\. Outer terminal spine of endopod 3 of leg 4 about 1.5× length of inner terminal spine; endopod 3 of leg 4 2–3× longer than broad ... . *D. bicuspidatus* (Claus, 1857)
– Outer terminal spine of endopod 3 of leg 4 about 2× length of inner terminal spine; endopod 3 of leg 4 3–4.2× longer than broad .... *D. bicuspidatus thomasi* (S. A. Forbes, 1882)
9\. Leg 4 endopod 3, outer margin with seta 10
– Leg 4 endopod 3, outer margin with spine .... *D. nearcticus* (Kiefer, 1934)
10\. Leg 4 endopod 3 with 2 terminal spines 11
– Leg 4 endopod 3 with outer spine and inner seta .... *D. jeanneli* (Chappuis, 1929)
11\. Leg 4 endopod 3 stout, about 1.5–1.7× longer than broad 12
– Leg 4 endopod 3 slender, about 2.2–2.5× longer than broad 13
12\. Innermost terminal caudal seta shorter than outermost; caudal rami 5–7× longer than broad ... . *D. bisetosus* (Rehberg, 1880)
– Innermost terminal caudal seta longer than outermost; caudal rami 3–4.5× longer than broad .... *D. yeatmani,* new name
13\. Caudal rami 8–10× longer than

broad; leg 4 endopod 3, length of endopod about 1.9 × length of inner terminal spine .... *D. haueri* (Kiefer, 1931a)

– Caudal rami 4.5–6 × longer than broad; leg 4 endopod 3, length of endopod about 1.3 × length of inner terminal spine .... *D. palustris,* new species

Family Canthocamptidae Sars, 1906
Attheyella (*Mrazekiella*) *americana* (Herrick, 1884)

Material examined.—1 ♀, dissected on 2 slides; 5 ♀♀, 2 ♂♂, alcohol-preserved; USNM 232188.

Remarks.—The Rock Creek Park population varies little from those from North Carolina and Wisconsin, exhaustively described by Coker (1934). Two Rock Creek females bear two setae rather than one on the inner margin of leg 3 exopod article 2; Coker noted similar variability in the setation of endopod article 2 of this leg in females. The anal opercula of Rock Creek females bear 10–15 teeth, while those of the two males bear 12 and 14 teeth; Coker mentioned variations in this character also, his specimens from North Carolina having 12–18 "spinules", and those from Wisconsin having 20–24 "spinules".

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TANAIDACEA (CRUSTACEA: PERACARIDA) OF THE GULF OF MEXICO. V. THE FAMILY PSEUDOTANAIDAE FROM LESS THAN 200 METERS, WITH THE DESCRIPTION OF *PSEUDOTANAIS MEXIKOLPOS,* N. SP. AND A KEY TO THE KNOWN GENERA AND SPECIES OF THE WORLD

Jürgen Sieg and Richard W. Heard

Abstract.—No published records exist for pseudotanaid tanaidaceans in the Gulf of Mexico. In this study three species, *Iungentitanais primitivus* (Sieg, 1973), *Pseudotanais mortenseni* Sieg, 1973, and *P. mexikolpos,* n. sp. are reported from the Gulf or immediately adjacent waters of the Florida Keys. *Iungentitanais primitivus* and *P. mortenseni* were previously known only from their type localities, both at San Thomas Harbor in the West Indies. *Pseudotanais mexikolpos* is described from a single location in the West Flower Garden Banks off Texas. It most closely resembles two Mediterranean species, *P. mediterraneus* G. O. Sars, 1882, and *P. unicus* Sieg, 1977. It can be separated from *P. mediterraneus* by having a much longer disto-sternal seta on the propodus of peraeopods 4–6 and from *P. unicus* by its shorter cephalothorax and distinctly larger peraeopod 3. A key to the five known genera and 25 described species of the family is included and taxonomic problems concerning several species are briefly discussed.

There are no published records of the tanaidacean family Pseudotanaidae for the Gulf of Mexico. Of the 24 described species only three, *Iungentitanais primitivus* (Sieg, 1973), *Pseudotanais kurchatovi* Kudinova-Pasternak & Pasternak, 1978, and *P. mortenseni* Sieg, 1973, have been reported from the Caribbean region. During the past 10 years, three species of pseudotanaids were collected from less than 200 m in conjunction with several environmental baseline studies conducted in the Gulf of Mexico and the immediately adjacent waters of the Florida Keys. These specimens were made available to us for study and are the subject of this report.

The family Pseudotanaidae was originally established by Sieg (1973, 1977) for those species having a marsupium formed by a single pair of sheet-like oostegites. As in all other tanaidaceans except the Tanaidae, the eggs develop between the oostegites. The Tanaidae are the only other family with one pair of oostegites. This group is unique, however, in having the oostegites transformed into sack-like structures, termed "ovisacs" by Lang (1960), in which the eggs are incubated (see Sieg 1980, 1984; Johnson & Attramadal 1982). Other characters of the Pseudotanaidae given by Sieg (1977) were the: (1) reduced size of the first two peraeonites, (2) maxilliped with basis completely fused, (3) first antenna of females with 3 or 4 segments, and (4) mandibles with pars molaris reduced.

Males are known only for the genus *Pseudotanais* G. O. Sars, 1882. They are rarely collected and are distinctly dimorphic, with a body shape similar to the males of *Leptognathia* and *Typhlotanais.* The pleon is strongly enlarged and distinctly longer than one-third of the total body length (rostrum to tip of telson); whereas in females the pleon is approximately one-fifth of the total body length (Fig. 1: *Pseudotanais*). Each pleonite contains large bundles of dorso-ventral musculature to move the strongly developed pleopods which are characteristic of all males, even for those species in which the females lack pleopods. The first antenna has 7 segments with the first 2 dorsoventrally depressed and probably functioning as a unit. The third peduncle segment is distinctly smaller and movable. The four flagellar segments each bear aesthetascs distally (segments 1–3 with a cluster of aesthetascs and segment 4 with a single terminal aesthetasc). The second antenna is like that of the female. The mouthparts are lacking except for the maxilliped, which is slightly smaller than that of the female. Unlike the female the lateral margins of the maxilliped are fused with the carapace fold. The chelipeds are slightly larger, and the peraeopods and uropods appear more slender than in the female.

In a monograph of the family, Sieg (1977) grouped the known species into two subfamilies, the Cryptocopinae and the Pseudotanainae. The Cryptocopinae is represented by four genera: *Cryptocope* G. O. Sars, 1882; *Cryptocopoides* Sieg, 1977; *Iungentitanais* Sieg, 1977; and *Paraiungentitanais* Sieg, 1977. The subfamily Pseudotanainae has only the type genus, but contains most of the family's described species. Sieg (1977) also divided the genus *Pseudotanais* into the subgenera *Pseudotanais,* s.s. and *Akanthinotanais* Sieg, 1977.

Since 1977 three species of *Pseudotanais,* two species of *Cryptocopoides,* and two species of *Cryptocope* have been described: *Pseudotanais guillei* Shiino, 1978, from the Kerguelen Islands; *P. kurchatovi* Kudinova-Pasternak & Pasternak, 1978, from deep water in the Caribbean, and *P. siegi* Kudinova-Pasternak, 1985, from the North Atlantic; *Cryptocopoides rostralis* Tzareva, 1982, which was transferred to the genus *Typhlotanoides* Sieg, 1983 (Sieg 1986a:102) and *Cryptocopoides rotundata* Tzareva, 1982 (which was synonymized with the neuter of *Mirandotanais vorax* Kussakin & Tzareva, 1974 by Sieg 1986a:138–139). Within *Cryptocope* Kudinova-Pasternak (1982) described *C. longa* and *C. vitjazi,* both from the deep waters of the Mediterranean Sea. Finally, Kudinova-Pasternak & Pasternak (1978:187–188) mentioned a specimen of *Cryptocope* sp. from deep water in the Caribbean Sea, but with reservations they later reassigned it to the genus *Leptognathia* G. O. Sars, 1882 (Kudinova-Pasternak & Pasternak 1981:117).

A key to the known genera and all the described species of the family is presented here. For bibliographic, taxonomic, and zoogeographic information see Sieg (1983). For terminology refer to Sieg (1977, 1980).

The following abbreviations are used in the key and figures: A.1 = first antenna, A.2 = second antenna, L = labrum, Md(r) = right mandible, Md(l) = left mandible, Mx.1 = first maxilla, Mx.2 = second maxilla, La = labium (paragnaths), Mxp = maxilliped, Epi = epignath (=maxillipedal epipodite), Che = cheliped, P.1–P.6 = peraeopod 1 to peraeopod 6, Pl.1–Pl.5 = pleopod 1 to pleopod 5, Plt = pleotelson, and Uro = uropod.

Key to the Genera and Species of Pseudotanaidae

1. A.1 7-segmented (Fig. 1: *Pseudotanais*) .... males
– A.1 4- or 3-segmented 2
2. A.1 4-segmented (Fig. 1: subfamily Cryptocopinae) 3
– A.1 3-segmented (Fig. 1: subfamily Pseudotanainae) 6
3. Pleopods reduced, without setae (Fig. 1: Pl.3); Mx.1 with 9 terminal spines .... *Cryptocope abbreviata* (G. O. Sars, 1868)

– Pleopods well developed and with setae; Mx.1 with 5 short or 9 longer terminal spines 4

4. Cheliped slender, with carpus and propodus elongate (Fig. 1: Che.1, Che.2); A.1 elongate; pleopodal endopodite with one distal inner seta and exopodite with pilose proximal seta (Fig. 1: Pl.1) 5

– Cheliped (Fig. 1: Che.3) and A.1 stout; pleopodal exopodite and endopodite each only with some distal outer setae (Fig. 1: Pl.2) .... *Cryptocopoides arcticus* (Hansen, 1913)

5. Without eyes (Fig. 1); cheliped with carpus 4 times as long as broad (Fig. 1: Che.2); Mx.1 with 9 well developed terminal spines .... *Paraiungentitanais longidigitatus* (Kudinova-Pasternak, 1975)

– With eyes (Fig. 1); cheliped with carpus 5 times as long as broad (Fig. 1: Che.1); Mx.1 with 5 small terminal spines .... *Iungentitanais primitivus* (Sieg, 1973)

6. Carpal spines of P.2–P.6 of typical shape (Fig. 1: 1 subgenus *Akanthinotanais*) 7

– Carpus of P.2–P.6 with 1 transformed blade-like spine (Fig. 1: 2 subgenus *Pseudotanais* s. str.) ... 14

7. With eyes; pars molaris always pointed 8

– Without eyes; pars molaris pointed or ending in several blunt processes 12

8. Merus of P.4–P.6 with 2 short spine-like setae of equal size 9

– Merus of P.4–P.6 with 1 short and 1 long spine-like seta 10

9. Uropodal exopodite nearly as long as endopodite .... *Pseudotanais gerlachi* Sieg, 1977

– Uropodal exopodite only slightly longer than first segment of endopodite ..... *Pseudotanais malayensis* Sieg, 1977

10. Cheliped with carpus elongate (at least 2.5 times longer than broad) and elongate chela (Fig. 1: 4); ischium of P.3–P.6 with 1 long seta 11

– Carpus of cheliped stout (less than twice as long as broad) and chela of typical shape (Fig. 1: 3); ischium of P.3–P.6 with short seta ....*Pseudotanais guillei* Shiino, 1978

11. Peraeonites 4 and 5 relatively small, broader than long, lateral margins convex .... *Pseudotanais mortenseni* Sieg, 1977

– Peraeonites 4 and 5 large, at least as long as broad, lateral margins straighter, with a protuberance at articulation of peraeopods .... *Pseudotanais siegi* Kudinova-Pasternak, 1985

12. Cheliped with carpus elongate (about 3.5 times longer than broad) and elongate chela (Fig. 1: 4); pars molaris with several blunt processes (Fig. 1: 9) .... *Pseudotanais longipes* Hansen, 1913

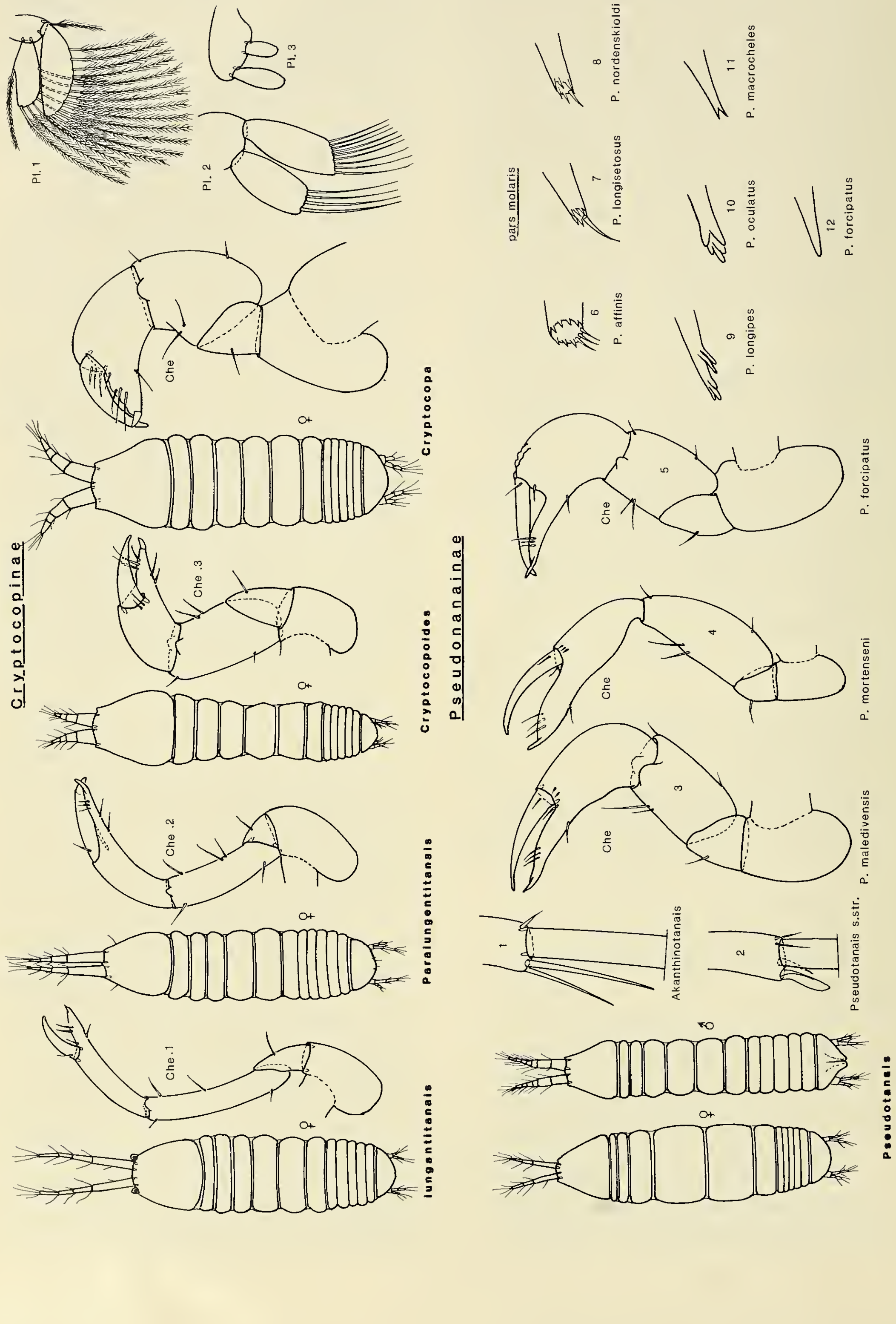
– Carpus of cheliped stout (less than twice as long as broad) and of typical shape (Fig. 1: 3); pars molaris pointed (Fig. 1: 12) 13

13. Sternal border of propodus in P.4–P.6 with 2 distal spine-like setae, longer than claw; propodus 3 times as long as claw .. *Pseudotanais gaussi* Vanhöffen, 1914

– Sternal border of propodus in P.4–P.6 with 1 distal spine-like seta, shorter than claw; propodus twice as long as claw .... *Pseudotanais similis* Sieg, 1977

14. With eyes; pars molaris ending in blunt processes (Fig. 1: 10) or simple point (Fig. 1: 12) 15

– Without eyes; pars molaris of vari-


Cryptocopinae
Pl. 1
Pl. 2
Pl. 3
Che
♀
Cryptocopa
Che. 3
♀
Cryptocopoides
Che. 2
♀
Paraiungentitanais
Che. 1
♀
Iungentitanais
Pseudonanainae
pars molaris
6
P. affinis
7
P. longisetosus
8
P. nordenskioldi
9
P. longipes
10
P. oculatus
11
P. macrocheles
12
P. forcipatus
Che
5
P. forcipatus
Che
4
P. mortenseni
Che
3
P. maledivensis
1
Akanthinotanais
2
Pseudotanais s.str.
♂
♀
Pseudotanais

able shape (broad with several spine-like setae; thin with several pointed or blunt processes; bifurcate or simple point (Fig. 1: 6–8, 11–12) 18

15. Pars molaris ending in several blunt spine-like processes (Fig. 1: 10) .... *Pseudotanais oculatus* Hansen, 1913 (syn. *Paratanais nanaimoensis* Fee, 1927)

– Pars molaris pointed (Fig. 1: 12) 16

16. Cephalothorax longer than broad; P.3 distinctly smaller than P.2 .... *Pseudotanais unicus* Sieg, 1977

– Cephalothorax broader than long, P.3 as large as P.2 17

17. Propodus of P.4–P.6 distally with one long sternal seta, distinctly longer than claw .... *Pseudotanais mexikolpos,* n. sp.

– Propodus of P.4–P.6 with one sternal distal seta, about as long as claw ....*Pseudotanais mediterraneus* G. O. Sars, 1882

18. Pleopods present 20

– Pleopods absent 19

19. Chela with a gap between fixed finger and articulation of dactylus (Fig. 1: 5); pars molaris pointed (Fig. 1: 12) ..*Pseudotanais forcipatus* (Lilljeborg, 1864)

– Cheliped without gap between fixed finger and articulation of dactylus (Fig. 1:3); pars molaris with 3 blunt processes .... *Pseudotanais lilljeborgi* G. O. Sars, 1882

20. Chela with a gap between fixed finger and articulation of dactylus (Fig. 1: 5); pars molaris pointed (Fig. 1: 12) 21

– Chela without gap between fixed finger and articulation of dactylus (Fig. 1: 3); pars molaris not pointed 22

21. Exopodite of uropod at most as long as first segment of endopodite; endite of maxilliped completely fused medially, without notch or setae ... *Pseudotanais jonesi* Sieg, 1977

– Exopodite of uropod distincly longer than first segment of endopodite; endite of maxilliped with 1 pair of small setae on each side of the disto-medial notch ....*Pseudotanais abyssi* Hansen, 1913

22. Pars molaris bifid (Fig. 1: 11) .... *Pseudotanais macrocheles* G. O. Sars, 1882

– Pars molaris broad or tapered, but always with several pointed processes (Fig. 1: 6–8) 23

23. Pars molaris broad, with 3 small distal setae in addition to pointed processes (Fig. 1: 6) .... *Pseudotanais affinis* (Hansen, 1887)

– Pars molaris tapered, without distal setae 24

24. Endopodite and exopodite of uropod nearly equal in length (pars molaris tapered and with several pointed processes of nearly equal size) .... *Pseudotanais vitjazi* Kudinova-Pasternak, 1966

– Exopodite of uropod distinctly shorter than endopodite 25

25. Pars molaris with 1 process distinctly longer than others (Fig. 1: 7); carpus of P.4–P.6 with 1 long sternal seta (as long as propodus) *Pseudotanais longisetosus* Sieg, 1977

– Pars molaris with all processes of nearly equal size (Fig. 1: 8); carpus of P.4–P.6 with short sternal seta

←

Fig. 1. Major characteristics of the different pseudotanaid subfamiliar taxa.

. . . . *Pseudotanais nordenskioldi* Sieg, 1977

Remarks.—Two species recently referred to the genus *Cryptocope, C. longa* Kudinova-Pasternak, 1982, and *C. vitjazi* Kudinova-Pasternak, 1982, are not included in the key, since they both appear to be most closely related to *Leptognathia* (Leptognathiinae). Both species differ distinctly from the described species of *Cryptocope* in the overall shape of the body and chela, the morphology of the pars incisiva, and the setation of the pleopods. The pars incisiva in *Cryptocope* is deeply incised while those of *Leptognathia* spp., *C. longa* and *C. vitjazi* are only slightly crenulated (see Sieg 1986b; Kudinova-Pasternak 1982:figs. 3, 4). The pleopodal exopodite and endopodite of *Cryptocope* only have distal setae (see Sieg 1977), whereas those of *C. longa* and *C. vitjazi* like *Leptognathia* spp. also each bear one proximal seta (see Kudinova-Pasternak 1982:figs. 3, 4). Based on these observations, we tentatively transfer *C. longa* and *C. vitjazi* to the genus *Leptognathia*, as diagnosed by Sieg (1986b).

Pseudotanais borceai Bačescu, 1960, is not included in the key because of apparent inconsistencies in the original and only description. The type material has been lost (Bačescu, pers. comm.), and at present it is not possible to determine its taxonomic status. Additional specimens from the type locality are needed to clarify this problem.

We also excluded *P. kurchatovi* Kudinova-Pasternak & Pasternak, 1978 from the key because it does not belong to *Pseudotanais*. Our reasons are based on the following criteria. In their original description Kudinova-Pasternak & Pasternak (1978: 188–190, fig. 5) described and illustrated the antenna 1 with the second segment short and annular as well as the third segment being distinctly longer. In all other known species of *Pseudotanais* the second segment is nearly as long as the third. Other morphological differences that make the systematic position of *P. kurchatovi* uncertain are: (1) the shape of the cheliped (especially that of the chela), (2) the proportion of peraeonites (peraeonites 1 and 2 atypically long and peraeonites 4 and 5 atypically broad), (3) the shape of dactylus and its terminal spine on P.4–P.6 (in all other species of *Pseudotanais* a short claw is present while in *P. kurchatovi* the dactylus and spine are unfused with a combined length nearly equal to that of propodus), and (4) the shape of the pars molaris is more reminiscent of species belonging to the Typhlotanaidae rather than to the genus *Pseudotanais.*

It also should be mentioned that at least in *P. nordenskioldi* Sieg, 1977, *P. longisetosus* Sieg, 1977, and *P. oculatus* Hansen, 1913, the figures of the pars molaris given by Sieg (1977) are misleading, since there are no distinct spines or setae as illustrated (see Figs. 43, 46, 49). In these species the pars molaris ends in several spine-like teeth, not spines or setae.

Subfamily Cryptocopinae Sieg, 1977

Iungentitanais primitivus (Sieg, 1973)

Figs. 2–4, 12

Material. — FLORIDA MIDDLE GROUNDS: Sta 151, 28°32′13″N, 84°18′40″W, 25–28 Jun 1979, 31.3–33.0 m, coral reef, dive, 1 female, Marine Science Consortium (MESC) Cat. No. 6157-10495.—Same station, 15–19 Oct 1978, 1 female, MESC Cat. No. 6157-10499 and 2 females, Cat. No. 6157-10500.—Sta 481, 29°30′52″N, 84°18′59″W, 6–8 Oct 1978, 28.5–33.0 m, coral reef, dive, 1 female, MESC Cat. No. 6157-10496.—Same station, 14–18 Oct 1978, 1 female, MESC Cat. No. 6157-10498.—Sta 247, 28°32′16″N, 84°18′36″W, 26–30 Jan 1979, 31.3–33.0 m, coral reef, dive/grab, 1 female, MESC 281261.

FLORIDA KEYS: Pumpkin Creek, Key Largo, 25°19′N, 80°16′W, no depth information, 2 Jun 1981, 2 females, Invertebrate Zoology Collection of the Gulf Coast Re-

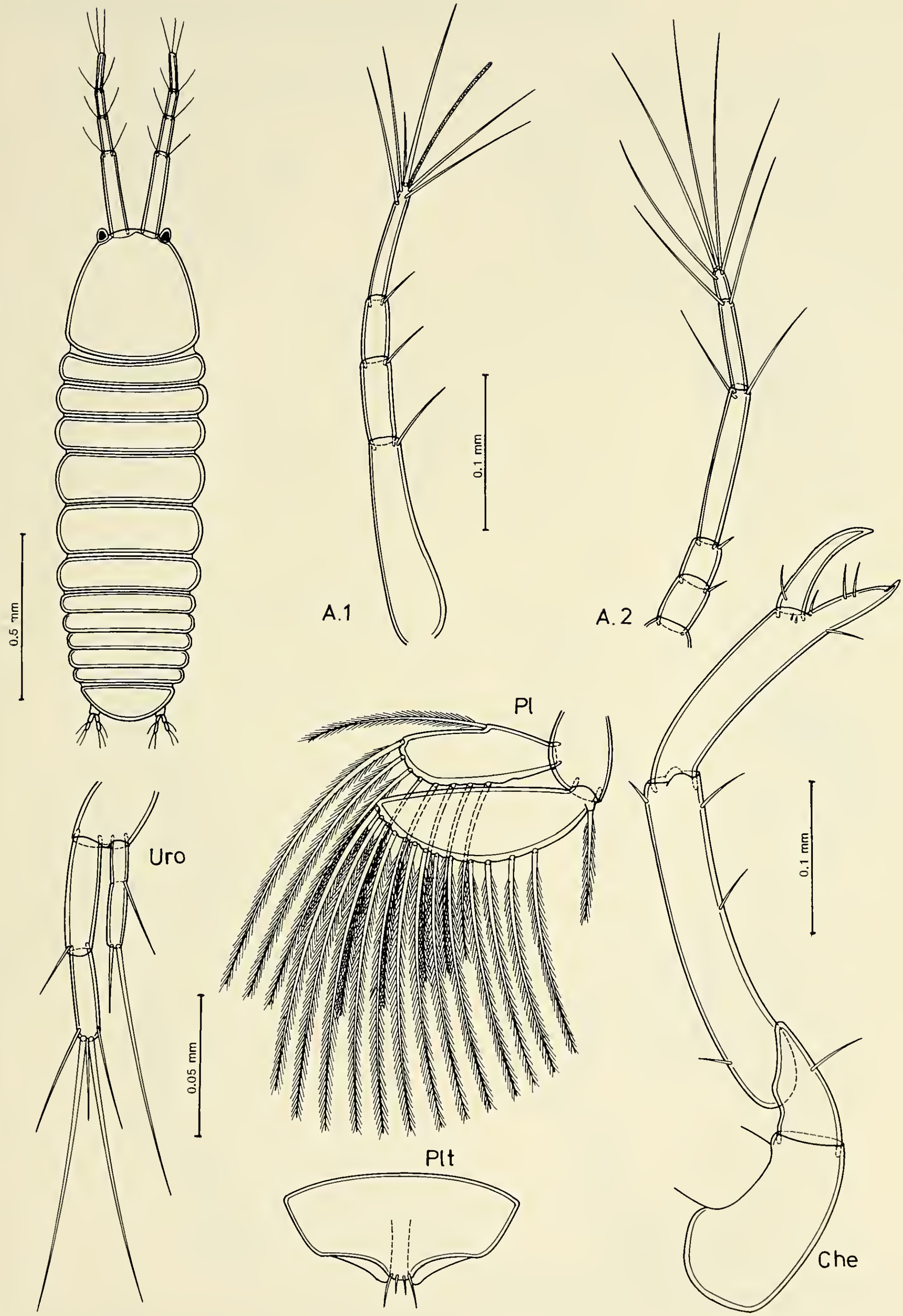


Fig. 2. *Iungentitanais primitivus* (Sieg, 1973), female.

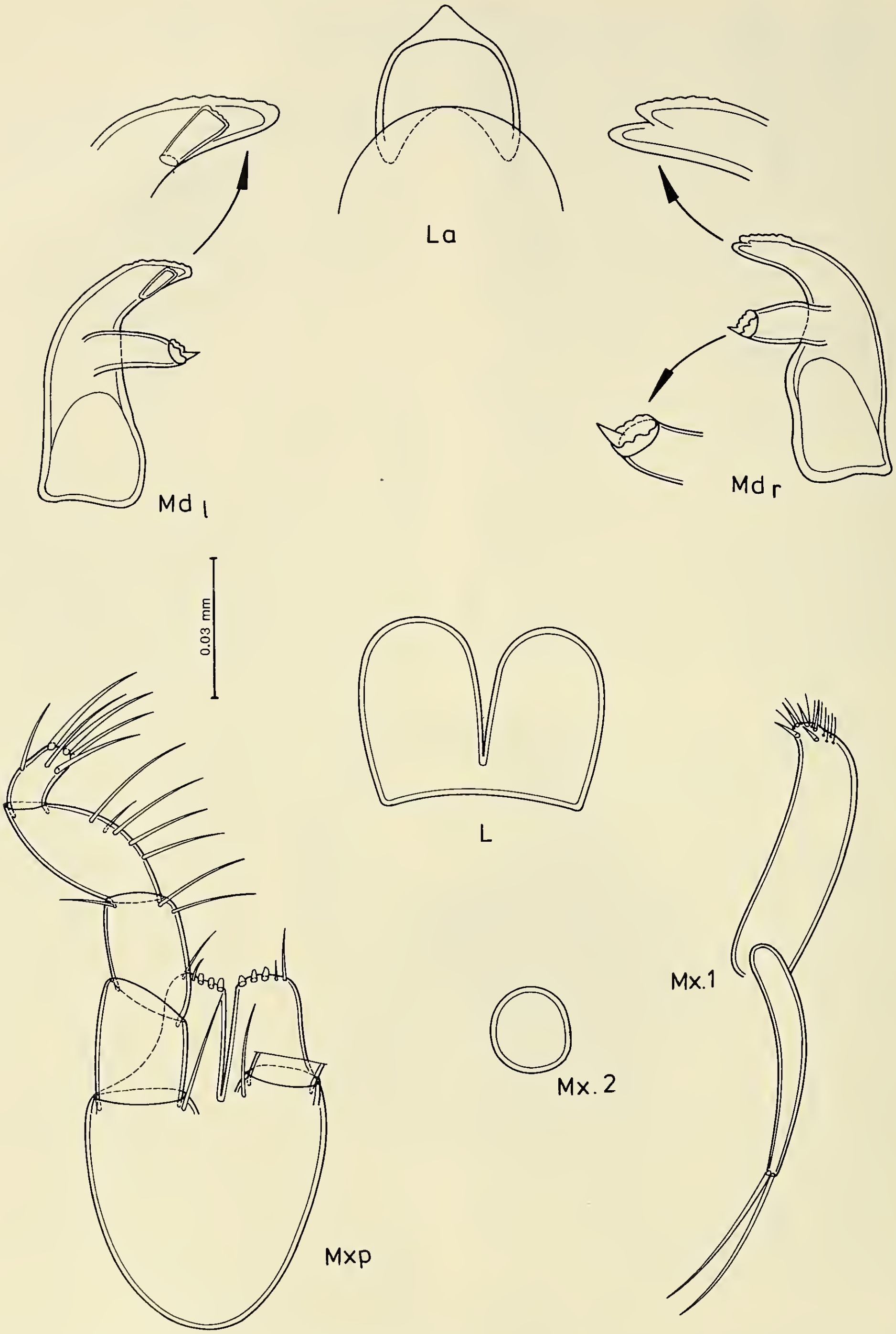


Fig. 3. *Iungentitanais primitivus* (Sieg, 1973), female.

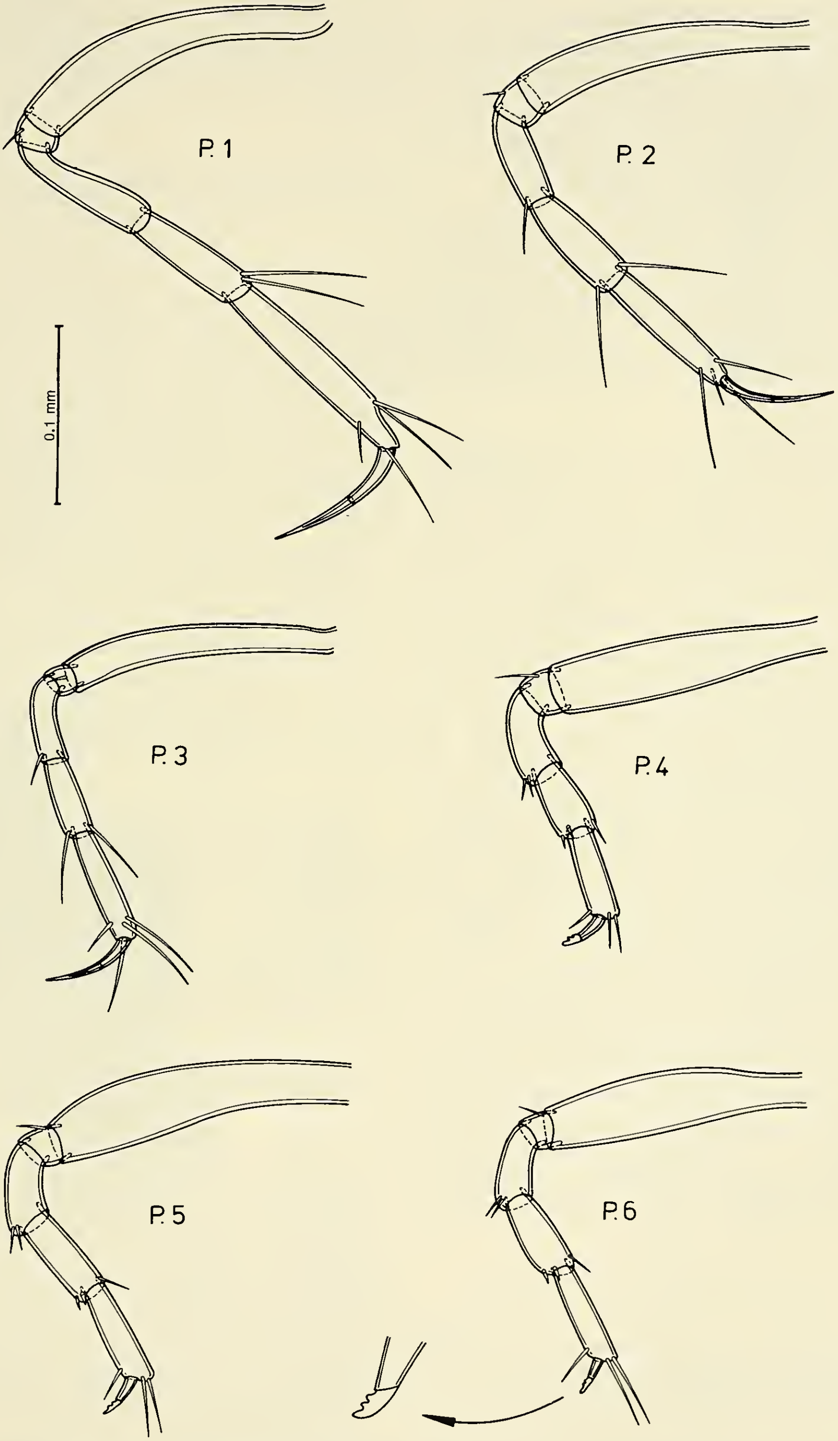


Fig. 4. *Iungentitanais primitivus* (Sieg, 1973), female.

search Laboratory (GCRL) Museum, Cat. No. I 86-1127.—Shark Channel, between lower Saddlebunch Keys and Big Coppitt Key, no depth information, 5 Jan 1982, 24°36′N, 81°39′W, 2 females dissected in Sieg Coll. and 1 female (lost).

Remarks.—*Iungentitanais primitivus* is characterized by a slender cheliped and a 4-segmented antenna 1. The presence of well developed eye-lobes containing clearly pigmented visual elements distinguishes the species from its closest relative *Paraiungentitanais longigigitatus* (Kudinova-Pasternak, 1975).

The mouthparts of two specimens were dissected to supplement the original description. As noted by Sieg (1977:12) both mandibles of the holotype, the only specimen then available, were lost during dissection. The mandibles (Fig. 3) do not differ markedly from those of *Paraiungentitanais longidigitatus.* Each mandible is well developed and has a broad pars molaris. The surrounding wall of the crushing area is slightly indented and has 1 tooth-like process. The distal margin of the pars incisiva of the right mandible is crenulated. The tip is bifid, and the lower tooth probably represents the fused lacinia mobilis. On the left mandible the lacinia mobilis is small and not fused with the pars incisiva.

Distribution (Fig. 12).—The holotype was collected from the harbor of Saint Thomas, West Indies, at a depth of 18.2–27.3 m. Our records from the Florida Keys and Florida Middle Grounds indicate that the species may have a broad distribution throughout the tropical waters of the Gulf of Mexico and the Caribbean (about 18–33 m).

Pseudotanais G. O. Sars, 1882

Remarks.—In our material each of the two subgenera established by Sieg (1977) is represented by a single species. The subgenus *Akanthinotanais* is characterized by having long meral spines on P.4–P.6 while *Pseudotanais,* s.s. has one transformed blade-like spine. *Pseudotanais mortenseni* Sieg, 1977 belongs to the former subgenus and *Pseudotanais mexikolpos,* n. sp. to the latter.

Pseudotanais (*Akanthinotanais*) *mortenseni* Sieg, 1977

Figs. 5–7, 12

Material.—FLORIDA KEYS: Pumpkin Creek, Key Largo, 25°19′N, 80°16′W, no depth information, 2 Jun 1981, 1 female, dissected in Sieg Coll.—Shark Channel, between lower Saddlebunch Keys and Big Coppitt Key, 24°36′N, 81°39′W, no depth information, 1 Jan 1982, 1 female, dissected in Sieg Coll. and 1 female (lost).

Remarks.—*Pseudotanais mortenseni* is distinguished from the other members of the subgenus *Akanthinotanais* by the following combination of characters: (1) presence of eyes, (2) a pointed pars molaris, (3) the shape of the cheliped, and (4) the armament of the merus (see key and Figs. 5–7).

Distribution (Fig. 12).—This is the first report of this species since its original description from the harbor of Saint Thomas, West Indies. Like *Iungentitanais primitivus* (Sieg, 1973), it may have a broad distribution in the tropical waters of the Gulf of Mexico and the Caribbean.

Pseudotanais (*Pseudotanais*) *mexikolpos,* new species

Figs. 8–11, 12

Synonymy.—cf. *Paratanais* sp. A., Anonymous (Texas A&M University), 1978:772.

Material.—Holotype: 1 female, National Museum of Natural History, USNM 231765; off Texas coast, East Flower Garden Bank, 72 m, Sta 902, 27°54′36.64″N, 93°32′53.27″W. Paratypes: 1 females, dissected in Sieg Coll., Sta 899-4-SED, 1 neuter, Sta 896-6b-SED, Invertebrate Zoology Collection of the Gulf Coast Research Laboratory Museum Cat. No.; 1 female, Sta

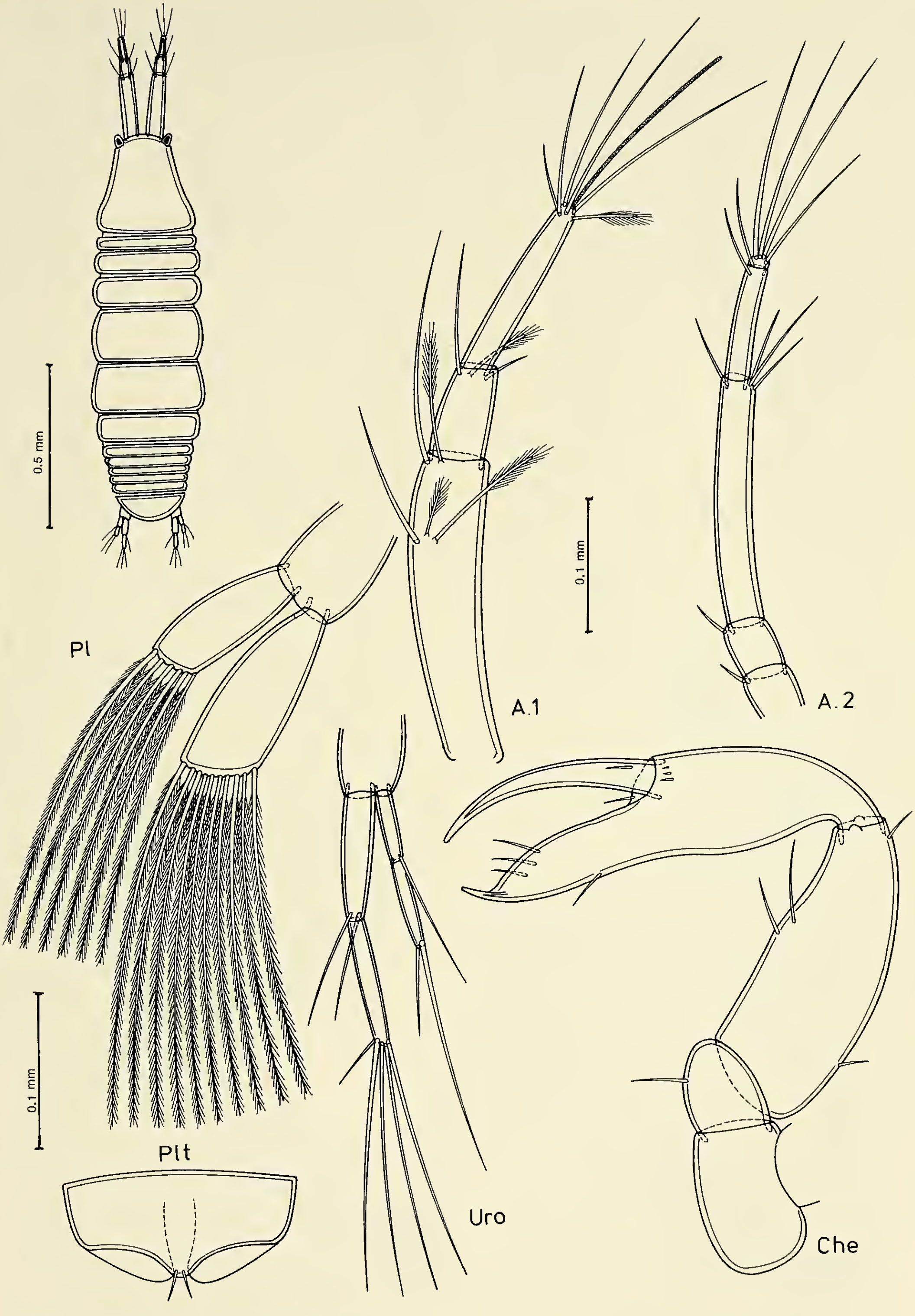


Fig. 5. *Pseudotanais mortenseni* Sieg, 1977.

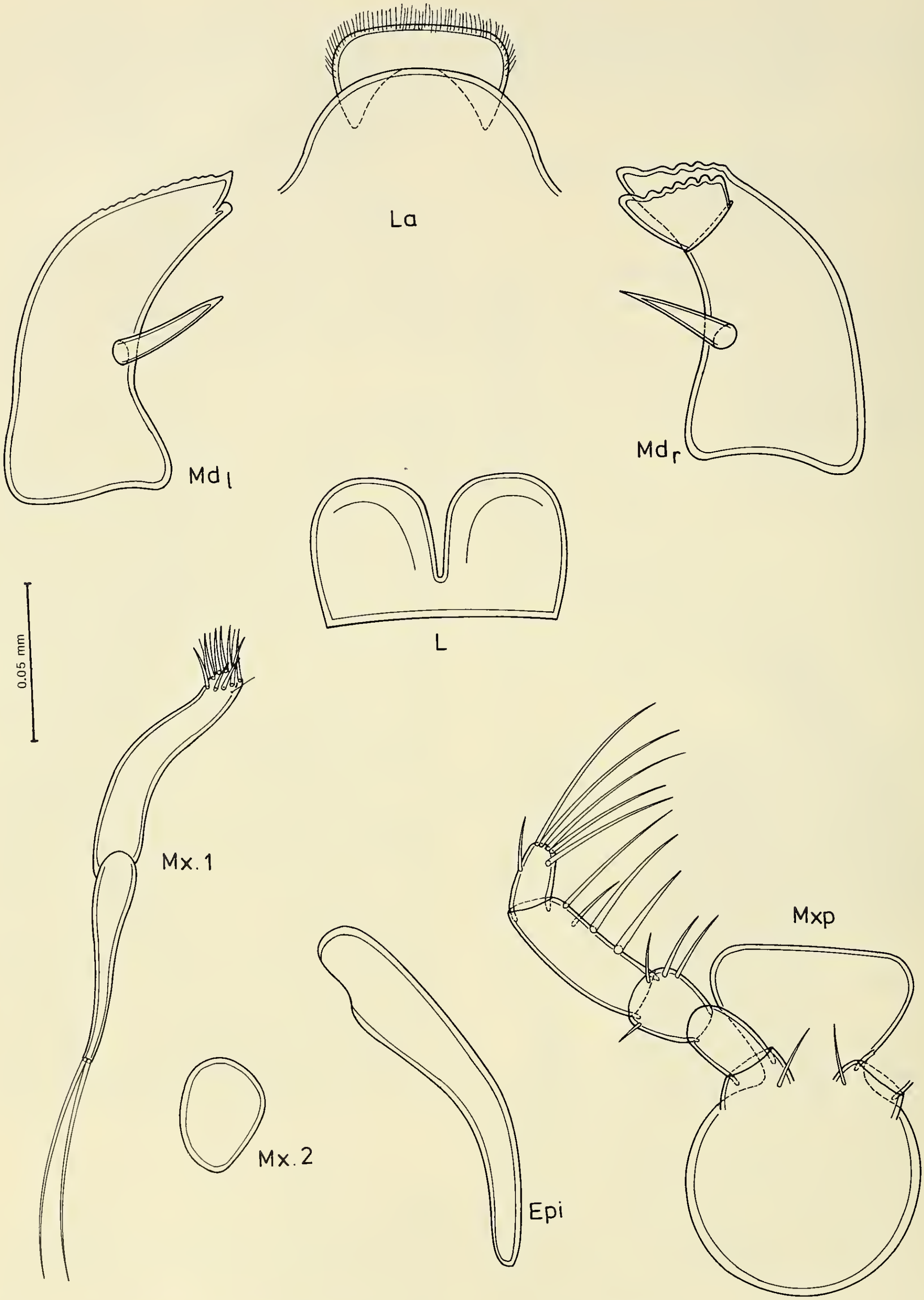


Fig. 6. *Pseudotanais mortenseni* Sieg, 1977.

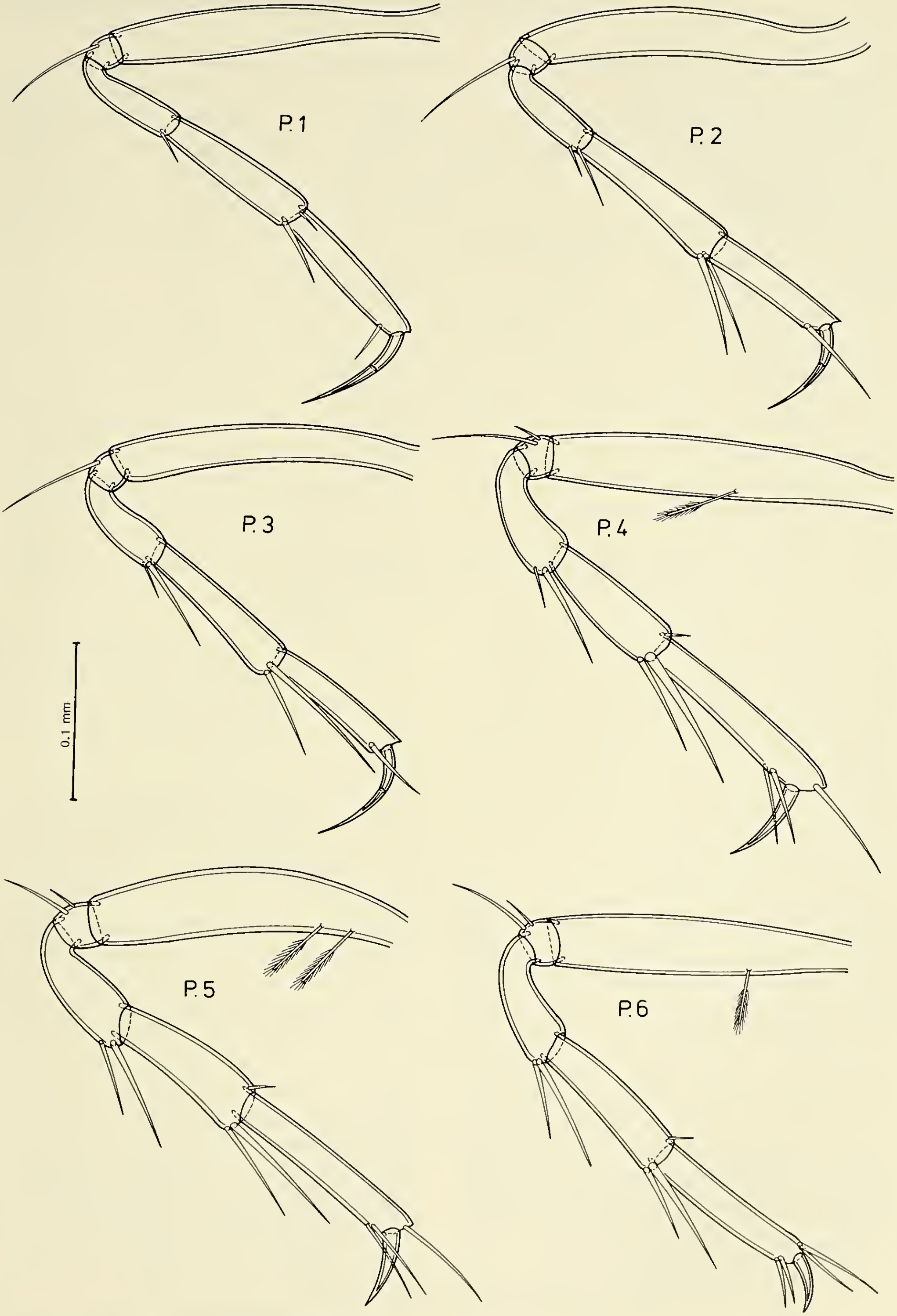


Fig. 7. *Pseudotanais mortenseni* Sieg, 1977.

896-3-4, USNM 231766; 1 neuter, Sta 897-8-3, USNM 231768; 1 neuter, Sta 896-6b-4, USNM 231769; all from type locality.

Additional material.—2 females of Texas coast, Stetson Bank, 28°09′N, 94°16′W, lost in slide preparation.

Type locality.—East Flower Garden Bank, off Texas coast, 27°54′36.64″N, 93°34′53.27″W, 72 m.

Etymology.—The first part of the name is taken from Mexico while the second part is of Greek origin (kolpos = bosom).

Description of female (paratype).—Length of adult female reaching about 1.5 mm, about 4.2 times longer than broad (Fig. 8).

Cephalothorax: Short, 1.1 times broader than long; eye-lobes well developed and with visual elements; rostral area convex, anterior ⅓ smallest, broadest posteriorly and corners rounded; no setae.

Peraeonites: Lateral margins of all peraeonites rounded in dorsal view, bearing no setae, spines, or peaks. First to third peraeonites small, first 6.9 times, second 5.5 times, and third 3.5 times broader than long; fourth and fifth peraeonites largest, fourth only 1.7 times and fifth 1.8 times broader than long; sixth peraeonite broadest posteriorly, margins strongly convex, about 2.3 times broader than long.

Antenna 1 (Fig. 8): Three-segmented. First segment 3.9 times longer than broad, with 1 seta at midlength and one seta, 1 setule, and 3 feathered hairs distally. Second 2.3 times longer than broad, with 2 distal setae. Third segment elongate, nearly 3.9 times longer than broad, tip with 1 aesthetasc, 2 normal setae, and 4 setae having bifid tips.

Antenna 2 (Fig. 8): Six-segmented. First segment small, partly fused with cephalothorax, and unarmed. Second stout, as long as broad, outer border with 1 spine-like distal seta. Third segment also short, but 1.5 times longer than broad, outer border with 1 spine-like distal seta. Fourth segment elongate, bent sternally, 4.6 times longer than broad, with 3 setae and 1 feathered hair distally. Fifth nearly 2.9 times longer than broad, 1 distal seta. Sixth segment very small, conical, with 2 short and 3 long setae.

Labium (Fig. 9): Hood-shaped, covered with fine setules.

Mandibles (Fig. 9): Not strongly calcified, but well developed and of typical shape. Pars molaris reduced, small, thin, with pointed tip. Left mandible with slightly crenulated pars incisiva, lacinia mobilis well developed, with 1 large and 4 small teeth. Right mandible with crenulated pars incisiva, lacinia mobilis fused to pars incisiva, represented only by well-developed edge.

Labium (Fig. 9): Consisting of 1 lobe, outer lobe totally lacking; inner lobe deeply incised at middle.

Maxilla 1 (Fig. 9): Endite bearing circle of 9 spines. One-segmented palp as long as endite, with 2 terminal setae.

Maxilla 2 (Fig. 9): Of typical shape, oval, lacking setae.

Maxilliped (Fig. 9): Well developed, without coxae. Basis fused medially, with a small seta near articulation of palpus; inner lobe of normal size, totally fused, distal margin undulate (wave-like), with 2 rows of 4 setules. Palpus 4-segmented; distal margin of first segment slanted towards inner border, trapezoidal, 1.3 times longer than broad, unarmed; second segment also trapezoidal, but inner border longer than outer, inner border with 2 setae; third segment elongate, about 2.4 times longer than broad, inner border with 3 strong setae. Fourth about 2.6 times longer than broad, outer border with 1 seta, inner border with 4 strong setae.

Epignath (Fig. 9): Of typical shape; elongate, tip rounded and unarmed.

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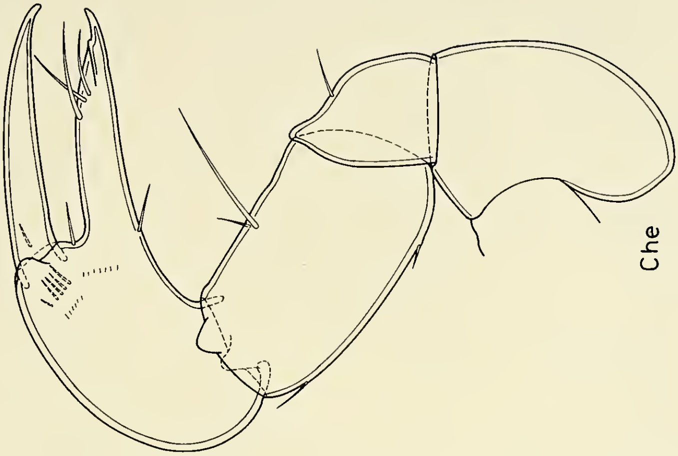
Fig. 8. *Pseudotanais mexikolpos*, n. sp., female, paratype.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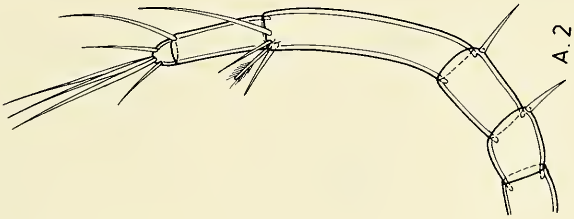
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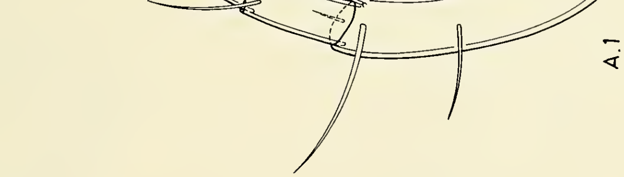
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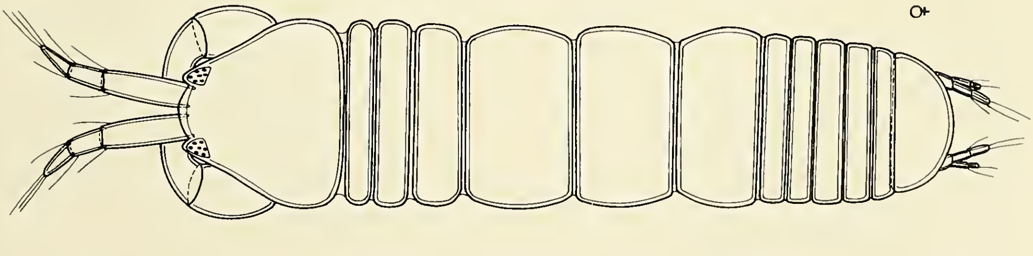
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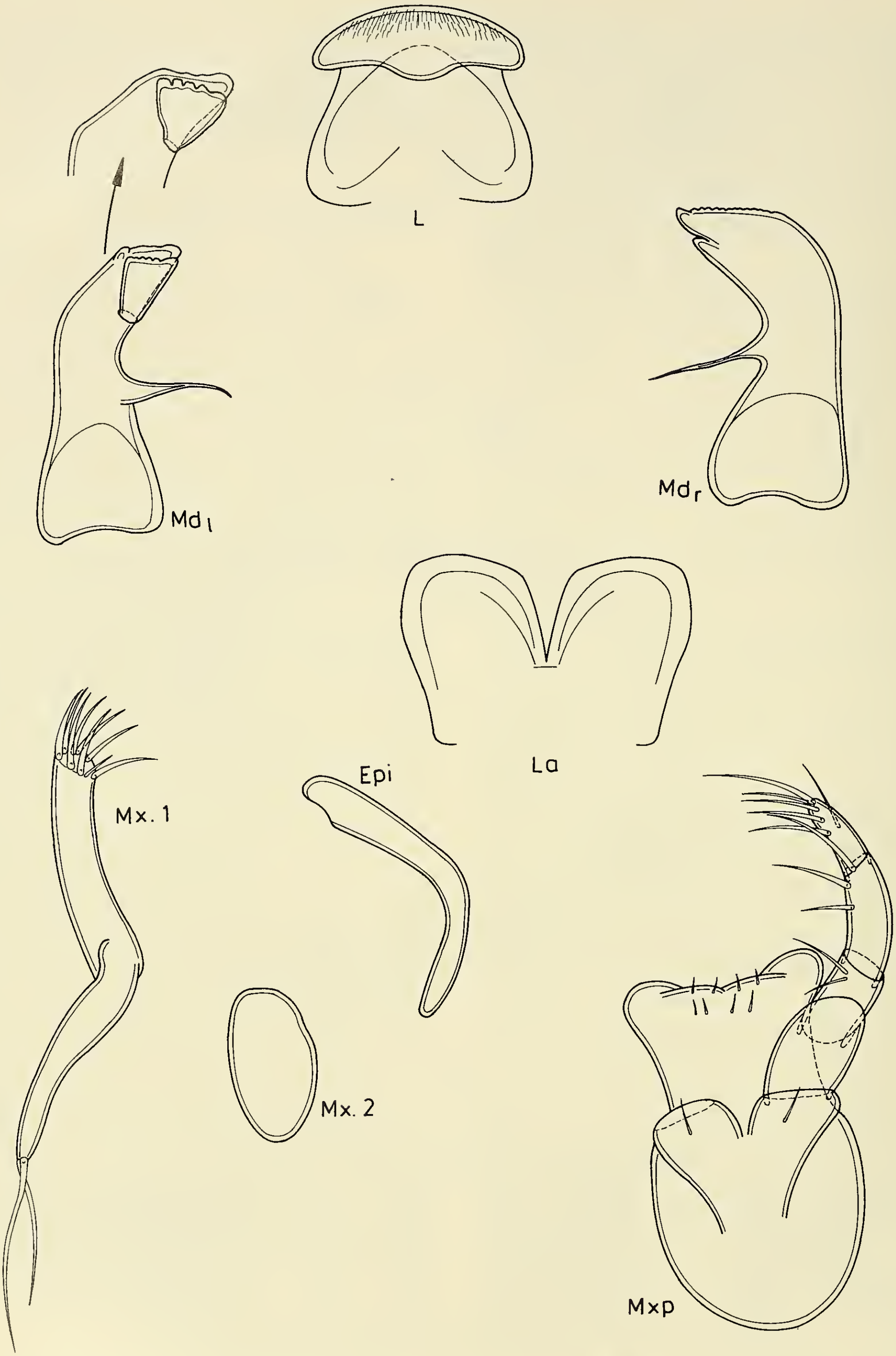

Fig. 9. *Pseudotanais mexikolpos,* n. sp., female, paratype.

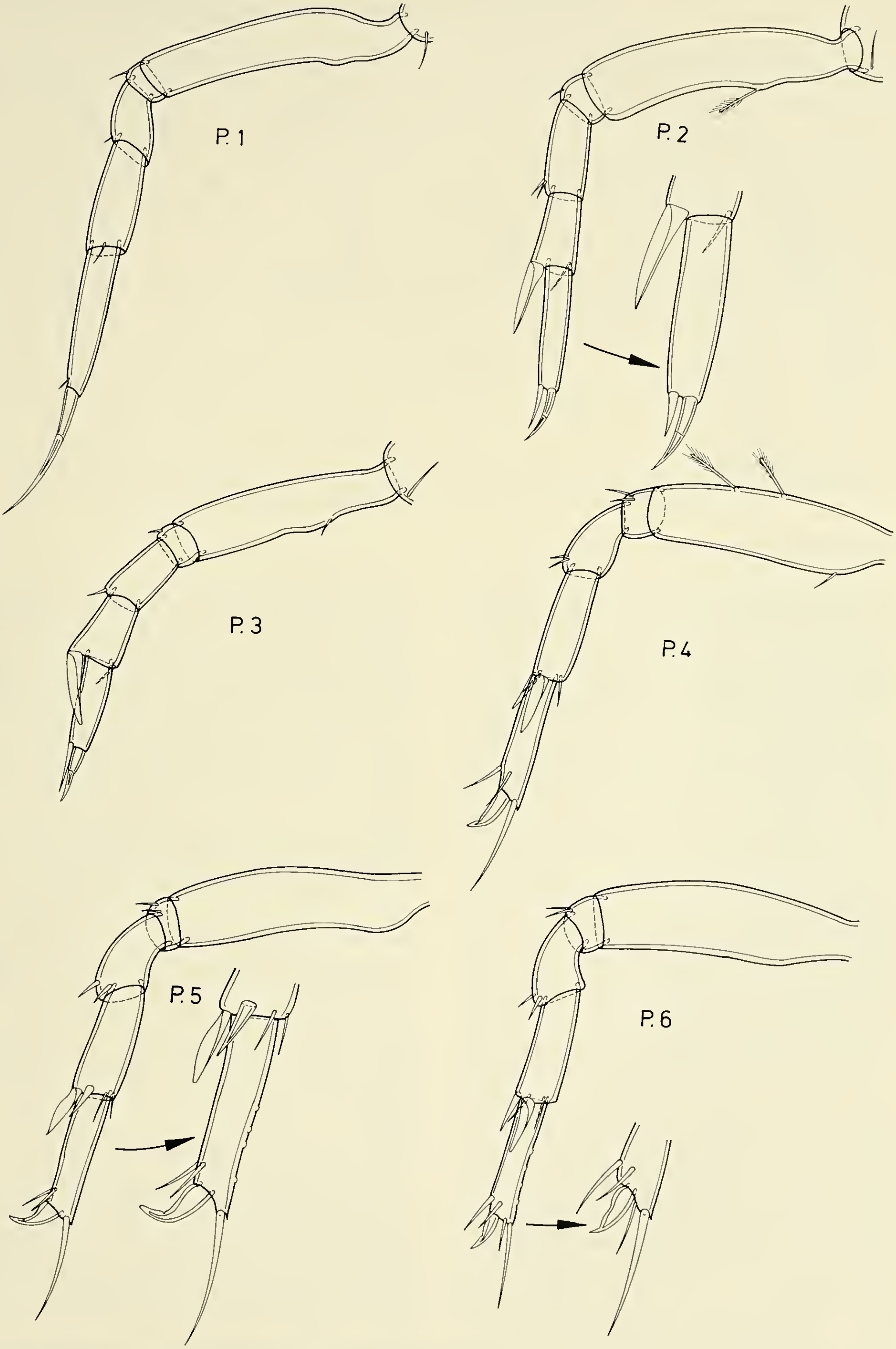

Fig. 10. *Pseudotanais mexikolpos*, n. sp., female, paratype.

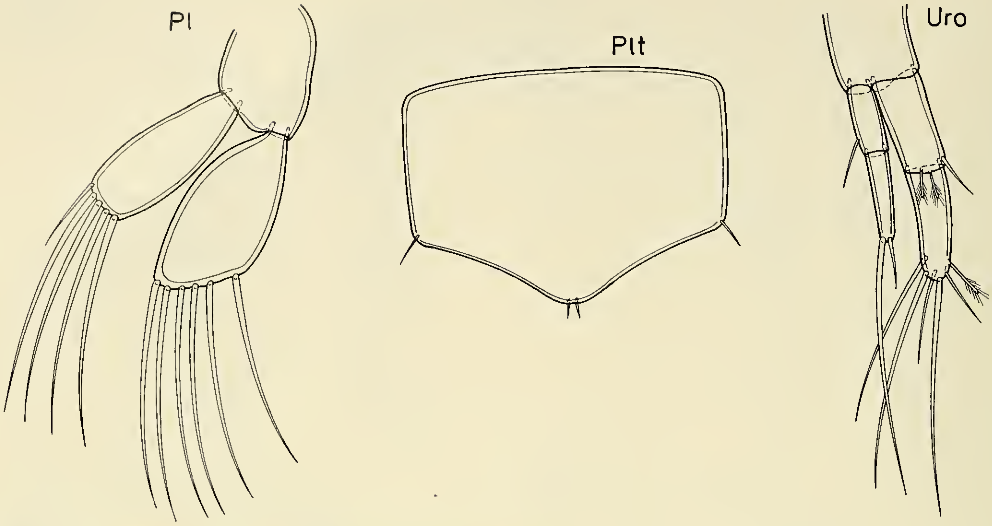

Fig. 11. *Pseudotanais mexikolpos,* n. sp., female, paratype.

Cheliped (Fig. 8): Well developed, of typical shape, chela with small gap. Side-piece of normal size, articulating with basis behind a distal conjunction. Basis stout, about 1.6 times longer than broad, unarmed. Merus small, triangular, with 1 midsternal seta. Carpus relatively short, 1.6 times longer than broad, tergal border with 1 small proximal and 1 small distal seta; sternal border with 1 short and 1 long seta at midlength. Propodus with fixed finger elongate, nearly 3 times longer than broad, with "comb" at base of dactylus consisting of five small setae, with 2 groups of setules nearby; fixed finger with 3 tergal setae, tip not markedly sclerotized, sternal border with 1 small seta; with 1 small seta close to articulation of dactylus. Dactylus straight, with 1 small proximal seta.

Peraeopod 1 (Fig. 10): Slender; coxa not fused with peraeonite, with 1 seta. Basis 5.4 times longer than broad, unarmed. Ischium annular, with 1 tergal seta. Merus nearly 1.5 times longer than broad, with 1 tergal setule. Carpus 2.4 times longer than broad, with 1 distal rostral seta. Propodus elongate, five times longer than broad, with 1 distal tergal setule. Dactylus and terminal spine not fused, combined length nearly equal to that of propodus.

Peraeopod 2 (Fig. 10): Shorter than P.1; coxa not fused with peraeonite, having 1 seta. Basis slightly bent sternally, 4.6 times longer than broad, sternal border with 1 feathered hair at midlength. Ischium annular, with 1 tergal setule. Merus slightly over 2 times longer than broad, tergal border with 1 rostral and 1 caudal seta distally. Carpus shorter, 1.8 times longer than broad, tergal border with 1 strong blade-like spine reaching about 0.6 times length of propodus, with 1 additional caudal seta. Propodus about 4.6 times longer than broad, with 1 tergal spine-like seta distally. Dactylus and terminal spine unfused, short, combined length reaching 0.45 times that of propodus.

Peraeopod 3 (Fig. 10): Similar to P.2, except propodus 2.4 times longer than broad, therefore carpal blade-like spine appearing smaller than in P.2, but in reality of same size.

Peraeopod 4 (Fig. 10): Somewhat stouter than P.1–P.3. Coxa fused to peraeonite, no setae. Basis nearly 3.6 times as long as broad, tergal border with 2 feathered hairs, sternal border with 1 proximal setule. Ischium annular, with 2 tergal setae. Merus bent sternally, 1.5 times longer than broad, tergal border with 1 rostral and 1 caudal spine-like seta distally. Carpus elongate, about 3 times longer than broad, tergal border dis-

Fig. 12. Distribution of the pseudotanaid species in the Caribbean and the Gulf of Mexico. ● *Iungentitanais primitivus* (Sieg, 1973). ■ *Pseudotanais mortenseni* Sieg, 1977. ▲ *Pseudotanais mexikolpos,* n. sp.

tally with 1 rostral blade-like spine and 1 spine, sternal border distally with 1 caudal seta. Propodus slightly longer than carpus, 4.2 times longer than broad, tergal border with 1 rostral and 1 caudal spine-like setae distally, sternal border with 1 spine-like seta, which is distinctly longer than terminal segment. Dactylus and terminal spine fused to claw.

Peraeopod 5 (Fig. 10): Similar to P.4. Basis unarmed, dactylus bearing 1 additional seta, and sternal border of propodus with 3 to 4 tubercles.

Peraeopod 6 (Fig. 10): Similar to P.4 and P.5, except propodus bearing distally 1 additional small seta on sternal border.

Pleopods (Fig. 11): All 5 pairs of pleopods similar. Basis small, slightly longer than broad, unarmed. Exopodite 1-segmented, with 6 setae on outer border. Endopodite 1-segmented, with 1 small seta appearing articulated to inner border, outer border with 4 setae, none appearing pinnate.

Pleotelson (Fig. 11): Of typical shape, not elongate, 1.4 times broader than long; caudal point protuberant, with 2 small medial setae; 1 additional seta at each caudal corner.

Uropods (Fig. 11): Biramous. Basis short, as long as broad, unarmed. Endopodite 2-segmented; first segment 2.1 times as long as broad, with 2 feathered hairs and 1 seta distally; second segment as long as first, but more slender, about 2 times longer than broad, 2 small, 3 long, and 1 feathered hair at tip. Exopodite 2-segmented, reaching slightly more than ¾ length of endopodite; first segment 2.5 times longer than broad, 1 distal seta; second more slender, 3.8 times longer than broad, with 1 long and 1 short seta at tip.

Remarks.—This species appears to be most closely related to *P. unicus* Sieg, 1977 and *P. mediterraneus* G. O. Sars, 1882, both from the Mediterranean. *Pseudotanais mexikolpos* can be separated from *P. unicus* by its short cephalothorax and peraeopod 3, which is distinctly smaller in *P. unicus.* It is distinguished from *P. mediterraneus* by having a much longer disto-sternal seta on propodus of P.4–P.6.

Distribution (Fig. 12).—*Pseudotanais mexikolpos* is presently known from the type locality, in the vicinity of Golum Lake, a hypersaline seep, on the East Flower Garden Bank, and from Stetson Bank, both off Texas coast.

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DIACRIA PICCOLA AND *DIACRIA MACULATA*: TWO NEW PTEROPOD MOLLUSC SPECIES FROM THE ATLANTIC AND PACIFIC OCEANS

J. Bleeker and S. van der Spoel

Abstract.—A few specimens of *Diacria* from the northwestern Pacific Ocean were described as intermediates between *D. trispinosa* forma *trispinosa* and *D. rampali* (cf. Van der Spoel 1982). New records from this *Diacria* form from the Pacific and Atlantic prove that these 'intermediates' are a common phenomenon, not an incidental occurrence. The co-occurrence of this *Diacria* form with other related species of the genus made it acceptable that a good species is involved, for which the name *Diacria maculata* is proposed.

In one of the Northwestern Pacific Ocean sediment samples very small *Diacria trispinosa*-like specimens were found. Though it is known that the western Pacific representatives of *D. trispinosa* may be small (Rampal 1975), the present material, twice as small as the smallest previously known specimen, is considered to represent a species new to science for which the name *D. piccola* is proposed.

Diacria piccola, new species
Figs. 2–4

Material.—Locality data of *D. piccola* with numbers of specimens in parentheses: Holotype USNM 276782 and paratype USNM 859098, both from *Albatross* sta 5236, Philippines, off Magabao Is., E. Mindanao, 8°50′45″N, 126°26′52″E, 494 fms, fine gray sand, 12 feet Agassiz beam trawl, 11 May 1908 (2).

Description.—The specimens collected from the sediment are subfossils or Recent specimens which have been buried in the sediment for a long period, as evidenced by decalcification. No color patterns remain visible. In the holotype the caudal spine is broken off below the closing septum, the width near the septum (> 15% of shell width) is relatively large compared to other species (< 15% of shell width). The lateral spines are worn off. The dorsal side shows 3 ribs; the central one is especially broad and flattened. The lateral sides between the closing septum and the lateral spines are nearly straight and meet at an angle of 66°. The dorsal lip is curled dorsally. The ventral lip is slightly curved ventrally. The 2 lateral ribs on the ventral side are indistinct. Measurements of the holotype: shell width 2.52 mm, shell length 3.32 mm, length between lateral spines and closing septum 1.60 mm, distance between lateral spines and closing septum 2.00 mm, distance between lateral spines and centre of upper lip 1.80 mm, width of shell aperture 1.08 mm, height of shell aperture 0.49 mm, angle of lateral sides 66°.

The paratype is slightly smaller than the holotype and damaged at the upper shell lip; it is filled with sediment.

Type material.—Deposited at the Smithsonian Institution. The holotype USNM 276782 and one paratype USNM 859098 are both from *Albatross* sta 5236, 494 fms, fine gray sand.

Type locality.—Philippines, off Magabao Is., E. Mindanao, 8°50′45″N, 126°26′52″E.

Etymology.—The small size and resemblance to a small pipe is reflected in the Italian word piccolo. It is here treated as a neo-Latin adjective.

Diacria maculata, new species
Figs. 4, 5, 8, 9

Material.—Locality data of *D. maculata* with numbers of specimens in parentheses; geographic positions between square brackets are added by the present authors: Holotype USNM 283052 and paratypes USNM 859099 (8), both from: *Albatross* sta 5470, Philippines, Lagonboy Gulf, E. Luzon, 13°37′30″N, 123°41′09″E, 560 fms (estimate), 18 Jun 1909 (9).

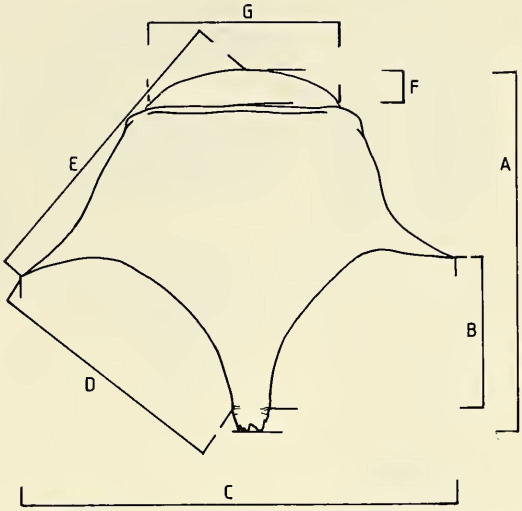
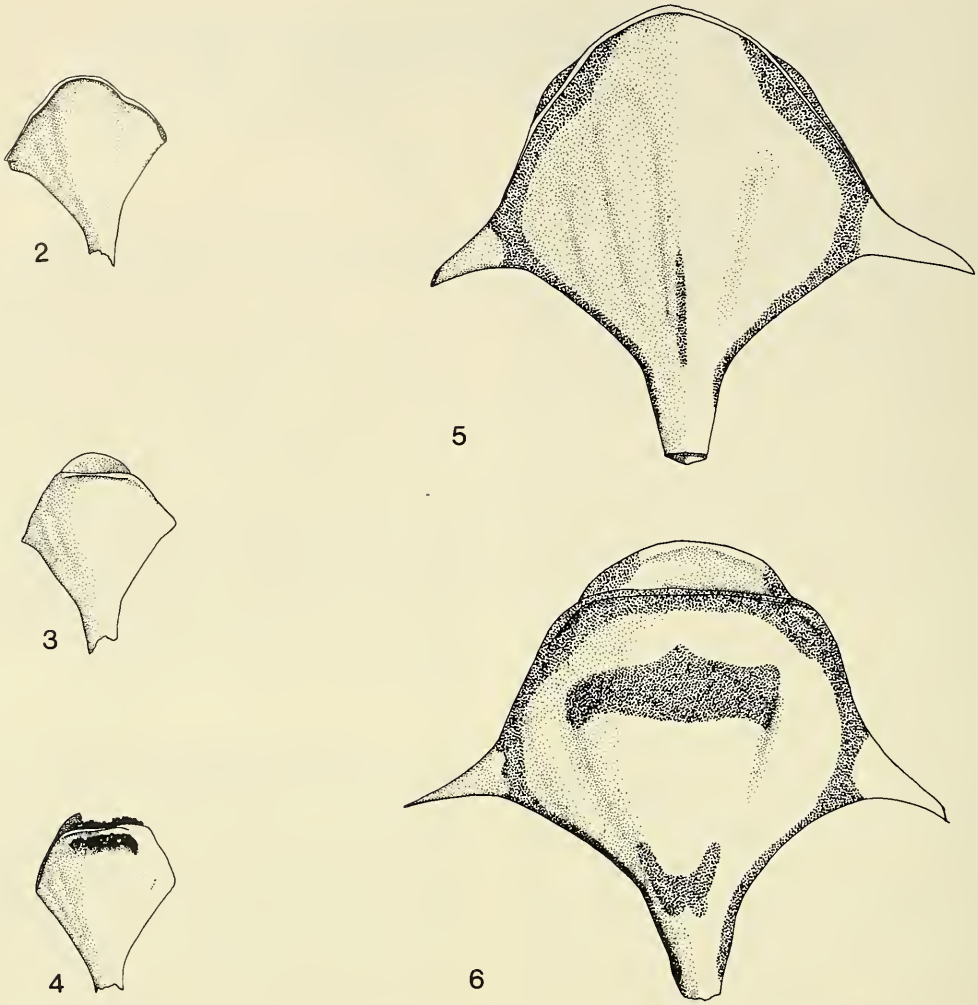


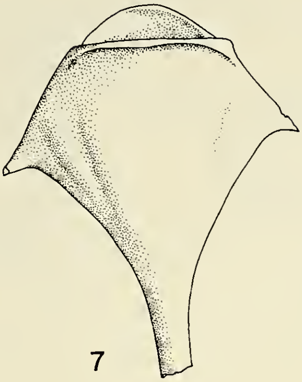
Fig. 1. *Diacria* shell showing measurements referred to. A, Shell length; B, Length between lateral spines and closing septum; C, Shell width; D, Distance between lateral spines and closing septum; E, Distance between lateral spines and center of upper lip; F, Height of shell aperture; G, Width of shell aperture.

USNM 859100: *Fish Hawk* sta 1154, off Martha's Vineyard, 39°55′31″N, 70°39′W, 193 fms (1).—USNM 38491: *Albatross* sta 2222, S of Martha's Vineyard, 39°03′15″N, 70°50′45″W, 1537 fms (2).—USNM 859101, *Albatross* sta 2760, off Bahia, Brazil, 12°07′00″S, 37°17′00″W, 1019 fms, ooze (1).—USNM 859102, *Albatross* sta 5580, Darvel Bay, Borneo, 23 m, W of Sibutu, 4°52′45″N, 119°06′45″E, 162 fms, brown sand and coral (2).—USNM 258143: *Albatross* sta 5238, Philippines, off Pt. Lambajon, E. Mindanao, 7°34′45″N, 126°38′15″E, 380 fms, green mud (4).—USNM 274767: *Albatross* sta 5394, Philippines, off Dumurug Masbate, 12°00′30″N, 124°05′36″E, 153 fms, green mud (5).—USNM 276003: *Albatross* sta 5265, Philippines, off Matocot Pt., W. Luzon, 13°41′15″N, 120°00′50″E, 135 fms, sand and mud (1).—USNM 859103, *Albatross* sta 5236 Philippines, off Magabao Is., E. Mindanao, 8°50′45″N, 126°26′52″E, 494 fms, fine gray sand (4).—USNM 281794: *Albatross* sta 5392, Philippines, off Adyagan Is., E. Masbata, 12°13′15″N, 124°05′03″E, 135 fms, green mud and sand. (5).—USNM 284465: *Albatross* sta 5314, China Sea, off Pratas Is., 21°41′N, 116°46′E, 122 fms, sand and broken shells (1).—USNM 284819: *Albatross* sta 5313, China Sea, off Pratas Is., 21°30′N, 116°49′E, 150 fms, sand (2).—USNM 288113: *Albatross* sta 5425, Philippines, Jolo Sea off Cagayan Is., 9°37′45″N, 121°11′E, 495 fms, gray sand, mud, coral and sand (9).—USNM 289069: *Albatross* sta 5453, Philippines, Albay Gulf, off Legaspi light, E. Luzon, 13°12′N, 123°49′18″E, 146 fms (1).—USNM 289259: *Albatross* sta 5429 Philippines, off Fondeado Is., E. Palawan, 9°41′30″N, 118°50′22″E, 766 fms, green mud. (1 + cf. 2).—USNM 289640: *Albatross* sta 5459, Philippines, Albay Gulf, E. Luzon, 13°10′21″N, 123°59′54″E, 201 fms (2).—USNM 289802: *Albatross* sta 5582, Borneo, off Si Amil Is., 4°19′54″N, 118°58′38″E, 890 fms, gray mud and fine sand (1).—USNM 334804: [21°15′N, 158°W] *Albatross* sta 3908, Hawaiian Is., S. coast Oahu Is., 304–308 fms, fine white sand and mud. (1).—USNM 859104 *Albatross* sta 2644, off Cape Florida, 25°40′00″N, 80°00′00″W, 193 fms, gray sand (1).—USNM 357699: *Eolis* sta 118, Miami, Florida, off Govt. cut NE, 30 fms (1).—USNM 859105: [25°35′N, 80°05′W] *Eolis* sta 153, off Foway light, Fla., SE 3,5 mi. (1); USNM 859106: [25°35′N, 80°05′W] *Eolis* sta 174,



Figs. 2–6. *Diacria piccola*: 2, Holotype, dorsal view; 3, Holotype, ventral view; 4, Paratype, ventral view. *Diacria maculata:* 5, Holotype, dorsal view; 6, Holotype, ventral view.

off Foway light, Florida, ENE, 58 fms (1).—USNM 859107: [25°30′N, 80°11′W] *Eolis* sta 302, off Sand Key, Florida, 100 fms. (1).—USNM 859108: [25°30′N, 80°11′W] *Eolis* sta 324, off Sand Key, Florida, 100 fms (11).—USNM 859109 *Eolis* sta 329, off Sambo Reef, Florida, 135 fms (8).—USNM 859110: [25°35′N, 80°05′W] *Eolis* sta 340, off Foway light, Florida, 209 fms. (3).—USNM 429577: Johnson Smithsonian Exp. sta 32, 18°25′50″N, 67°14′55″W 200–280 fms (1).—USNM 859115: Johnson Smithsonian Exp. sta 93, 18°38′00″N, 65°09′30″W, 350–400 fms (2).—USNM 859111: Johnson Smithsonian Exp. sta 25, 18°32′15″N, 66°22′10″W, 240–300 fms (1).—USNM 859112: State University of Iowa Exp. sta 25, off Pelican Is., Barbados, 80 fms, coarse sand (1).—USNM 859113: [13°57′S, 59°33′W] State University of Iowa Exp. sta 54, off cable station, Barbados, 33 fms rocky (1).—USNM 859114 coarse sand (1); 59°33′W] (1).—USNM 859114 *Albatross* sta 2711, New Jersey, 38°59′00″N,



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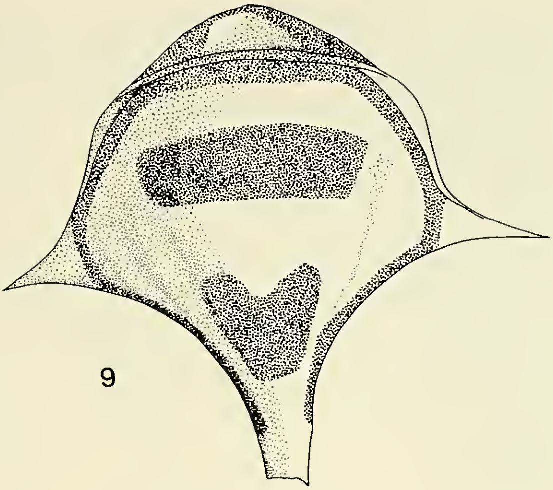

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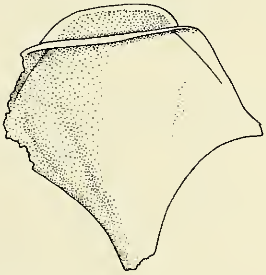

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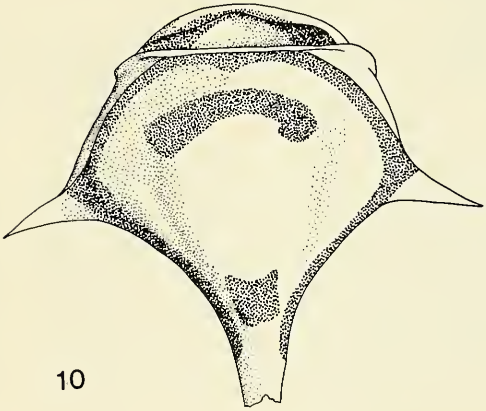

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Figs. 7–10. 7, *Diacria piccola* × *D. rampali,* ventral view; 8, *Diacria piccola* × *D. trispinosa,* ventral view; 9, *Diacria maculata* from the Pacific Ocean; 10, *Diacria maculata* from the Atlantic Ocean.

70°07′00″W, 1544 fms globigerina ooze (1).

Description.—The type series was collected from the sediment but no decalcification has occurred, and the color pattern is well preserved so that very recently sedimented specimens are represented. In the holotype the caudal spine is broken off below the closing septum, the width at the closing septum shows similarity to that in *Diacria trispinosa,* for example. The lateral spines are straight and sharp, slightly directed caudally. The dorsal side shows 3 moderately developed ribs. The central rib is most elevated in the caudal part, the lateral ones in the middle. The lateral sides between lateral spines and closing septum are nearly straight and form an angle of 109°. Growth lines are evident on both sides. The color pattern on the dorsal side consists of a continuous band along upper and lateral shell margins; a separate patch of color is found on the caudal half of the median dorsal rib. The upper lip is curved only slightly dorsally. The ribs on the ventral side are very indistinct, the ventral aperture lip curves prominently ventrally. The color pattern on the ventral side also forms a continuous band along upper and lateral shell margins, and a roughly quadrangular color patch is found on the upper half of the ventral side, as well as a patch on the narrowing caudal part of the ventral side. Sizes in the holotype are: shell width 8.80 mm, shell length 7.36 mm, length between lateral spines and closing septum 3.20 mm, distance between lateral spines and closing septum 4.80 mm, distance between lateral spines and center of upper lip 5.68 mm, width of shell aperture 3.20 mm, height of shell 0.72 mm, aperture angle between lateral sides 109°.

Type material.—Deposited at the Smithsonian Institution. The holotype USNM 283052 and 8 paratypes USNM 859099 are all from *Albatross* sta 5470, 560 fms (estimate).

Type locality.—Philippines, Lagonboy Gulf, E. Luzon, 13°37′30″N, 123°41′09″E.

Etymology.—The color spots (=maculata) on both sides give this species its name.

Discussion.—Sediment samples are used throughout as the forms described as new in this paper are not recorded from the plankton. In the large collections of plankton samples studied from the areas concerned no comparable specimens were found so that it is not excluded that the new species are fossil or subfossils.

The measurements given in the descriptions and table are indicated in Fig. 1.

Diacria piccola is distinct from all related species by its small size and narrow angle between the lateral sides. *D. maculata* is distinct from all other species by its color pattern.

Diacria is composed of the following taxa: the *Diacria trispinosa* group: *Diacria trispinosa* forma *trispinosa* (De Blainville, 1821), between 40°N and 40°S in all oceans.

Diacria trispinosa forma *atlantica* Dupont, 1979, between 40°N and 70°N in the Atlantic Ocean.

Diacria trispinosa forma *atlantica* Dupont, 1979 upwelling type (cf. Hilgersom & Van der Spoel 1988) in upwelling area off NW Africa.

Diacria rampali Dupont, 1979, between 30°N and 30°S in all oceans.

Diacria major (Boas, 1886), in Central waters of all oceans.

Diacria maculata, n. sp., in NW boundary currents of Atlantic and Pacific Oceans.

Diacria piccola, n. sp., W tropical Pacific near Philippines.

The *Diacria quadridentata* group (cf. Van Leyen & Van der Spoel 1982):

Diacria quadridentata (De Blainville, 1821). Indo-Pacific between 30°N and 30°S.

Diacria costata Pfeffer, 1879. Central water form (cf. Van Leyen & Van der Spoel 1982) of the Pacific.

Diacria costata Pfeffer, 1879. Equatorial water form (cf. Van Leyen & Van der Spoel 1982) of Indian and Pacific Oceans.

Diacria danae Van der Spoel, 1968. Equatorial waters of all oceans.

Diacria schmidti schmidti Van der Spoel, 1971. Eastern Tropical Pacific.

Diacria schmidti occidentalis Van Leyen & Van der Spoel, 1982. Western Tropical Pacific near Philippines.

Diacria erythra erythra Van der Spoel, 1971. Red Sea and Western Indian Ocean.

Diacria erythra crassa Van der Spoel, 1971. Red Sea.

Variation and distribution.—*Diacria picola* is known currently only from near the Philippines, thus any conclusion on its distribution is excluded. Further, the two specimens available cannot give an indication of variation. In the sample with the type material, however, two specimens also were found that were somewhat larger and resemble in shape *D. rampali* (Fig. 7) or *D. trispinosa* (Fig. 8). This may indicate that interbreeding of *D. piccola* with related species is still possible. Deformation or abnormal growth are not expected to generate shells of the type described here as all aberrant shells found show either asymmetry or

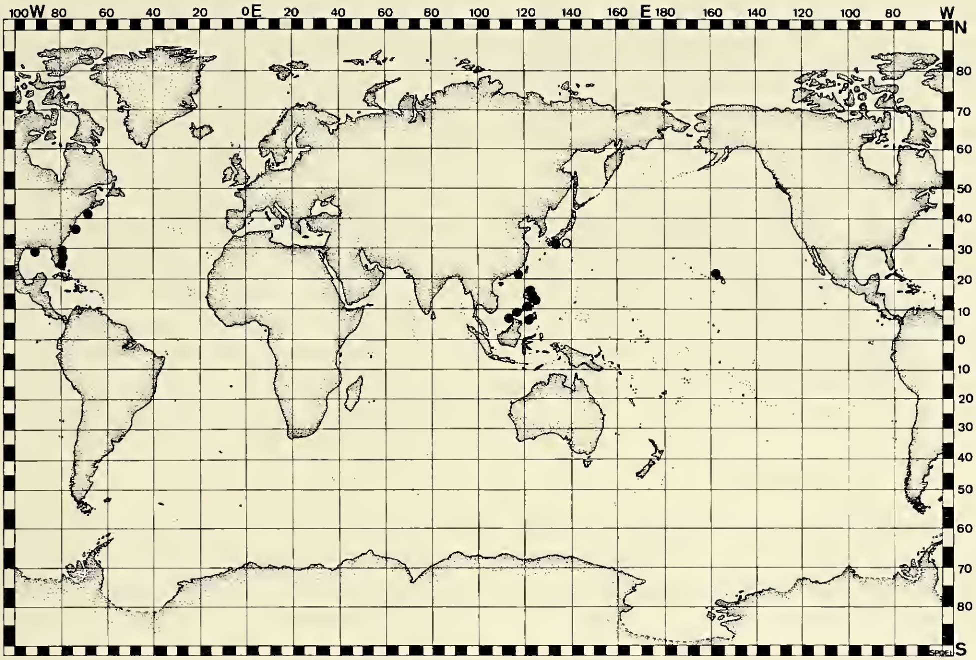

Fig. 11. Distribution of *Diacria maculata* (closed circles) and *D. piccola* (open circles).

different aberrations in different growth regions of the shell, which is not the case in *D. piccola.*

Rampal (1975) described the size variation of *Diacria trispinosa* in the Pacific Ocean, but though a tendency towards smaller sizes is clear, it is not acceptable that *D. piccola* forms the extreme of a size variation of one of the two mentioned species. The gap between the size range of *D. piccola* and the other species is too large and size variation will be binomial with a separate maximum for *D. piccola.*

Diacria maculata is found in the western North Pacific and in the western North Atlantic oceans (Fig. 11). Though the distribution of this species probably is not completely known, it is evident that it does not occur along the eastern borders of the oceans. An endemic occurrence in western boundary waters is not known for other species, though a few (distant) neritic taxa have their range in these water masses. Probably *D.*

Table 1.—Morphometric data (minimum–maximum) in mm based on the present material and literature data showing the unique position of *D. picola* and the more intermediate position of *D. maculata.*

Species	Shell width	Shell length	Aperture height	Angle of lateral sides
D. major[1]	7.0–11.0	7.5–9.0	0.5–1.0	—
D. t. dark type[2]	7.0–10.0	6.0–8.0	—	—
D. maculata[3]	9.8	7.4	0.9	100–110°
D. t. atlantica[1]	6.5–12.0	6.0–9.5	0.4–0.8	—
D. major	6.5–8.0	7.2–8.4	0.5–0.9	100–110°
D. maculata	**5.5-8.8**	**5.0-7.2**	**0.5-0.8**	**100-110°**
D. t. trispinosa[1]	5.5–9.0	5.0–6.5	0.5–0.9	—
D. t. trispinosa	5.6–7.8	5.4–6.8	0.5–0.8	80–90°
D. rampali[1]	5.5–8.5	5.0–7.0	0.5–0.8	—
D. rampali	5.5–6.9	5.5–6.6	0.5–0.7	80–90°
D. piccola	**2.0-2.4**	**2.5-2.8**	**0.24**	**65-80°**

[1] After Dupont 1979.

[2] After Hilgerson & Van der Spoel 1988.

[3] After Van der Spoel 1982.

maculata is a neritic taxon in the *Diacria trispinosa* group of oceanic species. Atlantic and Pacific specimens do not differ in color pattern and shape, the Pacific ones are only slightly larger than the Atlantic ones, as can be seen in Table 1.

In shape *D. maculata* is closest to *D. major* and in shape to *D. rampali,* but many characters, like the closing membrane in the caudal spine, make it look like a *D. trispinosa,* so that it was originally considered an intermediate between both (Van der Spoel 1982).

Acknowledgments

Dr. C. F. E. Roper and M. Sweeney kindly provided the material on which this publication is based and commented on the manuscript.

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DEEP-SEA TUBIFICIDAE (OLIGOCHAETA) FROM THE GULF OF MEXICO

Christer Erséus

Abstract.—Four bathyal species of the subfamily Phallodrilinae (*Phallodrilus constrictus,* n. sp., *P. grasslei* Erséus, 1984, *Bathydrilus connexus,* n. sp., and *B. longiatriatus* Erséus, 1983) are reported from the northern part of the Gulf of Mexico. *Phallodrilus constrictus* is characterized by bifid penial setae (three per bundle), and heavily muscular atria and copulatory sacs, the latter enclosing pendant penes. *Bathydrilus connexus,* which belongs to the '*B. adriaticus* group,' has more or less single-pointed setae in postclitellar segments, and blunt, somewhat chisel-shaped penial setae (two, occasionally three, per bundle).

Marine oligochaetes collected during a study of the northern Gulf of Mexico continental slope were sent to the author for identification from LGL Ecological Research Associates, Inc. (Bryan, Texas). The material contained four bathyal species belonging to the subfamily Phallodrilinae, of which two are new to science. The taxonomy of these species is treated here. Other tubificids found are *Limnodriloides monothecus* Cook, 1974 (Limnodriloidinae) and a species of *Tubificoides* (Tubificinae), but they occurred only at stations of about 350 m depth. The latter of these two will be treated by the author elsewhere.

The specimens studied here were collected by boxcore sampling along two transects, south of Louisiana and south of western Florida, respectively. Some worms were stained with paracarmine by the author; all individuals were then mounted whole in Canada balsam. The material is deposited at the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Phallodrilus Pierantoni, 1902
(Generic definition: see Erséus 1984a)

Phallodrilus constrictus, new species
Figs. 1A–C

Holotype.—USNM 113701, from S of W Florida, 28°16′42″N, 86°15′06″W, 625 m, 16 Apr 1984.

Paratypes.—USNM 114501–114502, 2 specimens: 1 from 28°07′05″N, 86°19′15″W, 860 m, 18 May 1985; 1 from 28°21′45″N, 86°48′05″W, 852 m, 20 May 1985.

Description.—One paratype 3.2 mm long, 20 segments (other specimens not complete). Width at XI (compressed, whole-mounted specimens) 0.14–0.17 mm. Clitellum extending over ½X–½XII. Somatic setae (Fig. 1A) bifid, with upper tooth thinner and slightly longer than lower, at least anteriorly. These setae 28–47 μm long, about 1–1.5 μm thick, 3–4 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae (Fig. 1B; C, ps) slender, bifid, with upper tooth thinner and shorter than lower, about 45–50 μm long, 2 μm thick, 3 per bundle. Male pores paired ventrally and posteriorly in XI. Spermathecal pores paired in line with ventral setae, anteriorly in X.

Pharyngeal glands in IV–VI. Male genitalia (Fig. 1C) paired. Vas deferens not observed. Atrium oval, 53–63 μm long, 33–37 μm wide, with 3–8 μm thick lining of muscles, and ciliated and somewhat granulated inner epithelium. From ectal end of atrium short, narrow duct leading into oval, heavily muscular copulatory sac, 47–49 μm long, 30–40 μm wide. Penis present, narrow and pendant within copulatory sac. Ante-

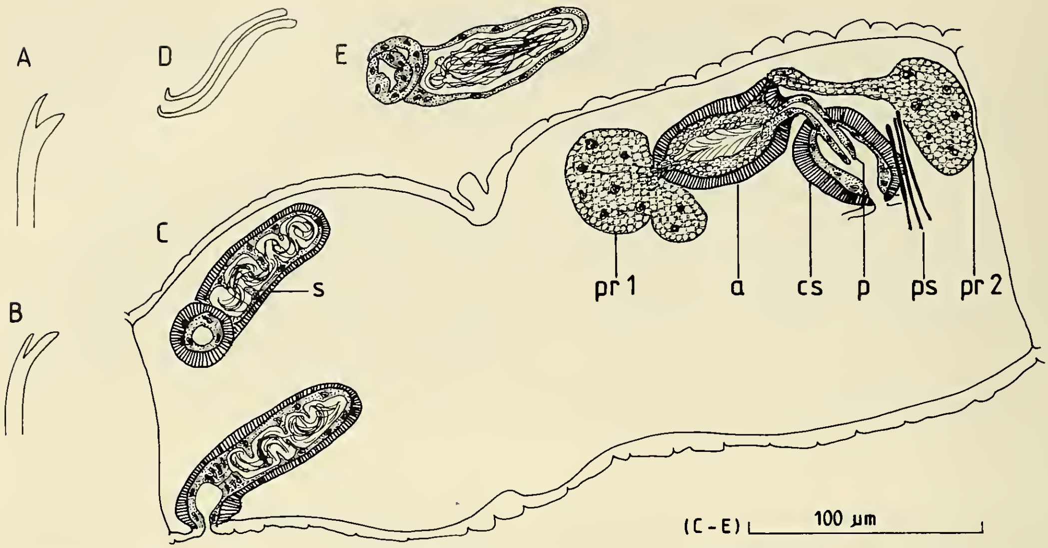

Fig. 1. A–C, *Phallodrilus constrictus,* n. sp.: A, Free-hand drawing of somatic seta; B, Free-hand drawing of penial seta; C, Somewhat ventral view of spermathecae and one of male ducts in segments X–XI (note: septum between X and XI not observed). D–E, *Phallodrilus grasslei* Erséus: D, Penial setae; E, Spermatheca. Abbreviations: a atrium; cs copulatory sac; p penis; pr 1 anterior prostate gland; pr 2 posterior prostate gland; ps penial seta; s spermatheca.

rior prostate gland attached to apex of atrium. Posterior prostate attached to ectal end of atrium, near exit of narrow duct. Spermathecae (Fig. 1C, s) cylindrical, 82–94 µm long, 21–28 µm wide, consisting of short, partly hollow ducts, and slender ampullae, all with 2–4 µm thick lining of muscles; sperm in small compartments within ampullae.

Remarks.—*Phallodrilus constrictus* is named for the distinct 'constriction' on the male duct between the atrium proper and the muscular copulatory sac. The species bears resemblance to *P. vulnus* Erséus, 1983 and *P. cristolatus* Erséus, 1983, two bathyal species from the NE Atlantic which also have bifid penial setae and penial structures (latter termed pseudopenes by Erséus 1983). [Note that the illustrations of *P. vulnus* and *P. cristolatus* were transposed in the original paper; the legend of Erséus' (1983) fig. 1 actually refers to the drawing of fig. 2 and vice versa.] *Phallodrilus contrictus* is, however, easily distinguished from both of these by its very conspicuous, muscular copulatory sacs and by the morphology of its spermathecae. Another close relative of the new species is probably *P. davisi* Erséus, 1984, known from the continental shelf off Massachusetts (Erséus 1984c). It has well developed copulatory sacs and penes, as well as compartmented spermathecae. The male ducts and the spermathecae of *P. davisi* are, however, not as muscular as those of *P. constrictus,* and the species lacks penial setae.

Distribution and habitat.—Northern Gulf of Mexico. Upper continental slope sediment, 625–860 m.

Phallodrilus grasslei Erséus, 1984
Fig. 1D, E

Phallodrilus grasslei Erséus, 1984b:101–103, figs. 1–3.

Type material.—USNM 96493–96495, holotype and 2 paratypes from 1789 m depth, S of Massachusetts, NW Atlantic (see Erséus 1984b).

New material examined.—USNM 113702, 1 specimen from S of Louisiana, 28°04'18"N, 86°34'24"W, 1330 m, 17 Apr 1984.

Remarks.—This species was previously known only from off Massachusetts. The new individual conforms well to the original description. For instance it has sigmoid, hooked penial setae, 2 per bundle (Fig. 1D), which is the most striking feature of *P. grasslei.* The spermathecal ampullae of the original material had thick walls (Erséus 1984b: fig. 1). The spermathecae of the new material are, however, more thin-walled (Fig. 1E).

Distribution and habitat.—Northern Gulf of Mexico (new record), S of Massachusetts. Continental slope sediments, known from 1330–1789 m depth.

Bathydrilus Cook, 1970
(Generic definition: see Erséus 1981, and modification by Erséus 1983)

Bathydrilus connexus, new species
Fig. 2A–C

Holotype.—USNM 113703, from S of W Florida, 28°09'36"N, 86°25'00"W, 845 m, 17 Apr 1984.

Paratypes.—USNM 113704–113710 and 114503–114505, 10 specimens from S of W Florida and Louisiana: 1 from 26°57'48"N, 89°31'00"W, 2490 m, 28 Nov 1983; 2 from 26°58'00"N, 89°31'48"W, 2467 m, 29 Nov 1983; 1 from 26°56'54"N, 89°36'12"W, 2377 m, 13 Apr 1984; 2 from 28°16'42"N, 86°15'06"W, 625 m, 16 Apr 1984; 1 from 28°00'24"N, 86°38'48"W, 2853 m, 18 Apr 1984; 2 from 28°14'50"N, 86°09'47"W, 618 m, 16 May 1985; and 1 from 28°00'10"N, 86°38'43"W, 2902 m, 21 May 1985.

Description.—Length (2 complete worms) 7.8–12.9 mm, 43–55 segments. Width at XI (compressed, whole-mounted specimens) 0.23–0.39 mm. Epidermal glands not observed. Clitellum extending over ½X–XII. Somatic setae (Fig. 2A, B) 45–75 μm long, 2.5–3 μm thick, 2–3(4) per bundle anteriorly, 2(3) per bundle in postclitellar segments. In segments II–VIII, setae bifid, with upper tooth thinner and shorter than lower (Fig. 2A). From IX, setae sharply single-pointed or with very much reduced upper tooth (Fig. 2B). Penial setae (Fig. 2C, ps) straight or somewhat curved, (3) per bundle, 60–85 μm long, entally 5–6 μm wide (ectally narrower), with blunt, somewhat chisel-shaped tips directed towards and located near midventral line. Male pores paired in line with ventral somatic setae, posteriorly in XI. Spermathecal pores paired in lateral lines, in anteriormost part of X. In several specimens, male and spermathecal pores elevated on bulbous protuberances.

Pharyngeal glands in IV–VII. Male genitalia (Fig. 2C) paired. Vas deferens 7–12 μm wide, slightly longer than atrium, entering latter somewhat ectal to middle, together with anterior prostate gland. Atrium spindle-shaped, 100–175 μm long, 50–56 μm wide at middle, with very thin outer lining of muscles and ciliated inner epithelium. Middle part of atrium densely granulated. Posterior prostate glands attached to apical, inner end of atrium. Ectally, atrium terminating in simple pseudopenis. Spermathecae (Fig. 2C, s) with short, indistinct ducts and large, sacciform ampullae; latter with a few large roundish 'spermatozeugmata.'

Remarks.—This species is named *connexus* (Latin meaning 'linked together' or 'bordering upon'), because of its close relationship with a whole group of, largely shallow-water, species of *Bathydrilus* [*B. adriaticus* (Hrabe, 1971), *B. litoreus* Baker, 1983, and others] characterized by more or less erect, spindle-shaped atria, bisetal or trisetal penial bundles, and sacciform spermathecae with sperm arranged in 'spermatozeugmata.' *Bathydrilus connexus* is in fact very similar to *B. adriaticus,* but is regarded as a separate species because of the detailed morphology of its setae. Sharply single-pointed postclitellar setae (Fig. 2B), are not known from any other member of

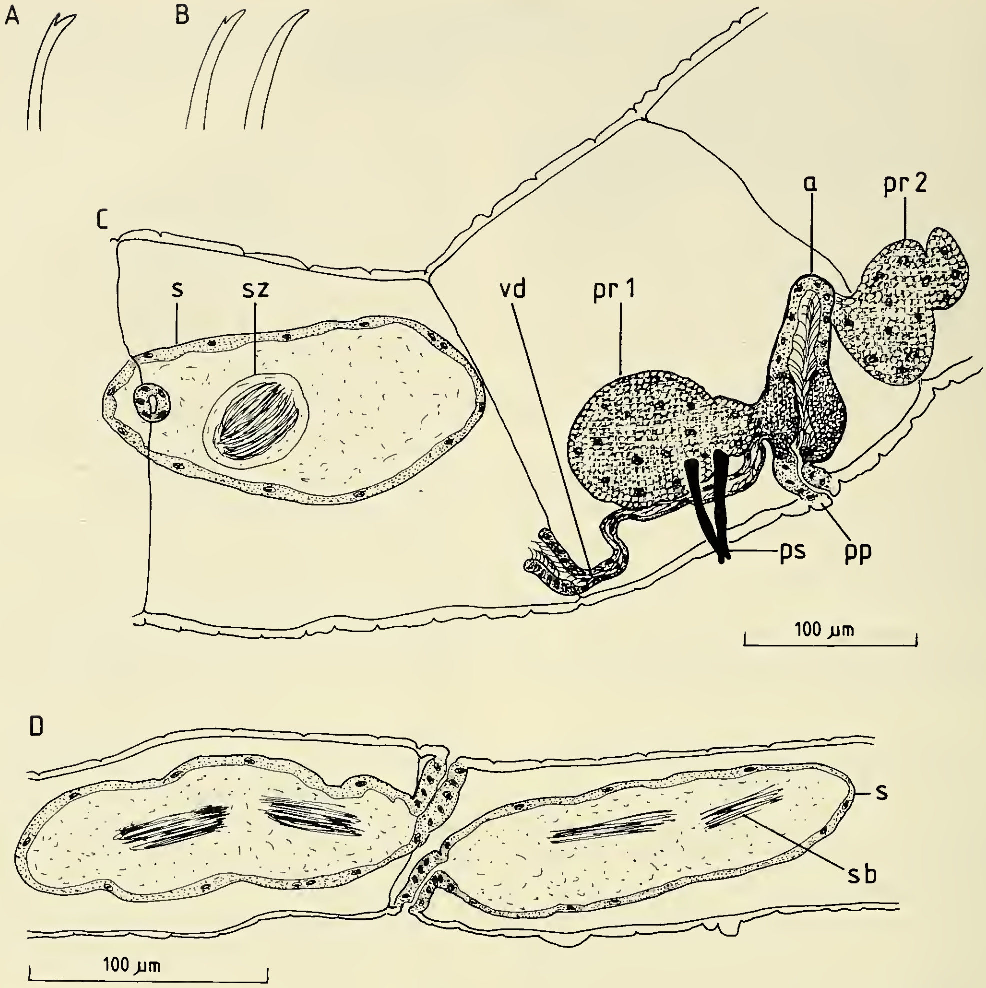

Fig. 2. A–C, *Bathydrilus connexus,* n. sp.: A, Free-hand drawing of anterior seta; B, Free-hand drawing of postclitellar setae; C, Lateral view of spermatheca and male duct in segments X–XI. D, *Bathydrilus longiatriatus* Erséus: spermathecae in segments IX–X. Abbreviations: a atrium; pp pseudopenis; pr 1 anterior prostate gland; pr 2 posterior prostate gland; ps penial seta; s spermatheca; sb sperm bundle; sz 'spermatozeugma'; vd vas deferens.

this group. Moreover, the penial setae of the new species are blunt, those of *B. adriaticus* are pointed.

Distribution and habitat.—Northern Gulf of Mexico. Continental slope sediments, known from 618–2902 m depth.

Bathydrilus longiatriatus Erséus, 1983
Fig. 2D

Bathydrilus longiatriatus Erséus, 1983:143–144, fig. 10.

Type material.—USNM 72988, holotype from about 2850 m depth, N of Surinam (see Erséus 1983).

New material examined.—USNM 113717–113722 and 114506, 7 specimens from S of W Florida and Louisiana: 3 from 26°58′00″N, 89°31′48″W, 2467 m, 29 Nov 1983; 1 from 27°28′24″N, 89°46′48″W, 1390 m, 13 Apr 1984; 1 from 28°09′36″N, 86°25′00″W, 845 m, 17 Apr 1984; 1 from 27°27′41″N, 89°47′19″W, 1506 m, 15 Nov

1984; 1 from 28°35′22″N, 86°46′26″W, 622 m, 13 May 1985.

Remarks.—*Bathydrilus longiatriatus* was originally described on the basis of a single specimen from off Surinam. Very long, muscular atria (about 300–400 μm long in new material), extending to the end of segment XII, characterize the species. The holotype was precopulatory, but in some of the new individuals the spermathecae contain an amorphous granular mass with a few bundles of sperm (Fig. 2D). Some of the worms from the Gulf of Mexico have fine particles adhering to the cuticle.

Distribution and habitat.—Northern Gulf of Mexico (new record) and N of Surinam. Continental slope sediments, known from 622–2953 m depth.

Acknowledgments

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A NEW CRAB, *SEORSUS WADEI,* FROM THE LATE CRETACEOUS COON CREEK FORMATION, UNION COUNTY, MISSISSIPPI

Gale A. Bishop

Abstract.—A fossil dakoticancroid crab, *Seorsus wadei,* new genus and species, is described from the early Maastrichtian Coon Creek Formation of Union County, Mississippi. This crab belongs to the *Dakoticancer* Assemblage previously described from the Blue Springs locality. The only known specimens consist of a nearly complete, crushed, carapace steinkern and a partial carapace steinkern. *Seorsus* differs from other members of the Dakoticancridae in carapace proportions, shape and ornamentation.

Collection of the Blue Springs locality (Bishop 1983) on 10 Mar 1984, resulted in the discovery of a new fossil crab. The Blue Springs locality is situated geographically in the Mississippi Embayment, an ancient arm of the Cretaceous Tethys Seaway that occupied much of present Mississippi, Alabama, and western Tennessee. Two specimens were collected from the sandy claystone shelf sediments of the Coon Creek Formation of early Maastrichtian Age (Russell et al. 1983). Correlation with other North American Cretaceous rocks indicates an absolute age of approximately 67 million years before present. Both specimens are internal casts of the carapace and are preserved as steinkerns.

Systematic Paleontology

Order Decapoda Latreille, 1803
Superfamily Dakoticancroidea Rathbun, 1917
Family Dakoticancridae Rathbun, 1917
Seorsus, new genus

Type species.—The type species of *Seorsus* is *Seorsus wadei,* n. sp.

Diagnosis.—Carapace of moderate size, longer than wide (L/W = 1.10), widest at anterior ⅓; lateral margins distinctively convergent posteriorly; grooves broad, moderately defined; areolations very tumid, especially epibranchial lobes; cardiac region with small central tubercle; metabranchial region with subtle transverse and submarginal ridges. Claws and legs unknown.

Etymology.—"Seorsus" is derived from the Latin; apart, separate, severed, to indicate the carapace shape which sets this taxon apart from the other dakoticancroid genera and also the fragmented or severed nature of both specimens. The gender is masculine.

Occurrence.—*Seorsus* is known from a single species based on two carapace specimens from the Coon Creek Formation, early Maastrichtian, of Union County, Mississippi.

Seorsus wadei, new species
Fig. 1A–F

Diagnosis.—Carapace longer than wide (L/W = 1.10), widest at anterior ⅓; lateral margins distinctively convergent posteriorly. Grooves and areolations similar to those in other members of family. Carapace evenly granulate.

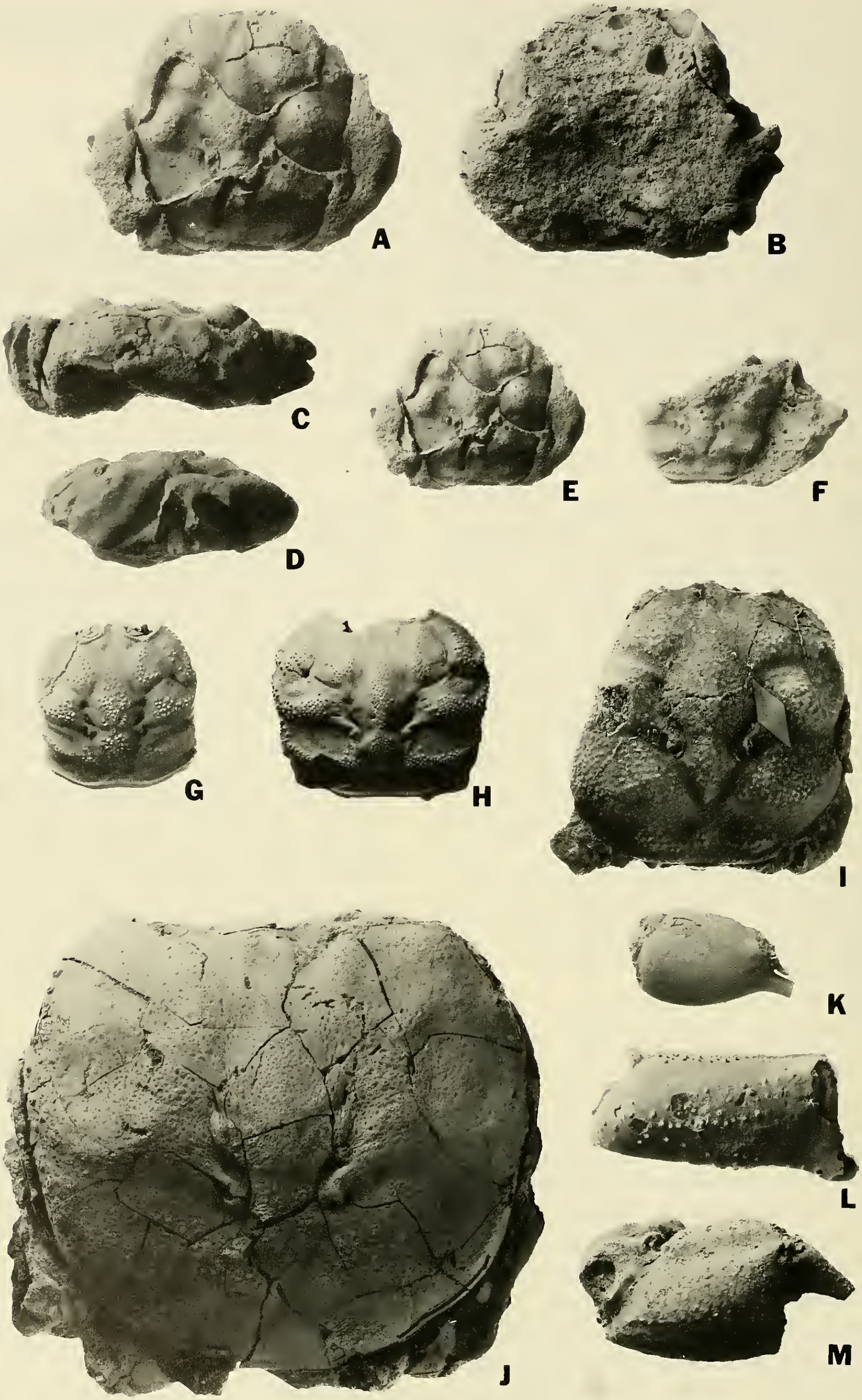
Description.—Carapace 1.10 times longer (23.3 mm) than wide (21.1 mm), widest at anterior ⅓; front relatively straight; anterolateral margin broadly rounded; lateral margins relatively straight, converging posteriorly; posterolateral margins tightly rounded; hind margin straight. Carapace regions tumid but poorly differentiated because of broad shallow grooves. Cervical groove sinuous, posteriorly reflexed around large mesogastric region; hepatic groove and longitudinal gastric grooves poorly defined but present; branchiocardiac and cervical grooves define epimeral peninsula; anterior branchial groove very shallow; posterior marginal groove sharply defined. Cephalic arch differentiated into large mesobranchial, intermediate protogastric, and small hepatic regions each raised into a granulate tumid areolation. Scapular arch differentiated into sagittal ridge consisting of cardiac and intestinal regions; and branchial regions consisting of raised epibranchial ridge, a smaller mesobranchial ridge, and metabranchial area. Cardiac region with low medial boss. Hind margin raised into a posterior rim. Transverse, low submarginal bosses on posterior of metabranchial regions. Orbits large and broad occupying 48% of carapace width. Carapace regions evenly granulated except for more coarsely granulated highest parts of hepatic and epibranchial regions. Legs very granulate, decreasing in size posteriorly, P_5 very small. Sternum and abdomen poorly exposed. Abdomen narrow (male) and abdominal somite A_1 with longitudinal ridge and transverse ridge.

Comparison.—Seorsus wadei is an enigmatic fossil. As with many fossil crabs represented by unique or only a few specimens, diagnostic characteristics necessary to confidently assign the species or genus to a higher taxonomic unit are often lacking. Assignment in such cases can only be made on the basis of circumstantial evidence such as general similarities in carapace shape, carapace morphology, and carapace ornamentation. Although admittedly not the best possible criteria, assignment to a family seems better than to such taxa as "Family Indeterminate," or not describing them at all. Once such a taxon is described it is available for scientific discussion and possible reassignment as other carcinologists evaluate the data.

Seorsus wadei has a generalized carapace lacking clearly definitive characteristics. Based solely on shape, *Seorsus* is most similar to trapezohedral members of the Family Geryonidae but differs from them by lacking the dentate front and the large orbits. *Seorsus* also resembles some members of the Family Goneplacidae in its trapezohedral shape but differs from them in having clearly divided orbits. The carapace areolation of *Seorsus* resembles closely that of members of the Family Dakoticancridae. If *Seorsus* is viewed obliquely from the front, this similarity is enhanced and the trapezohedral carapace outline becomes quite similar to that of *Dakoticancer* Rathbun, 1917. The carapace ornamentation of *Seorsus wadei* consists of low, intermittent granulation similar to that of *Dakoticancer, Avitelmessus* Rathbun, 1923, and *Tetracarcinus* Weller, 1905, 1907. Because of these similarities, *Seorsus* is assigned to the Family Dakoticancridae.

Seorsus wadei differs from other dakoticancroid crabs by its trapezohedral shape. *Seorsus wadei* is more arched and much smaller than *Avitelmessus grapsoideus* Rathbun, 1923, but larger than *Tetracarcinus subquadratus* Weller, 1905, and trapezohedral rather than quadrate. *Seorsus wadei* most resembles *Dakoticancer* in areolation and ornamentation. *Seorsus wadei* is trapezohedral whereas *D. australis* Rathbun, 1935, is nearly rectangular. *Seorsus wadei* is most similar to *D. overanus* Rathbun, 1917, which is slightly trapezohedral in carapace outline, but differs by being much more trapezohedral, having a relatively larger cephalic arch, and nearly lacking the prominent epimeral peninsulas of *D. overanus.*

Variation.—Because this species is represented by only two specimens, variation is undefinable. The mode of preservation as a steinkern preserves basic body shape and,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because of compression of the exterior mold onto the interior mold, some of the carapace ornamentation. Description of a new species based on two specimens is justified by sampling (a collection of about 1500 fossil decapods) which indicates that this species is such a minor taxon in the Blue Springs *Dakoticancer* Assemblage that additional specimens may not be collected for some time. Such low abundances in fossil and recent assemblages necessitate the description of new taxa based on few specimens when discovery of additional specimens cannot reasonably be expected for some time.

Type locality.—The only known specimens, the holotype (GSCM 1693) and paratype (GSCM 1694), were collected from the Coon Creek Formation in Union County, Mississippi, in the NE¼, NW¼, SE¼, section 9, T. 8S., R. 4E. The holotype is deposited in the collection of the GSC Museum (Georgia Southern College, Statesboro, Georgia 30460-8161).

Etymology.—The trivial name "wadei" honors the stratigrapher and paleontologist, Bruce Wade, whose pioneering efforts built the foundation for subsequent studies of Cretaceous fossils of the Mississippi Embayment.

Remarks.—The specimens collected are phosphatic steinkerns (internal molds) that are grayish orange (10 YR 714) to yellowish gray (5 Y 712) in color. The carapaces are broken by compression and show two sizes (0.5 mm and 1.2 mm) of open burrows within them. The crabs' legs have been broken away by weathering but were partly replicated by dental impression wax for study. This is the typical mode of preservation at the Blue Springs locality.

The *Dakoticancer australis* Assemblage

The Blue Springs *Dakoticancer* Assemblage (Bishop 1983 fig. 3, table 1) consists of 11 decapods and is dominated by a few taxa (*D. australis* (49.0%), *Protocallianassa mortoni* (Pilsbry, 1901) (26.9%), and *Hoploparia tennesseensis* Rathbun, 1926 (10.1%)) and eight other taxa present in very small numbers (Bishop 1985). *Seorsus wadei* constitutes less than 0.1% of it. The assemblage is thought to represent a preserved community fraction (Bishop 1981) of a Cretaceous decapod-dominated community that periodically inhabited the Cretaceous sea bottom (Bishop 1986a).

The Superfamily Dakoticancroidea and Family Dakoticancridae were erected by Rathbun (1917:385) to contain the crab *Dakoticancer overanus* described from the Western Interior Cretaceous (South Dakota). In 1935 Rathbun described *D. overanus australis* and reassigned *Tetracarcinus subquadratus* to the Family Dakoticancridae. Glaessner (1960:46) remarked on similarities and reassigned *Avitelmessus grapsoideus* to Dakoticancridae. This classification is the currently accepted model (Glaessner 1969:R491). Bishop (1983:426) raised *D. overanus australis* to species level rank. Rathbun (1937:26) described *D. olssoni,* but it should be assigned to another genus. The current constitution of the Superfamily Dakoticancroidea is presented below with diagnoses and illustrations (Fig. 1).

←

Fig. 1. North American Cretaceous dakoticancroid crabs. A–F, *Seorsus wadei,* n. sp.: A–D, Holotype (GSCM 1693) in dorsal, ventral, anterior, and left lateral views, ×2.0; E–F, Comparative dorsal views of Holotype and Paratype (GSCM 1694). G–M, Comparative views of other dakoticancroid taxa: G, *Tetracarcinus subquadratus* Weller, 1905, carapace (GAB 37-1113); K, Same, right claw, ×2.0; H, *Dakoticancer overanus* Rathbun, 1917, carapace (GAB 4-2006, ×1.5); L, Same, right claw (GAB 4-B4, ×2.0); I, *Dakoticancer australis* Rathbun, 1935, carapace (USNM 73840, ×1.5); M, Same, right claw (GAB 37-1094, ×2.0); J. *Avitelmessus grapsoideus* Rathbun, 1923, carapace (USNM 25411, ×2.5).

Superfamily Dakoticancroidea Rathbun, 1917
nom. correct. Glaessner (1969, R491)
(pro Dakoticancroideae Rathbun, 1917)

Diagnosis.—"Carapace rectangular to transversely ovoid, front narrow; orbits well developed, median part of cardiac groove weak, branchiocardiac groove strong, no lineae; third maxillipeds elongate; sternum of female without longitudinal grooves, fifth pereiopods subdorsal, small." (Glaessner 1969:R491).

Family Dakoticancridae Rathbun, 1917

Diagnosis.—Characters of superfamily.

Genus *Dakoticancer* Rathbun, 1917

Diagnosis.—"Carapace rectangular to transversely ovoid, wider than long, front narrow, orbits well developed, bilobed; median part of cardiac groove weak, gastric regions hardly separated from cardiac-intestinal region, branchiocardiac groove well developed, pleural sutures on carapace sides; genital openings on coxae, female on third leg and male on fifth; fifth legs much reduced. Chelae equal." (Bishop 1983:424).

Dakoticancer overanus Rathbun, 1917
Fig. 1H, L

Diagnosis.—Carapace moderate size, slightly wider than long, widest across epibranchial regions, sides sinuous, slightly convergent posteriorly, well-differentiated by grooves, cervical groove prominent; ornamented by granules over areolations; posterior shelf narrow, rim upturned. Claws equal, much longer than high.

Dakoticancer australis Rathbun, 1935
Fig. 1I, M

Diagnosis.—"Carapace large, slightly longer than wide, widest across branchial and hepatic regions (sides nearly parallel), well differentiated by grooves, ornamented by granules over entire surface. Claws similar, equal, short, stout, and crested; carpal articulation very oblique; fingers short, downturned." (Bishop 1983:426).

non *Dakoticancer olssoni* Rathbun, 1937

Remarks.—Rathbun assigned this Cretaceous crab to *Dakoticancer* with no comparison. The specimen in question (USNM 495104) was examined by me on 26 Aug 1977 at which time I made the note, "This is *not* a *Dakoticancer.*" The specimen has probable affinity to the Necrocarcinids, possibly being assignable to *Protonecrocarcinus* Förster, 1968, or to *Cyphonotus* Bell, 1863.

Genus *Tetracarcinus* Weller, 1905
Tetracarcinus subquadratus Weller, 1905
Fig. 1G, K

Diagnosis.—Carapace small, subquadrate, widest across epibranchial region, length nearly equals width; sides sinuous; areolations low, granulate, cardiac region large; weakly differentiated by smooth grooves, particularly peripherally, on cephalic arch, and deeper on scapular arch. Claws equal, inflated proximally, fingers small.

Seorsus, new genus
Seorsus wadei, new species
Fig. 1A–F

Genus *Avitelmessus* Rathbun, 1923
Avitelmessus grapsoideus Rathbun, 1923
Fig. 1J

Diagnosis.—Carapace very large, flat, circular, widest at midlength anterolateral margin spinose. Grooves poorly developed except for those delimiting sagittal ridge and epimeral peninsula; sagittal ridge well-differentiated, epibranchial somewhat tumid, other regions not well-differentiated; regions relatively level, especially peripherally. Claws equal, short, crested, granulate; fingers large, downturned, fluted, and toothed.

Biogeography

Dakoticancroid crabs are confined to the latest Cretaceous rocks (Santonian-Maastrichtian) of North America on the shallow shelves of the Tethys Sea. The taxa are more or less endemic but with boundaries of their distributions somewhat overlapping. *Tetracarcinus subquadratus* is abundant on the Northern Atlantic Coastal Plain and in the Mississippi Embayment, with but one record in the Western Interior Seaway. *Avitelmessus grapsoideus* is found on the Southern Atlantic Coastal Plain and is abundant in the Mississippi Embayment where it occurs in the dominant *Avitelmessus* Assemblage in thin layers over large areas. The unusually large size of this crab, its abundance, and its occurrence in laminated shales and calcareous sandstones are correlated with yet undefined environmental conditions. *Dakoticancer australis* is the predominant decapod in the *D. australis* Assemblage of Northern Mississippi (Bishop 1983), and *Seorsus wadei* is a minor element in it. *Dakoticancer overanus* is the predominant decapod in the repeated *D. overanus* Assemblages of the middle Western Interior Seaway (Bishop 1981). Little has been substantiated about evolutionary development of the dakoticancroid crabs. It is apparent, however, that *Tetracarcinus* is the oldest known dakoticancroid, with abundant Santonian–Campanian records on the Northern Atlantic Coastal Plain, and that *Dakoticancer* probably evolved from *Tetracarcinus* and migrated into the Western Interior during the Late Campanian and into the Mississippi Embayment during the Maastrichtian (Bishop 1986b:129).

Acknowledgments

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SCIONELLA PAPILLOSA, A NEW SPECIES OF POLYCHAETE (POLYCHAETA: TEREBELLIDAE) FROM THE SOUTHWEST FLORIDA CONTINENTAL SHELF

Gary Tourtellotte and Henry Kritzler

Abstract.—*Scionella papillosa*, a new species of terebellid polychaete from the southwest Florida continental shelf is described. It more closely resembles the only other Atlantic species, *S. lornensis* Pearson, 1969, than the Pacific species, *S. japonica* Moore, 1903, *S. estevanica* Berkeley & Berkeley, 1942, and *S. vinogradovi* (Ushakov), 1955, in lacking a ridge on segment 4, but it differs from all four in having densely packed small digitiform papillae on the ventrolateral surfaces of the second segment.

From collections made in December, 1983 on the southwest Florida continental shelf by Environmental Science and Engineering, and LGL Ecological Research Associates under a contract with the Minerals Management Service, U.S. Department of the Interior, there were segregated a number of specimens of an unidentifiable terebellid polychaete whose closest affinities seemed to be with the genus *Scionella* Moore, 1903. This genus had hitherto been known only from the cold waters of the North Pacific and Scotland.

Family Terebellidae
Subfamily Amphitritinae
Scionella Moore, 1903

Type species.—*Scionella japonica* Moore, 1903, by monotypy.

Material examined.—North Atlantic Ocean, Gulf of Mexico, 26°17′4.5″N, 082°19′57″W, 16 m, 6 Dec 1983 (Environmental Science and Engineering, Inc., Tampa, Florida and LGL Ecological Research Associates, Inc., collectors). Holotype, USNM 99376, paratype USNM 99377, numerous other specimens in the collections of the senior author.

Description.—Holotype, complete specimen with 20 thoracic and about 65 abdominal segments, 17 mm long and 1 mm wide. Body cylindrical in section. No distinct ventral glandular scutes. Fused prostomium and peristomium forming a collar surrounding terminal mouth. Numerous tentacles arising from dorsal and lateral surfaces of collar. Eyespots lacking. First segment bearing small lateral lappets. Second segment having large, translucent lateral lappets, ventrolateral surfaces of which covered with densely packed, small digitiform papillae (Fig. 1a). Second segment also with median, V-shaped, opaque pad accentuating appearance of lateral lappets of this and following segments. From anterior dorsal edge of second segment, one pair of bottle-brush branchiae arising, each consisting of stout, ringed stalk bearing on its distal ⅔ a cluster of filaments arranged in whorls, too densely packed to reveal manner of insertion (Fig. 1b).

All specimens having one small and one large branchia, smaller being about ⅓ size of larger. In holotype, larger equal in length to first 7 segments.

Third segment bearing largest lateral lappets. Smallest on fourth, on which appearing first notosetae, continuing through segment 20. In anterior setigers, notopodia very

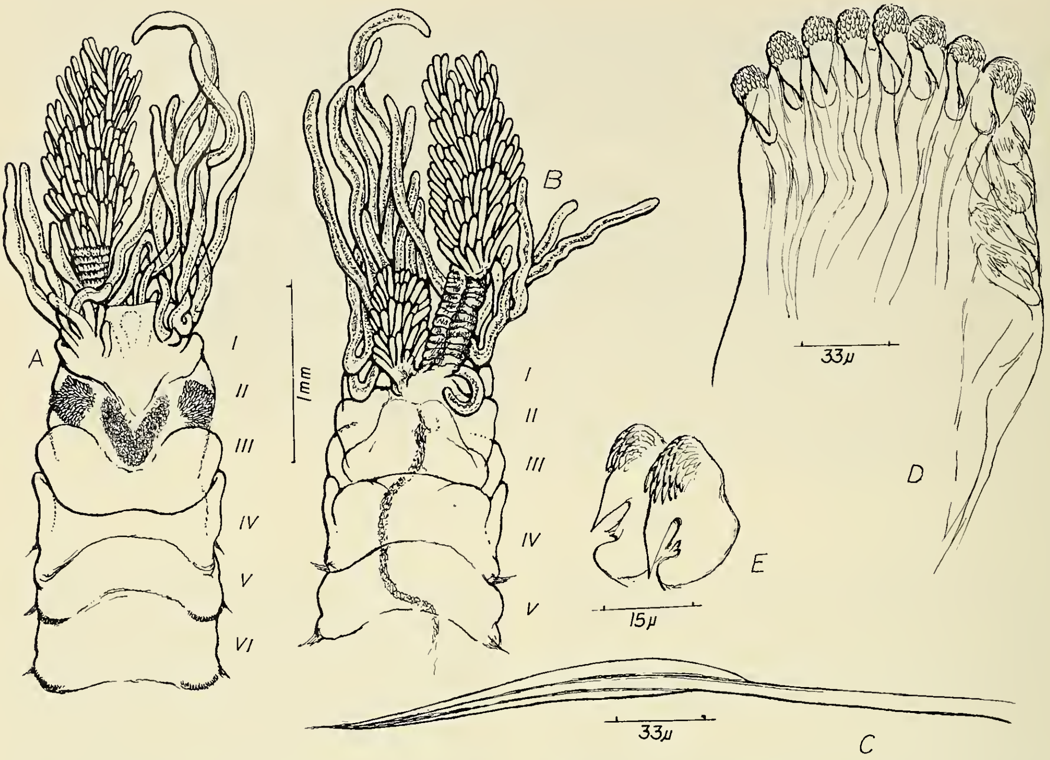

Fig. 1. *Scionella papillosa,* holotype. A, Anterior end, ventral view; B, Anterior end, dorsal view; C, Notoseta; D, Abdominal uncinigerous pinnule; E, Thoracic uncinus.

short, each bearing 6–7 smooth-tipped bilimbate setae. Limbs on one side slightly wider than on opposite (Fig. 1c). In posterior thorax, notopodia somewhat more prominent, although still no more than short rounded protuberances bearing up to 12 similar setae. Avicular uncini, none of which having elongate basal stalks, as in *Pista,* borne in single rows of 25–30 on segments 5–10 and in double rows of 10–20, interlocking face to face, on segments 11–20. Abdominal uncini occurring in single rows, having prominent suspensory ligaments and borne on well-developed, flap-like pinnules (Fig. 1d). Throughout, uncini having several rows of denticles forming a crown above main fang (dental formula MF:8:9:10:∼) (Fig. 1e). Terminal anus surrounded by 4 short, rounded protuberances.

Etymology.—The specific name, *papillosa,* derived from Latin, refers to the patches of digitiform papillae on the ventrolateral surfaces of the second segment.

Remarks.—The most useful treatment of the genus *Scionella* is that of Pearson (1969). In his key (pp. 513–514) the four species then known fall into two groups, those with a dorsal ridge on segment 4 (*S. japonica* Moore, 1903, *S. estevanica* Berkeley & Berkeley, 1942, and *S. vinogradovi* (Ushakov, 1955)), and those without (then only *S. lornensis* Pearson, 1969). Perhaps some significance may be attached to the fact that the first group occurs only in the Pacific, whereas the second has been found only in Atlantic waters. *Scionella papillosa,* also an Atlantic species and lacking a dorsal ridge on the fourth segment, may be grouped with

S. lornensis. Scionella papillosa, however, differs from the latter in having lateral lappets on the first 4 segments; in that the lateral lappets on the second segment are less prominent than those on the third, a condition which is reversed in *S. lornensis*; in that it lacks well-developed ventral glandular scutes; and in that none of its gill filaments are dichotomously branched.

It is not possible to state how *S. papillosa* compares with the others with respect to nephridia. This character which was given much weight by Pearson and was a principal basis for classification by Hessle (1917) has not been useful in dealing with the generally very small polychaetes from the Gulf of Mexico offshore continental shelf. Certainly, *S. papillosa* does not have the large bottle-shaped nephridial papillae on the fourth segment, as depicted by Hartman (1969) for a California specimen of *S. japonica.*

The number of uncini per segment, much larger in *S. japonica* (up to 160 thoracic and 65 abdominal) than in *S. papillosa,* may not be a significant difference, the numbers possibly being a function of the size of the specimens.

The collar-like fused prostomium and peristomium of *S. papillosa* bears little resemblance to the trefoil-shaped structure in *S. japonica,* as described by Moore and figured by Hartman (1969:635, fig. 1) or, presumably, to these structures in *S. estevanica.*

Were it not for the dorsal ridge on the fourth segment, *S. estevanica* would easily fit in with the *S. papillosa, S. lornensis* group, for its gills also arise from segment 2 and, apparently, its lateral lappets lack the alate configuration and increasingly more dorsal insertion which set off the other two species so plainly.

In any case, *S. papillosa* is distinguished from all the others by the patches of papillae on the second segment.

Accordingly, Pearson's key may be updated as follows:

Key to the Species of *Scionella* Moore, 1903

1a. Segment 4 with a prominent dorsal ridge 3
1b. Segment 4 without a ridge .. 2
2a (1b). Lateral lappets on the first three segments .... *S. lornensis* Pearson
2b (1b). Lateral lappets on the first four segments .... *S. papillosa,* n. sp.
3a (1a). Gills carried on segment 4 . 4
3b (1a). Gills carried on segment 2 .. .. *S. estevanica* Berkeley & Berkeley
4a (3a). Edges of segment 4 lappets crenulate .... *S. vinogradovi* (Ushakov)
4b (3a). Edges of segment 4 lappets smooth ..... *S. japonica* Moore

Ecology and distribution.—*Scionella papillosa* has been dredged from relatively shallow depths in the subtropical waters of the Gulf of Mexico, whereas the other four species have been found in greater depths in the cold waters off California, Japan, Western Canada, the Sea of Okhotsk, and Scotland. It lives in mucous tubes adorned with fine sand grains, buried in medium to fine, mainly calcareous, sediments. The salinity of the overlying water was 35.1‰ and the dissolved oxygen 7.3 mg/liter. It is associated with other polychaetes: *Cirrophorus* sp., *Axiothella mucosa, Mediomastus californiensis, Exogone dispar, Pseudovermilia* sp.; the amphipods *Ampelisca sp., Tiron tropakis,* and *Eudeuenopus honduranus*; the cumaceans *Oxyurostylis smithi,* and *Cyclaspis* spp.; the decapod *Lucifer faxoni*; and the cephalochordate *Branchiostoma caribaeum.*

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STREPTOSPINIGERA ALTERNOCIRRUS, A NEW SPECIES OF POLYCHAETA (SYLLIDAE: EUSYLLINAE)

Takashi Ohwada

Abstract.—A new species of Eusyllinae, *Streptospinigera alternocirrus*, from Aburatsubo Bay on the Pacific coast of Central Japan is described. Although it is most closely related to *S. heteroseta* Kudenov in possessing enlarged acicula, composite spinigers, and both superior enlarged and capillary simple setae, it is distinguished from the latter in the morphology and arrangement of the dorsal cirri.

Streptospinigera Kudenov, 1983, was described as a genus closely related to *Streptosyllis* Webster & Benedict, 1884, in having enlarged anterior setae, but differing from the latter in possessing composite spinigers and superior capillary simple setae. During the course of my study on the settlement and recruitment of polychaete larvae (Ohwada 1986) numerous tiny syllids were collected. Some of them fit well in the genus *Streptospinigera*, but differ from *S. heteroseta* Kudenov, the only known species in the genus, in their morphology and arrangement of the dorsal cirri. They are described below as a new species.

Type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), British Museum (Natural History), London (BM(NH)), and National Science Museum, Tokyo (NSMT).

Streptospinigera alternocirrus, new species
Figs. 1, 2

Material examined.—Misaki, Kanagawa, Japan: Aburatsubo Bay (35°09′18″N, 139°36′55″E), 2 m, clean medium sand, coll. T. Ohwada, 19 Nov 1984, holotype (USNM 01494); 22 Oct 1984, paratype (USNM 01495); 25 Jan 1985, paratype (BM(NH)ZB 1986.695); 20 May 1985, paratype (NSMT-Pol. P 236). Material examined represents a selection of material available.

Description.—Holotype, sexually mature, 1.37 mm long, 0.23 mm wide without parapodia at middle widest part of body, with 32 setigers. Three paratypes 1.09 to 1.75 mm long, 0.10 to 0.17 mm wide with 26 to 33 setigers. Body generally lacking pigmentation in alcohol preservation.

Prostomium wider than long, with palps large, fused basally, directed anteroventrally, laterally incised, distally rounded, lacking palpal cirri (Fig. 1a, b). Three antennae smooth, clavate; with long median antenna in middle of prostomium, lateral antennae lateral to small ocular spots (Fig. 1a). Four lenticular eyes in trapezoidal arrangement (in holotype, anterior right eye as 2 separate spots, in paratype (USNM 01495), anterior left eye as 2 separate spots), and 2 small ocular spots lateral to bases of lateral antennae (Fig. 1a, b). Peristomium a complete ring dorsally and laterally, with 2 pairs of smooth clavate tentacular cirri; dorsal pair slightly longer than ventral pair.

Pharynx completely everted in paratype (USNM 01495), unarmed, thickly sclerotized, distal border surrounded by 10 papillae proximal to smooth anterior end of sclerotized part (Fig. 1b), extending to about middle part of setiger 3, almost as long as proventriculus. Proventriculus barrel-shaped, about twice as long as wide, ex-

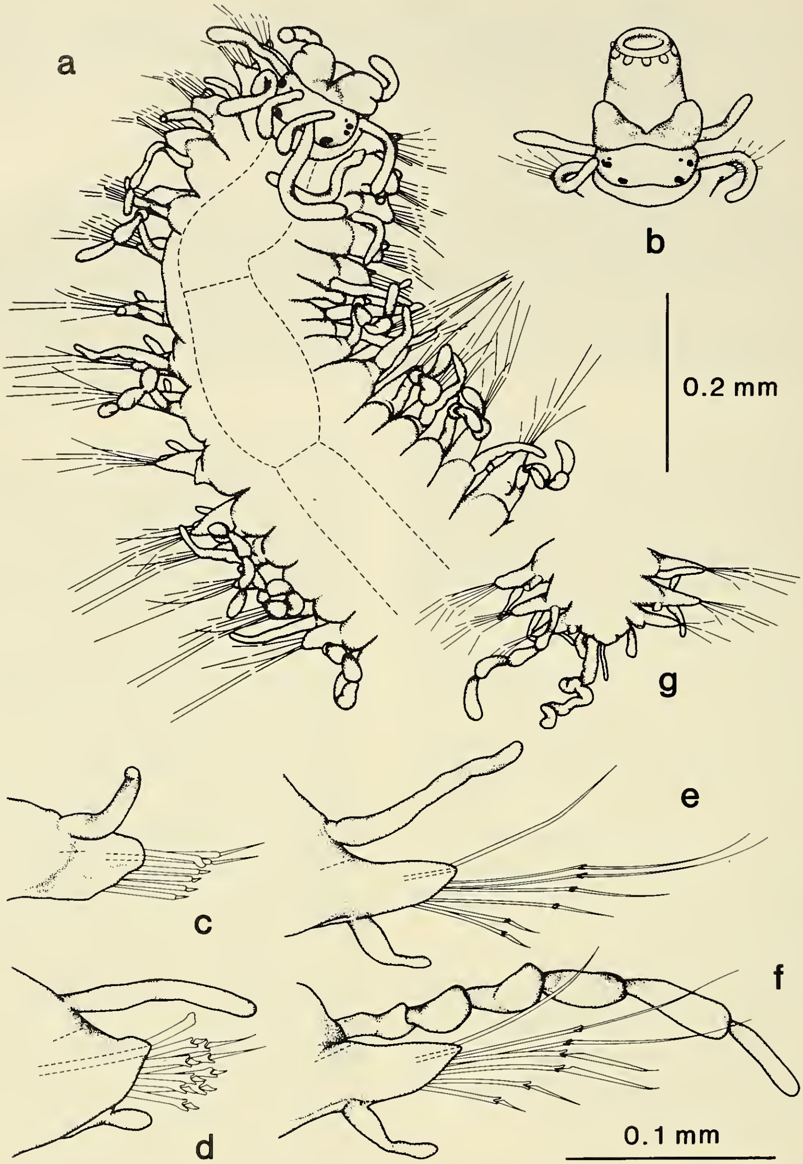

Fig. 1. *Streptospinigera alternocirrus*: a, c, holotype (USNM 01494), b, paratype (USNM 01495), c–f, paratype (BM(NH)ZB 1986.695), g, paratype (NSMT-Pol. P 236): a, Anterior half, dorsal view, pharynx partially everted; b, Dorsal view, anterior end with pharynx everted, antennae not shown (positions dotted); c, Parapodium from setiger 3, dorsal view; d, Same, anterior view; e, Parapodium from setiger 20, anterior view; f, Parapodium from setiger 25, anterior view; g, Posterior end, dorsal view, long right anal cirrus missing.

tending from setiger 7 through 10 in holotype whose pharynx partially everted (Fig. 1a), with about 30 transverse rows of muscle points, also arranged in 2 opposite, diagonal planes.

Parapodia of setigers 1 to 5 large, distally truncate (Fig. 1c, d). Parapodia from setiger 6 smaller and conical (Fig. 1a, e, f). Dorsal cirri of setiger 1 long, resembling tentacular cirri but slightly longer; those of setigers 2, 3, 5 smooth, cirriform (Fig. 1a, c, d). In setiger 4 dorsal cirri longer, with 2 articulations (Fig. 1a). Dorsal cirri of setiger 6 with 4 rather large articles (Fig. 1a). Dorsal cirri of setigers 7 and 8 smooth, thick, subulate, thereafter as long as setae with 4–6 large articles (Fig. 1f) on odd-numbered setigers and smooth, thick, subulate, extending beyond parapodial lobes (Fig. 1e) on even-numbered setigers to end of body (Fig. 1a, g). Each article containing dense yellowish-brown granules. Ventral cirri smooth throughout, short, blunt, inflated on setigers 1–3 (Fig. 1d), thereafter becoming elongate to setiger 7, then subulate to posterior end (Fig. 1e, f).

Neuroacicula of setigers 2–5 twice as thick as followings, with dorsally curved tips (Fig. 2b–e, h). Those from setigers 1 and 6, to end of body slender, distally beak-shaped (Fig. 2a, f, g). Notoacicula very slender, needle-like (Fig. 2i) present in all setigers; those in few anterior setigers especially thin.

Superior simple seta present in all setigers. Those of setigers 1–5 distally falcate, rather short, as long as shafts of compound spinigers; those of setigers 2–5 enlarged (Figs. 1c, d, 2j). From setiger 6 to end of body, stout simple seta replaced by long slender capillary seta, slightly curved dorsally and finely serrated on lower curved side (Figs. 1e, f, 2k) (sometimes transitional forms between two types of simple setae on setiger 6).

Setigers 1–5 each with 10–11 thick composite setae including 6–9 falcigers having short unidentate blades (Fig. 2l, n) and 2–4 spinigers having long blades (Fig. 2m), all with saw-tooth cutting margins, lacking distal hoods and sheaths; those of setigers 2–5 thicker than those of setiger 1. Shaft tips smooth with rather pointed superior branch and rounded inferior branch; cup-shaped socket for blade between two branches (Fig. 2o).

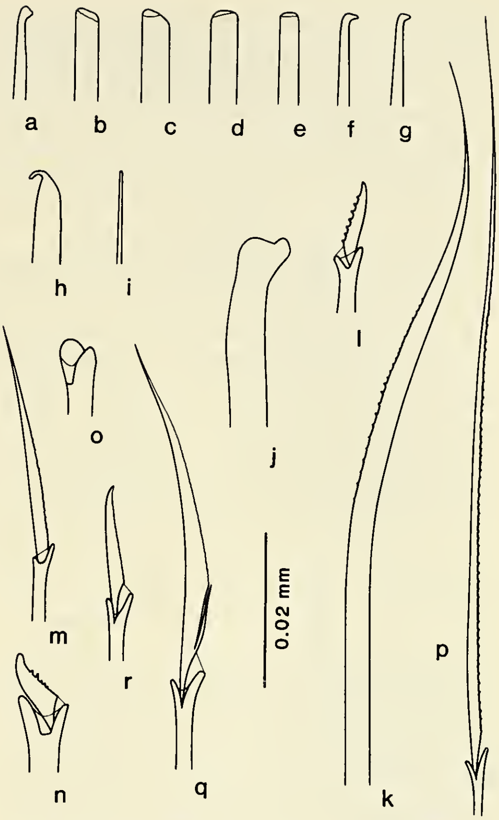

Fig. 2. *Streptospinigera alternocirrus*, paratype (BM(NH)ZB 1986.695): a–g, Neuroacicula, dorsal views: a, Setiger 1; b, Setiger 2; c, Setiger 3; d, Setiger 4; e, Setiger 5; f, Setiger 6; g, Setiger 20; h, Neuroaciculum, setiger 3, anterior view; i, Notoaciculum, setiger 20, anterior view; j, Enlarged superior simple seta, setiger 4, posterior view; k, Superior capillary seta, setiger 10, posterior view; l, Medial composite falciger, setiger 1, anterior view; m, Upper composite spiniger, setiger 1, anterior view; n, Medial composite falciger, setiger 5, posterior view; o, Shaft tip of same, dorsoposterior view; p, Superior composite spiniger, setiger 15, posterior view; q, Medial composite spiniger, setiger 16, posterior view; r, Inferior composite falciger, setiger 22, posterior view.

Setigers 6 to end of body each with 6–9 slender composite setae including 2–3 superior spinigers having very long finely serrated blades of similar length (Fig. 2p), 2–4 medial spinigers having long minutely serrated blades (Fig. 2q) and 2–4 inferior falcigers having rather short unidentate blades with minutely serrated cutting margins (Fig. 2r) becoming shorter ventrally (Fig. 1f); all lacking distal hoods and sheaths. Medial spinigers sometimes with basal spur (Fig.

2q). Shaft tips smooth, similar to those of setigers 1–5, but socket for blade generally inconspicuous, not recognized in superior spinigers. Inferior simple seta absent throughout body.

Pygidium very small with 3 smooth anal cirri including short filiform midventral and 2 long lateral ones (Fig. 1g).

In holotype, gametes present from setiger 10 to end of body.

Remarks.—*Streptospinigera alternocirrus* agrees with *S. heteroseta* in having enlarged acicula in the anterior region, composite spinigers and both enlarged and capillary superior simple setae. *Streptospinigera alternocirrus,* however, differs from *S. heteroseta* in having not only articulate dorsal cirri but also subulate dorsal cirri after setiger 7. In addition, while articulate dorsal cirri become long only on setigers 6, 9, 11, 13, 16, 18 in *S. heteroseta,* long articulate dorsal cirri occur on setiger 6 and, alternately with smooth thick subulate dorsal cirri from setiger 9 to end of body in *S. alternocirrus.* Dorsal cirri of setiger 4 are short, smooth, subulate to cylindrical in *S. heteroseta,* and rather long with two articles in *S. alternocirrus.*

Streptosyllis pettiboneae Perkins, 1980, agrees with *Streptospinigera alternocirrus* in having similar arrangement of articulate and smooth dorsal cirri; *S. pettiboneae,* however, has only composite falcigers and stout superior simple setae.

Ecology.—*Streptospinigera alternocirrus* occurs abundantly in clean medium to fine sands. Epitokes were occasionally found. In these epitokes, four lenticular eyes are enlarged, and several very long natatory setae develop superior to usual capillary simple seta on the segments swollen with reproductive material. Larval settlement occurred mainly from April to June in the type locality, and the highest density of 25,000 inds./m^2 was recorded during this settling season (Ohwada 1986). The adult population disappeared soon after the breeding season.

Etymology.—The specific name, *alternocirrus,* derives from the Latin, *alterno,* meaning alternate, and *cirrus* meaning curls; it is used as a noun in apposition.

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NEOTROPICAL MONOGENEA. 11. *RHINOXENUS,* NEW GENUS (DACTYLOGYRIDAE: ANCYROCEPHALINAE) WITH DESCRIPTIONS OF THREE NEW SPECIES FROM THE NASAL CAVITIES OF AMAZONIAN CHARACOIDEA

D. C. Kritsky, W. A. Boeger, and V. E. Thatcher

Abstract.—Rhinoxenus, new genus is proposed for ancyrocephalines characterized by 1) possessing a pair of dorsal haptoral spikes which replace or are modifications of the dorsal anchor/bar complex; 2) lacking a dorsal bar; and 3) having hook pair 2 situated on two bilateral lobes of the trunk. Species of *Rhinoxenus* infest the nasal cavities of Neotropical charcoid fishes. Three new species are described: *R. piranhus,* new species, from *Serrasalmus nattereri* (Kner), *R. arietinus,* new species, from *Schizodon fasciatum* Agassiz and *Rhytiodus argenteofuscus* Kner, and *R. nyttus,* new species from *S. fasicatum.* Two undescribed species of *Rhinoxenus* are reported from *S. fasciatum* and *Hydrolycus scomberoides* (Cuvier), respectively.

Relatively few species of Dactylogyridae have been recorded from nasal cavities of freshwater fishes. In North America, Rogers (1967) described *Aplodiscus nasalis* (Dactylogyrinae) from the nose of the Alabama hogsucker, *Hypentelium etowanum* (Catostomidae). Dechtiar (1969) described two species of Dactylogyrinae, *Pellucidhaptor catostomi* and *P. nasalis,* from the nasal cavities of *Catostomus catostomus* and *C. commersoni* (Catostomidae), respectively, in Ontario. Recently, Klassen and Beverley-Burton (1985) reported *Ligictaluridus monticellii* (Ancyrocephalinae) from the nose of *Ictalurus nebulosus* (Ictaluridae) in Ontario. The latter species had previously been reported from the nasal cavities of North American Ictaluridae imported into Europe (Cognetti de Martiis 1924, Prost 1973). Additional records of Dactylogyridae from the nose of freshwater fishes exist from Europe, the USSR, and Asia (Smirnova et al. 1964, Strelkow & Ha Ky 1964, Gussev and Strijak 1972). At present there are no reports of dactylogyrids from the nares of Neotropical or Ethiopian freshwater fish.

Recently, we examined the nasal cavities of a few species of freshwater fish collected from the Manaus area in Brazil. These preliminary collections from four species of Characoidea, one species of Siluriformes and one clupeid host have revealed several new monogenean species and genera, suggesting that the nose of fishes may be a specific site of infestation for an unique fauna in the Neotropical Region. The present study includes the description of dactylogyrids comprising a new genus from the characoid hosts.

Materials and Methods

Fish were collected by net from the environs of Manaus, Amazonas, Brazil, during 1983 and 1984. The host brain and spinal cord were destroyed by pithing, after which the nasal cavities of each fish were washed with a strong current of 1:4000 formalin solution. After this washing, the nasal cavity was disrupted with a probe and again washed with the formalin solution. The washings were collected and examined with a dissecting microscope; parasites were removed with a fine probe and fixed in a 3% formalin solution. Preparation of helminths for study followed the procedures outlined by Kritsky, Thatcher & Boeger (1986). Measurements, all in micrometers, were made with the aid of a filar micrometer, except length of the cirrus was approximated using a Minerva curvimeter on camera lucida drawings. Type specimens were deposited in the helminth collections of the Instituto Nacional de Pesquisas da Amazônia (INPA), the U.S. National Museum (USNM), and the University of Nebraska State Museum (HWML).

Rhinoxenus, new genus

Diagnosis.—Dactylogyridae, Ancyrocephalinae. Body robust, divisible into cephalic region, trunk, haptor (peduncle absent). Tegument thin, smooth. Cephalic lobes, head organs, cephalic glands present. Four eyes. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; intestinal caeca (2) confluent posterior to gonads, lacking diverticulae. Genital pore midventral. Gonads intercaecal, overlapping; testis dorsal to ovary. Vas deferens looping left intestinal caecum; seminal vesicle a dilation of vas deferens, frequently with constriction near midlength; copulatory complex comprising coiled cirrus with counterclockwise rings, accessory piece basally articulated to cirrus by proximal projection lying within rings of cirrus. Vagina sinistral in anterior trunk; seminal receptacle present. Vitellaria well developed, coextensive with caeca. Haptor armed with ventral pair of anchors, ventral bar, 6 pairs of hooks with ancyrocephaline distribution (Mizelle 1936) (hook pair 2 removed from haptor, lying in lateral or ventrolateral lobes on posterior half of trunk), one pair of dorsal spike-like structures which replace or represent modifications of dorsal anchors. Hooks with proximally inflated shank. Nasal parasites of Neotropical characoid fishes.

Type species, host, and locality.—*Rhinoxenus piranhus,* n. sp. from *Serrasalmus nattereri* (Kner), Ilha Marchantaria, Rio Solimões, near Manaus, Amazonas, Brazil.

Other species.—*Rhinoxenus arietinus,* n. sp. from *Schizodon fasciatum* Agassiz (type) and *Rhytiodus argenteofuscus* Kner (an apparent accidental host); *Rhinoxenus nyttus,* n. sp. from *Schizodon fasciatum*; *R.* spp. from *Schizodon fasciatum* and *Hydrolycus scomberoides* (Cuvier) (USNM 79264, 79265, respectively).

Etymology.—The generic name is from Greek (*rhin/o* = nose + *xen/o* = guest).

Rhinoxenus piranhus, new species

Figs. 1–8

Host.—*Serrasalmus nattereri* (Kner), the piranha cajú, Serrasalmidae.

Locality.—Ilha Marchantaria, Rio Solimões near Manaus, Amazonas, Brazil (type) 21 Sep 1983, 15 Aug 1984, 14 Sep 1984, 25 and 26 Nov 1984; Furo do Catalaõ, near Manaus, Amazonas, Brazil 27 Nov 1984.

Type specimens.—Holotype, INPA PA287-1; paratypes, INPA PA287-2 to PA287-11, USNM 79180, 79181, HWML 23307.

Description (based on 79 specimens; 20 measured).—Body 758 (582–1014) long, fusiform, slightly flattened dorsoventrally; greatest width 165 (132–206) in posterior trunk. Cephalic lobes poorly developed, 2 terminal, 2 bilateral; 2 pairs of head organs lying in cephalic lobes and adjacent cephalic area; cephalic glands unicellular, bilateral, posterolateral to esophagus. Eyes usually equidistant, members of anterior pair smaller than those of posterior pair; conspicuous lens associated with posterior eyes; eye granules ovate, small; accessory granules absent. Pharynx ovate, with distal sucker-like modification, 34 (27–39) in diameter. Haptor trapezoidal, 113 (93–136) wide, 111 (86–135) long. Ventral anchor 131 (120–137) long, with superficial root modified into ventromedial protuberances serving as articulation point for bar, evenly curved shaft, point with saucer-like termination; base 25

(20–32) wide. Anchor filament conspicuous, basal. Dorsal haptoral spike 116 (97–130) long, with small bulbous proximal end, tapered distal point; each termination with conspicuous cap of tissue. Ventral bar 52 (46–55) long, flattened, with small terminal protuberances. Hook pair 2–24 (23–25) long, lying in small lobe on ventral surface of posterior trunk, stout, with heavy point, erect thumb, inflated proximal ⅔ of shank. Haptoral hooks 27 (24–29) long, elongate, delicate, with curved point, erect thumb, shank slightly inflated proximally. FH loop extended to near beginning of shank dilation. Cirrus a coil of about 2½ rings; base with bilaterally sclerotized lobes, ring diameter 28 (25–31), cirrus length 175. Accessory piece spathulate distally, with lateral rod-like thickening, proximal projection extending along distal one-half cirral ring serving as cirral guide; length of distal spathulate portion 51 (45–55). Testis elongate ovate, 126 (115–144) long, 36 (34–37) wide; seminal vesicle with medial constriction; prostatic reservoirs not observed. Ovary elongate, with varying diameter, greatest width 34 (23–48), length 183 (137–202); oviduct short; ootype, uterus not observed; genital pore posterior to intestinal bifurcation; vagina with distal double cavity from which simple tube arises; seminal receptacle a dilation of vaginal tube, lying diagonally to left of body midline. Egg lacking filaments, with proximally thickened shell.

Remarks.—Rhinoxenus piranhus is the type species for the genus. The specific name is derived from the common or local name of the host.

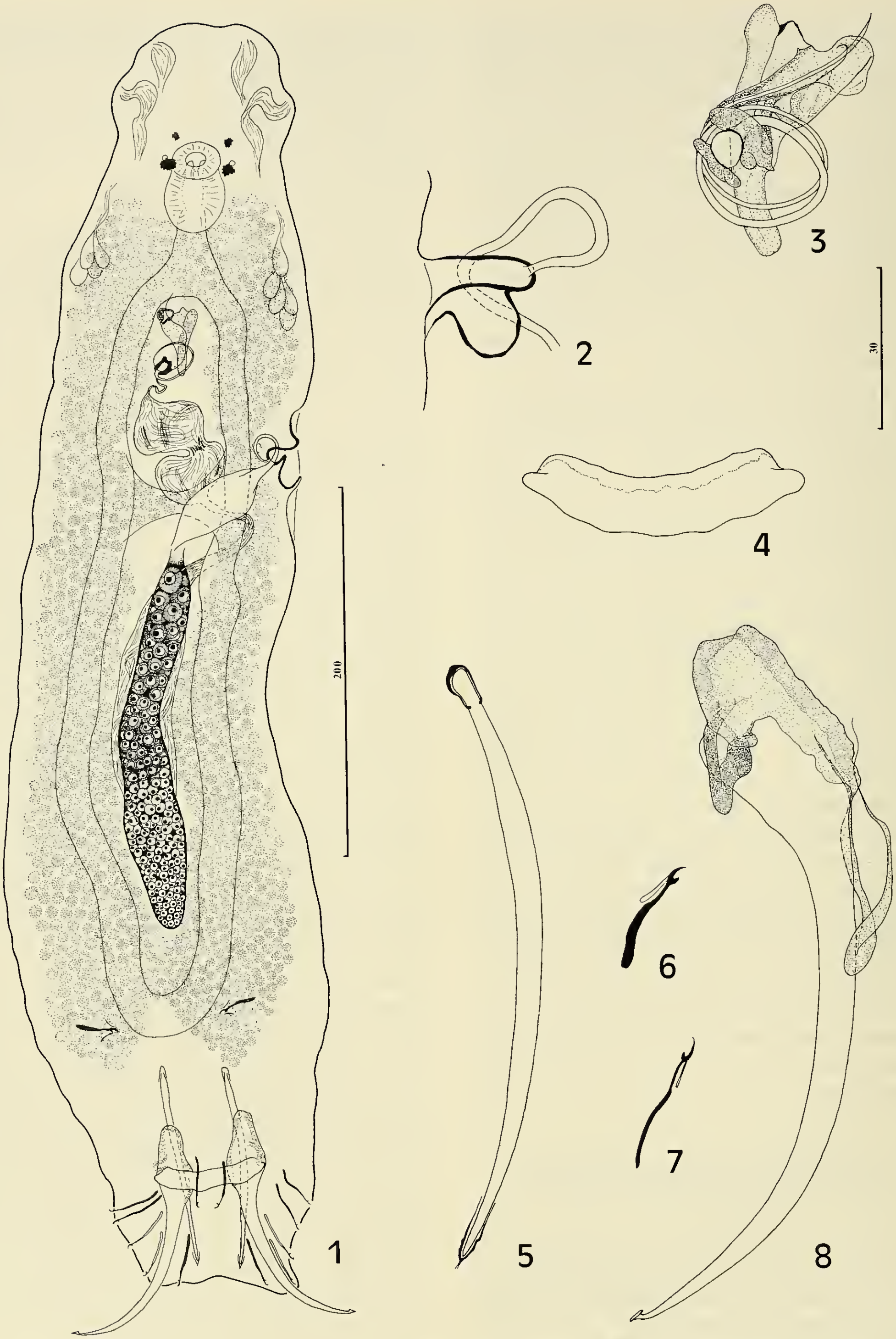
Rhinoxenus arietinus, new species
Figs. 9–17

Hosts.—Schizodon fasciatum Agassiz, the aracú pintado, Anostomidae (type), and *Rhytiodus argenteofuscus* Kner, the aracú pau de negro, Anostomidae.

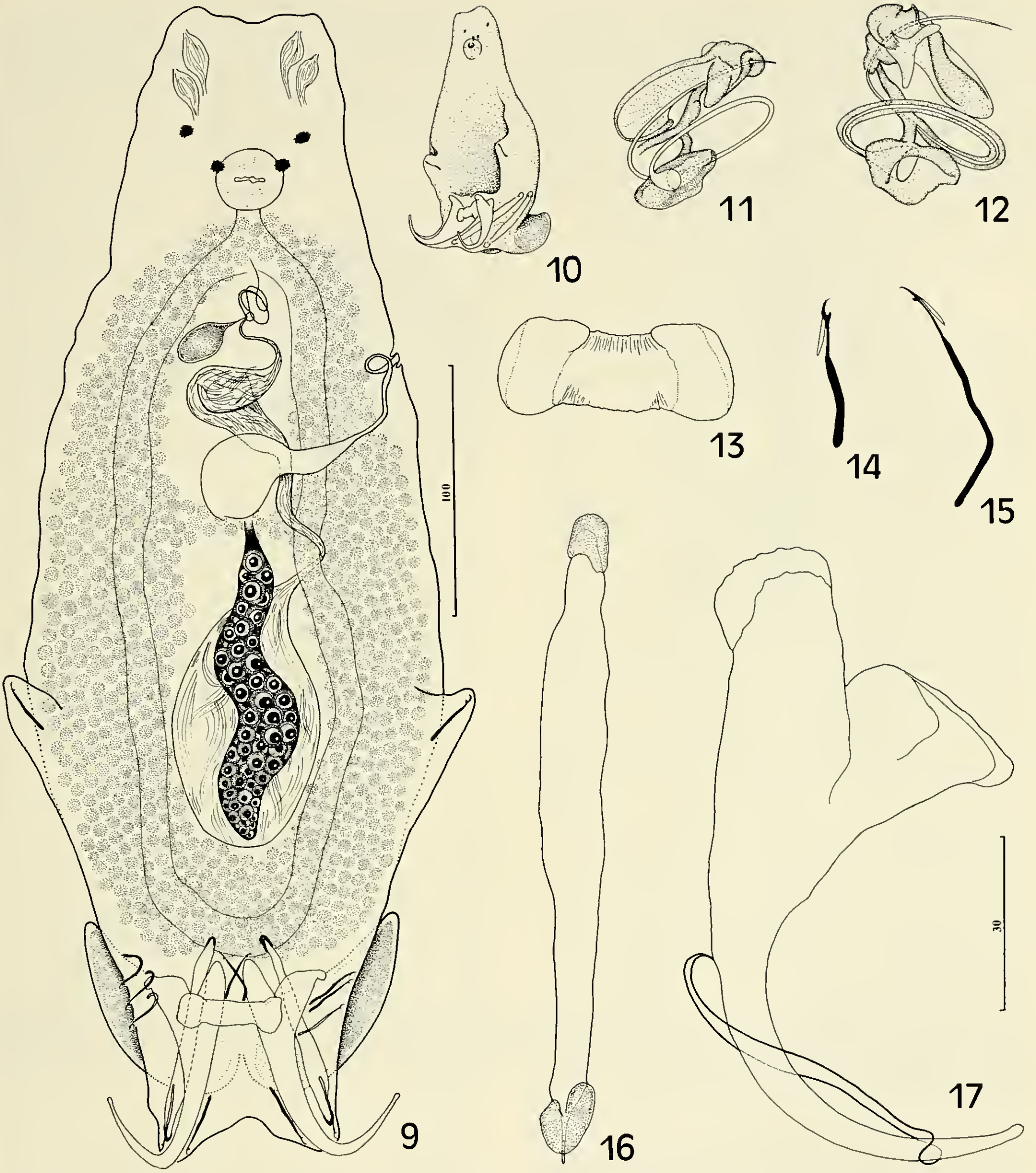
Locality.—Ilha Marchantaria, Rio Solimões, near Manaus, Amazonas, Brazil (type) *S. fasciatum,* 25 Nov 1983; aquarium, INPA, Manaus, Amazonas, Brazil (*R. argenteofuscus,* 8 Feb 1984.

Type specimens.—Holotype, INPA PA288-1; paratypes, INPA PA288-2 to PA288-4, USNM 79183, 79184, HWML 23309, 23310.

Description (based on 17 specimens).—Body flattened dorsoventrally, with lateral margins of trunk curled ventrally (Fig. 10); length 395 (310–501) greatest width 169 (133–202) in posterior trunk at level of gonads. Cephalic area with 2 poorly developed terminal lobes; head organs conspicuous, usually 2 pairs; cephalic glands indistinct, posterolateral to pharynx. Eyes subequal; members of anterior pair approximately twice the distance apart of members of posterior pair; eye granules ovate, small; accessory granules absent or few in cephalic region. Pharynx spherical, 23 (20–27) in diameter. Haptor subquadrate, with 2 large posteriorly directed pads shaped as horns of a ram; pads dense staining, apparently glandular; haptor 126 (111–138) wide, 108 (89–131) long. Ventral anchor 106 (88–115) long, robust, with large base, well-developed roots, evenly curved shaft and point, obtuse point tip; base 54 (50–61) wide. Anchor filament well developed. Dorsal haptoral spike 110 (89–126) long, variable in width, robust, with distal acute tip, proximal and distal tissue caps. Ventral bar 43 (41–46) long, subrectangular, with slightly expanded ends. Hook pair 2 lying on lateral lobe of trunk just posterior to body midlength, with heavy point, erect thumb, proximal ⅔ of shank inflated. Haptoral hooks elongate, delicate, with blunt thumb, proximal ¾ of shank dilated. FH loop extending to near level of termination of shank inflation. Cirrus a coil of about 1½ rings, base with large sclerotized lobes, ring diameter 29 (26–33), cirrus length 107–110. Accessory piece basally articulated to cirral base, proximally follows first cirral ring, with ornate termination; length of terminal portion 32 (27–36). Testis ovate, 80 (78–83) long,

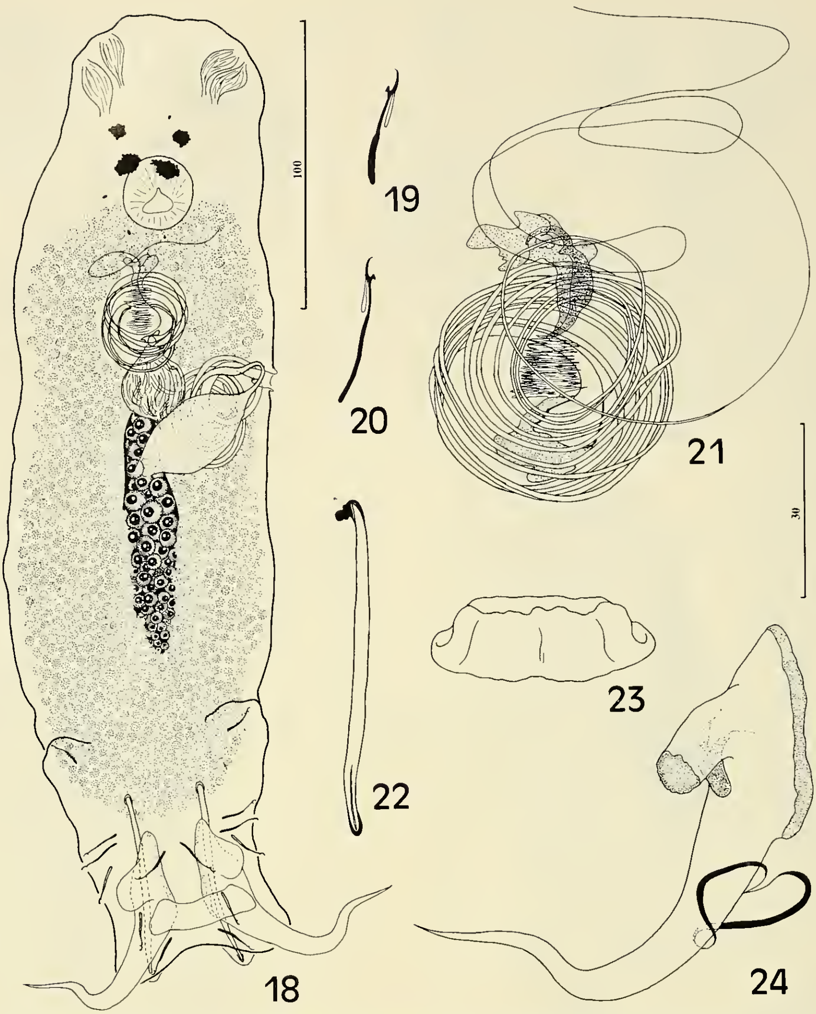


Figs. 1–8. *Rhinoxenus piranhus*: 1, Holotype (ventral); 2, Vagina (dorsal); 3, Copulatory complex (dorsal); 4, Ventral bar; 5, Dorsal haptoral spike; 6, Hook pair 2; 7, Haptoral hook; 8, Ventral anchor. All figures are drawn to the 30-micrometer scale except Fig. 1 (200-micrometer).



Figs. 9–17. *Rhinoxenus arietinus*: 9, Holotype (ventral); 10, Ventrolateral illustration showing relationship of haptoral anchors, pads, and spike, and bilateral body lobes; 11, 12, Copulatory complexes; 13, Ventral bar; 14, Hook pair 2; 15, Haptoral hook; 16, Dorsal haptoral spike; 17, Ventral anchor; Figs. 11–17 are drawn to the 30-micrometer scale; Fig. 9 to the 100-micrometer scale.

36 (29–43) wide, seminal vesicle with inconspicuous medial constriction, one prostatic reservoir lying to right of cirral base. Ovary 85 (81–88) long, 21 (18–23) wide, usually an elongate sigmoid organ which may appear subovate in contracted specimens as a result of margins between curves being closely appressed; oviduct short; ootype, uterus not observed; genital pore posterior to or at level of intestinal bifurcation; vagina sclerotized, tubular, with distal loop, expanding proximally to large pyr-



Figs. 18–24. *Rhinoxenus nyttus*: 18, Holotype (ventral); 19, Hook pair 2; 20, Haptoral hook; 21, Copulatory complex; 22, Dorsal haptoral spike; 23, Ventral bar; 24, Ventral anchor. All drawings are to the 30-micrometer scale except Fig. 18 (100-micrometer).

iform seminal receptacle. Vitellaria dense, coextensive with gut.

Remarks.—This species is unique among the Dactylogyridae by possessing two posterior lobes on the haptor. The lobes are apparently glandular and serve in attachment within the nasal cavity of the host. The specific name is from Latin (*arietinus* = like a ram's head) and is based on the dorsal haptoral lobes which impart a ram's head appearance to the haptor.

Rhinoxenus nyttus, new species
Figs. 18–24

Host.—*Schizodon fasciatum* Agassiz, the aracú pintado, Anostomidae.

Locality.—Ilha Marchantaria, Rio Solimões, near Manaus, Amazonas, Brazil 25 Nov 1983.

Type specimens.—Holotype, INPA PA 286-1; paratypes, USNM 79182, HWML 23308.

Description (based on 3 specimens).—Body foliform; length 334 (299–358), greatest width 92 (88–96) at various points along trunk. Cephalic lobes poorly developed or absent; 4 head organs in anterolateral cephalic region; cephalic glands inconspicuous, lying posterolateral to pharynx. Members of posterior pair of eyes larger, closer together than those of anterior pair; eye granules ovate, small; accessory granules few or absent in cephalic area and anterior trunk. Pharynx subspherical, 24–25 in diameter; gut obscured by vitellaria. Haptor subrectangular, 81 (70–93) long, 66 (65–67) wide. Ventral anchor lacking roots, base with 2 superficial projections articulating to ventral bar, shaft curved, point undulated; anchor 76 (71–80) long, base 25 (24–26) wide. Anchor filament well developed. Dorsal haptoral spike 59 (57–60) long, delicate, with distal hollow point, proximal and distal caps. Ventral bar subtrapezoidal, with short posterolateral protuberances; bar 41 (39–42) long. Hook pair 2–18 (16–20) long, lying on 2 bilateral lobes on posterior trunk, with delicate point, erect blunt thumb, shank dilated along proximal half. Haptoral hooks 21 (20–22) long, delicate, with fine point, blunt thumb, slightly dilated proximal shank; FH loop extending to near beginning of dilated portion of shank. Cirrus comprising a coil of 10–15 rings, simple base; ring diameter 35 (33–39); cirrus 1300 long. Accessory piece basally articulated to cirrus, proximally twisted and lying within cirral rings, distally serving as a cirrus guide; accessory piece 29–30 long. Testis, vas deferens, prostatic reservoirs not observed; seminal vesicle pyriform. Ovary elongate, fusiform, 15–16 wide, 54–55 long; oviduct short; ootype, uterus not observed; vagina comprising an elongate coiled tube expanding into large fusiform seminal receptacle; vitellaria dense, scattered throughout trunk.

Remarks.—Based on the morphology of the haptoral bar, the dorsal haptoral spikes, and the ventral anchor base, *Rhinoxenus nyttus* is most closely related to the type species, *R. piranhus.* The coiled cirrus and vaginal tube, each comprising numerous rings, and the acute and doubly bent anchor point in *R. nyttus* serve to differentiate these species. The specific name is a neologism suggested by the Greek (*Nyss/o* = to prick) and refers to the presumed action of the dorsal haptoral spike.

Discussion

Although the morphology of the internal organ systems of *Rhinoxenus* species is not unique among the Dactylogyridae, the genus is characterized by some outstanding features not found among members of other genera in the family. Most notable among these are: 1) the modification of the dorsal anchors into paired haptoral spikes which lack an articulating bar and 2) the removal of hook pair 2 from the haptor to bilateral lobes on the trunk. In a few species of Dactylogyridae (some *Cosmetocleithrum* spp., among others), hook pair 1 may be located on the peduncle, but this condition is not considered as significant as that shown by species of *Rhinoxenus.* In *Cosmetocleithrum,* hook pair 1 remains in close proximity to the haptor and probably functions similarly to that of other dactylogyrids with normal hook distributions. Modifications of the haptors of *Rhinoxenus* species apparently relate to the needs for attachment determined by the physical surface of the host's nares. However, collection techniques precluded a determination of how the parasites utilize their highly modified haptors at specific attachment sites within the nasal cavity. Determination of haptoral and hook 2 function in *Rhinoxenus* species will most likely depend on observations of living specimens on their hosts.

The uniqueness of *Rhinoxenus* precludes determination of closely related genera, even though the genus clearly is a member of the Ancyrocephalinae (sensu Yamaguti 1963) based on anatomy of the internal organ systems (digestive and reproductive). It is unlikely that it belongs in the Dactylogyrinae, which includes most North American parasites from nasal cavities of fishes (*Aplodiscus, Pellucidhaptor*), since the anchor/bar complex is ventral (dorsal in Dactylogyrinae), 4A hooks are lacking, and species of *Rhinoxenus* parasitize characoid fishes (primarily Cyprinidae in Dactylogyrinae).

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AEGA LEPTONICA, A NEW SPECIES OF AEGID ISOPOD CRUSTACEAN FROM THE TROPICAL WESTERN ATLANTIC, WITH NOTES ON *ROCINELA OCULATA* HARGER AND *ROCINELA KAPALA,* NEW SPECIES

Niel L. Bruce

Abstract.—*Aega leptonica,* n. sp. is described and figured. The status and distribution of *Rocinela oculata* is reviewed and a new name, *Rocinela kapala,* is provided for Australian material previously identified as *R. oculata.* Remarks are given on the presence of the mandibular molar process in aegids, and the mouthparts of the family are rediagnosed.

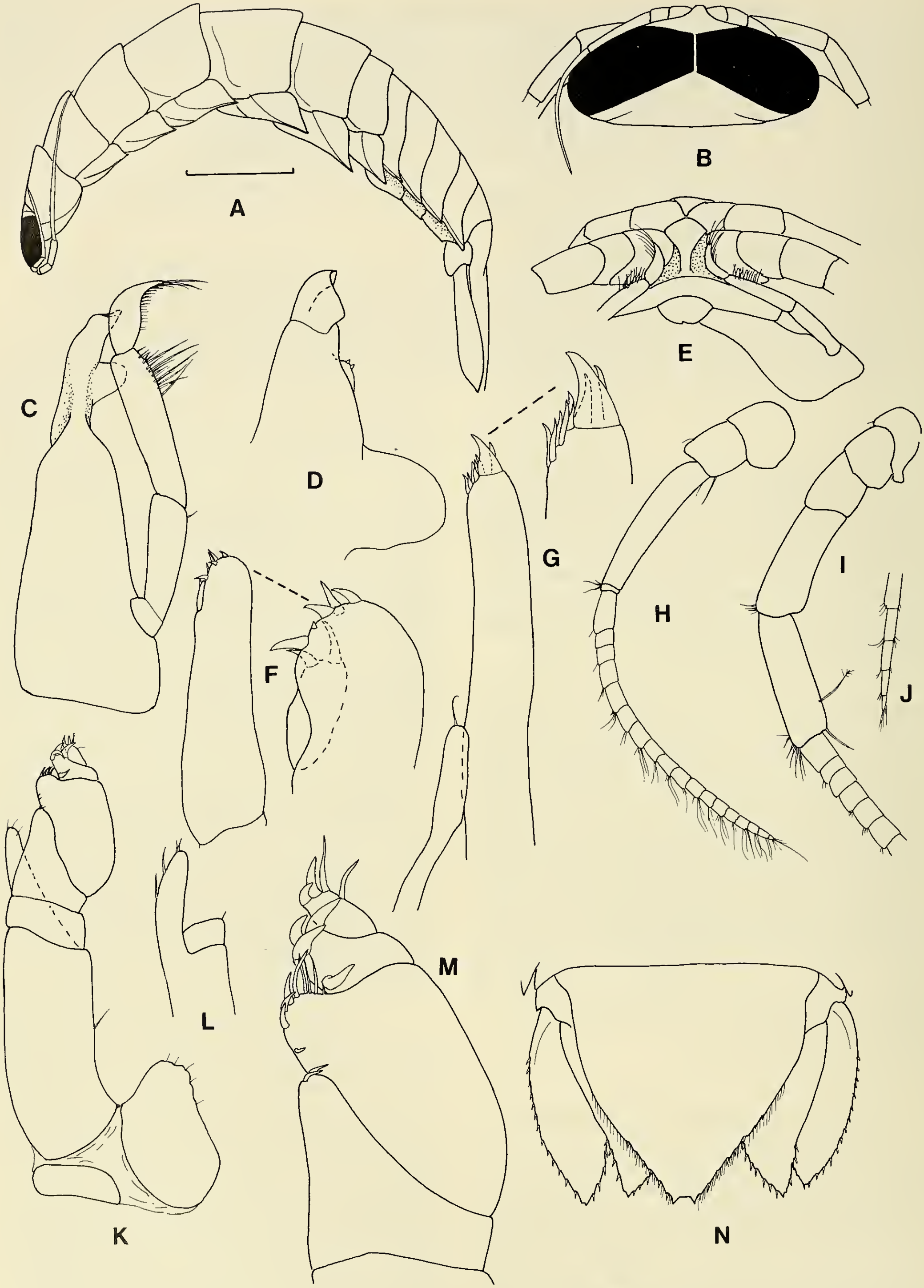
The Aegidae of the United States have been little studied, the only major work since Richardson's (1905) monograph being that of Brusca (1983) on the East Pacific *Aega* species. The only recent new record of Atlantic aegids was of *Aega monophthalma* Johnston (Treat 1980).

While examining collections at the Smithsonian I came across a new species of *Aega,* and also material identified as *Rocinela oculata.* This Atlantic material, identified as *R. oculata,* proved not to belong to that species, but also led to a re-evaluation of the status of Australian material identified as *R. oculata,* which is here described as a new species. The following abbreviations are used: AM–Australian Museum; NSW—New South Wales, Australia; USNM—U.S. National Museum of Natural History, Smithsonian Institution; QM—Queensland Museum.

Mouthpart Morphology of the Aegidae

Some confusion over the presence or absence of the mandibular molar process in the Aegidae has appeared in recent literature. Brusca (1983), in his diagnosis to the family, stated "mandible without lacinia mobilis, spine row, or molar process." This was later repeated by Brusca and Iverson (1985), and Bowman (1986) stated that the aegid mandible lacked the molar process. This seems to be due to a misinterpretation of Brusca's (1983) figs. That the family Aegidae possess a molar process has been amply demonstrated, most notably by Hansen (1890) who figured it for *Barybrotes agilis* (plate 9, fig. 3f), *Aega psora* (plate 9, fig. 4c, d) and *Rocinela danmoniensis* (plate 10, fig. 1b–e). The figs. for *Aega vigilans. A. laevis, A. lethrina, A. coroo, A. beri, Rocinela oculata* and *Alitropus typus* given by Bruce (1983) all show a molar process on the mandible. The molar process of *Aega vigilans* has small spines on the anterior margin. *Aega leptonica* described herein retains a very reduced spine row, also noted in other aegids by Hansen (1890).

There are several other aspects of mouthpart morphology frequently not noted. The mandible palp has 4 articles, the proximal one often fused to the second, also figured by Hansen (1890). The maxilla is made up of two articles, the large one usually termed lateral lobe, to which is attached the very much smaller medial lobe (there is never a basal lobe with two distinct terminal lobes as figured by Brusca (1983), this appearing to be an artifact caused by folding under a slide coverslip). The maxilla is essentially the same as that of the Cymothoidae. The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maxillule is nearly always figured without a medial lobe, but in *Aega leptonica* this small lobe is present.

The maxilliped of *Aega* has an article often not figured. This article is the coxa, the article lateral to it is the epipod as figured and identified by Hansen (1890), and not part of a divided coxa. In males the epipod may be small, or with a few marginal setae; in females the maxilliped develops large laminar lobes, one from the basis and one from the coxa.

The mouthparts of the Aegidae are here rediagnosed: Mandible incisor narrow, molar process present, lacinia mobilis and spine row (usually) absent; palp of 3 or 4 articles, articles 1 and 2 often coalesced. Maxillule slender, styliform with terminal spines. Maxilla with 2 articles, small distomedial lobe joined to larger lateral lobe, each lobe with 2 or more apical spines. Maxilliped with endite and epipod; palp with 3–5 articles, at least articles 3 and 4 with large hooked spines.

Aega leptonica, new species
Figs. 1, 2

Material.—Female Holotype, 28.5 mm, off Tortugas, Florida, 30 Jul 1932, 1048 m, *Fish Hawk* sta 65–32 (USNM 227124).

Type locality.—Off Dry Tortugas, Florida, U.S.A., ca. 24°00′N, 83°00′W.

Description.—Body about 3 times as long as wide. Cephalon with median rostrum; eyes large, united, medially occupying about 0.25 length of cephalon. Pereonites 4–7 with partial transverse impressed line. Coxae becoming more acute posteriorly; all coxae with oblique carina. Pleonites all visible; pleonites 1–4 each with horizontal carina. Pleotelson slightly wider than long, lateral margins convex, converging to narrow apex; each margin with 6 large spines and marginal setae; apex with subrectangular excision, lateral margins of which diverge.

Antennule peduncle article 3 longest, exceeding combined lengths of articles 1 and 2; peduncle article 4 fused to 3; flagellum with 17 articles, extending to middle of pereonite 1. Antenna peduncles articles 1–3 short; 4 and 5 about equal in length, each longer more than twice as long as article 3; flagellum with 27 articles, extending to anterior to pereonite 3.

Frontal lamina approximately pentagonal, posterior part stem-like; anterior margins slightly convex. Mandible incisor truncate; molar process prominent, vestigial spine row present; palp 4 articled, article 1 short, fused to article 2, distolateral margin of article 3 and most of lateral margin of article 4 with stiff setae. Maxillule with 1 broad-based triangular spine and 8 slender spines. Maxilla with 2 gently curved spines on endopod, exopod with 3 large curved spines, 1 curved and 1 straight spine. Maxilliped palp medial margins with 2 slender spines at distal angle of article 2, 5 spines and 4 setae on article 3, 4 large recurved spines on article 4, and 2 curves spines and 2 setae on article 5; endite with 4 setae.

Pereopods all slender. Pereopods 1–3 with slender propodus and elongate dactylus which exceeds length of propodus; 2 small spines on posterior margin of carpus, 1 small spine on posterior margin of merus, 1 small spine on anterodistal angle of ischium. Pereopods 2 and 3 with more numerous and larger spines than pereopod 1. Pereopod 7 basis with evenly spaced setae along anteromedial margin; posterior margins of is-

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Fig. 1. *Aega leptonica,* holotype: A, Lateral view; B, Cephalon; C, Mandible; D, Mandible, detail; E, Clypeal region; F, maxilla and detail; G, maxillule and detail; H, Antennule; I, Antenna; J, Antennal flagellum, distal articles; K, Maxilliped; L, Maxilliped endite; M, Maxilliped palp; N, Pleotelson and uropods. Scale bar represents 5 mm.

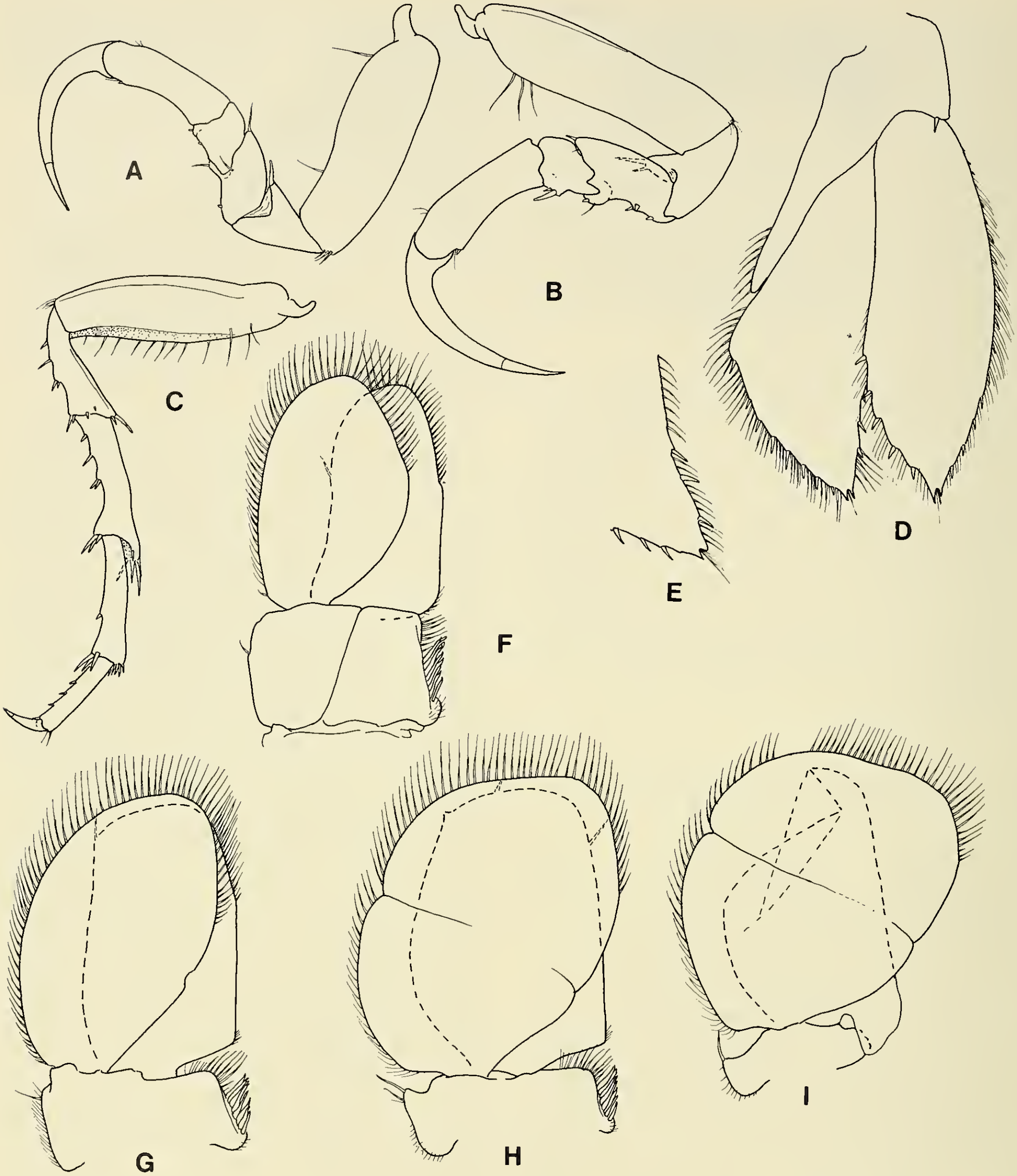

Fig. 2. *Aega leptonica,* holotype: A, Pereopod 1; B, Pereopod 2; C, Pereopod 7; D, Left uropod, ventral view; E, Right uropod, endopod apex, dorsal view; F–I, Pleopods 1–3, 5 respectively.

chium and merus indented, each indentation with spines as well as spines at distal angles; carpus with 1 spine on posterior margin; propodus with 3 spines on posterior margin.

Pleopods with only endopod of pleopod 5 naked; endopods of pleopods 3 and 4 with setae only on distomedial margin; endopods 3–5 with small acute process on mediodistal angle. Peduncle of pleopod 1 with 9 cou-

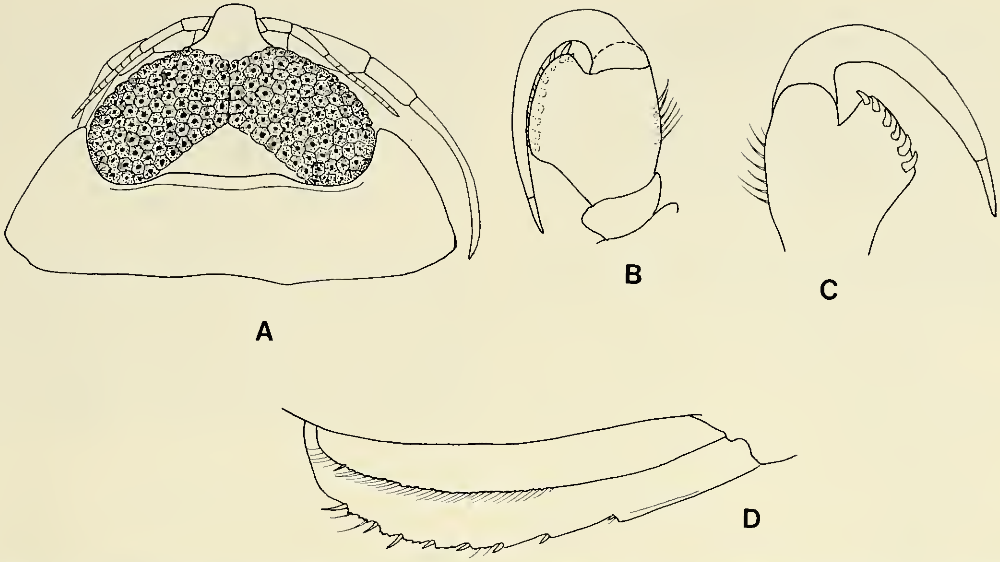

Fig. 3. *Rocinela oculata,* holotype. A, Dorsal view of cephalon; B, Propodal palm, pereopod 1; C, Propodal palm of peropod 2; D, Lateral margins of right uropodal rami.

pling hooks decreasing to 7 on peduncle 4. Uropods extending to apex of pleotelson, rami about equal in length. Exopod lateral margin convex, with 15–16 marginal spines and continuous marginal setae, medial margin with 5 spines and continuous marginal setae. Endopod lateral margin sinuate, with continuous marginal setae and three spines; medial margin with continuous marginal setae and 8 spines; apices of both rami bifid.

Male.—Not known.

Color.—On collection label: "Pink on posterior three somites . . . eyes chestnut."

Remarks.—The shape of the pleotelson, medially united eyes, and slender anterior pereopods readily identify this species. *Aega leptonica* is most similar to those species which have a prominently excised pleotelson apex: *Aega beri* Bruce, and *Aega quadratisinus* Richardson. Characters common to all three species include antennule, antennal, clypeal, pereopodal, pleopodal and uropod morphology. *Aega leptonica* differs from those two species in having medially united eyes, and more slender anterior pereopods.

The similar species *Aega excisa* Schioedte & Meinert, 1879, differs in having smoothly convex pleotelson lateral margins, and the pletoelson excision is V-shaped, not rectangular.

Etymology.—The specific epithet is derived from combining the Greek words *leptos* (slender, thin) and *onychos* (talon or claw).

Rocinela oculata Harger
Fig. 3

Rocinela oculata Harger, 1883:97, pl. III, figs. 2–2a, pl. IV, fig. 1.—Richardson, 1898:9; 1900:219; 1901:523; 1904:34, 35; 1905:191, fig. 195.—Schultz, 1969:199, fig. 314.

Not *Rocinela oculata.*—Bruce, 1983:778, figs. 15, 16 (=*Rocinela kapala,* new species).

Material.—Holotype, immature (13.3 mm), off Georgia, U.S.A. (MCZ 3910).

Remarks.—The single specimen is too fragile to allow dissection, but additional figures of appendages in situ are given.

Material in the Smithsonian collections from the Caribbean and Florida identified as *R. oculata* (USNM 7513, USNM 90440) are not that species, the morphology and spination of pereopods 1 to 3 being incompatible with Harger's holotype. This material appears to be an undescribed species of *Rocinela.*

Distribution.—Known only from the type locality, off Georgia, U.S.A.

Rocinela kapala, new species

Rocinela oculata.—Bruce, 1983:778, figs. 15, 16 (not *R. oculata* Harger, 1883).

Material.—HOLOTYPE male (41.5 mm), east of Clarence River mouth, NSW, Australia, 29°25.2′S, 153°49.5′E, 12 Oct 1975, 450 m, coll. NSW State Fisheries on F.R.V. *Kapala* (AM P31740) (specimen figured by Bruce 1983). PARATYPES. 4 males, 2 females, same data as holotype (AM P31705). Other paratypes detailed by Bruce (1983) AM P17950, P21014, P31704, QM W10464.

New records.—Male (36.0 mm), female (48.0 mm), off Sydney, NSW, 33°47′S, 151°58′E, 6 Dec 1972, 765 m (AM P37143); male (48.0 mm), off Sydney, NSW, 33°42′S, 151°57′E, 25 Sep 1984, 632 m (AM P37142); female (41.0 mm) off Clarence River, NSW, 29°46′S, 153°42′E, 26 Apr 1978, 405 m (AM P37141); all coll. NSW State Fisheries, FRV *Kapala.*

Remarks.—This material was described in detail by Bruce (1983) and identified as *R. oculata.* Under remarks Bruce (1983) commented that specificity of Australian and western Atlantic material would only be confirmed by examination of adult specimens of *R. oculata* from off the U.S.A.

Re-examination of the holotype of *R. oculata* showed that the two populations cannot be considered conspecific, and the Australian species is here named as new.

Rocinela kapala can easily be distinguished from *R. oculata* by: shorter, anteriorly rounded rostrum; pereopods 1 to 3 with palm less produced, posterior margin convex; pereopods 4–7 less spinose; pereonites 4 to 7 become elongated in adults.

Etymology.—Named after the New South Wales Fisheries vessel, FRV *Kapala.*

Acknowledgments

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PANDEA CYBELES, A NEW MEDUSA FROM THE SARGASSO SEA (COELENTERATA: ANTHOMEDUSAE: PANDEIDAE)

Angeles Alvariño

Abstract.—A new medusa is described and illustrated. It is compared to related species in the genus, *Pandea conica* (Quoy & Gaimard, 1827) and *Pandea rubra* Bigelow, 1913. It differs from those species in the proportions of the umbrella and its conical process, number of ribs on the umbrella, number of marginal tentacles, ocelli on the basal bulb of tentacles, and the large size of the stomach. The diagnostic characteristics of these species and *Pandea cybeles* are compiled in a table. Information is included on the distribution of the species throughout the world.

The genus *Pandea* Lesson, 1843, includes two valid species, *Pandea conica* (Quoy & Gaimard, 1827) and *Pandea rubra* (Bigelow, 1913. Mayer (1910) recognized five species of Pandeidae: *Pandea conica* (Quoy & Gaimard, 1827), *P. saltoria* (Sars, 1835), *P. minima* von Lendenfeld, 1884, *P. violacea* Agassiz & Mayer, 1899, and *P. maasi* Maas, 1904.

According to Kramp (1965) *P. maasi* is a synonym of *Euphysa flammea* (Linko, 1905); *P. minima* and *P. violacea* are juvenile stages of indeterminable Tiaridae, placing also *P. violacea* under *Merga violacea* (Agassiz & Mayer, 1899); and *P. saltoria* is a species of *Aglantha.*

During the Sargasso Sea Biowat cruise on the R/V *Knorr* in Apr 1975, plankton collections were obtained, and some specimens of Medusae, Siphonophora, and Ctenophora were kindly sent to me by Michael Latz (Department of Biological Sciences, University of California, Santa Barbara) for identification. The medusae included three specimens of a new species of *Pandea*, described below.

Pandea cybeles, new species
Figs. 1, 2

Material.—NE Sargasso Sea, Biowat Cruise of R/V *Knorr*, Apr 1975, from tows with Tucker ½ m net with 333 μm mesh: Sta 240, 34°53.22′N, 70°06.01′W, ca. 100 m depth, 20 Apr 1975, holotype, USNM 77473.—Sta 231, 33°55.74′N, 69°59.11′W, ca. 1 m depth, 19 Apr 1975, paratype, USNM 77474. A third specimen from Sta 230, 33°55.74′N, 69°59.11′W, ca. 1 m depth, 19 Apr 1975, was left at the University of California, Santa Barbara.

Description.—Umbrella bell-shaped, slightly higher than wide (heights 18, 20 and 25 mm, widths 14.5, 16.3 and 20 mm respectively), with conical apical process about 5 mm long (measurements included in total height) in largest medusa (Fig. 1). Exumbrella with ridges reaching from tip of apical process to each marginal tentacle, alternating with grooves running from tip of apical process to spaces between tentacles at edge of umbrella. Crest of each ridge with thin whitish band, probably formed by rows of nematocysts. The four wide radial canals with rough margins. Circular or ring canal simple, about half width of radial canals, with smooth margins (Fig. 1). Centripetal canals lacking. Velum narrow.

Marginal tentacles about 40, 10 at each space between perradii, long, of same size, hollow. Base of tentacle with thick conical laterally compressed bulb or spur clasping margin of umbrella. Abaxial spur of each tentacle having 1 red ocellus.

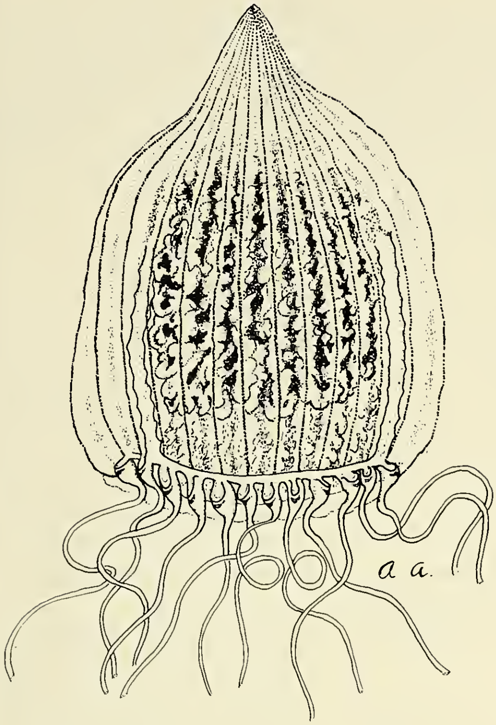

Fig. 1. *Pandea cybeles,* habitus.

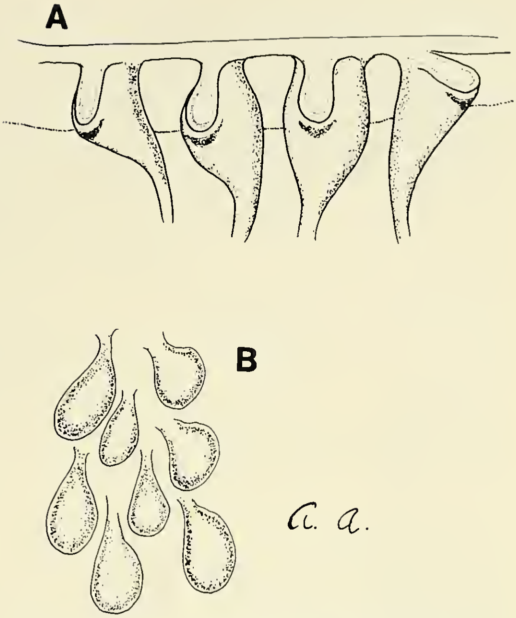

Fig. 2. *Pandea cybeles:* A, Detail of bulbs in marginal tentacles; B, Detail of internal ovular formations in gonads.

Stomach large, completely filling subumbrellar cavity, attached for about ⅓ of its length to subumbrella perradii.

Mouth with 4 perradial lips deeply and complexly folded, with crenulated edges, reaching border of umbrella.

Gonads extending over interradial and perradial zones, completely covering stomach, forming irregular network of sinuous ridges and pits, latter corresponding to internal ovular formations (Fig. 2B).

Color of stomach, mouth, gonads, and border of umbrella pinkish, with light purple and violet tones. Thick jelly umbrella and conical apical process, crystal clear with violet tones, revealing darker tones of stomach and gonads within.

Etymology.—Named after Cybele, goddess of nature.

Remarks.—Differential morphological characteristics of *Pandea cybeles, P. conica,* and *P. rubra* are given in Table 1.

Pandea cybeles differs from *P. conica* in the proportion of length to width of the umbrella, the number of ribs, the number of marginal tentacles, and the size of the stomach.

Pandea cybeles differs from *P. rubra* in having a conical apical process of the umbrella, and ribs and nematocyst tracks on the umbrella, all of which structures are absent in *P. rubra.* The circular canal is broader in *P. rubra* than in *P. cybeles.* The number of marginal tentacles is different in the two species, and *P. rubra* does not have ocelli on the basal bulb of the tentacles.

The stomach of *P. rubra* reaches to half the length of the subumbrellar cavity; in *P. conica* it occupies about ⅓ or ½ of the length of the subumbrellar cavity, whereas in *P. cybeles* it fills completely the subumbrellar cavity, reaching the margins of the umbrella.

Differences between *Pandea rubra* and *Pandea cybeles* are obvious and do not require further discussion. However, *Pandea*

Table 1.—Principal differential characteristics of the species of *Pandea* and the new species.

Characteristics	*Pandea conica* (Quoy & Gaimard, 1827)	*Pandea rubra* Bigelow, 1913	*Pandea cybeles*, n. sp.
Umbrella	Bell barrel-shaped, about twice as high as wide, jelly fairly thick, with apical process	Bell-shaped, as high or slightly higher than wide, with rounded summit, without apical process. Thin soft walls	Bell-shaped, slightly higher than wide, of thick jelly, with thick apical conical process
Umbrella size	20–30 mm height, 10–15 mm wide	30–40 mm height up to 75 mm	18–25 mm height and 14.5–20 mm wide
Velum	Narrow	Narrow	Narrow
Apical conical process	Conical at summit, with apical ectodermal thickening	Not present	Present, long conical ectodermal thickening at top of umbrella
Ribs and ridges	16 or in the 20's. Exumbrellar nematocyst ribs	No ribs or exumbrellar nematocyst tracks	Present 40 exumbrellar ribs with nematocyst band at crest edge, extending from tip of conical process to edge of umbrella
Radial canals	4 broad, smooth or jagged	4 broad with wavy or jagged outlines	4 broad with jagged outline
Circular canal	Narrower than radial canals, smooth outlines	Broad, with smooth outlines	Narrower than radial canals, about half width, smooth outlines
Marginal tentacles	16 or in the 20's, smooth, hollow, with conical laterally compressed basal bulb, without well developed abaxial spur, with one abaxial ocellus. No rudimentary marginal tentacles	18–24 of various sizes, hollow, smooth, with large conical basal bulb, not laterally compressed, with distinct abaxial spur clasping margin of umbrella. No ocelli. No rudimentary marginal tentacles	About 40, 10 from perradial to perradial, hollow, long, with conical laterally compressed basal bulb, with abaxial spur and ocellus. No rudimentary marginal tentacles
Stomach	Large, pyramidal, almost filling upper ⅓ of subumbrellar cavity, attached about ⅘ of length to subumbrellar perradii	Large, with broad base, about half-height of subumbrellar cavity, attached to subumbrellar perradii for about ⅘ of its length	Large, filling completely subumbrellar cavity, attached ⅓ of its length to subumbrellar perradii
Mouth	4 perradial lips with folded crenulate edges	4 lips with folded crenulate margins	4 perradial lips with complexly folded crenulate edges reaching border of umbrella
Gonads	On entire interradial walls of stomach, forming coarse meshwork of ridges and pits, surrounding the stomach	Very fine meshwork of pits, interradially on stomach, close-meshed irregular network of ridges with pits between them	Extended over interradial and perradial zones covering completely stomach, forming network of ridges and oval pits

Table 1.—Continued.

Characteristics	*Pandea conica* (Quoy & Gaimard, 1827)	*Pandea rubra* Bigelow, 1913	*Pandea cybeles*, n. sp.
Color	Stomach and gonads reddish, brownish or yellowish. Mouth lips reddish or pink, tentacles milky yellow, ocelli red or reddish brown. Subumbrella colorless	Subumbrella, stomach, mouth, gonads and marginal tentacles deep brownish red or chocolate	Stomach, mouth, gonads and border of umbrella pink with light purple and violet tones
Distribution	Atlantic, Mediterranean	Bermuda, NW Pacific, Bering Sea, British Columbia. Probably inhabiting deep waters	Sargasso Sea

conica and *Pandea cybeles* are more closely related, as both have a long conical process at the top of the umbrella. Therefore, a discussion on the descriptions of *Pandea conica* published by various authors will enlighten the separation of the species.

There is some disagreement among the various authors on the number of marginal tentacles, as well as in the proportion of height and width of the umbrella. It appears in some instances that authors were including under *Pandea conica* specimens belonging to different species.

However, all authors basically agree, when defining *Pandea conica,* that the height of the umbrella is about twice its width, the manubrium extends only along the upper ⅓ or half of the subumbrellar cavity, and the number of ribs on exumbrella and marginal tentacles is in the 20's, about 24.

A chronological review of descriptions by various authors follows.

Quoy & Gaimard (1827) first described the medusa as *Dianaea conica,* collected near the Strait of Gibraltar, as body elongated conically pointed at the top, "tentacles small, filamentous, in the 20's, with reddish spot at their base. The umbrella presented as many striae as tentacles. Manubrium with 4 small short arms, pink in color, the rest of the medusa transparent." Their illustration of the medusa shows size proportions of umbrella, stomach and tentacles.

Maas (1904) found abundant specimens of *Pandea conica* at Monaco Bay, and those had 8, 16, or 20 tentacles.

Mayer (1910) described *Pandea conica* as "barrel-shape sides bluntly pointed, 21 mm high and 10 mm wide, with 8 to 24 well developed longitudinal rib-like ridges along exumbrella and equal number of marginal tentacles with abaxial ectodermal ocelli. Stomach wide and short with 4 folded lips having sinuous margins." The colors of gonads, tentacles, and ocelli were brownish red, yellowish-milky and dark purple, respectively. Mayer's illustration (1910:117) shows short additional ridges extending up to ⅓ from the border of the umbrella, and the conical top is missing. Either this is an illustration of a newly-born medusa or it is not *P. conica.*

Vanhöffen (1911) indicated *P. conica* 12.5 mm high and 10 mm wide with conical process of 2 mm, 4 radial canals and ring canal. The largest specimens had 19 or 20 tentacles. Other characteristics agreed with descriptions by other authors.

Hartlaub (1913) also indicated the umbrella extending into a conical process at the top, being 21 mm high and 10 mm wide, with 24 marginal tentacles, and the stomach extending along the upper ⅓ of the subumbrellar cavity. Gonads and color agree with previous descriptions. Figure 286 on page 339 of Hartlaub 1913 illustrates his description.

Browne (1916) referred to *Pandea* juvenile specimens obtained at the Chagos Archipelago, which could be related to *Pandea conica.* The smallest was about 2.5 mm in diameter.

Uchida (1927) discussed the characteristics of *Pandea conica* and *P. rubra.* He identified and described specimens obtained at Misaki, Japan, as *Pandea conica,* with "bell somewhat prismatic, with truncated top, 30 mm high and 17 mm wide; exumbrella with 44 longitudinal ridges. 4 Radial canals, wide, jagged, widest in the lower half. Ring canal narrower. Tentacles 44, all of similar length, hollow. Manubrium wide and short, nearly filling the upper half of bell cavity, fused with the upper part of subumbrella." The rest of the descriptive part agrees with other authors, in gonads, color, etc. He explained, "Ocellus could not be found in preserved specimens."

The truncate top of the umbrella of Uchida's specimens indicates that those specimens apparently do not belong to *Pandea conica* (see fig. 38, page 214 of Uchida 1927).

Ranson (1936) discussed the characteristics of species of *Pandea,* mainly referring to *P. conica* and *P. rubra.* The collections Ranson analyzed included abundant specimens or various sizes, enabling him to determine series of development of the medusa. A table on page 83 compiles the characteristics of *P. conica* as described by various authors. Analysis of data in that table suggests that under *P. conica* were included some specimens belonging to other species.

Russell (1953) described *P. conica* with higher than wide umbrella, conical summit, 16 to 24 longitudinal exumbrellar nematocyst ribs and corresponding number of marginal tentacles; jelly fairly thick. Velum narrow. Stomach pyramidal filling upper half of subumbrellar cavity, etc.

Kramp (1961) described *P. conica* "up to 21 mm high, 10 mm wide, with a conical apex terminating with a peculiar patch of thickened ectoderm; exumbrella with longitudinal ribs and ridges. Manubrium about half as long as bell cavity, with short mouth tube and folded lips. Radial canals fairly narrow, smooth. 16–24 tentacles with laterally compressed basal bulbs, with abaxial ocellus."

Radial canals in *P. conica* as described by Kramp (1961) do not agree with those in *P. cybeles,* which are wide with jagged outlines.

According to Kramp (1961) the *Pandea conica* of Bigelow (1918) found between Chesapeake Bay and Bermuda is possibly a new species.

The main anatomical features used to distinguish species of *Pandea* are: shape, dimensions, and characteristics of umbrella; shape and dimensions of stomach; characteristics of canals; number and characteristics of tentacles.

In *Pandea conica* according to most authors, the height of the umbrella is almost twice its width. The stomach occupies the upper ⅓ or probably half of the subumbrellar cavity. Ribs and tentacles are in the 20's, usually up to 24.

In *Pandea cybeles,* width and height of umbrella are rather similar, only slightly higher than wide. The stomach is large, filling completely the subumbrellar cavity, extending to the edge of the umbrella. Ribs and marginal tentacles number 40.

Differences between *P. conica* and *P. cybeles* are clear when comparing the illustrations by Quoy & Gaimard (1827), Hartlaub (1913), Russell (1953), and Kramp (1959, 1965), with those of *P. cybeles* in the present work.

Distribution.—The medusa is a meroplanktonic stage. Specimens of *Pandea,* including *Pandea cybeles* have been mainly obtained far offshore at oceanic localities.

Therefore, the medusae experience wide oceanic distribution, enjoying a long-lived pelagic medusoid stage. Kramp (1959) stated that the large size of the medusae may indicate a long pelagic life, which is advantageous for increasing dispersion of the population, with the opportunity to be transported by currents to regions distant from the normal habitat of the species. Kramp (1959) also suggested that in *Pandea conica,* wide oceanic distribution is due to the fact that its hydroid is attached to the shell of the pteropod *Cleodora cuspidata.*

Segura (1984) found specimens of *Pandea* sp. at several locations northwest of the Galapagos Islands, off Ecuador and Peru. They were juvenile specimens of some species of *Pandea,* with umbrella 1.0 to 3.0 mm high and 1.0 to 2.0 mm wide, with no apical projection, umbrella of thick mesoglea, exumbrella with longitudinal rows of nematocyst tracks in same number as marginal tentacles. Velum narrow. Stomach large, filling almost completely the subumbrellar cavity. Radial canals wide, circular canal narrow. Marginal tentacles up to 24, tentacular basal bulbs conical, laterally compressed. No ocelli at basal bulb of tentacles.

Pandea conica has been observed near Bermuda (Bigelow 1918, 1938), China (Chiu 1954), Gibraltar (Hartlaub 1913), Tristan de Cunha (Haeckel 1879), Alboran Sea, Tirrhenian Sea, Sidra Sea, Messina, Aegean Sea, Marmora Sea, Strait of Gibraltar (Kramp 1924), Japan and Philippine Islands (Kramp 1928), Gulf of Guinea (Kramp 1955), West Africa and off Argentina (Kramp 1957), Sargasso Sea, west of Spain, east of Azores (Kramp 1959), East Africa, Ceylon, East Australia, New Zealand, Vietnam (Kramp 1968), Strait of Gibraltar (Quoy & Gaimard 1827), Mediterranean Sea (Ranson 1936), Japan (Uchida 1927), Agulhas Current (Vanhöffen 1911), China Seas (Zhang 1979).

Pandea rubra has been recorded from British Columbia and Puget Sound (Arai & Brinckmann-Voss 1980), Gulf of Alaska, Aleutians, Southeast Kamchatka, Sea of Okhotsk, San Francisco (Bigelow 1913), Bermuda (Bigelow 1938), West Ireland (Kramp 1920), west of British Isles (Kramp 1929, Russell 1953), south and southwest of Iceland (Kramp 1926), South Africa, Weddell Sea, Antarctic (Kramp 1957a, b), Northwest Pacific, Ceylon, Northeast Pacific (Kramp 1965), USSR Far East waters (Naumov 1956), Cochin, Malabar-Trivandrum coastal waters (Vannucci et al.1970).

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PALEOCENE TURTLES FROM THE AQUIA AND BRIGHTSEAT FORMATIONS, WITH A DISCUSSION OF THEIR BEARING ON SEA TURTLE EVOLUTION AND PHYLOGENY

Robert E. Weems

Abstract.—The Piscataway Member of the Aquia Formation (upper Paleocene: Thanetian) has yielded remains of six species of turtles: *Aspideretes virginianus* (Clark), *Planetochelys savoiei* (n. gen., n. sp.), *Osteopygis roundsi* (n. sp.), *Dollochelys coatesi* (n. sp.), *Catapleura ruhoffi* (n. sp.), and *Allopleuron insularis* (Cope). The Brightseat Formation (lower Paleocene: Danian) has yielded three taxa: *Taphrosphys sulcatus* (Leidy), *Agomphus* sp., and *Osteopygis emarginatus* Cope. These faunas, when compared with Late Cretaceous and early Eocene marine turtle faunas, provide valuable insights into the evolutionary history of sea turtles from Late Cretaceous through Early Tertiary time. No catastrophic terminal Cretaceous extinction event among sea turtles is indicated by this succession. Rather, strong decline in the late Campanian is followed by modest recovery in the Thanetian and Ypresian. This decline and renaissance closely matches the global pattern of oceanic cooling and warming in Late Cretaceous–early Tertiary time.

Turtle remains have been reported from the Aquia Formation of the Pamunkey Group since 1895, but mostly from isolated fragments (for example, see Clark & Martin 1901). Not until Lynn (1929) described a fairly complete carapace of "*Amyda*" *virginiana* was there sufficient material adequate to characterize even one species. Even so, Lynn did not demarcate the suture boundaries on this specimen and the published illustration does not show them clearly. Since the publication of Lynn's paper, more chelonian material has turned up sporadically both in the Aquia Formation and in the underlying Brightseat Formation, but it has not been described. This new material, although far from ideal, is still sufficient to expand greatly our knowledge of the diversity and taxonomy of the turtles of Paleocene age and sheds new light on their anatomy.

Age of the Aquia and Brightseat Formations.—The Aquia formerly was considered to be a lower Eocene unit (Clark & Martin 1901), but Loeblich & Tappan (1957) demonstrated that it should properly be considered part of the upper Paleocene column on the basis of its contained planktonic Foraminifera. Greater refinement in the stratigraphic position of this unit has been achieved by Gibson and others (1980), whose work indicated that the entire Aquia lies within calcareous nannoplankton zones NP5 through NP9. The Aquia is divided into two members (Clark & Martin 1901), a lower member named the Piscataway which lies within NP5 through NP8, and an upper member named the Paspotansa which falls entirely within NP9. This division implies that the Piscataway accumulated 60 to 57 Ma and the Paspotansa accumulated 57 to 55 Ma (Fig. 1). Both members of the Aquia belong within the Thanetian Stage of the Paleocene (Hardenbol & Berggren 1978).

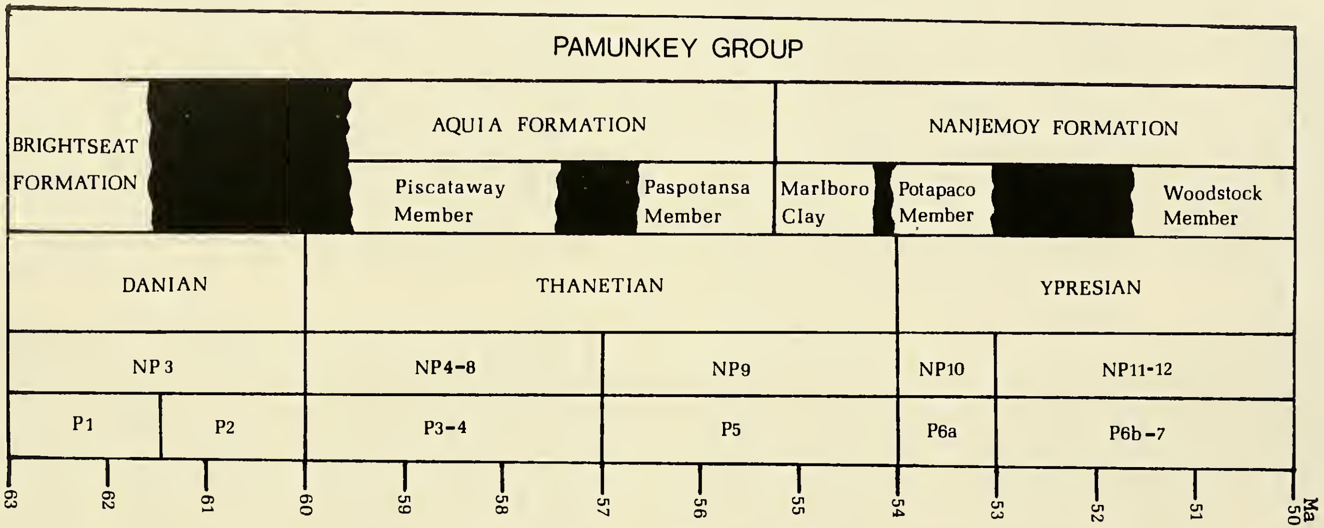


Fig. 1. Age ranges of the members and formations comprising the Pamunkey Group in Maryland and Virginia (after Clark & Martin 1901, Gibson et al. 1980).

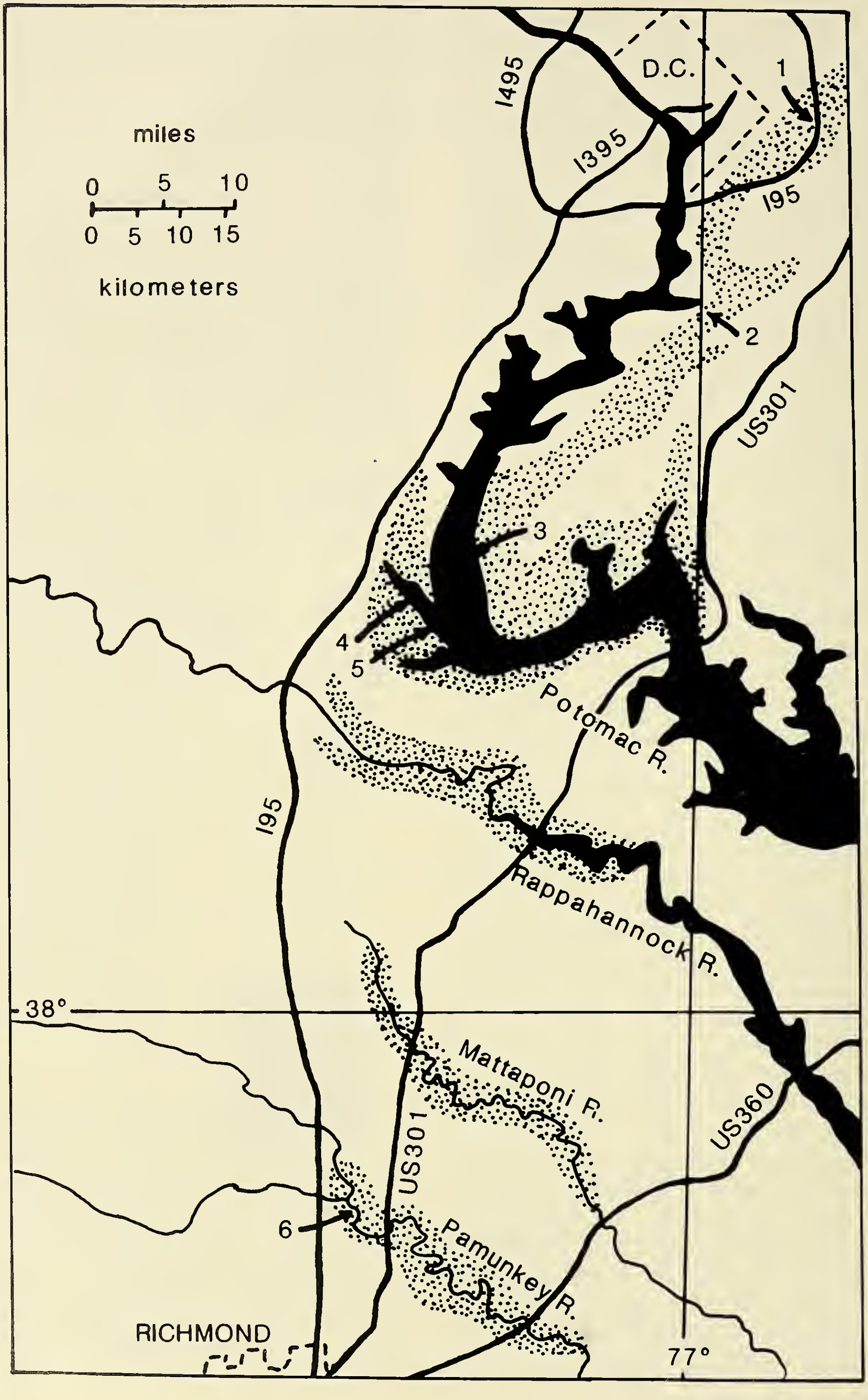
The Piscataway is richer in vertebrate remains than the Paspotansa, but both members are productive. All of the specimens described here from the Aquia Formation were found in outcrops of the Piscataway Member, within the outcrop belt of the Pamunkey Group (Fig. 2). There is no strong evidence from these occurrences to suggest that any of these turtles is restricted to only a part of this member. Since turtle remains have not yet been reported from the overlying Paspotansa Member, it is premature to say anything about the possible younger range limit for these species.

The underlying Brightseat Formation has yielded three recognizable turtle taxa. These are also known from a stratigraphically equivalent unit in New Jersey, the Hornerstown Sand. The Hornerstown has yielded a diverse, but poorly known, turtle fauna. Even so, the remains from the Hornerstown are complete enough to indicate that most of them differ from the Piscataway turtles at the species level or higher. The Brightseat, now recognized as a separate stratigraphic entity (Bennet & Collins 1952), was tentatively lumped with the Aquia as "Zone 1" by Clark & Martin (1901). It is now considered to be distinctly older (Danian) and known to have an invertebrate fauna and flora distinctly different from those found in the Aquia. In the past, the New Jersey equivalent of the Brightseat (the Hornerstown) often was regarded as Late Cretaceous in age, but this designation is no longer considered to be valid. Increasing refinement in the definition of the Cretaceous–Tertiary boundary has clearly put both the Brightseat and the Hornerstown within the Danian (Hazel 1969, Loeblich & Tappan 1957).

Within the Pamunkey Group, the only described species of turtle has been "*Trionyx*" *virginianus* (Clark 1895, 1896) from beds later known as the Piscataway Member of the Aquia. This species was transferred to *Amyda* (=*Trionyx*) by Lynn (1929), but its status was not changed otherwise. Elsewhere in the Atlantic Coastal Plain, Paleocene turtles have been described only from New Jersey. No amydid turtles remotely resembling "*Amyda virginiana*" have been reported in that state from the Paleocene, but a number of chelonioid species were described from the "greensand beds." These taxa were summarized by Hay (1908) and variously allotted to "Cretaceous greensands" and "Eocene greensands." It is now

Table 1.—Stratigraphic occurrences of type specimens of sea turtles described from the uppermost Cretaceous, Paleocene, and lower Eocene beds of the New Jersey Coastal Plain. *Atlantochelys mortoni,* from the greensands of Burlington County, is too vaguely referenced to be put in a specific stratigraphic unit but almost certainly came from either the Navesink (Upper Cretaceous) or Hornerstown (lower Paleocene). Locality data from Hay (1908) was sufficient to place other type specimens in specific units (J. P. Owens, oral communication 1984). *Peritresius ornatus* (=*Taphrosphys nodosus*) is known only from horizons lower than those shown here (Red Bank Formation and Navesink Formation) (Baird 1964). Stratigraphy after Minard and others (1969) and Owens & Sohl (1969); however Olsson (1963) and Gaffney (1975a) present an alternative view considering basal Hornerstown (and most of the Hornerstown vertebrate fossils) to be latest Maastrichtian in age.

Age	Unit	Holotype of:
Early Eocene	Manasquan Formation	*Chelonia parvitecta* *Lembonax polemicus* *Lembonax propylaeus*
Late Paleocene	Vincentown Formation	*Lembonax insularis* *Rhetechelys platyops*
Early Paleocene	Hornerstown Sand	*Osteopygis emarginatus* *Osteopygis gibbi* *Osteopygis robustus* *Osteopygis chelydrinus* *Osteopygis erosus* *Osteopygis borealis* *Osteopygis platylomus* *Catapleura repanda* *Catapleura ponderosa* *Lytoloma angusta* *Lytoloma jeanesi* *Lytoloma wielandi* (partly equals *Dollochelys atlantica*) *Erquelinnesia molaria*
Late Cretaceous	Tinton Sand	*Osteopygis sopitus*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known that parts of these greensands are actually Paleocene, and, for this reason, Table 1 relates the type specimens of these New Jersey species to the modern stratigraphic terms for the units from which they came. All of the "species" of *Osteopygis* (and *Erquelinnesia molaria*) have been combined into the single species *O. emarginatus* by Zangerl (1953), who considered all of these forms to be age and individual variants within a single population. I am inclined to agree with his conclusions and suspect that "*Catapleura ponderosa*" and "*Lytoloma angusta*" (at least the jaw) may also prove to be junior synonyms of *O. emarginatus.* All of these specimens were found in what is now known as the Hornerstown Sand of the Rancocas Group of early Paleocene (Danian) age and are of approximately the same age. The one possible exception is the type specimen of "*Osteopygis sopitus*" which came from an older horizon (the Upper Cretaceous Tinton Sand) than any of the other synonymized taxa. The type is too fragmentary to determine most of the anatomy of this turtle; therefore future collecting might show that it is a valid separate species from *O. emarginatus.*

As Hay (1908) pointed out, *Lembonax polemicus* and *L. propylaeus* came from a single horizon and locality and may well represent a single species or even individual. *Lembonax insularis,* which comes from a lower horizon that is stratigraphically equivalent to the Paspotansa Member of the Aquia Formation, probably represents a distinct species. Of the remaining forms, *Rhetechelys platyops* is most distinctive. *Atlantochelys mortoni* (which cannot be clearly assigned to a unit), "*Chelonia*" *parvitecta,* and *Catapleura repanda* are fragmentary but probably diagnostic. The jaw elements referred by Hay (1908) to his species "*Lytoloma wielandi*" were later referred by Zangerl (1953) to *Osteopygis emarginatus.* As Hay had specifically designated the type of "*L. wielandi*" to be one of the jaw elements, the carapace was left apparently unnamed. To this carapace, Zangerl (1953) gave the name *Toxochelys atlantica.* Later, Zangerl (1971) erected the genus *Dollochelys,* using *D. casieri* from France as the type species, and referred his species *atlantica* to this genus.

Thus only three chelonioid species (*Catapleura repanda, Dollochelys atlantica,* and *Osteopygis emarginatus*) may be present in the lower Paleocene Hornerstown Sand. The upper Paleocene Vincentown Formation has yielded *Lembonax insularis* and *Rhetechelys platyops;* the lower Eocene Manasquan Formation has yielded *Lembonax polemicus* (=*L. propylaeus*?) and "*Chelonia*" *parvitecta.* Because these species are found so close to the Maryland-Virginia area, many will be mentioned in the following discussion.

Turtles from the Brightseat Formation

Family Pelomedusidae

Taphrosphys sulcatus (Leidy)

Fig. 3D, E

Referred specimen.—USNM 357714, fragment of a carapace including the supra-

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Fig. 2. Map showing general localities from which the turtles described in this report were excavated. Shaded areas are outcrop belts of the Pamunkey Group. 1, Hampton Mall, Maryland, at intersection of Central Avenue and Interstate 95 (reference locality for *Taphrosphys sulcatus, Agomphus* sp., and *Osteopygis emarginatus*); 2, Piscataway Creek, Maryland, at Indian Head Highway bridge (type locality for *Catapleura ruhoffi*); 3, Liverpool Point, Maryland (type locality for *Dollochelys coatesi* and reference locality for *Osteopygis roundsi*); 4, Aquia Creek bluffs, Virginia, (upper end) where "Zone 2" of Clark & Martin (1901) is exposed (type locality for *Planetochelys savoiei*); 5, Aquia Creek bluffs, Virginia, (lower end) where "Zone 6" of Clark & Martin (1901) is accessible (type area for *Aspideretes viginianus*); 6, Pamunkey River bluffs, Virginia, northwest of U.S. Route 301 bridge (type locality for *Osteopygis roundsi*).

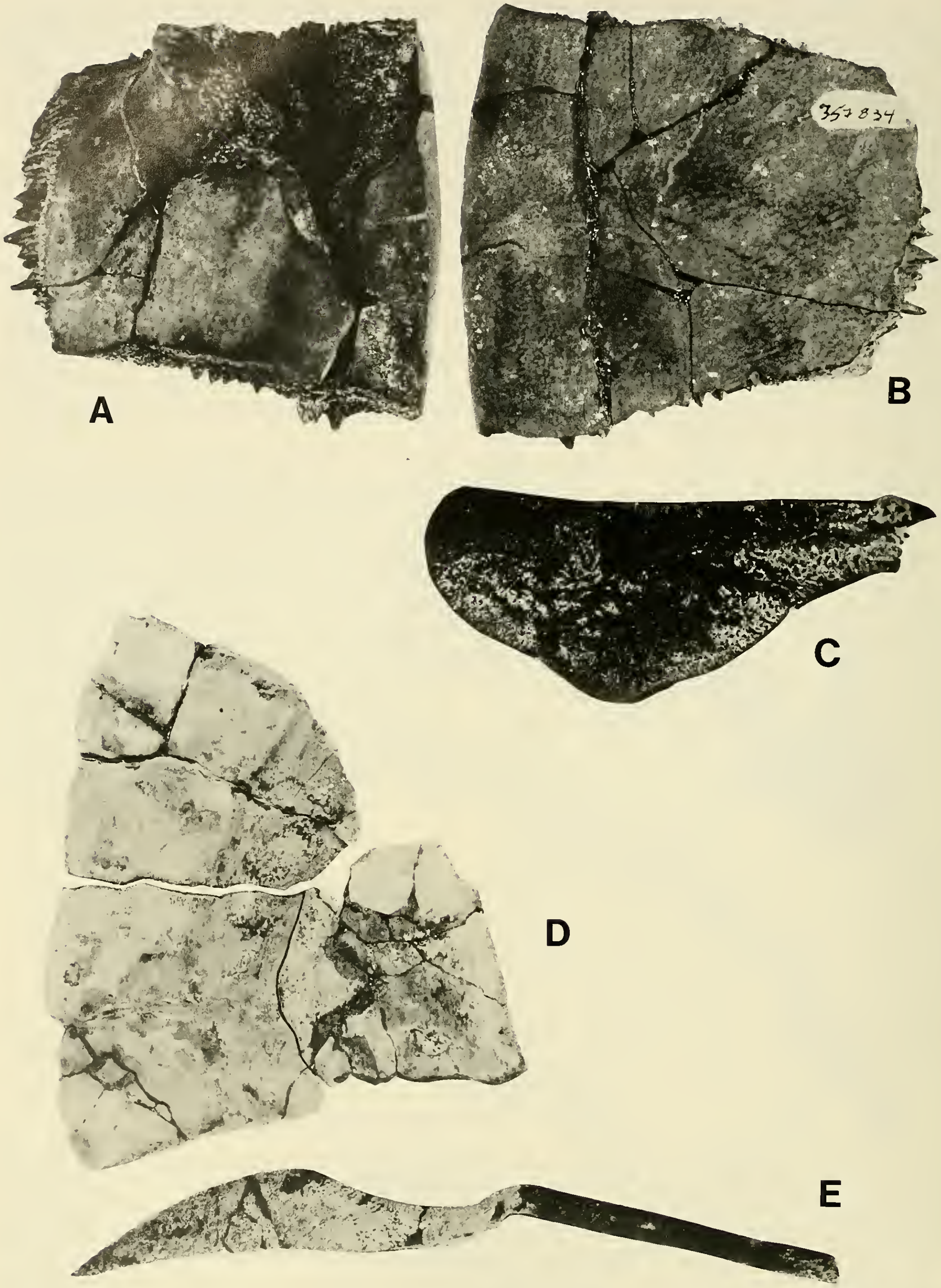

Fig. 3. Specimens of *Agomphus* and *Taphrosphys* from the Brightseat Formation of Maryland. A, Ventral, B, Dorsal, and C, Anterior view of the third right peripheral element of *Agomphus* sp. Maximum dimension of

pygal, pygal, and eleventh left peripheral elements.

Locality and horizon.—Found in the Brightseat Formation at the Hampton Mall (near the junction of Central Avenue and Interstate 95) in Prince Georges County, Maryland, by Albert Myrick.

Discussion.—This side-necked turtle is a fairly common faunal component of the Hornerstown Sand in New Jersey. A number of nominal species have been described, but these have been reduced to the single taxon *Taphrosphys sulcatus* by Gaffney (1975a), who concluded that the various type materials represent individual variants within a single population. The Maryland specimen shows no significant differences from the New Jersey material and is therefore included in the same taxon.

Family Adocidae
Agomphus sp.
Fig. 3A–C

Referred specimen.—USNM 357834, a third right peripheral element.

Locality and horizon.—Probably found in the Brightseat Formation at the Hampton Mall in Prince Georges County, Maryland.

Discussion.—The great thickness of this element, its incorporation into a massive plastral bridge, the lack of well developed surface sculpturing, and the presence of a very thin sulcal groove all characterize this specimen as an element of *Agomphus.* Although *Agomphus tardus* and *Agomphus masculinus* (Wieland 1905) are based on fairly complete material, the types of *A. firmus, A. petrosus, A. turgidus, A. oxysternum,* and *A. pectoralis* are based on very fragmentary specimens. It is unclear if more than one variable taxon is represented. In the absence of adequate material to resolve this issue, the specimen from Maryland is merely designated as *Agomphus* sp. The original donor card, which indicates no collector, stated that the specimen came from the Aquia Formation at Hampton Mall rather than the Brightseat Formation. However, examination of the matrix clinging to the specimen shows that it contains muscovite flakes but lacks glauconite or phosphate grains. Because the Brightseat is micaceous but not glauconitic at this locality, while the Aquia is glauconitic but not micaceous, the specimen almost certainly came from the Brightseat rather than the Aquia (Lauck W. Ward, pers. obs. 1987). *Agomphus* is found frequently in the Hornerstown Sand of New Jersey, which is age equivalent to the Brightseat, but is unknown from any other Aquia Formation locality. Therefore, this specimen can be assigned to the Brightseat, rather than the Aquia, with considerable confidence.

Family Cheloniidae
Subfamily Osteopyginae
Osteopygis emarginatus Cope
Figs. 3D, E, 4

Referred specimen.—USNM 412113, palate composed of premaxillaries, maxillaries, and vomer.

Locality and horizon.—Found in the Brightseat Formation at the Hampton Mall in Prince Georges County, Maryland, by George Fonger.

Discussion.—This specimen (Fig. 4, Fig. 11A–C) consists of the major part of a secondary palate. The angle of the beak indicates a broad, blunt snout. These characteristics are typical for *Osteopygis emarginatus.* Although the secondary palate is well developed, it is not so long as in the other known osteopygine genera (*Rheteche-*

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specimen is 8.9 cm. D, Ventral and E, Left lateral view of carapace fragment of *Taphrosphys sulcatus.* Ventral view includes pygal (lower left), suprapygal (lower right), and eleventh peripheral (top) elements. Maximum dimension of specimen is 17.8 cm.

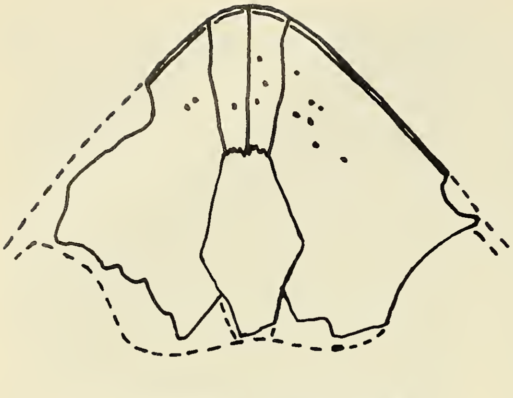

Fig. 4. Palate of *Osteopygis emarginatus* Cope based on USNM 412113 from the Brightseat Formation of Maryland.

lys, Erquelinnesia) or in the new species of *Osteopygis* described below. The type material of *O. emarginatus* comes from the Hornerstown Sand of New Jersey, correlative with the Brightseat, so the occurrence of this species in both units is not surprising.

Osteopygis and the Osteopyginae were considered to be toxochelyids by Zangerl (1953, 1971), but Fastovsky (1985) considered their affinities to lie closer to the more advanced family Cheloniidae, on the basis of shared derived cranial characters. This newer taxonomic association is followed here. So far, the Osteopyginae are known only from the Western Hemisphere (Foster 1980, Pritchard 1984).

Turtles from the Aquia Formation

Family Sinemydidae

Planetochelys, new genus

Diagnosis.—Shell small, rounded in dorsal aspect, highly arched and thin. Neural series depressed relative to costals on both sides, producing medial saddle in shell. One suprapygal present. Plastron not sutured to carapace, but a flattened region for abutment of hypoplastral buttresses extending back to middle of seventh peripheral. Ilia not fused to carapace.

Etymology.—The generic name, from Greek *planetos* (wanderer) and *chelys* (turtle), is an allusion to its apparent familial origins in China.

Planetochelys savoiei, new species

Figs. 5–8

Diagnosis.—Because the genus is currently monotypic, the diagnosis is at present the same as that for the genus.

Etymology.—The species name is for Kurt Savoie, who found the type specimen.

Holotype.—USNM 412107, posterior half of a carapace, found along the western bank of Aquia Creek at the base of Clark & Martin's (1901) "Zone 2" by Kurt Savoie, 1974.

Discussion.—The lack of fusion between the carapace and ilia indicates that this specimen is a cryptodire. The strongly arched carapace lacks a sutured plastral bridge, but does have a flattened area along the ventromedial border of the seventh peripheral (and presumably on the fourth, fifth, and sixth peripherals, which are missing) for abutment of a plastral bridge. Despite its small size and thin bones, there is no sign of any costoperipheral fontanelles. This combination of characters is typical of the Sinemydidae, which were first recognized from Lower Cretaceous beds of eastern Asia (Wiman 1930). Since the description of the type species, *Sinemys lens,* two taxa have been added to this family: *Manchurochelys manchouensis* from the Jurassic of Manchuria (Endo & Shikama 1942) and *S. wierhoensis* from the Cretaceous of Xinjiang, China (Yeh 1973). Recognition at the family level was established by Yeh (1963). Mlynarski (1976) considered the Sinemydidae to be of uncertain affinities, although similarities were noted in the plastron to the plastra of the Dermatemydidae and Kinosterninae. Zangerl (1953) considered the possibility that the Sinemydidae were ancestral to the sea turtles, but he saw no compelling evidence

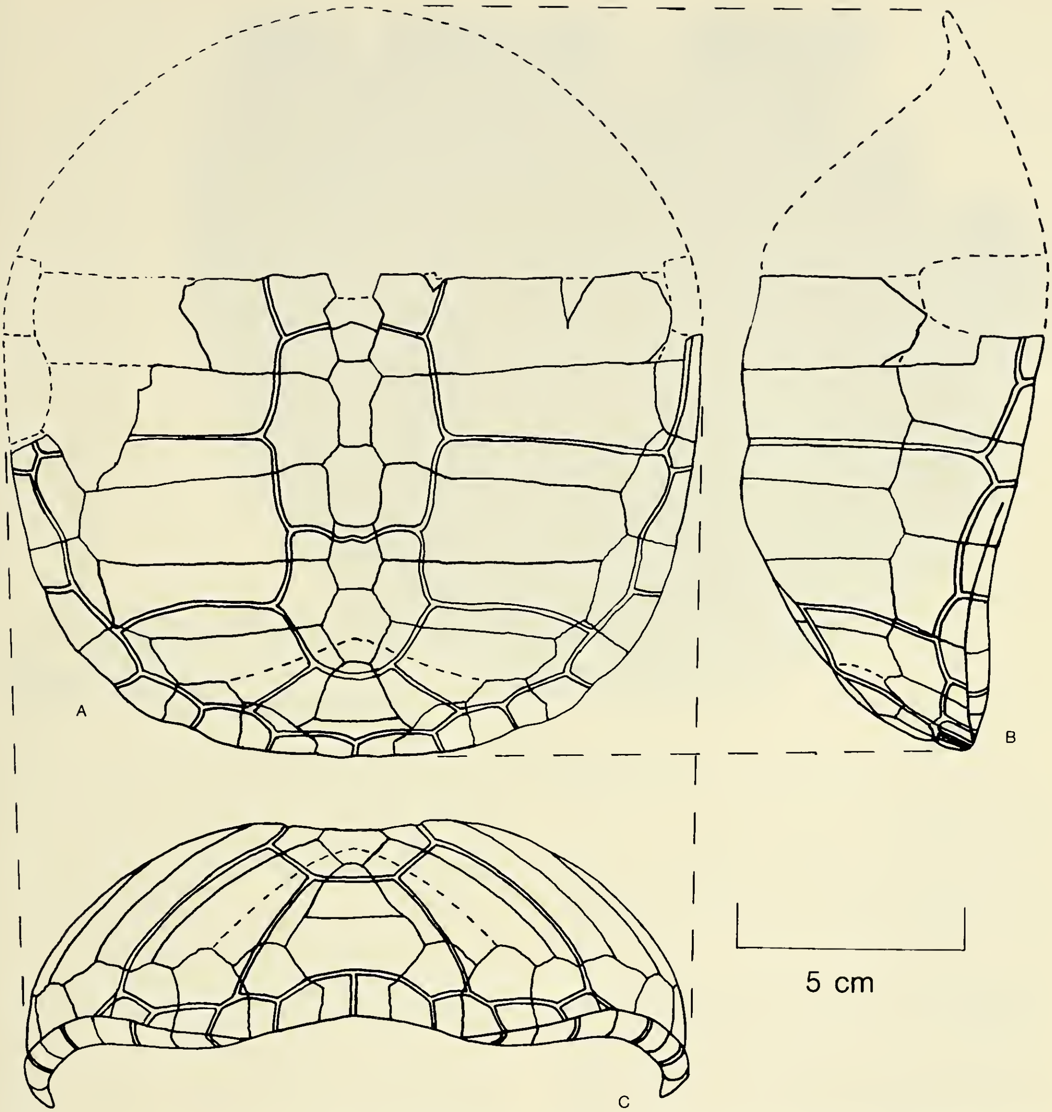

Fig. 5. A, Dorsal, B, Lateral, and C, Posterior views of the carapace of the type specimen of *Planetochelys savoiei* (new genus and species) (USNM 412107).

for this possibility. Recently, Shuvalov & Chkhikvadze (1979) associated the Early Cretaceous *Hangaiemys* with this family; previously it was considered to be a macrobaenid.

Although the specimen at hand is remote in time and space from other members of the Sinemydidae, its character states are compatible only with this family. Only the Chelydridae and the chelonioid families also lack a sutured plastral bridge, but they have costoperipheral fontanelles when they are as small as this specimen, and they are much flatter in cross section. Even in the late Paleocene, the Chelydridae have their typical strongly crenulated carapace margin (Erick-

Fig. 6. Dorsal view of the posterior carapace of *Planetochelys savoiei* (USNM 412107).

son 1973), and, by that time, all of the chelonioid families were far more specialized than this form (Zangerl 1953).

The presence of a longitudinal groove centered along the neural series is reminiscent of *Hangaiemys,* and the presence of a single postneural might be a logical evolutionary result of the trend seen in *Sinemys,* in which only one large postneural remains and the other is greatly reduced. Small size is also a characteristic feature of this group. In all of these traits, the Aquia specimen seems to show sinemydid affinities. Therefore, it is provisionally assigned to that family.

Planetochelys differs from *Manchurochelys* in that the latter form still has a partially sutured plastral bridge and two well developed postneurals. *Planetochelys* also differs from *Sinemys* in having only one postneural and a median longitudinal saddle. *Hangaiemys* has two and sometimes three postneurals. Because *Planetochelys* is so remote in time and space from these other forms, it will probably prove to have many other unique features when better material becomes available. Known portions are shown in Figs. 5 through 8.

Family Trionychidae
Subfamily Trionychinae
Aspideretes virginianus (Clark), 1895
Figs. 9, 10

Holotype.—USNM 9354, fragments of two costal plates.

Locality and horizon.—Found at Aquia Creek bluffs, Stafford County, Virginia. Horizon unreported but almost certainly Piscataway Member, Aquia Formation, judging from Clark & Martin (1901:75).

Referred specimen.—USNM 11944, largely complete carapace except for the distal portions of the fourth through seventh costals on the left side.

Locality and horizon.—Found at Aquia Creek bluffs, Stafford County, Virginia, Piscataway Member, Aquia Formation.

Fig. 7. Ventral view of the posterior carapace of *Planetochelys savoiei* (USNM 412107).

Discussion.—This species is assigned to the subfamily Trionychinae because it lacks peripheral elements, possesses a nuchal that is about five times wider than it is long, and it has a type III disc (Meylan 1984). Hay (1908) accepted the traditional assignment of this species to *Trionyx* (*Amyda*) with a query because the type is so fragmentary. Since Lynn's (1929) description of a fairly complete carapace of *A. virginianus,* no significant new material has been collected. Fragments of this species, common throughout the Piscataway, are easily recognizable by their great thickness and vermiform to pitted sculpture. Only a photograph of Lynn's specimen was published in his paper, and no attempt was made to define the individual shell elements. Much of the periphery of the shell was pieced together, but the central portion of the carapace does not appear to have been reconstructed accurately. By doggedly piecing together the fragments of the central region of Lynn's specimen, I have managed to determine the location of the costal and neural sutures.

As Figs. 9 and 10 show, a large preneural element is present. This element, which may be really the first neural (Meylan 1984), is characteristic of *Aspideretes* but not of *Trionyx.* For this reason, Clark's species is transferred to *Aspideretes.* Probably *Trionyx* proper does not occur in beds older than Eocene (Carpenter 1981). As Hummel (1929:390) has shown, even modern *Trionyx* occasionally can develop a large preneural element. Similarly, the rest of the carapace in modern *Trionyx* can also show a lot of individual variation. Yet preneurals seem to be very exceptional in Eocene to Recent *Trionyx,* whereas they are the rule for Cretaceous to Paleocene *Asperidetes* (Carpenter 1981). A population of shells should be examined to determine accurately

Fig. 8. Oblique (postero-dorsal) view of the posterior carapace of *Planetochelys savoiei* (USNM 412107).

which generic designation is correct, but this is not yet possible. For now, the Paleocene age of this form, the very large size of the preneural in the one nearly complete carapace available, and the absence of evidence for unusual shell development elsewhere in the anterior carapace region serve to characterize this species as a member of *Aspideretes.*

Trionychoids are thought of as exclusively freshwater turtles but have been observed alive in marine waters (Hay 1908:514). The abundance of *Aspideretes virginianus* in the marine Aquia Formation suggests that this form was an inhabitant of marine waters in the late Paleocene (Thanetian). Additionally, the exceptional size, thickness, and massiveness of the carapace and plastron are compatible with life in sea water, which is more buoyant than fresh water.

Family Cheloniidae
Subfamily Osteopyginae
Osteopygis roundsi, new species
Figs. 12A, 13, 14A, 15

Diagnosis.—Anterior portion of beak blunt and wide; internal edges of maxillary beak project toward anterior midline at an angle of nearly 90°; roof of mouth has an extensive secondary palate. Width to length ratio of vomer 0.68; vomer having prominent medial keel. Back edge of palate formed by contribution from pterygoids. Carapace and plastron, so far as known, typically osteopygine, costoperipheral fonta-

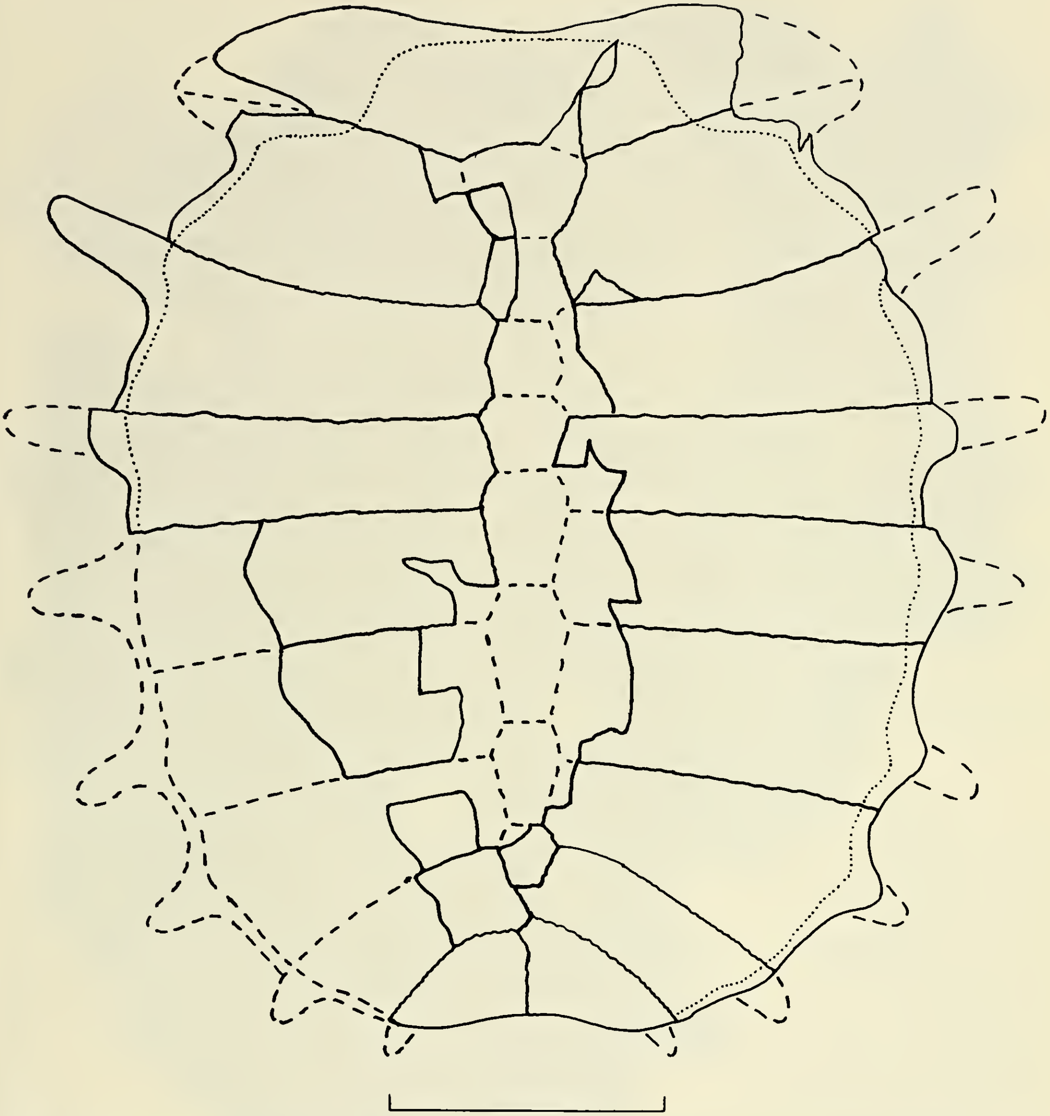

Fig. 9. Reconstruction of the carapace elements of *Aspideretes virginianus* (Clark) based on USNM 11944.

nelles possibly more persistent than those in *O. emarginatus.* Carapace not sculptured, sulci deeply impressed, costal rib heads subrounded in shape.

Etymology.—For Thomas Rounds, who discovered the type specimen.

Holotype.—USNM 412108; a crushed and slightly exploded skull, imbedded in a nodule. Only the ventral surface is clearly visible (Fig. 12A).

Locality and horizon.—Pamunkey River bluffs, upriver from U.S. Highway 301, in the Ashland 7.5-minute quadrangle. Found in shell bed about 1 ft above basal boulder bed, Piscataway Member, Aquia Formation, by Thomas Rounds.

Paratypes.—USNM 357713, poorly preserved skull and associated carapace fragments, including costal fragments, one neural, and three peripherals. River bluff

Fig. 10. Carapace of *Aspideretes virginianus* (USNM 11944).

0.5 mi. south of where the North Anna and South Anna rivers converge to form the Pamunkey River, Ashland 7.5-minute quadrangle. Found in shell bed 2 ft above basal boulder bed, Piscataway Member, Aquia Formation, by Robert E. Weems, Carrol Chewning, Mary Jane Chewning, 1971.—USNM 357710, left hyoplastron and left hypoplastron. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in shell bed comprising "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Calvin Allison.

Fig. 11. Anterior end of skull of *Osteopygis emarginatus* (USNM 412113). A, Dorsal, B, Lateral, and C, ventral view; length as preserved 5.5 cm; D, Eleventh right peripheral element of *Catapleura ruhoffi*, greatest length 5.5 cm (USNM 358865); E, F, Distal end of tibia of *Dollochelys coatesi* (USNM 412110); G, H, Femur of *Dollochelys coatesi* (USNM 412110).

Discussion.—This species differs from *Osteopygis emarginatus* in being much larger and in possessing a more strongly developed secondary palate. The pterygoids are incorporated into the back of the palate, and the groove receiving the cutting edge of the lower beak is relatively much deeper (Fig. 13). A prominent medial ridge is developed on the vomer; this ridge is developed only faintly in *O. emarginatus*. The general shape of the skull is *Osteopygis*-like and unlike that of *Rhetechelys*, which has a more pointed snout. Although the palate is longer than that in *O. emarginatus*, it is less extremely developed than in either *Erquelinnesia* or *Rhetechelys*.

A second specimen of *O. roundsi* (USNM 357713) also includes a very poorly preserved skull. Little detail is preserved, but the size and the shape of the snout leave little doubt that this specimen represents the same species (Fig. 14A). Associated with the skull were a number of costal fragments, one well preserved neural, and three peripherals. The neural is flat and notably anteroposteriorly elongate (Fig. 15A). One of the peripherals (Fig. 15B) has a broad notch on its internal border above the socket that received the tip of the costal rib. This feature is also typical of the peripherals of *O. emarginatus*. In *O. emarginatus* the costoperipheral fontanelles eventually closed in mature animals. This closure does not seem to have occurred in the later and more highly derived *Erquelinnesia*. Because *O. roundsi* is intermediate in time and specialization, I suspect that costoperipheral fontanelles may be more persistent in *O. roundsi* than they are in *O. emarginatus*. A partial plastron (USNM 357710) found at Liverpool Point seems typically osteopygine in nature and is tentatively referred to *O. roundsi* (Fig. 15C). The hyoplastron has a long ascending process, as it does in *O. emarginatus*, pre-

Fig. 12. A, Ventral view of skull of *Osteopygis roundsi* (USNM 412108); B, Right anterior side of carapace of *Dollochelys coatesi* (USNM 412109).

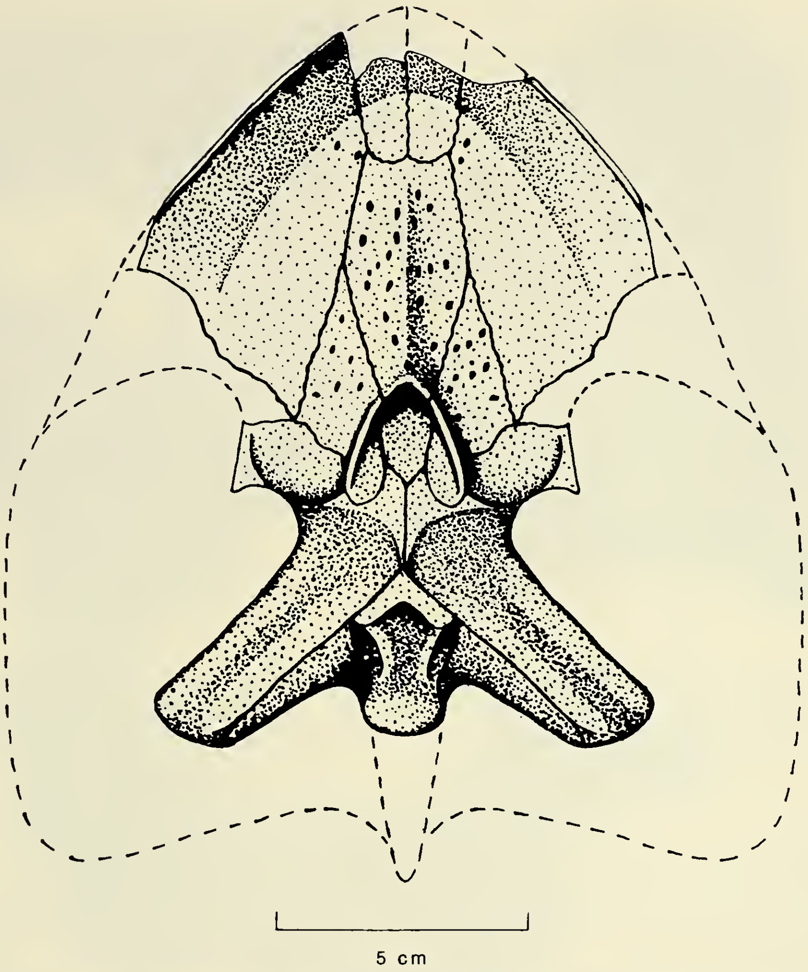

Fig. 13. Reconstruction of the ventral skull elements of *Osteopygis roundsi* (new species) (USNM 412108).

sumably for insertion into the second peripheral. Another specimen questionably referrable to *O. roundsi* is USNM 9357, which is a costal fragment figured by Clark & Martin (1901:10, fig. 7) as "*Euclastes* sp." It is too large for *Planetochelys* or *Catapleura,* too thick for *Dollochelys* or *Lembonax,* and much too thin and smooth for *Aspideretes.* Therefore, it may be *Osteopygis* by default even though it lacks positive diagnostic characters.

Subfamily Eochelyinae

Catapleura ruhoffi, new species

Figs. 16–19, 20A

Diagnosis.—Dentaries flat and fused along a long, narrow symphesis that includes over two-thirds of length of each element; carapace flattened in lateral aspect, suboval in dorsal aspect. Costoperipheral fontanelles (so far as known) persistent beyond second peripheral. Nuchal much wider than long.

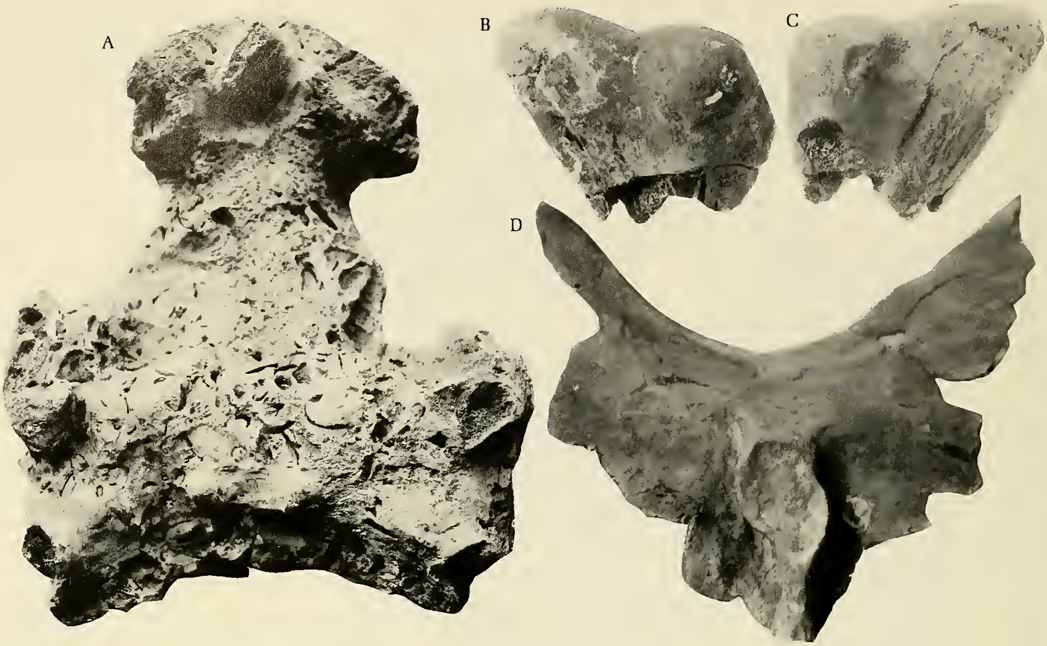

Fig. 14. A, Poorly preserved skull of *Osteopygis roundsi,* length 19 cm (USNM 357713); B, C, Proximal end of humerus of *Dollochelys coatesi* (USNM 412110); D, Ventral view of nuchal element of *Psephophorus* sp. (from Chandler Bridge Formation (upper Oligocene), Charleston region, South Carolina).

First peripheral much wider along external border than along internal border. Neurals flat anteriorly, slightly keeled posteriorly. Carapace unsculptured, thin boned, sulci lightly impressed onto bone. Costal rib heads subrounded in shape.

Etymology.—For Theodore B. Ruhoff, who discovered the type specimen.

Holotype.—USNM 358865, a disarticulated partial skeleton consisting of the fused dentaries, nuchal, right and left first peripherals, right and left second peripherals, right third peripheral, fifth, sixth and ninth left peripherals, eleventh right peripheral, parts of right and left first costals, part of the right second costal, sixth right costal, first neural, part of fourth neural, eighth neural, and first suprapygal.

Locality and horizon.—West bank of roadcut, Indian Head Road near Piscataway Creek, Prince Georges County, Maryland. Found in Piscataway Member, Aquia Formation (in excavation for crocodile) by Theodore B. Ruhoff, 1949.

Discussion.—The fused dentaries of this form (much narrower than one could expect for *Osteopygis roundsi*), a long, narrow symphyseal region, and slightly keeled posterior neurals make this species distinct from all other Piscataway turtles described here (Fig. 16). The fused dentaries are very reminiscent of the Eocene cheloniid *Puppigerus,* and this species may be an ancestral form of that genus. Moody (1974) noted that the length of the dentary symphysis correlated strongly with the length of the secondary palate, and the same correlation probably holds in osteopygines as well. On this basis, the species described here also probably had a secondary palate, a character suggestive of eocheloniine rather than toxochelyine affinities for this form. This species differs from *Puppigerus,* however, in that two fontanelles are present between the first costals and the nu-

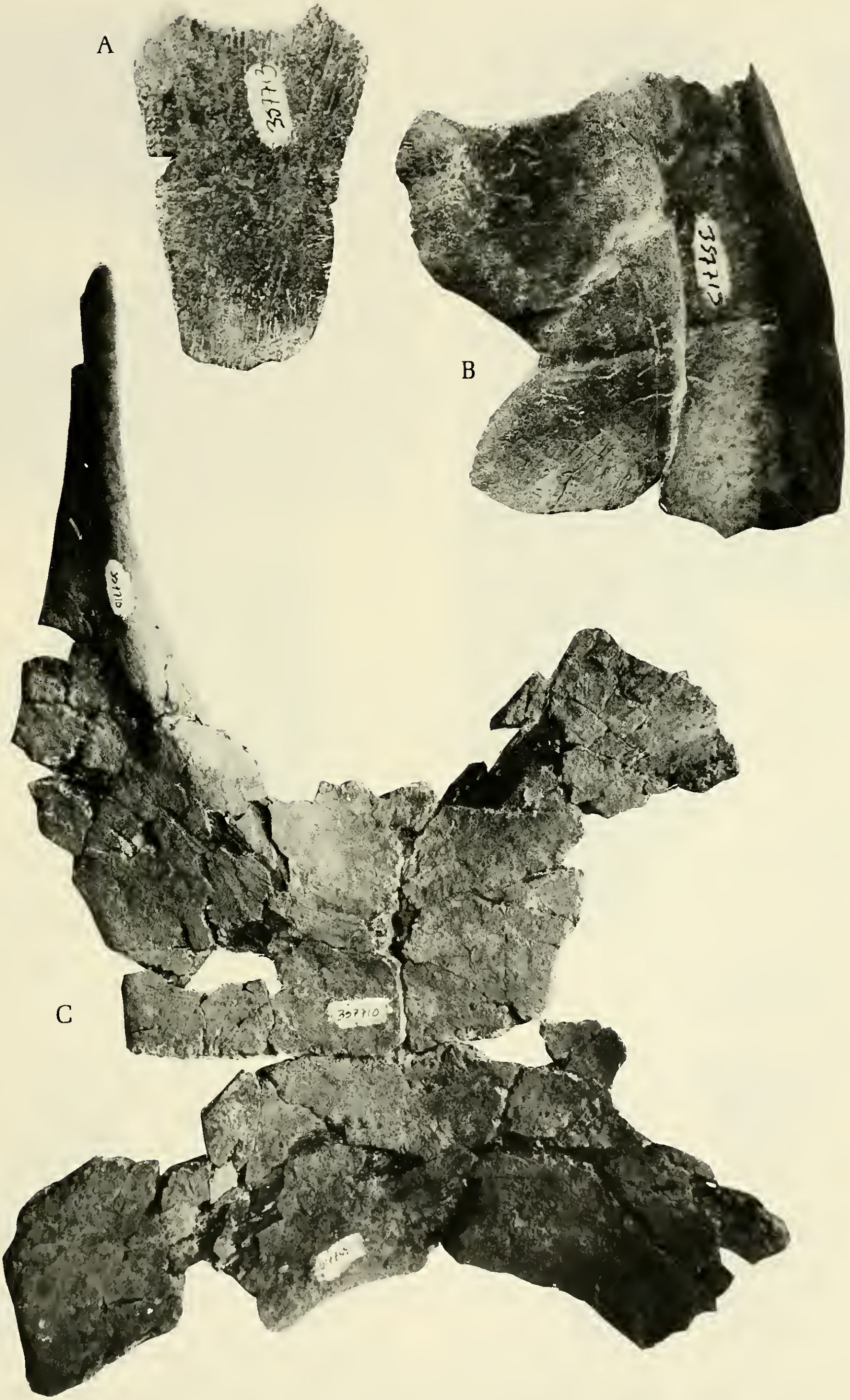

Fig. 15. Elements of *Osteopygis roundsi*: A, Dorsal view of neural element, length 6 cm (USNM 357713); B, Dorsal view of peripheral element, length 7 cm (USNM 357713); C, Internal view of left hyoplastron and hypoplastron, total length 29 cm (USNM 357710).

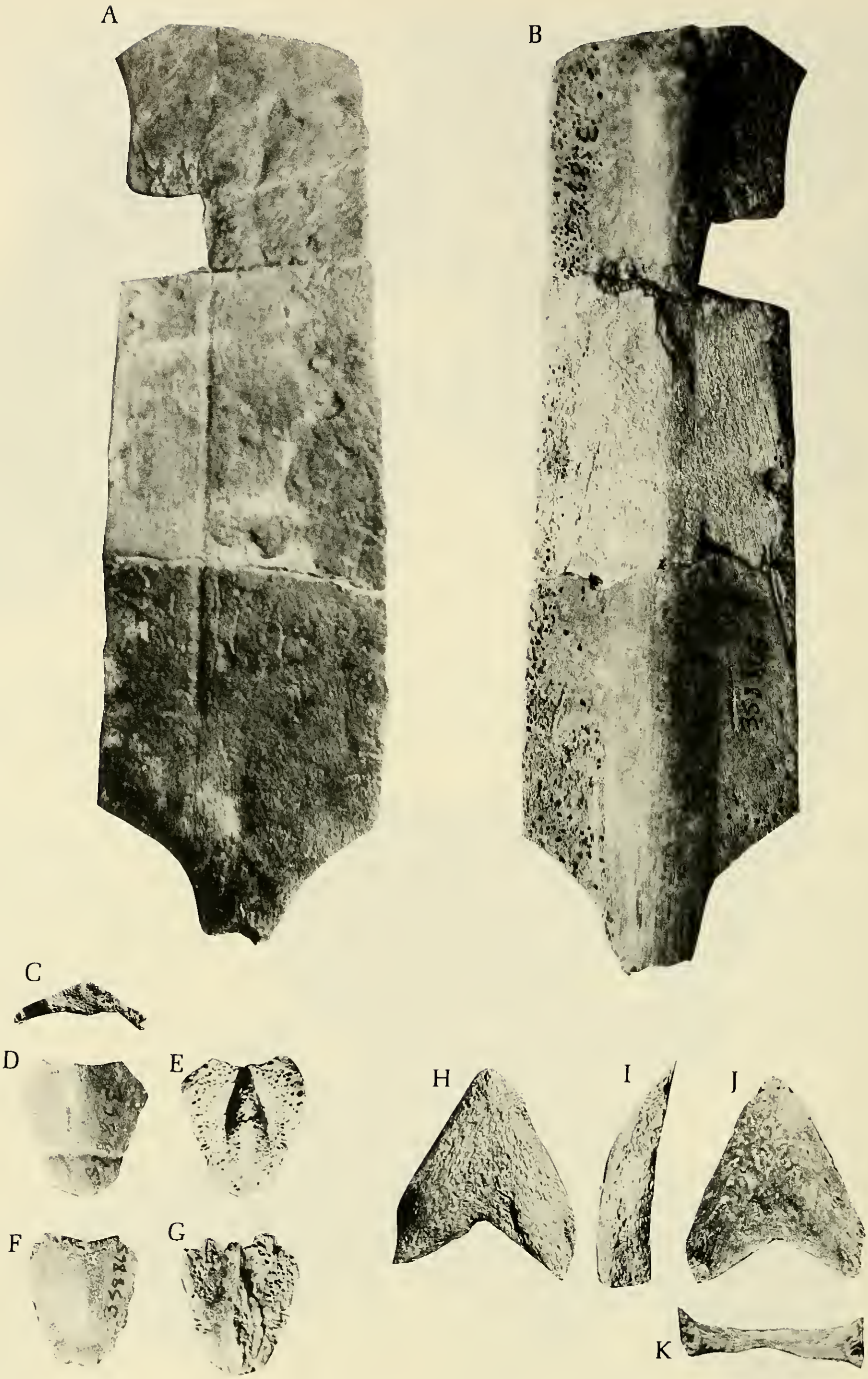

Fig. 16. Elements of *Catapleura ruhoffi* (USNM 358865): A, B, Sixth right costal in dorsal and ventral view, length as preserved 14 cm; C, D, E, Eighth neural in (C) anterior, (D) dorsal, and (E) ventral view, length 2.3 cm; F, G, First preneural in (F) dorsal and (G) ventral view, length 2.2 cm. H, I, J, K, Fused dentaries in ventral, lateral, dorsal, and posterior view, length 3.4 cm.

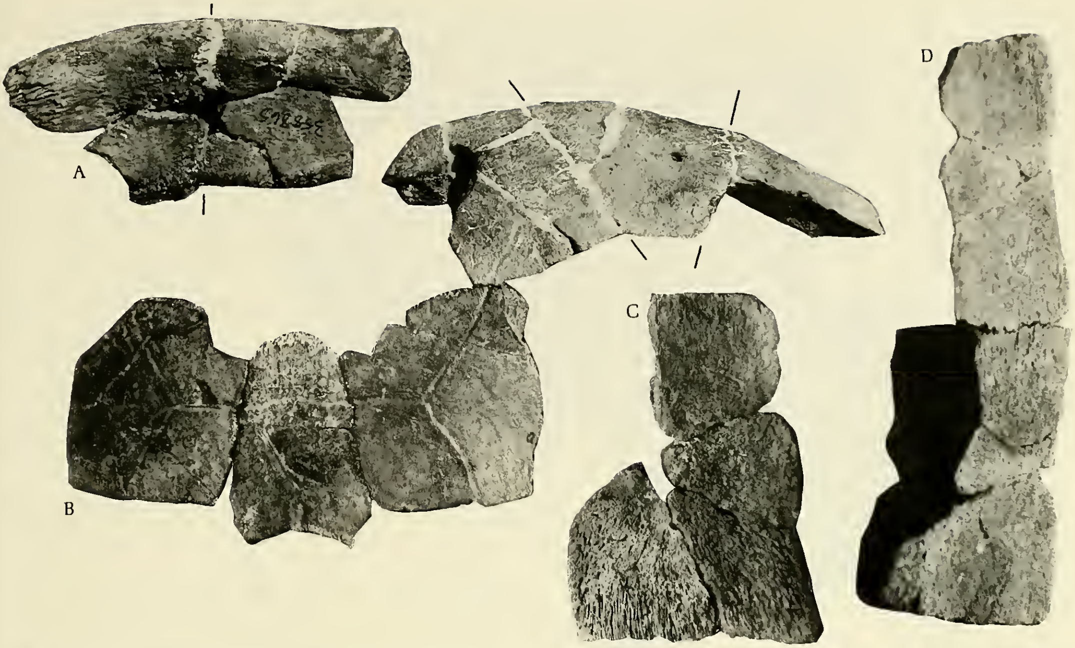

Fig. 17. Elements of *Catapleura ruhoffi* (USNM 358865): A, First and second left peripherals in ventral view, width 8.5 cm; B, First neural, proximal end of first right and left costals, right side of nuchal, first peripheral (edge marked by black lines), and part of second peripheral; neural length 5 cm; C, Ninth left peripheral element, length 7.3 cm; D, Parts of sixth and seventh left peripheral elements, maximum combined length 12.5 cm.

chal in young specimens (Fig. 17) and that the costoperipheral fontanelles apparently are persistent. Probably at an advanced age, the costonuchal fontanelles do become overgrown by a thin layer of bone, as an isolated costal from Liverpool Point shows (USNM 357707, Fig. 20A). Juvenile *Puppigerus* do not appear to have these fontanelles at all. Therefore, although this species may be ancestral to *Puppigerus,* it does not seem to be close enough in morphology to be included in that genus.

Catapleura repanda, from the Hornerstown Sand of New Jersey, is more similar to the Aquia specimen than *Puppigerus.* The type of this species is fragmentary but sufficient to match it to any future, more complete specimens from the Hornerstown. Significant characters are the lack of sculpture, the persistent presence of costoperipheral fontanelles behind the second peripheral, the wide nuchal, and the nearly triangular shape of the first peripherals. In all of these traits except the last, the new species described here is similar to *C. repanda.* Even in the last character, *C. ruhoffi* approaches *C. repanda,* for the internal margin of the first peripheral is only about one-third to two-thirds as long as the external margin (see Figs. 17 through 19). *Catapleura repanda* is a poorly known type, but its geographic proximity to the new species, despite its temporal distance from it, makes it a genus to which the new form could be assigned. Nothing would be gained at this point by erecting a new genus, because *Catapleura* will probably prove to be the correct generic name when its type species is better known.

Catapleura ruhoffi is placed in the family Cheloniidae because of indirect evidence that this species had a secondary palate (inferred from the long symphyseal region that is present on the fused dentaries) and because of its morphological similarities with

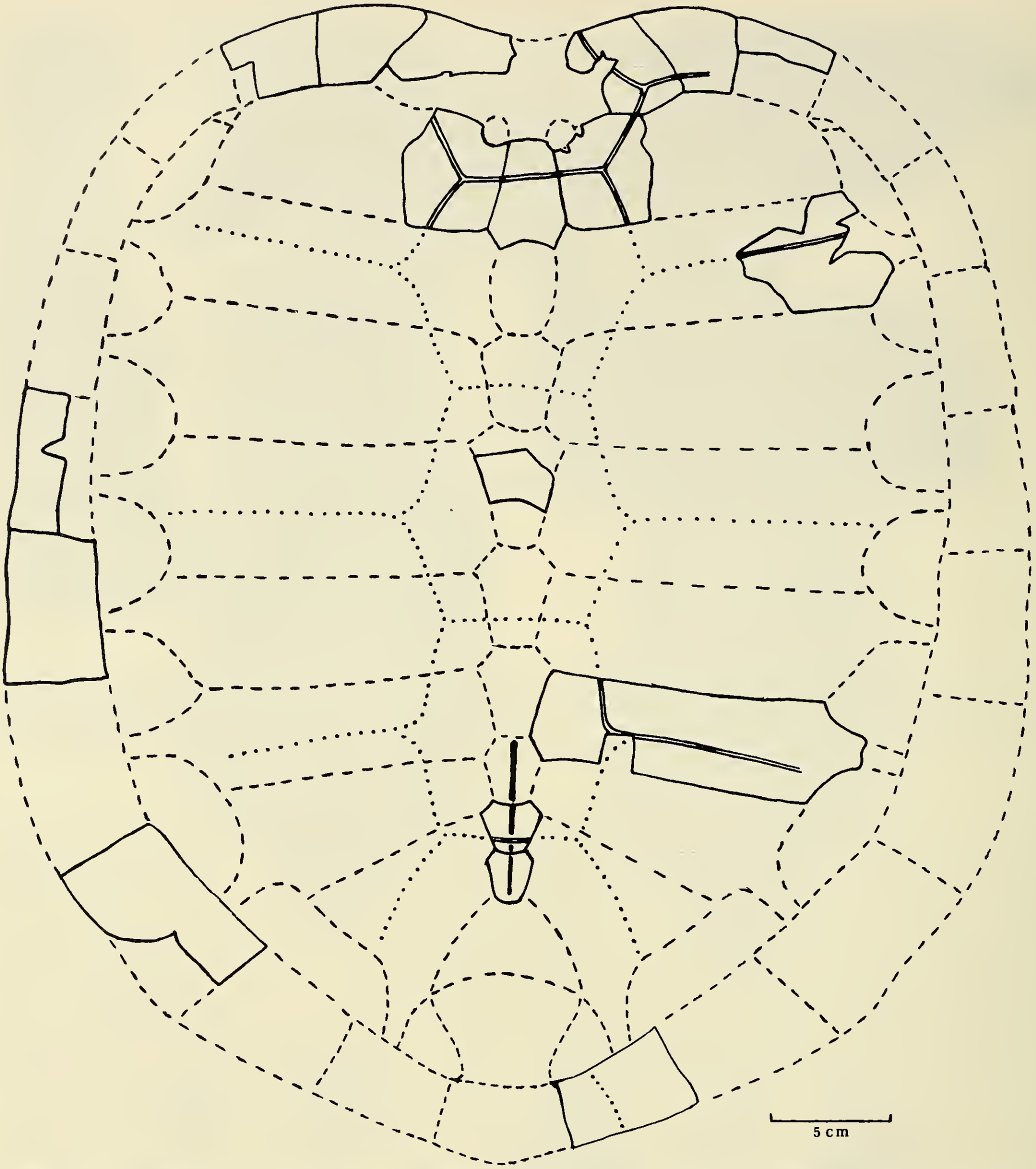

Fig. 18. Reconstruction of the carapace elements of *Catapleura ruhoffi* (new species) based on the type (USNM 358865).

Puppigerus, which is accepted as a primitive cheloniid. Since the Cheloniidae are derived ultimately from generalized toxochelyid stock, early members of this family should be expected to retain some primitive toxochelyid traits. *Catapleura ruhoffi* is no exception, because it has toxochelyid-like costonuchal fontanelles that became overgrown by bone as the animal matured. The presence of costonuchal fontanelles suggests the possibility that *C. ruhoffi* might be retained within the Toxochelyidae. But *C. ruhoffi* lacks epineural elements or serrations along the external margins of the peripherals, so placement of this species in the Lophochelyinae is precluded. Therefore, *C. ruhoffi*

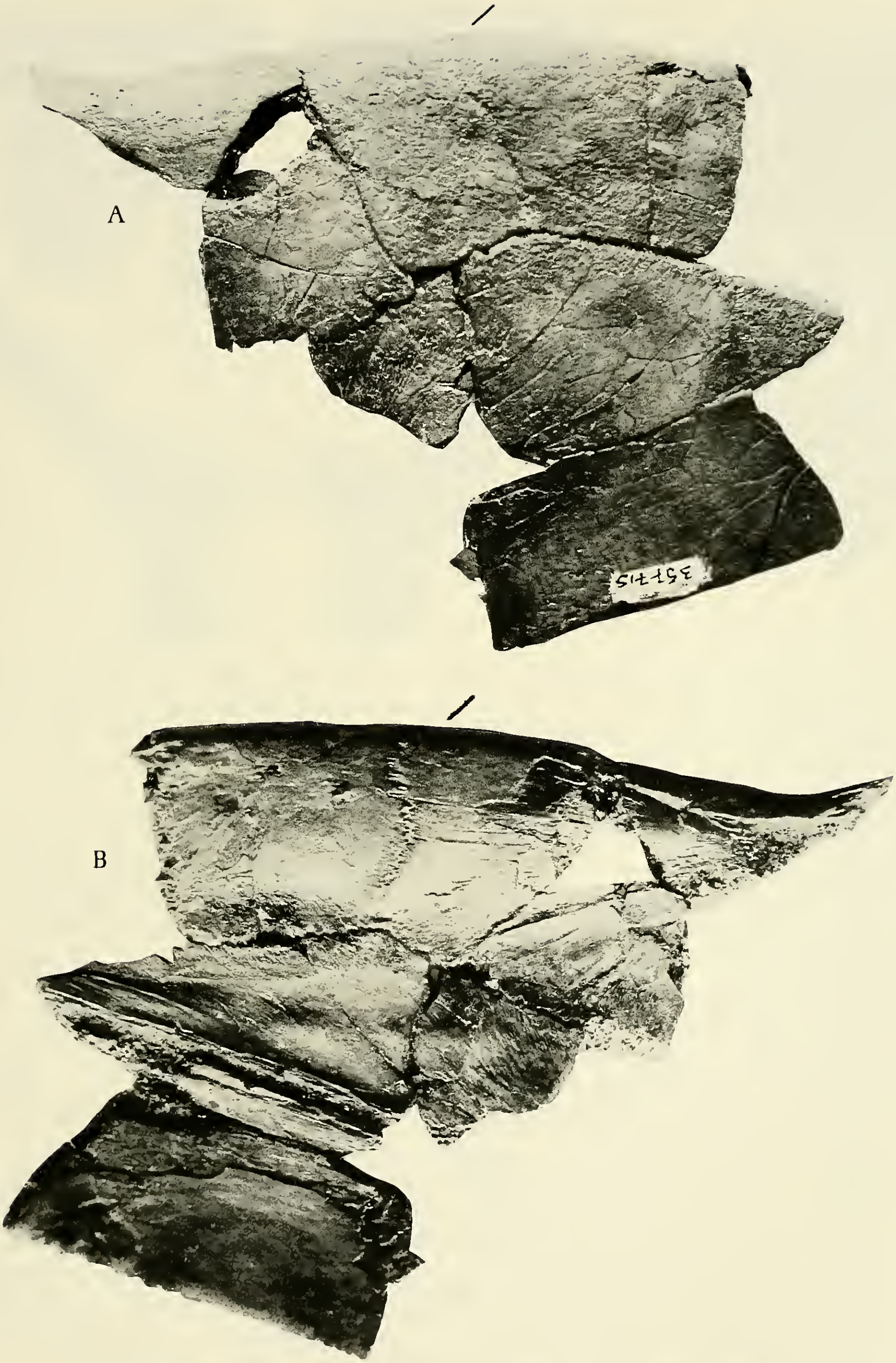

Fig. 19. First peripheral, part of nuchal, and part of first costal of *Catapleura ruhoffi* (USNM 357715): A, Dorsal view; B, Ventral view. Dark lines mark nuchal/first peripheral suture. Maximum width 15 cm.

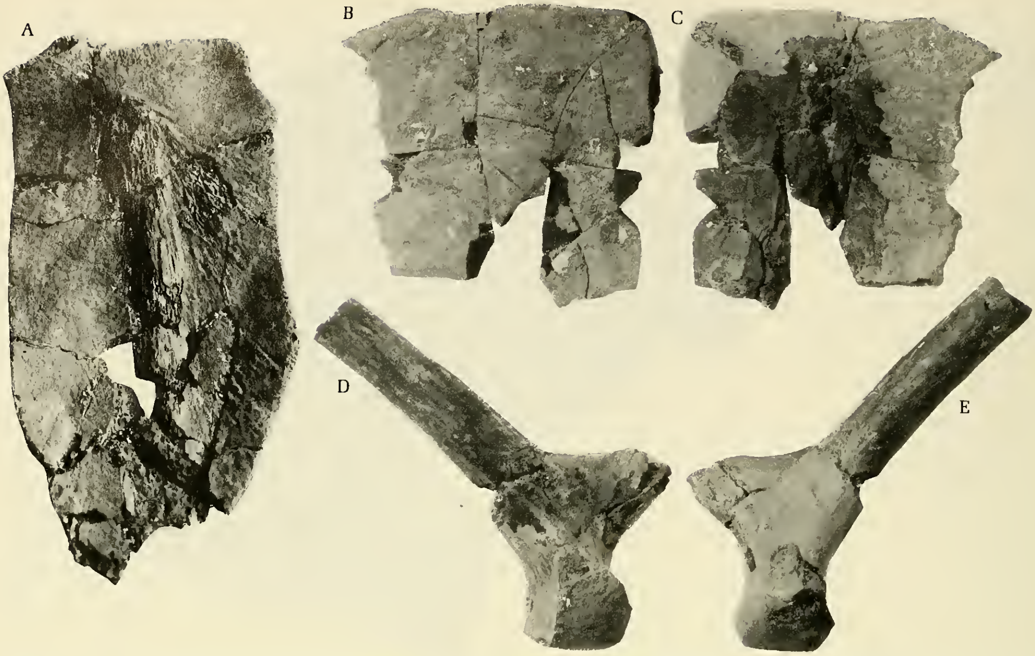

Fig. 20. A, Internal view of first left costal of *Catapleura ruhoffi* (USNM 357707) showing area of thin bone (upper right corner) where costonuchal fontanelle was present but later thinly overgrown by bone, length 11.8 cm; B, C, Proximal end of second right costal of *Dollochelys coatesi* (USNM 412110) in dorsal and ventral view; D, E, Scapula of *Dollochelys coatesi* (USNM 412110).

could be retained only within the persistently conservative subfamily Toxochelyinae, where it does not fit well because it probably had a long, typically cheloniid secondary palate. Among the Cheloniidae, *C. ruhoffi* cannot be considered an osteopygine, because it lacks a pit for reception of an anteriorly directed spur from the hyoplastron, it has no notches along the internal margin of the peripherals, and the long, narrow shape of the snout is atypical of the Osteopyginae. Therefore, it seems best to view *Catapleura arkansaw* of the Late Cretaceous, *Catapleura repanda* of the early Paleocene, and *Catapleura ruhoffi* of the late Paleocene as representing the primitive cheloniid stock that evolved from generalized toxochelyid ancestors into the modern cheloniid stock. In taxonomic terms, these turtles could be retained as part of the overall Late Cretaceous toxochelyid radiation, but, in evolutionary terms, they already were becoming primitive cheloniids. Therefore, they should be grouped with the stock toward which they were evolving and not with the stock from which they were derived.

Family Toxochelyidae
Subfamily Toxochelyinae
Dollochelys coatesi, new species

Figs. 20B–E, 21, 22

Diagnosis.—First neural scute (and presumably more posterior missing neural scutes by analogy) longer than wide, in contrast with *D. casieri* (type species) and *D. atlantica* which both have neural scutes wider than long; anterior neural elements also proportionally narrower than in the other two species.

Etymology.—For Anthony G. Coates of The George Washington University, my former Ph.D. adviser, who has long worked on the Aquia Formation.

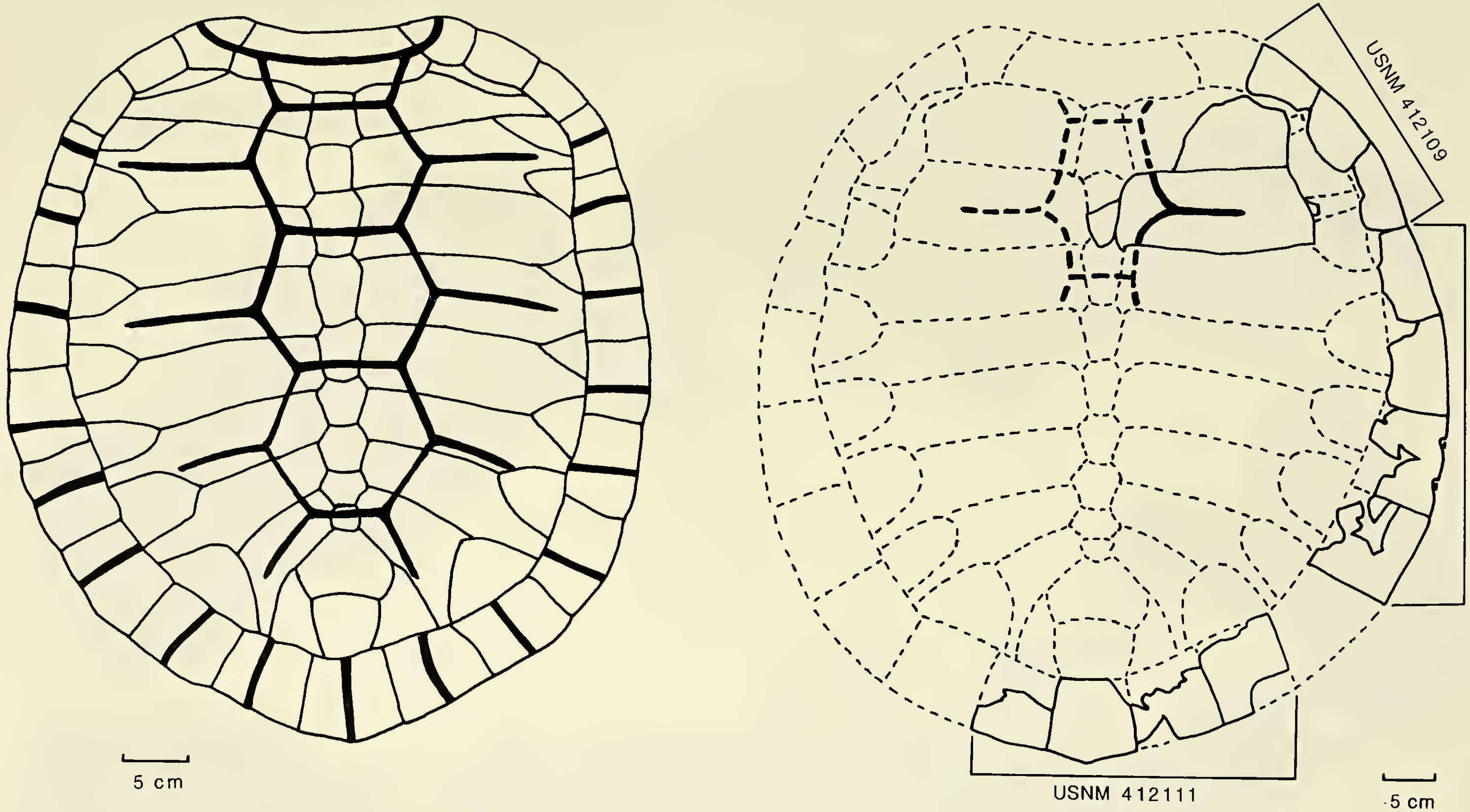

Fig. 21. Tentative restoration of the carapace of *Dollochelys coatesi* based on USNM 412109, USNM 412110, and USNM 412111 (left side). USNM 412110 also includes the proximal end of the second right costal and some limb and girdle elements (Figs. 11, 14, and 20). Restoration of *D. atlantica* (From Parris and DeTample 1986) is shown for comparison. Note the marked differences in the proportions of the neural elements and the outlines of the first neural scutes.

Fig. 22. Elements of *Dollochelys coatesi*: A, Fifth, sixth, seventh, and eighth peripherals (USNM 412110); B, Tenth right peripheral, eleventh right peripheral, pygal, and eleventh left peripherals in ventral view (USNM 412111).

Holotype.—USNM 412109, part of right first costal, second costal, part of second neural, second through fourth right peripheral. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Robert E. Weems and Stephen R. Horman, 1983.

Paratypes.—USNM 412110, second right costal fragment, pygal fragment, fifth through eighth right peripherals; fragments of the hyoplastra, hypoplastra, and xiphiplastra; scapula, proximal end of right humerus, left femur, distal end of tibia. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Robert E. Weems, Marguerite Kingston, and Terri Purdy, 1977.—USNM 412111, pygal, right and left eleventh peripherals, right tenth peripheral. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Stephen R. Horman and Robert E. Weems, May 1983.

Discussion.—The notably thin (2–4 mm thick) costal and neural material of this taxon is typically toxochelyid and cannot be assigned to either of the two thicker-shelled cheloniid turtles previously described in this paper. All three specimens appear to represent a turtle much larger than the new species of *Catapleura* described previously, and the forward extent of the costoperipheral fontanelle (Fig. 21) also is much greater than in *Catapleura* (Fig. 18) even though *Catapleura* represents a much smaller form. The fontanelles in sea turtles tend to close up partly or entirely with age. Therefore, if this material represented an old individual of the same species shown in Fig. 18, the fontanelles should be relatively much more closed. Although the overall carapace size is comparable to that of *Osteopygis roundsi*, the costal and neural elements are only about half as thick in specimens of comparable size and the peripherals lack the distinctive osteopygine notches on their internal borders (see Fig. 15B).

Among toxochelyids, this material can be assigned only to *Dollochelys* on the basis of USNM 412111 (Fig. 22), which has the characteristic *Dollochelys* pygal shape (as long or longer than wide with a single point at its posterior extremity, see Fig. 21). Other toxochelyid genera all have pygals notably wider than long. The width/length ratio of the pygal in the Piscataway form (0.82) is greater than that for the one well known specimen of *D. casieri* (0.72) but is in the range known for *D. atlantica* (between 0.7 and 1.0). Two other specimens (USNM 412109 and USNM 412110) can be referred confidently to the same taxon on the basis of their relatively large size, very thin shell, lack of notches on the internal border of the peripherals, and extreme development of costoperipheral fontanelles. These specimens are shown on Figs. 12B and 22A and a tentative reconstruction of the carapace, based on all of these specimens, is shown in Fig. 21. The general proportions of the neural and costal elements are similar to those of the same elements in *D. atlantica*, as shown in Fig. 21, though the neurals are somewhat narrower. The most striking difference, however, is shown by the impressions of the sulci which indicate that, in life, the first neural scute (and by analogy probably the other neural scutes as well) was very much narrower than the neural scutes in either *D. casieri* or *D. atlantica*. The carapace fragment shown in Fig. 22A was associated with some limb and girdle elements (Figs. 11E–H, 14B–C, 20B–E) all of which are typically toxochelyid in their morphology. Because limb and girdle elements are poorly known in the other two species, more detailed comparisons of these elements cannot be made.

Fig. 23. A, Anterior portion of carapace of *Allopleuron insularis* (USNM 359002).

Family Dermochelyidae
Subfamily Allopleurinae
Allopleuron insularis (Cope)
Figs. 23, 24

Referred specimen.—Nuchal, first neural, right and left first peripherals, right and left second peripherals, left third peripheral. Found in bluff between Aquia Creek and Potomac Creek, western bank of Potomac River, Stafford County, Virginia, by Kurt Savoie. Label data do not give exact horizon, but nanofossils in the matrix of the specimen indicate that it came from NP8 (Laurel Bybell, written communication, 1978), which would place it in "Zone 6" of Clark & Martin (1901), Piscataway Member, Aquia Formation.

Discussion.—This fragmentary specimen (Figs. 23 and 24) represents only the anteriormost portion of a very large, lightly built turtle whose carapace was probably over 2 m long. The carapacial bones of this turtle are extremely thin for its size, and the carapace is built very much like a large kite. On the basis of its large size, its deeply indented nuchal, the forwardly projected position of the first peripherals, and its occurrence at only a slightly lower stratigraphic horizon (NP8) than the Vincentown Formation of New Jersey (NP9), this specimen seems identical to *Lembonax insularis* Cope. Unfortunately the type species for *Lembonax, L. polemicus,* is based on only two fragments of plastron and a fragment of scapula, none of which are diagnostic. Therefore, *"Lembonax"* must be considered a nomen dubium, even though the species "*Lembonax*" *insularis* and "*Lembonax*" *propylaeus* Cope are apparently based on diagnosable material and therefore valid. Fortunately, the well known European turtle genus *Allopleuron* Ruschkamp agrees with all of this material in its most striking features, so there is no difficulty in assigning both "*L.*" *insularis* and "*L.*" *propylaeus* to that well known genus.

Cope and later Hay (1908) recognized that the first peripheral in *A. insularis* was located in a very peculiar position. Although Cope correctly recognized that this element was the first peripheral, Hay was uncertain and thus speculated that the same element might be the eleventh peripheral. Reference to the present specimen shows that much of the confusion resulted from the fact that the first peripheral has been ontogenetically drawn forward, so that the second peripheral makes broad contact with the nuchal behind it. This very unusual ontogeny has caused the first peripherals to form the inner edges of two horns that project forward on either side of the neck. Correlatively, the nuchal edges have been drawn forward to give the nuchal a deep, saddle-shaped anterior border similar to that found in *Allopleuron propylaeus* and *A. hoffmani,* both of which are close to this form but differ significantly from the Aquia specimen in the details of the shape of the nuchal. On the basis of the unsutured inner margin of the second and third peripherals, *A. insularis* appears to have had a long, open costoperipheral fontanelle. The first neural is notable for being nearly triangular in shape and much wider than it is long. The costals are unknown. The wide neural is very reminiscent of the condition found in *Eosphargis breineri* (Nielsen, 1964), a primitive dermochelyoid turtle (Rhodin 1985:766), and even the Cretaceous form of *Allopleuron* shows a trend in this direction, its neurals being about as wide as they are long.

Recently, a partial skeleton with a *Psephophorus*-type dermal shield was found in the upper Oligocene Chandler Bridge Formation near Charleston, South Carolina. Associated with this specimen was a thin nuchal plate having a deeply emarginated anterior border (Fig. 14D). On the basis of this association, as well as the similarities of *Allopleuron* with *Eosphargis,* it seems clear that *Allopleuron insularis* is part of the ancestral stock of the modern *Dermochelys.* However, this ancestral stock (*Glyptochelone, Allopleuron, Protosphargis,* and *Eos-*

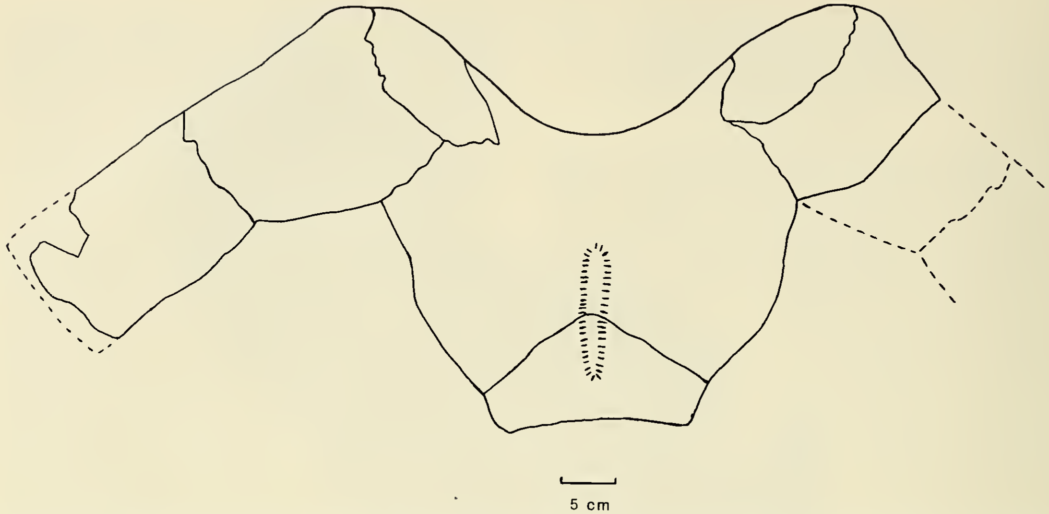

Fig. 24. Restoration of the anterior part of the carapace of *Allopleuron insularis* (Cope) based on USNM 359002.

phargis) completely lacks the uniquely dermochelyid armor of polygonal mosaic plates and so merits separate subfamilial rank. It is considered best to use the well known genus *Allopleuron* as the namesake for this subfamily. The Allopleurinae can be defined as including large, relatively very thin-shelled, strongly fontanellized sea turtles having strongly reduced, anteroposteriorly elongate plastral elements, a deeply excavated nuchal element, but no development of dermochelyid mosaic armor.

Implications for the Phylogeny of Sea Turtles

The foregoing descriptions suggest that the Paleocene sea turtles of New Jersey, Maryland, and Virginia provide an evolutionary link between the Late Cretaceous sea turtles of the American western interior and the Eocene sea turtles of England and Belgium. Zangerl (1971) suggested that the toxochelyids appeared and persisted later in western Europe than they did in North America, and argued that this phenomenon was the result of their slow dispersion over geologic time from west to east. Recently, however, Moody (1980b) has pointed to recent discoveries of Cretaceous toxochelyids from Ireland and France indicating that the family was widespread throughout the North Atlantic Basin in Late Cretaceous time. Because Eocene sea turtles are very poorly known in both the Atlantic and Gulf Coastal Plains of America, nothing meaningful can be inferred about their American distribution at that time, but there is currently no positive evidence to suggest that sea turtles in Europe or America were strongly endemic. Although exactly equivalent faunal horizons on each continent cannot so far be matched, the presence in the American Paleocene of forms that seem close to the expected ancestral condition for European Eocene forms strongly suggests that migration back and forth across the Atlantic was as easy then as it is for sea turtles today.

Although Zangerl (1953) did not attempt to draw a phylogenetic chart of American Cretaceous sea turtles, such a chart can be produced readily from his taxonomic treatment. The present perspective (and a much more complete knowledge of Paleocene forms) seem to warrant reinterpretation of the phylogeny of sea turtles as envisioned by Zangerl. This reinterpretation results from changing the taxonomic position of just two closely related genera, *Desmatochelys* and *Corsochelys.* Zangerl considered both to be early cheloniids, largely because of basicranial specializations that also are seen in modern cheloniids. Yet, because parallelism is common in closely related lineages, it is reasonable to expect different lineages of sea turtles to evolve one trait (or a few functionally related traits) in parallel. In some traits, particularly the strong forward projection of their nuchals, *Corsochelys* and *Desmatochelys* are uniquely specialized sea turtles. In other respects, however, recent workers have tended to find greatest similarities with the Dermochelyoidea. Pritchard (1979) associated *Desmatochelys* with the dermochelyoids, and Rhodin (1985) has shown that *Corsochelys* had vascularized chondroepiphyses, a character state otherwise known only among the dermochelyoids. Also, both genera show an early trend toward large size and strong reduction in the carapace. Another notable dermochelyid trait is the fact that both the left and the right rows of plastral elements are drawn strongly away from the midline and compressed side to side to leave a medial fontanelle across the entire central half of the plastral area. This pattern is typical of that found in the Allopleurinae and Dermochelyinae. In contrast, the Protostegidae retain primitive, squarish, plate-like elements (Zangerl 1953, Collins 1970), and the Cretaceous chelonioid families have their plastral elements compressed anteroposteriorly toward the midline to leave large antero-lateral and postero-lateral fontanelles but only a narrow median fontanelle (see Fig. 25 for comparisons).

Although the plastral elements appear compressed, the likely ontogenetic mechanism to effect this appearance probably was the establishment of a line or lines of polarity, perpendicular to which growth was retarded. By slowing growth along one axis of plastral elements, intervening cartilaginous areas remained unreplaced. This reduced weight and the need to ingest as much phosphorus to generate more bone. Strength along the axis parallel to the line or lines of polarity, however, was not sacrificed because the narrow but elongate plastral elements still formed bracing struts. Thus a balance was struck between the advantages of lightening the shell and the disadvantages of weakening it.

The fact that the protostegids retain essentially plate-like plastral elements, yet in other respects are readily allied with the dermochelyids rather than with the chelonioids (see Fig. 26), strongly suggests that ontogenetic mechanisms to effect extreme plastral reduction evolved independently in chelonioids and dermochelyids. Similarly, because chelonioid turtles and dermochelyid turtles effect the reduction of their plastrons by contraction of elements along axes with orthogonal polarities, it is difficult to envision an ancestor which could have had character states common to both strategies. The modern genus *Chelonia* is the only sea turtle known to develop both longitudinal and (secondarily in the late Tertiary) lateral compression of its plastron. All other sea turtles seem to follow one pattern of condensation to the exclusion of the other. This strong contrast in developmental style offers two obvious derived character states which can be used to separate chelonioid from dermochelyid turtles.

On the basis of all of the above derived character traits, it is most reasonable to ally *Desmatochelys* and *Corsochelys* with the Dermochelyidae. However, they obviously merit rank as a discrete subfamily, the Desmatochelyinae, because they are readily distinguished within the Dermochelyidae by the presence of forwardly thrust nuchals. With the placement of *Desmatochelys* and *Corsochelys* in the Dermochelyidae, a taxonomy can be erected for sea turtles which also makes sense of their stratigraphic occurrences as well.

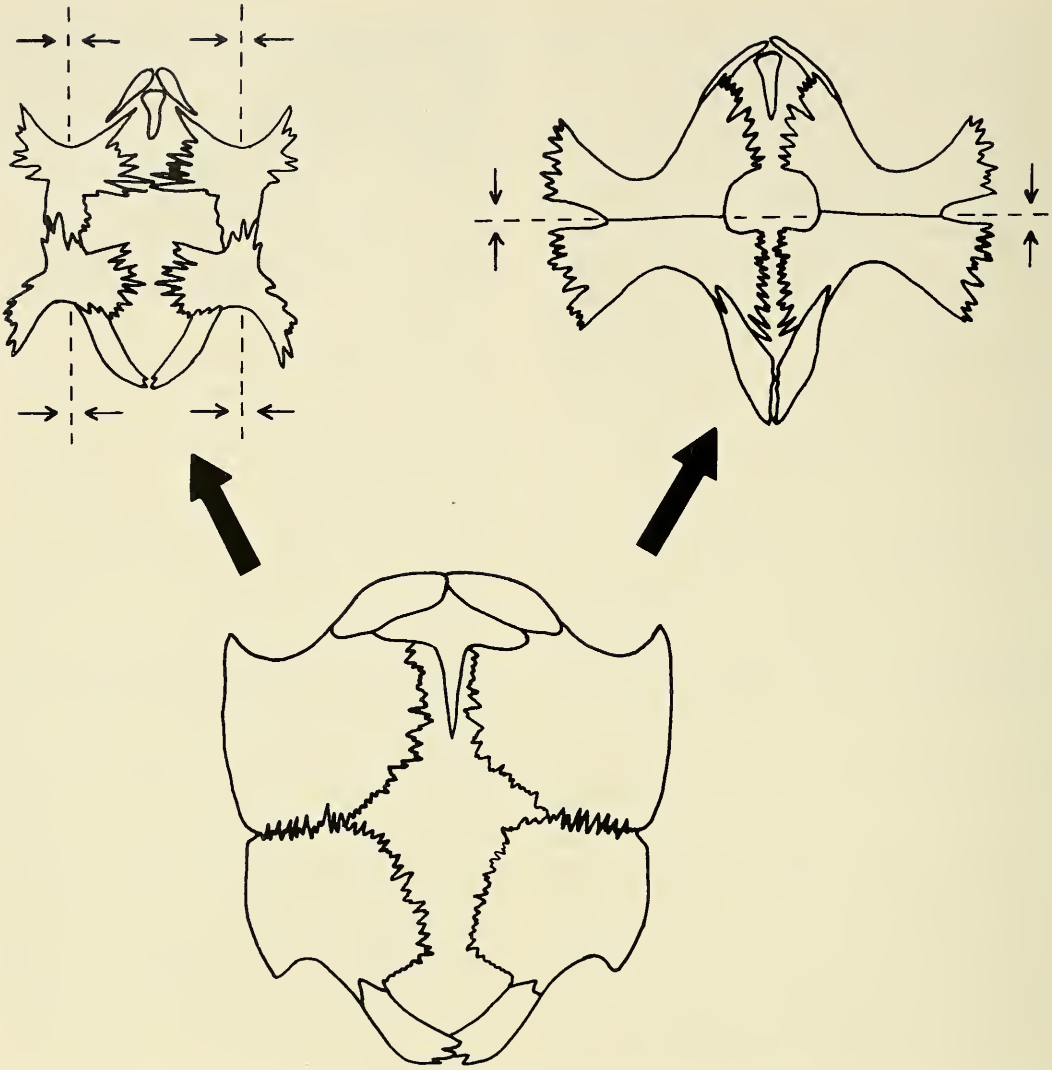

Fig. 25. Diagram showing the two major evolutionary trends in the plastrons of advanced sea turtles. Primitively the plastral elements are squarish and only slightly reduced, as illustrated by the Chelospharginae (bottom). In more advanced dermochelyoid forms, there is a tendency for the plastral elements to become more reduced by compression (shown by arrows) toward two axes (dashed lines) oriented in an anteroposterior direction, leaving a very broad medial plastral fontanelle (upper left). In cheloniid and toxochelyid turtles, the plastral elements tend to become compressed toward a single axis oriented transversely across the midline of the shell (upper right), leaving broad anterolateral and posterolateral plastral fontanelles. In the living *Chelonia mydas,* both types of compression seem to occur, but this is a highly derived condition, established in the Late Tertiary, atypical of other cheloniids.

Because the entire superfamily to which the Dermochelyidae belong is so thin-shelled and fontanellized, well-preserved specimens are rare. It therefore seems likely that many more species of Cretaceous and early Tertiary dermochelyids remain to be described and that any phylogeny of this family made at the present time will be necessarily sketchy and very incomplete. Similarly, the details of the phylogeny of the family Cheloniidae are still sketchy and incomplete due to lack of described material at many horizons. Nevertheless, at the subfamily and higher taxonomic levels, a cladistic phylogeny can be drawn relating all of the various known families and subfamilies of sea turtles on the basis of shared derived characteristics (see Fig. 26). This proposed phylogeny 1) entirely removes occurrences of apparently advanced cheloniids from the Cretaceous and 2) implies that the Dermochelyidae occur as far back in time as unequivocal members of the Toxochelyidae. *Kirgizemys,* which was described by Nessov & Khozatskiy (1978) as a Lower Cretaceous toxochelyid, is extremely primitive and shows only a few derived toxochelyid traits in its shell, such as developing lateral plastral fontanelles and a tendency toward anteroposterior constriction of the plastron toward the midline. The familial assignment is quite possibly correct, but without cranial material it is impossible to be certain based on so few observable derived toxochelyid character states.

Although the Dermochelyidae, as here defined, seem to stand in contrast to the Toxochelyidae and Cheloniidae, they do show some affinities with the Protostegidae, principally in the strongly reduced carapace, the proportions of elements in the shoulder girdle, and the morphology and histology of the humerus. Therefore, it is reasonable to associate these two families within the superfamily Dermochelioidea as an entirely separate line of sea turtle evolution from the Toxochelyidae and Cheloniidae, which can be associated together as the superfamily Chelonioidea. The four constituent families of these two superfamilies are the same four recognized by Gaffney (1975b) as containing all Cretaceous and Cenozoic sea turtles. The taxonomic organization of these various families and subfamilies, and the described genera which can be assigned confidently to them, are summarized in Table 2.

Table 2.—Taxonomy of the sea turtles, showing superfamily, family, and subfamily levels of classification and their organization. Below the subfamily level, phylogenetic pathways are not indicated and genera are listed *seriatim.*

- Superfamily Chelonioidea
  - Family Plesiochelyidae
    - *Plesiochelys, Portlandemys*
  - Family Toxochelyidae
    - Subfamily Toxochelyinae
      - *Dollochelys, ?Kirgizemys, Portochelys, Thinochelys, Toxochelys*
    - Subfamily Lophocheliinae
      - *Ctenochelys, Lophochelys, Neurochelys, Peritresius, Prionochelys*
  - Family Cheloniidae
    - Subfamily Osteopyginae
      - *Erquelinnesia, Osteopygis, Rhetechelys*
    - Subfamily Eocheloniinae
      - *Argillochelys, Catapleura, Eochelone, Glarichelys, Puppigerus, Tasbacka*
    - Subfamily Syllominae
      - *?Bryochelys, Kurobechelys, Syllomus*
    - Subfamily Cheloniinae
      - *Caretta, Carolinochelys, Chelonia, Eretmochelys, Lepidochelys, Procolpochelys*
- Superfamily Dermochelyoidea
  - Family Protostegidae
    - Subfamily Chelospharginae
      - *Calcarichelys, Chelosphargis, Rhinochelys*
    - Subfamily Protostegidae
      - *Archelon, Protostega*
  - Family Dermochelyidae
    - Subfamily Desmatochelyinae
      - *Corsochelys, Desmatochelys*
    - Subfamily Allopleuroninae
      - *Allopleuron, Eosphargis, Glyptochelone, Protosphargis*
    - Subfamily Dermochelyinae
      - *Cosmochelys, Dermochelys, Psephophorus*

Once *Desmotochelys* and *Corsochelys* have been removed from the Chelonioidea, the major evolutionary radiation of the Cheloniidae cannot be found before the beginning of the Tertiary. Persistently generalized sea turtles, possibly similar to *Thinochelys* and *Portochelys,* appear to have given rise to a primitive cheloniid, *Catapleura arkansaw,* by the Late Cretaceous

(Schmidt 1944). But only later, in the late Paleocene, did the major radiation of cheloniids begin. Late Cretaceous (Santonian through Campanian) radiations of sea turtles did occur, but these only involved the families Toxochelyidae, Protostegidae, and Dermochelyidae. This major radiation ended with the Campanian, however, and no protostegids of any kind are known to have survived into the Maastrichtian. The toxochelyines are known only from a single form in the Maastrichtian (*Toxochelys weeksi*), and *Dollochelys* is the only known Paleocene form. Similarly, the lophochelyines are represented only by *Peritresius* in the Maastrichtian and a single fragmentary form from the Danian (Wood 1973). In contrast, a modest radiation of the Allopleurines occurred in the Maastrichtian and the osteopygines make their first appearance. In general, though, both the Maastrichtian and Danian appear to have been times of relatively low sea turtle diversity. This general pattern of decline reverses in the Thanetian with the beginning of the cheloniid radiation. In the Ypresian (early Eocene), sea turtles reached their peak of Cenozoic diversity. Although lophochelyines make their last appearance in the form of *Neurochelys* (Moody 1980a), and osteopygines in the form of *Erquelinnesia* (Zangerl 1971), most of this assemblage consists of eochelyines and allopleurines. The later Tertiary history of the sea turtles so far is too poorly known to indicate exact relationships or to get a feeling for detailed changes in diversity.

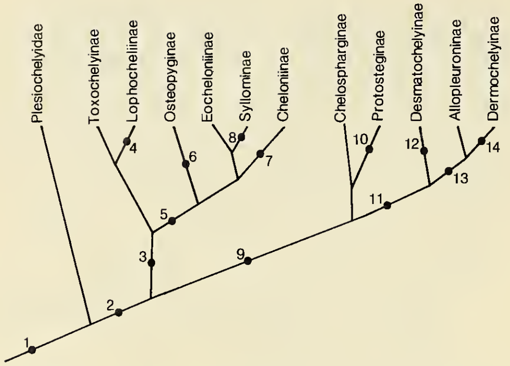

Fig. 26. Cladogram showing the relationships and key shared derived characters of the known families and subfamilies of sea turtles. Numbers refer to the following character states or character complexes: 1) Palatine and internal carotid arteries equal in diameter, basisphenoidal trabeculae lie close together; foramina anterius canalis carotici interni lie close together and are separated by relatively thin bar of bone; dorsum sellae high and separated from sella turcica and carotid foramina by prominent bone surface; posterior part of sella turcica not concealed by overhanging dorsum sellae (Gaffney 1975b, 1984). 2) Palatine artery and canalis caroticus lateralis larger than internal carotid artery and canalis caroticus internus; front limb with elongate digits and metacarpals forming a flipper with elements oriented in one plane (Gaffney 1975b, 1984). 3) Hyoplastra and hypoplastra reduced by constriction anteroposteriorly toward a transverse midline axis (see Fig. 25). 4) Neurals serrated, forming mid-dorsal keel, peripherals moderately to strongly serrated, connection between pygal and suprapygal very narrow or broken, hyoplastron, hypoplastron, and xiphiplastron with conspicuous ventral keel knobs, epineural elements present in advanced genera (Zangerl 1953). 5) Secondary palate present, postnuchal fontanelles lost at least in adult stages. 6) Prefrontal has an extended posterior process, nearly or entirely excluding frontal from orbit, fissura ethmoidalis deep, palate flat with low tomial ridge, vomer has straight contact with premaxillaries, enlarged complete secondary palate organized differently from that in the Cheloniinae (Fastovsky 1985). 7) Secondary palate completely developed, rear limbs markedly modified for swimming rather than walking. 8) Secondary palate lost, jaw margins develop pseudodont crenulations, deltopectoral crest of humerus moved far distally toward the middle of the humerus. 9) Much of dermal bone layer absent in carapace, resulting in costal ribs that are free of overlying bone; front flippers very long in relation to body; large radial crest of humerus displaced distally, humerus tends to develop vascularized chondroepiphyses; braincase partially cartilaginous in adult (Wieland 1906, Zangerl 1953, Gaffney 1984, Rhodin 1985). 10) Pointed and decurved beak; nasal elements lost; costals very greatly reduced, extending no farther down the axis of the rib than a distance equal to their width (Zangerl 1953). 11) Hyoplastra and hypoplastra reduced by constriction laterally toward two parallel anteroposterior axes (see Fig. 25). 12) Nuchal elongated to project forward over neck region, neurals longer than wide. 13) Nuchal element deeply emarginated, neurals as wide or wider than long. 14) Normal shell elements (reduced) overlain by mosaic of suturally interconnected dermal bones.

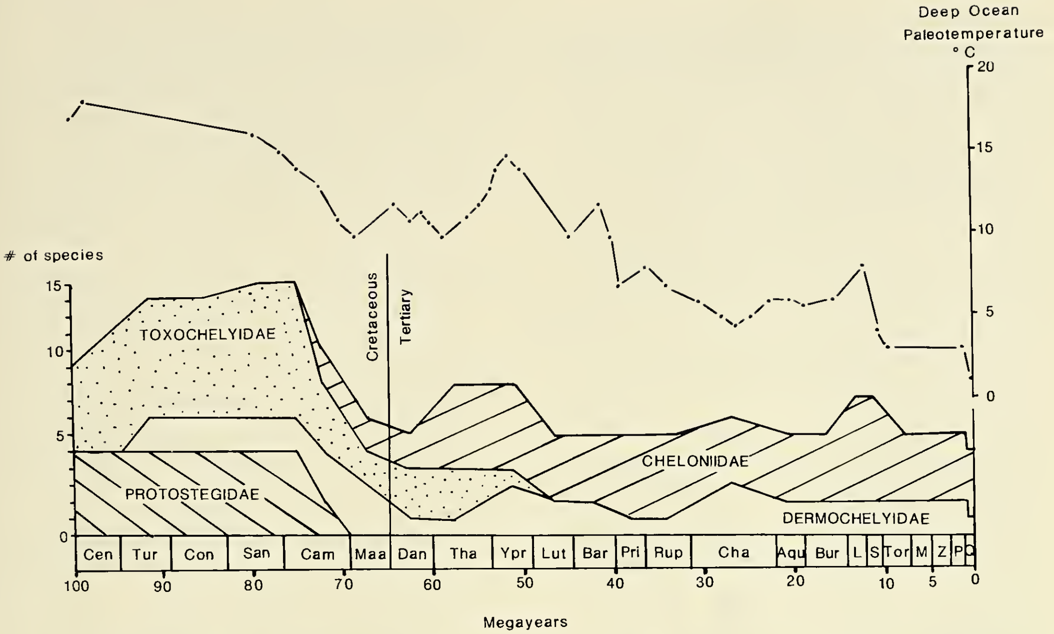

Fig. 27. Diversity in sea turtle families in comparison with the oxygen isotope derived oceanic paleotemperature curve for the northern mid-latitudes (temperature curve adapted from Douglas and Woodruff 1981). Many factors could explain the strong correlation between ocean temperature and sea turtle diversity, including (1) increased areal extent of shallow sea habitat during warm spells, (2) more efficient physiology during warm spells, or (3) better egg viability during warm spells. Cen = Cenomanian, Tur = Turonian, Con = Coniacian, San = Santonian, Cam = Campanian, Maa = Maastrichtian, Dan = Danian, Tha = Thanetian, Ypr = Ypresian, Lut = Lutetian, Bar = Bartonian, Pri = Priabonian, Rup = Rupelian, Cha = Chatian, Aqu = Aquitanian, Bur = Burdigalian, L = Langhian, S = Serravalian, Tor = Tortonian, M = Messinian, Z = Zanclian, P = Piacenzian, Q = Quaternary undifferentiated.

Generally, however, there has been decline since the early Eocene to the present diversity of five species worldwide.

Sea Turtles and the Cretaceous–Tertiary Transition

As indicated by the previous discussion, sea turtles seem to have had two periods of exceptional radiation and diversity, once in the Campanian and once in the Ypresian. In between those radiations, both the Maastrichtian and the Danian represent a time of exceptionally low diversity. No major extinction among sea turtles can be localized at the Maastrichtian–Danian boundary. Rather, the most dramatic time of extinction occurs near the end of the Campanian. This pattern of evolutionary expansion and contraction does not seem to be strongly affected either by the recently suggested meteoric impact event at the Maastrichtian–Danian boundary (Alvarez et al. 1980) or by the more gradual series of climatic and geologic changes suggested by Officer & Drake (1983), but does match nicely the changes in the estimated average oceanic temperatures for the mid-northern latitudes through the Late Cretaceous and early Tertiary (Fig. 27). The correlation is so close that the diversity of sea turtles seems to have been controlled either directly by average ocean temperatures around the world or by the same factors that controlled such temperatures, rather than by short-term dramatic events that may have occurred sporadically throughout geologic time. If extraterrestrial causes for this extinction are to be invoked, only a large interstellar dust and debris cloud which reduced the intensity of sunlight over an interval of millions of years would fit the pattern observed.

As a generally quiet period in sea turtle history, the Maastrichtian–Danian interval was a time of continuity and stability, marked by neither the radical changes nor great innovations that would occur later in Tertiary. Thus, at a time when many other animal and plant groups have been described as being in a period of massive change or decline, the sea turtles appear to have been essentially unaffected by any great changes taking place around them. As the early Tertiary global warming trend unfolded, the sea turtles concurrently underwent a new evolutionary radiation, undiminished in their evolutionary potential by the Cretaceous–Tertiary transition.

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A DESCRIPTION OF THE PIGMENTED AND NON-STYGOBIONTIC FEMALES OF *PODOBOTHRUS BERMUDENSIS* BARNARD & CLARK, 1985 (CRUSTACEA: AMPHIPODA: DULICHIIDAE)

Michael F. Gable, Eric A. Lazo-Wasem, and Adam J. Baldinger

Abstract.—The females of *Podobothrus bermudensis* (Amphipoda: Dulichiidae) are described. Three females and two males, all from the shallow subtidal zone, are compared with each other and with the single cave-dwelling male used by Barnard & Clark (1985) to establish the monotypic genus. Most significantly, all females are pigmented and all males are non-pigmented. The mandibular palp is judged to be the most useful character for distinguishing *Podobothrus* from the closely related *Podocerus*.

Podobothrus bermudensis Barnard & Clark, 1985, was described as a sea-cave amphipod species (and genus) from a male specimen collected from Green Bay Cave, Bermuda. Examinations of collections at the Yale Peabody Museum (YPM), made in Bermuda in 1985, and of United States National Museum (USNM) collections, made by M. L. Jones in the early 1980's, have uncovered five additional specimens of this new species including three females. Because these animals exhibit important morphological and habitat differences from the type specimen, we believe that descriptions of the specimens and remarks on their distribution will provide valuable information for amphipod taxonomists and stygobiologists.

Description.—Female: Body pigmented, most notably on abdomen and thoracic areas (Fig. 1). Pereonites dorsally smooth except for a slight mucronation on pereonite 2, spine groups on distoposterior corners of pereonites 2–4, 6 and pleonite 1. Pleonites 1–3 with slight dorsal carinations. Urosomites as in males.

Coxae reduced, subrectangular, distinctly larger than those of males, coxae 1–4 touching, coxae 5–7 overlapping. Head and eyes as in males, except eyes pigmented, appearing red in alcohol (Fig. 1).

Antenna 1, 118% body length, ratio to peduncle of antenna 2, 1:1; flagellum 50% of peduncular length, 5-articulate; accessory flagellum, 1-articulate, as in male. Antenna 2, proportion of peduncular article 4 to 5, 1:1.1, flagellum missing.

Mouthparts as in male except: lower lip with facial tubercles extending from internal margins of anterior lobes; medial margin of inner plate of maxilla 2 less setose, apical setae, plumose; setae of mandibular palp, distinctly pinnate (Fig. 2).

Gnathopod 1 similar to that of male with exception of dactyl, which in female lacks inner marginal spination, but possesses setae and a distal annulation (Fig. 2). Gnathopod 2 similar to that of male, but more weakly subchelate, palmar margin of article 6 finely serrated, dactyl distally annulated; pigment spots along the length of the appendage (Fig. 2). Pereopod 7 (others missing) with pigment spots along its length.

Pleopods as in male, except peduncular segments pigmented (Fig. 1). Uropods as in male, but uropod 3 lacking inner setule. Telson as in male.

Material examined.—YPM 8269: Ferry

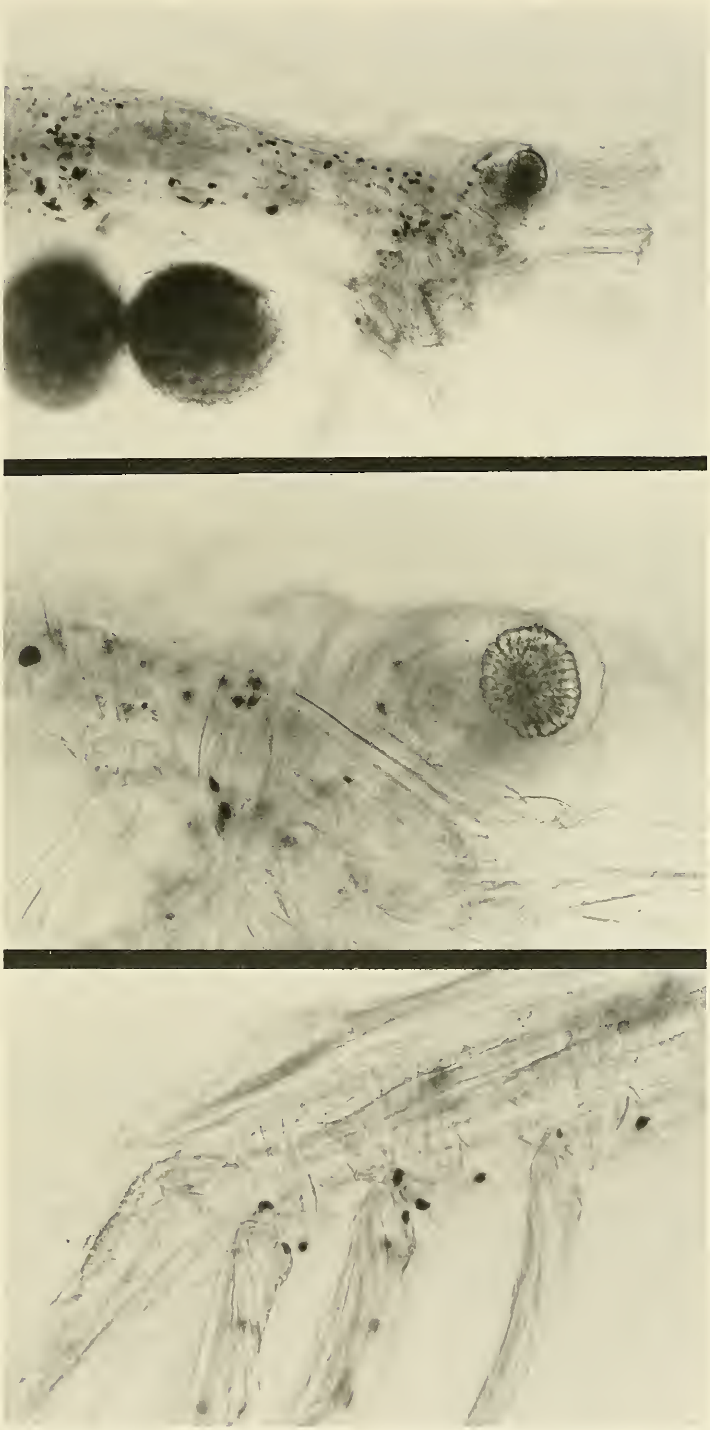

Fig. 1. *Podobothrus bermudensis,* ovigerous female, 2.2 mm. YPM No. 8269: Top, Lateral view of body pigmentation (4×); Middle, Close-up of pigmented eye and adjacent pigment granules (40×); Bottom, Lateral view of pigmentation on pleon and peduncular segments of pleopods (10×).

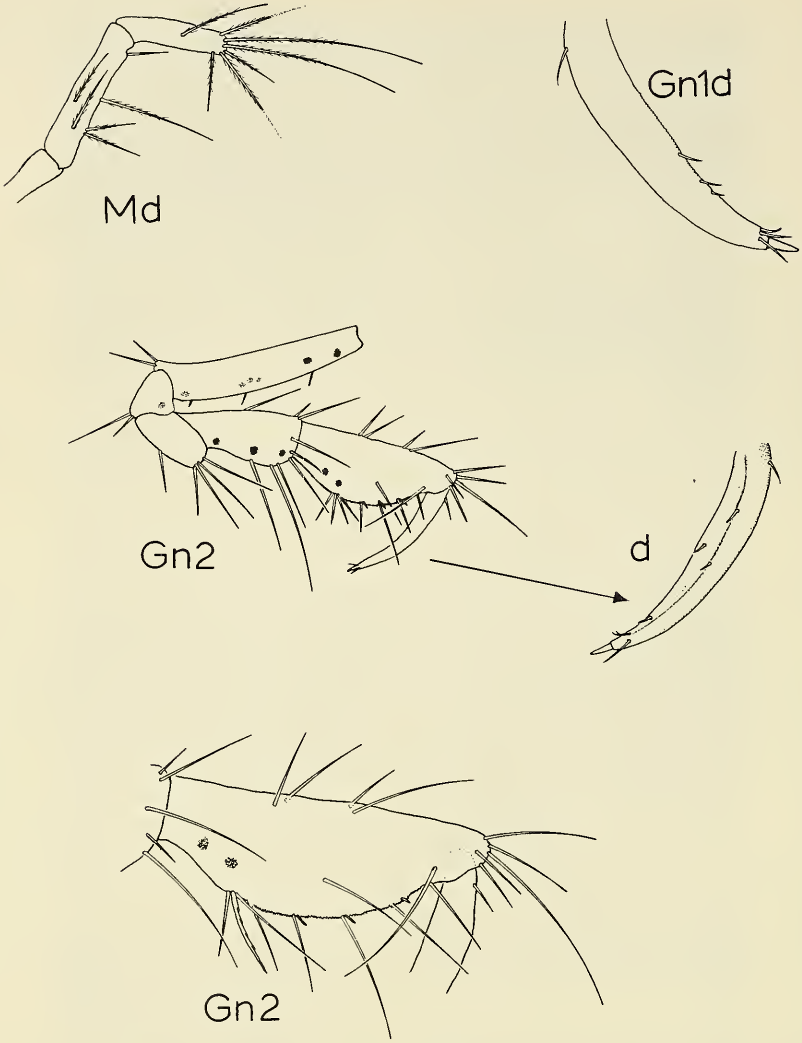

Fig. 2. *Podobothrus bermudensis,* female, 1.9 mm. USNM Acc. No. 346847. Legend: major body parts marked by abbreviations beginning with uppercase letters; enlargements of gnathopod articles marked by a lowercase "d." Abbreviations: Gn, gnathopod; Md, palp of mandible; d, dactyl.

Reach, St. George's, Bermuda, Cove W of BBS, M. F. Gable, 28 May 1985, 1 ovigerous female, 2.2 mm; Ferry Reach, St. George's, Bermuda, Cove W of BBS, M. F. Gable, 28 May 1985, 1 male, 1.7 mm. USNM Acc. No. 346847: Ferry Reach, Bermuda, adjacent to west side of dock at BBS, M. L. Jones, 2 Sep 1981, Cohen net through *Thalassia,* 2 females, 1.8 mm and 1.9 mm; Ferry Reach, St. George's, Bermuda, adjacent to west side of dock at BBS, M. L. Jones, 2 Sep 1983, 1 male, 1.8 mm.

Remarks.—Barnard & Clark (1985) mentioned a close resemblance between *Podobothrus* and the genus *Podocerus.* An undetermined species of *Podocerus* does occur in Bermuda. Because antennae and limbs of the two genera are often broken or missing in preserved specimens, we indeed found difficulty in distinguishing the two. Many characteristics of damaged specimens (e.g., spine lengths of the uropods) are too subjective for one not already versed in telling the two genera apart. We found that the best feature for quickly and decisively distinguishing *Podocerus* sp. from *Podobothrus bermudensis* is the third article of the mandibular palp, clearly visible without dissection, long, slender, and highly setose in the latter species, but somewhat short, stout, and with only a few short apical setae in the former species.

Differences between male and female *P. bermudensis* were mentioned in our description, but emphasis should be given to several notable differences. The last two articles of female gnathopod 2 differ significantly from those of the males, not unexpectedly. (An interesting dimorphism between right and left second gnathopods for the only male specimen with both gnathopods intact involves distinct differences in size and robustness of the appendages.) The pinnate setation on the mandibular palp is not shown by Barnard & Clark (1985), but we found this type of setation on both female and male specimens. The two most noteworthy differences, however, are the coxal plates and pigmentation. The coxal plates of all females are larger than those of our male specimens and of the specimen described by Barnard & Clark. Their male holotype, from a cave, is without pigmentation; our three females all have various degrees of pigmentation, including pigmented eyes, and our two males have none. All five of our specimens are from the shallow subtidal habitat, and pigmentation in this species, from the few specimens at hand, therefore appears to be sex-linked and to have nothing to do with habitat. Such knowledge might be useful for stygobiologists examining cave-related anatomical and morphological losses (e.g., pigmentation) to trace the evolutionary route of freshwater cavernicoles from marine ancestors (e.g., Stock 1986).

The habitats occupied by *P. bermudensis* support the statements made by Maddocks & Iliffe (1986) and Stock (1986) that certain island marine-cave and open-water taxa are often identical. Because of the great emphasis currently being placed on anchihaline and marine-cave fauna, care must be exercised in ascribing cavernicolous attributes to new species discovered in caves for those geographic areas and taxa, such as Bermuda and its amphipods, where shallow-water surveys are virtually non-existent. We have evidence to indicate that other cave amphipods described this decade from Bermuda may also be found with regularity in shallow-water marine habitats. Gable & Lazo-Wasem (1987) address this situation briefly in their review of the Bermuda caprellid amphipods. Further shallow-water surveys may indeed change the views on endemism (considerably higher in cave fauna than among littoral species) expressed by some for Bermuda (e.g., Iliffe, Hart & Manning 1983).

Acknowledgments

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A NOTABLE COLLECTION OF *CYCLORAMPHUS* (AMPHIBIA: LEPTODACTYLIDAE) FROM BAHIA, BRAZIL, WITH A DESCRIPTION OF A NEW SPECIES (*CYCLORAMPHUS MIGUELI*)

W. Ronald Heyer

Abstract.—Members of the frog genus *Cycloramphus* were unknown north of the Rio Doce, Espírito Santo, Brazil until 1986, when two species of the genus were collected in southern Bahia, Brazil. The first, *Cycloramphus fuliginosus,* was previously known from the states of Espírito Santo and Rio de Janeiro. The second species is new and described as *Cycloramphus migueli.*

Hypotheses are made to be tested by new data. Heyer & Maxson (1983:356) predicted that members of the frog genus *Cycloramphus* did not occur north of the Rio Doce within the Atlantic Forest Morphoclimatic Domain. The ecology of most *Cycloramphus* species is closely associated with small, fast-flowing mountain streams; topographic maps indicated that there were no areas north of the Rio Doce with enough topographic relief to provide suitable habitat. Prior to 1986, no *Cycloramphus* had been collected north of the Rio Doce. However, in October of 1986, Miguel T. Rodrigues collected two species of *Cycloramphus* from Fazenda Unacau and Rio de Una, Bahia, and saw one individual of a third (distinct, possibly new) species. Twelve specimens of *Cycloramphus fuliginosus* were collected along small (½–1½ m wide), fast flowing, clear streams with rocky bottoms. Most specimens were encountered in the forest, and a few where the forest was replaced by cacao plantations. Dr. Rodrigues also collected, among rocks about 100 m from a stream, a single specimen of *Cycloramphus* representing a new species, proposed herein as:

Cycloramphus migueli, new species

Fig. 1

Holotype.—MZUSP 63450, adult male, from Brazil: Bahia; São José (do Macuco), Fazenda Unacau, 15°09′S, 39°18′W; Miguel T. Rodrigues, 13 Oct 1986.

Diagnosis.—The webless species of *Cycloramphus* are *bolitoglossus, carvalhoi, catarinensis, diringshofeni, eleutherodactylus, granulosus, migueli, stejnegeri,* and *valae.* The toes are free of web and fringe and the dorsum is smooth in *C. migueli*; the toes are ridged or fringed and the dorsum warty-granular in *catarinensis, granulosus,* and *valae.* The leg is shorter in *C. migueli* (e.g., foot length 36% SVL) than in *diringshofeni* (average foot length 50% SVL in males) or *eleutherodactylus* (average foot length 48% in males). *Cycloramphus migueli* is most similar in appearance to *bolitoglossus, carvalhoi,* and *stejnegeri* (this grouping was previously recognized as the genus *Craspedoglossa* [see Heyer 1983, for discussion]). The venter and posterior thigh surfaces of *C. migueli* are dark with small, distinct, irregular light spots; the venter and posterior thigh surfaces of *C. carvalhoi* are uniform

Fig. 1. Dorsal and ventral views of holotype of *Cycloramphus migueli.*

brown; and the throat, chin, and posterior thigh surfaces of *C. stejnegeri* are dark brown with distinct light spots, while the belly is mostly unpigmented. In addition, *C. migueli* is smaller (male SVL 42 mm) than either *carvalhoi* (male SVL 59–62 mm) or *stejnegeri* (male SVL 45–47 mm). The ventral and posterior thigh patterns of *C. migueli* and *bolitoglossus* are similar. The two species differ in size (*C. migueli* male 42 mm SVL, *bolitoglossus* males 29–34 mm SVL) and *C. migueli* has a distinct fold, from the posterior corner of the eye to the shoulder, which is lacking in *C. bolitoglossus.*

Description of holotype.—Snout nearly round from above, slightly obtuse in profile; canthus rostralis indistinct; loreal convexly obtuse in cross section; tympanum hidden; vomerine teeth in obtuse series posterior to and between choanae; no vocal slits or vocal sac; first finger just longer than second; fingers lacking fringe or web; outer metacarpal tubercle large, square with rounded corners; inner metacarpal tubercle large, oblong, separated from subarticular tubercle of thumb by less than diameter of subarticular tubercle; thumbs lacking asperities; dorsal and ventral textures smooth; fold from posterior corner of eye to shoulder; inguinal gland large, circular, diameter greater than ⅓ length of thigh; toe tips rounded, not expanded; toes without fringe or web; subarticular tubercles under toes weakly developed; outer metatarsal tubercle large, rounded, elongate, about ½ size of oblong inner metatarsal tubercle; no tarsal or metatarsal folds; posterior surface of tarsus and sole of foot smooth.

SVL 42.1 mm, head length 16.1 mm, head width 19.2 mm, eye–nostril (middle of opening) distance 3.0 mm, thigh length 17.3 mm, shank length 14.0 mm, foot length 15.1 mm.

Dorsum with a dark, finely lichenous pattern of black and brown; brown interorbital band; face mostly black with three indistinct, slanted stripes from eye to edge of upper lip, most anterior stripe directed forward from eye, other two directed posteriorly; flank same color as dorsum; inguinal gland uniformly dark; upper limb surfaces barred black and brown; tips of digits white; venter black with small distinct white dots; under-surfaces of hands and feet gray with all tubercles and digit tips conspicuously white; posterior surface of thigh dark brown with small, irregular, distinct, light spots.

Etymology.—Named for Dr. Miguel T.

Rodrigues, who has made significant collections of frogs throughout much of Brazil.

Distribution.—Known only from the type locality (Fig. 2).

Discussion

The occurrence of *Cycloramphus fuliginosus* in the State of Bahia is surprising for two reasons. First, no member of any stream associated species group of *Cycloramphus* was expected north of the Rio Doce (Heyer & Maxson 1983:356). However, small, swift, clear streams obviously occur north of the Rio Doce, comparable in habitat to those found south of the river. Intensive collecting now will have to be done to ascertain the northern distributional limits of *Cycloramphus* in the Atlantic Forest system. Second, the occurrence of *C. fuliginosus* is in itself surprising. All other members of the same species group have much smaller geographic ranges (see Heyer 1983, and Heyer & Maxson 1983) than *C. fuliginosus.* As currently understood, *C. fuliginosus* is not continuously distributed throughout its range; rather it is known from three small areas in the State of Rio de Janeiro (in or near the city of Rio de Janeiro, Corcovado, and the Serra da Mangaratiba [Heyer 1983, fig. 38]); one locality in Espírito Santo (Santa Teresa); and now two nearby localities in southern Bahia (Fig. 2). There is no morphological differentiation among the samples from the states of Rio de Janeiro, Espírito Santo, or Bahia. In fact, all the Bahia and Espírito Santo individuals have the distinct tripartite odontoids on the lower jaw pointed out by A. Lutz (1929:10) as characterizing *C. fuliginosus.* As this characteristic often appears late in the ontogeny of *C. fuliginosus,* being found consistently only in large specimens (Lutz 1929:10), I did not include the character in my previous work (Heyer 1983). Additional data confirm Lutz's observation that *C. fuliginosus* is the only species of *Cycloramphus* to have bipartite or tripartite mandibular odontoids. Thus, it would appear that *C. fuliginosus* either (1) has until relatively recently had a continuous distribution but now is divided into relictual populations, or (2) has been separated for a longer period of time but has not undergone morphological differentiation characteristic of other species of *Cycloramphus* isolated for similar periods of time. Estimates of genetic relatedness among the Rio de Janeiro, Espírito Santo, and Bahia populations are needed to resolve the issue.

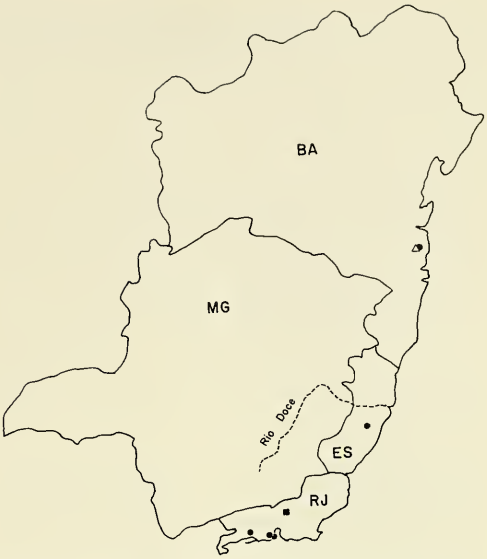

Fig. 2. Distribution of *Cycloramphus migueli* (triangle), *C. fuliginosus* (dots and triangle), and *C. stejnegeri* (square) in eastern Brazil. *Cycloramphus stejnegeri* geographically is the closest member of the species cluster to which *C. migueli* belongs. State initials, BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, RJ = Rio de Janeiro.

Cycloramphus migueli has a morphology indicative of a fossorial existence and, along with its presumed closest relatives (*bolitoglossus, carvalhoi,* and *stejnegeri*) most likely has some form of direct development (Heyer & Crombie 1979). These four species are allopatric, each with a small geographic range (*bolitoglossus* occurs in the Serra do Mar in the states of Paraná and Santa Catarina, *carvalhoi* in the Serra da Mantiqueira, and *stejnegeri* in the Organ Mountains, Fig. 2 and see Heyer 1983, figs. 30, 42). Assuming that *C. migueli* is closely related to *bolitoglossus, carvalhoi,* and *stejnegeri,* it is not surprising that a population found in Bahia would represent a new species, nor that a member of this cluster would occur in the Atlantic Forests north of the Rio Doce as species with direct development should be able to occur throughout the Atlantic Forest Domain.

From the same localities in Bahia, Dr. Rodrigues collected species of *Crossodactylus* and *Hylodes,* two genera typically found in the same streams as *Cycloramphus* south of the Rio Doce. Notable by its absence from these collections is a representative of the genus *Thoropa,* which elsewhere is found in the same types of habitats as *Cycloramphus.*

Acknowledgments

Dr. Miguel T. Rodrigues (Instituto de Biociências, Universidade de São Paulo) generously turned the Bahia *Cycloramphus* materials over to me for study and also provided his ecological notes for the specimens. Reginald B. Cocroft and Ronald I. Crombie (Smithsonian Institution) reviewed the manuscript.

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REDESCRIPTIONS OF TWO CHINESE *CUORA* (REPTILIA: TESTUDINES: EMYDIDAE)

Carl H. Ernst

Abstract.—Validity of the turtle *Cuora pani* Song, 1984, from Shaanxi Province, China, which has become available to American and European scientists via the pet trade, has been questioned. It has been confused with *Cuora yunnanensis* Boulenger, 1906, a poorly known species not seen since the type series was collected from two highland sites in Yunnan Province, China. Major differences exist, and the two species are redescribed and illustrated.

In the last year several taxa of Chinese box turtles, family Emydidae, have become available to the scientific community of North America and Europe through the pet trade. These turtles have all been mistakenly referred to as *Cuora yunnanensis* (Boulenger 1906), a highland species from Yunnan Province, China, and one that has not been collected since the type series. Most of the imported turtles are the recently named, but poorly described *Cuora pani* Song, 1984. The original descriptions of both *C. yunnanensis* and *C. pani* are vague and suggest many similarities that do not exist. *Cuora pani* was described in Chinese with a brief English summary, thus contributing to the confusion of non-Chinese readers. To clearly differentiate these two taxa, I offer the following descriptions and illustrations.

Methods and materials.—Straight-line measurements of each specimen were taken with dial calipers accurate to 0.1 mm of the greatest carapace length, carapace width and depth of the level of the seam between vertebrals 2 and 3, marginal width (the difference between the carapacial width and the width across the pleurals taken between the points of juncture of the marginals and pleurals at the level of the seam between vertebrals 2 and 3), greatest plastron length, greatest width and length of both plastral lobes, greatest bridge length, greatest width and length of vertebrals 1 and 2 and pleural 2, and the medial seam length and greatest width of all plastral scutes. Careful notes and drawings were made of head, neck, limb, carapacial, plastral, and bridge patterns. Colors were recorded from living turtles and color transparencies. Shell proportions are expressed as ratios of one measurement to another. Sixteen ratios proved useful (abbreviations used in the text are given in parentheses): width/length of cervical scute (W/L CS), width/length of first vertebral (W/L 1st V), width/length of second vertebral (W/L 2nd V), width/length of second pleural (W/L 2nd Pl), marginal width/carapacial width (MW/CW), marginal width/carapacial length (MW/CL), carapacial width/carapacial length (CW/CL), carapacial depth/carapacial length (D/CL), carapace depth/carapacial width (D/CW), plastral length/carapacial length (PL/CL), bridge length/plastral length (B/PL), bridge length/carapacial length (B/CL), length of anterior plastral lobe/plastral length (APL/PL), width of anterior plastral lobe/plastral length (APW/PL), length of posterior plastral lobe/plastral length (PPL/PL), and width of posterior plastral lobe/plastral length (PPW/PL). The number of rows of large scales at the lateral edge of the antibrachium between the claw of digit V and the first horizontal skin fold proximal to the elbow (presented in text as foreleg scale rows) was recorded.

Specimens from the following collections

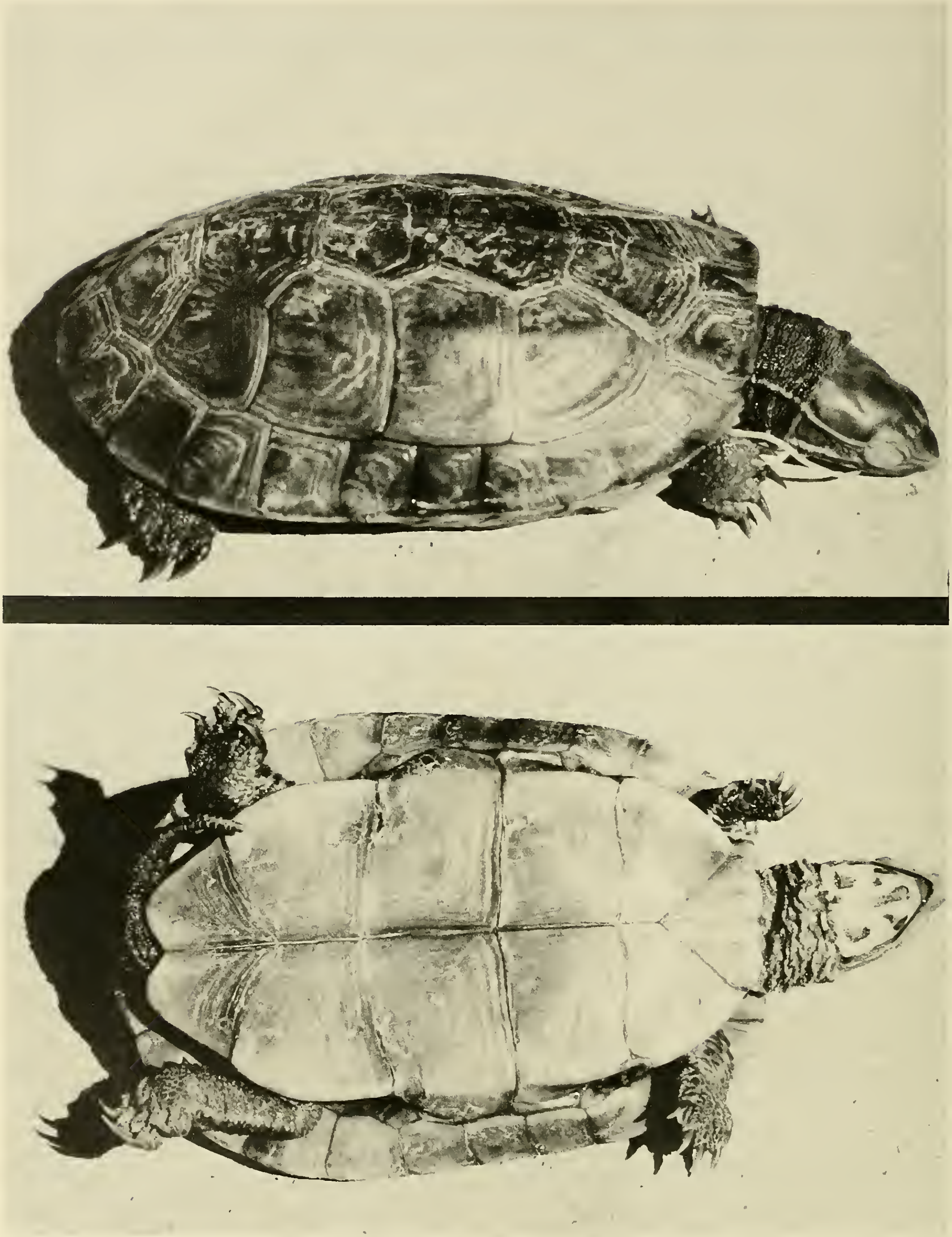

Fig. 1. Carapace and plastron of *Cuora yunnanensis.*

were examined (abbreviations used in the text are given in parentheses): British Museum of Natural History (BMNH), William H. Randel, Hatboro, Pennsylvania, personal collection (WHR), National Museum of Natural History, Smithsonian Institution (USNM).

Cuora yunnanensis (Boulenger, 1906)
Figs. 1, 2

Cyclemys yunnanensis Boulenger, 1906:567.
Cuora yunnanensis Smith, 1931:88.

Syntypes.—BMNH 1946.1.22.97 (female) from Tongchuan Fu, Yunnan Province, China, and 1946.1.22.98–99, 1946.1.23.1–3 (4 males, 1 female) from Yunnan Fu, Yunnan Province, China; John Graham.

Specimens examined.—BMNH 1946.1.-22.1–3; 1946.1.23.98–99.

Diagnosis.—A brown species of *Cuora* with a flattened, tricarinate carapace, a posteriorly notched plastron with a complete interanal seam, the plastral seams narrowly marked with dark pigment, brown skin, a light postorbital stripe, and large yellow or orange blotches on the chin and throat.

Description.—Carapace length to 140 mm (males 126, females 140, measurements of largest specimen taken from Boulenger 1906), elliptical, flattened (D/CL, 0.33–0.39, $\bar{x}$ = 0.352; D/CW, 0.49–0.51, $\bar{x}$ = 0.502; CW/CL 0.65–0.77, $\bar{x}$ = 0.704); widest at level of marginals 8–9, highest at posterior of vertebral 3 (posterior of vertebral 2 in one specimen). Sides straight with no indentation at the bridge. Marginals flared, those most posterior slightly serrated, the first anterior marginals widest, and those over the bridge narrowest (MW 11.0–16.6 mm, $\bar{x}$ = 13.2; MW/CW 0.18–0.215, $\bar{x}$ = 0.202; MW/CL, 0.13–0.17, $\bar{x}$ = 0.143). There is a slight notch between the twelfth marginals. Cervical scute longer than wide (W/L CS 0.76–0.89, $\bar{x}$ = 0.79). Each vertebral scute wider than long, but much narrower than the pleural scutes. The first and fifth vertebrals are flared, but the first does not extend to the seams separating marginals 1 and 2 on each side. General texture of carapacial scutes smooth in older individuals, but granulated with low, rounded rugosities in those up to 88 mm CL. Three longitudinal keels are present; that extending medially along the vertebrals is highest, while the lateral two, which extend along the dorsal third of the pleural scutes on each side, are lower and may be almost nonexistent in larger individuals. Carapace in preserved specimens is olive-brown to chestnut-brown with narrow black seams and some yellow along the pleural-marginal border.

Plastral length to 115.5 mm (males 115.5, females 62.4, but largest female reported by Boulenger (1906) not examined). PL/CL 0.92–0.94, $\bar{x}$ = 0.928; hinged between the pectoral and abdominal scutes, slightly upturned anteriorly and posteriorly notched. The posterior plastral lobe is longer and wider than the anterior lobe (APL/PL 0.42–0.45; $\bar{x}$ = 0.438; PPL/PL 0.56–0.58, $\bar{x}$ = 0.568; APW/PL 0.45–0.49; $\bar{x}$ = 0.480; PPW/PL 0.51–0.54, $\bar{x}$ = 0.526). Lateral margins of the femoral and anal scutes curved gradually toward the midline. Bridge moderate in length with a small axillary and a small inguinal scale; B/PL 0.28–0.31, $\bar{x}$ = 0.297; B/CL 0.26–0.29, $\bar{x}$ = 0.276. The average plastral formula is Abd. > Pect. > An. > Gul. > Fem. > Hum. The interanal seam is complete. Plastron light brown with dark brown or black seams. A dark bar is present on the bridge, and the undersides of the marginals are yellow with dark seams and some faded dark pigment.

The head is narrow, the snout pointed and only slightly projecting, and the upper jaw is slightly hooked. Coloration is olive to brown. A narrow yellow black-bordered stripe extends backward from the eye above the tympanum and onto the neck, and a second, similar stripe extends posteriorly from the corner of the mouth, passes below

Fig. 2. Head of *Cuora yunnanensis.*

the tympanum and onto the neck. The chin and throat are marked with large yellow to orange blotches. The jaws are yellow to tan. The neck is brown with two narrow yellow or orange, black-bordered, longitudinal stripes on each side.

The digits are fully webbed. The forelegs are brown with longitudinal stripes of yellow or orange spots. There are several large, band-like, transverse scales on the anterior surface of each foreleg; foreleg scale rows 9–11, $\bar{x} = 10$. The hindlegs are brown with a narrow outer fringe of small yellow scales. The tail is brown with two black-bordered, yellow dorsal stripes.

Males have concave plastra, and longer tails with the vent beyond the carapacial rim; females have flat plastra and shorter tails with the vent beneath the posterior marginals. The female carapace is more domed than that of the male.

Cuora pani Song 1984
Fig. 3

Holotype.—Shaanxi Institute of Zoology 80170 (adult male); *Allotype.*—SIZ 80171 (adult female), both from Xujiaba, Shaanxi Province, China; 17 Jun 1981, Song Ming-Tao.

Specimens examined.—WHR 1–11 (live; 5 males, 6 females) USNM 4 males).

Diagnosis.—A species of *Cuora* with reddish-brown vertebrals on an olive to dark brown, carinate carapace, a posteriorly notched plastron with a complete interanal seam, a plastral pattern of large, often separated, black blotches, yellow skin, a yellow postorbital stripe, and an unmarked chin and throat.

Description.—Carapace length to 156.5 mm (males 120 from Song 1984; females 156.5), oval, flattened. (D/CL 0.30–0.39, $\bar{x} = 0.352$; D/CW, 0.35–0.50, $\bar{x} = 0.467$; CW/CL 0.64–0.79, $\bar{x} = 0.729$); widest at level of marginal 8, highest near seam separating vertebrals 2 and 3. Sides straight with no indentation at the bridge. Marginals flared, those most posterior slightly serrated, the first anterior marginals widest, those along the sides may be slightly upturned (MW 9.2–18.8 mm, $\bar{x} = 12.7$; MW/CW 0.16–0.24, $\bar{x} = 0.197$; MW/CL 0.12–0.17, $\bar{x} = 0.143$). There is a slight notch between the twelfth marginals. Cervical scute longer than wide (W/L CS 0.35–0.91, $\bar{x} = 0.710$). Each vertebral scute wider than long, but narrower than the pleural scutes. The first and fifth vertebrals are flared. General texture of the carapacial scutes smooth in older individuals, but granulated with low, rounded rugosites in those to 84 mm CL. A low keel extends medially along the vertebrals; no lateral keels are present. Carapace in live individuals is olive-brown with chestnut-brown to reddish-brown pigment on the vertebrals, and occasionally as spots on the pleurals, and with a narrow yellow rim.

Plastral length to 146.5 mm (males 84.0, but PL not reported for large male in Song 1984; females 146.5); PL/CL 0.91–0.97, $\bar{x} = 0.932$; hinged between the pectoral and abdominal scutes, slightly upturned anteriorly and notched posteriorly. The posterior plastral lobe is longer and wider than the anterior lobe (APL/PL 0.40–0.46, $\bar{x} = 0.423$; PPL/PL 0.54–0.58, $\bar{x} = 0.560$; APW/PL 0.48–0.54, $\bar{x} = 0.502$; PPW/PL 0.51–0.60, $\bar{x} = 0.551$). Lateral margins of the femoral and anal scutes curve gradually toward the midline. Bridge moderate in length with a small axillary and a small inguinal scale; B/PL 0.27–0.35, $\bar{x} = 0.311$; B/CL 0.25–0.34, $\bar{x} = 0.290$. The average plastral formula is An. > Pect. > Abd. > Gul. > Fem. > Hum., but much variation exists in the 15 specimens examined, 4 had the average formula, 5 were An. > Abd. > Pect. > Gul. > Hum. > Fem.; 3 each were An. > Abd. > Pect. > Gul. > Fem. > Hum. and Pect. > An. > Abd. > Gul. > Fem. > Hum. The interanal seam is complete. Plastron yellow with large, triangular-shaped black blotches which may touch, but are often separated. A black bar is present on the bridge, and

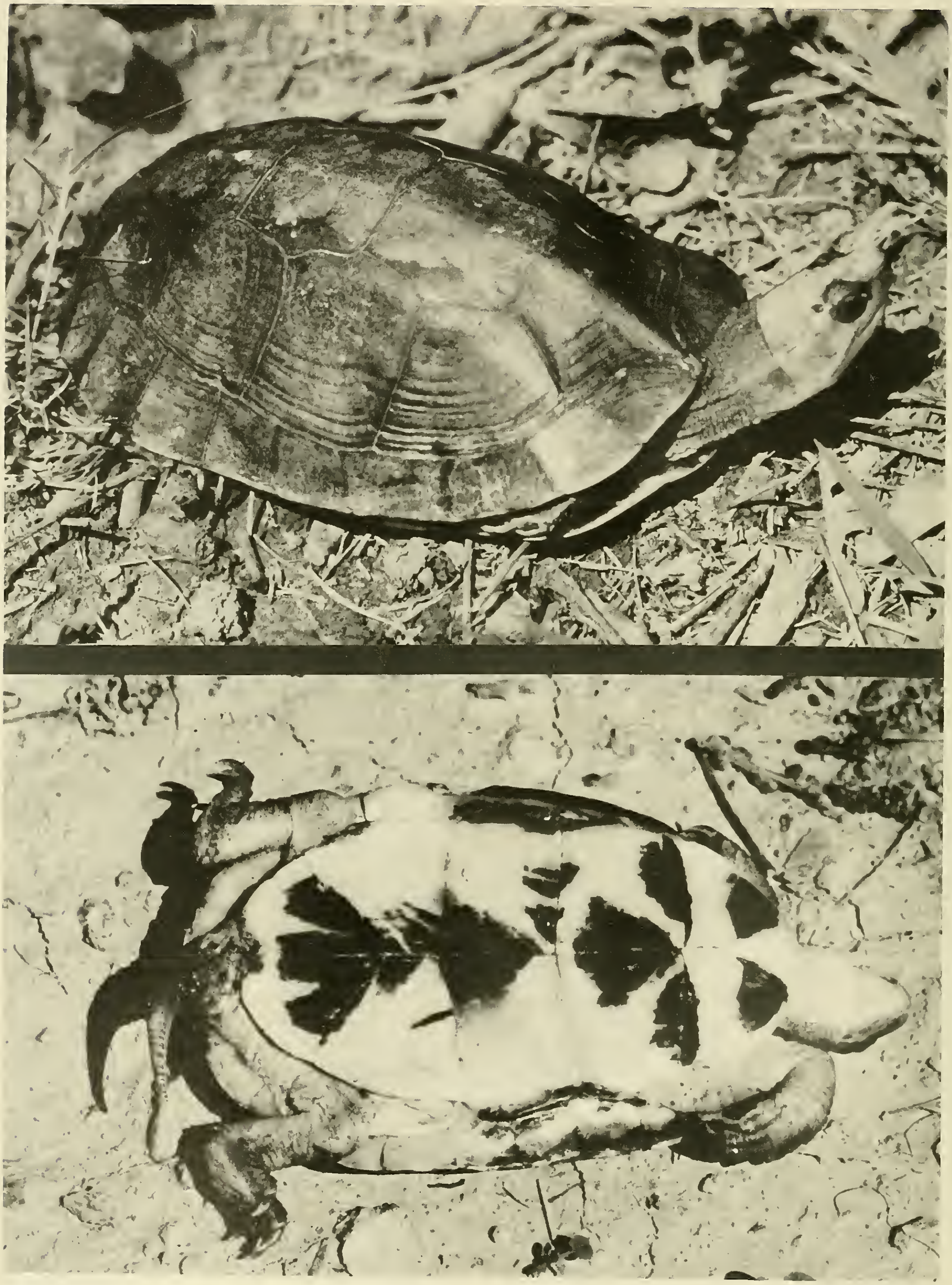

Fig. 3. Carapace and plastron of *Cuora pani.*

the undersides of the marginals are yellow, with some black pigment on those at the bridge.

The head is narrow, the snout is pointed but nonprojecting, and the upper jaw is slightly hooked. Coloration is lemon-yellow. A narrow, black-bordered stripe extends posteriorly from the eye onto the neck, and a second similar stripe runs backward from the corner of the mouth through the tympanum and onto the neck. Both of these stripes almost disappear in older individuals. The iris in life is greenish-yellow. The jaws, chin and throat are immaculate yellow. The neck is greenish-yellow dorsally and laterally, but yellow ventrally; narrow often broken, yellow stripes may occur on the sides or dorsal surface.

The digits are fully webbed. The limbs are olive on the outer surface but yellow to orange beneath. There are several large, band-like, transverse scales on the anterior surface of each foreleg; foreleg scale rows 10–15, $\bar{x} = 11.7$. The tail is olive with two black-bordered, yellow-dorsal stripes.

Sexual dimorphism as in *C. yunnanensis.*

Acknowledgments

I wish to thank William H. Randell for calling my attention to this problem, and for allowing me to examine his live specimens of *Cuora pani.* George R. Zug commented on an early draft of the manuscript, and Evelyn M. Ernst helped in the examination of the specimens.

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A NEW SPECIES OF *PORPHYRIO* (AVES: RALLIDAE) FROM ARCHEOLOGICAL SITES IN THE MARQUESAS ISLANDS

David W. Steadman

Abstract.—A new species of gallinule, *Porphyrio paepae,* is described from bones found in archeological sites on Hiva Oa and Tahuata, Marquesas Islands. This gallinule represents the only species of *Porphyrio* in the Pacific east of Samoa, Tonga, and Niue, where *P. porphyrio* occurs today. The occurrence of a species of *Porphyrio* in the Marquesas Islands, at the northeastern edge of Polynesia, suggests that congeners may have occurred through much of eastern Polynesia in prehistoric times.

Bones from Polynesian archeological sites have shown that the avifaunas of individual islands were much richer in species before human colonization. Here I describe a new species of gallinule of the genus *Porphyrio* from archeological sites on Hiva Oa and Tahuata islands in the Marquesas. The sites on Hiva Oa were described by Bellwood (1972, 1979:331–337) and Sinoto (1979). The site on Tahuata was excavated recently by B. Rolett, whose studies are in progress. The extinct landbirds from sites on both islands are reviewed briefly by Steadman (in press) and include new species of parrots (Steadman & Zarriello, 1987).

Materials and methods.—Comparative skeletons are from the Division of Birds, USNM. Aside from those of *Porphyrio* (see Tables 1–4), skeletons of *Gallirallus philippensis, Gallirallus owstoni, Gallicrex cinerea, Gallinula chloropus,* and *Fulica atra,* as well as fossils of undescribed species of *Gallirallus* from the Marquesas and elsewhere, were examined to determine generic relationships. Abbreviations: BPBM = Bernice P. Bishop Museum; USNM = National Museum of Natural History, Smithsonian Institution; yr B.P. = corrected radiocarbon years before present. Osteological terminology usually follows that of Baumel et al. (1979). Measurements were taken with dial calipers with 0.05 mm increments, rounded to the nearest 0.1 mm.

Systematic Paleontology

Class Aves
Order Gruiformes
Family Rallidae
Genus *Porphyrio*

Following Olson (1973:409), I regard the genus *Porphyrio* to include "*Porphyrula*" and "*Notornis.*" The fossil material is referred to *Porphyrio* rather than to other large rails (*Gallirallus, Gallicrex, Gallinula, Fulica*) because of the following characters. Carpometacarpus—processus pisiformis extends farther cranially; fovea carpalis caudalis deeper; great distance from processus pisiformis to departure of os metacarpi majus and os metacarpi minus; short distal symphysis of os metacarpi majus and os metacarpi minus. Synsacrum—stout overall; strongly bent ventrally in caudal portion. Femur—more obtuse angle formed at the junction of the impressiones obturatoriae and trochanter femoris; similar size and position of the impressiones iliotrochanteria and linea intermuscularis caudalis; medial margin of the condylus medialis oriented roughly parallel to the shaft rather than diagonal. Tibiotarsus—deep sulcus

Fig. 1. The femur of *Porphyrio* in cranial (A–C) and caudal (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* holotype, BPBM 165649, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

musculo fibularis; sharp cranio-medial and cranio-lateral margins of the shaft; deep incisura intercondylaris. Tarsometatarsus—extremely thin proximo-medial portion of shaft; more distinct fossa metatarsi. Pedal phalanx—more elongate.

Porphyrio paepae, new species
Figs. 1–4

Holotype.—Femur lacking only the medial portion of facies articularis acetabularis, BPBM 165649, from Hanatekua Shelter No. 2 Site (MH3-12), square E2-F2, 100–140 cm, Hiva Oa, Marquesas Islands, 19 Dec 1967, P. Bellwood. (This site has been referred to as Hanatukua, with an earlier Bishop Museum site designation of MH-11.)

Paratypes.—Hiva Oa, 1967, P. Bellwood: Pelvis—BPBM 165656, Hanatekua Shelter No. 2 Site (MH3-12), square D1, 80–100 cm. Femur (tentatively referred)—BPBM 168539, Hanatekua Beach Site (MH3-13, formerly designated MH-12), test pit 24, 40+ cm. Four tibiotarsi—BPBM 165651, Hanatekua Shelter No. 2 Site (MH3-12), square E1-H1, layer 10 (section collapse); BPBM 165652, Hanatekua Beach Site (MH3-13), test pit 2, layer 4; BPBM 167496, Hanatekua Beach Site (MH3-13), test pit 22, layer 4, 40+ cm; BPBM 165654, Hanaui Site (MH-22), test pit 8. Two tarsometatarsi—BPBM 165650, Hanatekua Shelter No. 2 Site (MH3-12), square E2-F2, 100–150 cm; BPBM 165653, Hanatekua Beach Site (MH3-13), test pit 23, 30+ cm.

Tahuata, Hanamiai Site (MT1), 1985, B. Rolett: Carpometacarpus—BPBM 166427, square L11, layer I37. Synsacrum—BPBM 166432, square L10, layer G/H16 (240–250 cm). Four femora—BPBM 166434, square I12, layer G/H14 (230–240 cm); BPBM 166430, square L11, layer I36; BPBM 166426, square L11, layer I37; BPBM 166424, square K9, layer F10 (180+ cm).

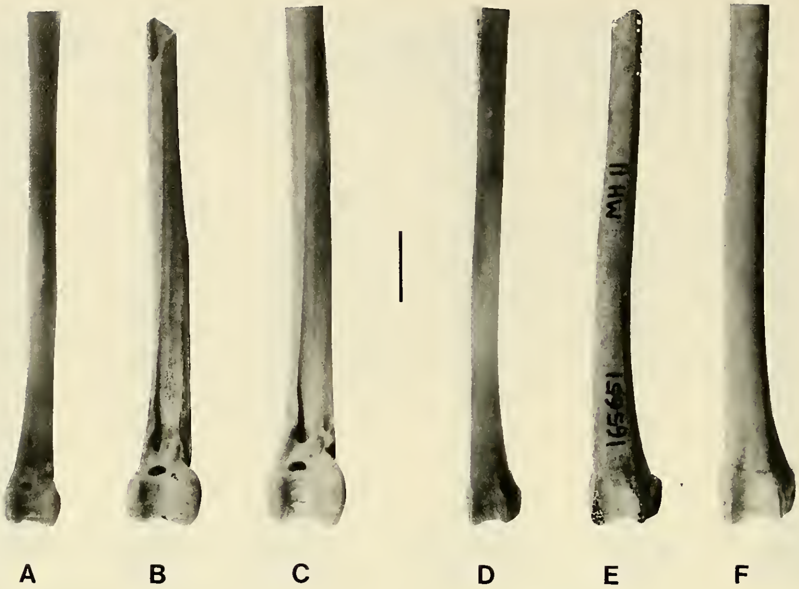

Fig. 2. The tibiotarsus of *Porphyrio* in cranial (A–C) and caudal (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* BPBM 165651, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

Two tibiotarsi—BPBM 166428, square M13, layer H31 (255–260 cm); BPBM 166433, square N13, layer H33 (260–265 cm). Two tarsometatarsi—BPBM 166429, square K11, layer G/H16 (220–230 cm); BPBM 166425, square K10, layer G13 (220–230 cm).

Diagnosis.—Smaller than any species of *Porphyrio* except the "*Porphyrula*" group (*P. martinica, P. alleni, P. flavirostris*) (Tables 1–4). Carpometacarpus: short; os metacarpi minus and os metacarpi majus fused proximally for a greater distance. Femur: shaft broader than in *P. martinica*; shaft straighter than in *P. porphyrio, P. poliocephalus,* or *P. pulverulentus*; sulcus patellaris broader than in *P. martinica*; impressio ligamentum cruciati caudalis deeper than in *P. martinica*; in medial aspect, condylus medialis joins caudal surface of the shaft nearly perpendicularly (more obtuse angle in all others); in lateral aspect, the proximal margin of crista trochanteris less rounded than in *P. porphyrio.* Tibiotarsus: shaft relatively shallower than in *P. porphyrio*; incisura intercondylaris relatively broader and deeper than in all others; proximal portion of condylus lateralis more rounded and joins the shaft more perpendicularly (an obtuse angle is formed in all others).

Etymology.—From the Marquesan word *paepae,* which is a prehistoric rectangular stone platform that served as a base for various dwellings (Bellwood 1979:333 and fig. 12.3). Like the extinct gallinule described here, the *paepae* is no longer an active part of Marquesan culture, although its remains are scattered on the islands.

Remarks.—No skeletons were available for *Porphyrio alleni* of Africa or *P. flavirostris* of South America. The former is about the size of *P. martinica,* while the latter is smaller than *P. martinica.*

Discussion

The chronology of the Hanatekua Shelter No. 2 Site is poorly defined, although the bones of *Porphyrio paepae* from this site may be from pre-cultural levels (Y. H. Sin-

Fig. 3. The tarsometatarsus of *Porphyrio* in dorsal (A–C) and plantar (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* BPBM 165650, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

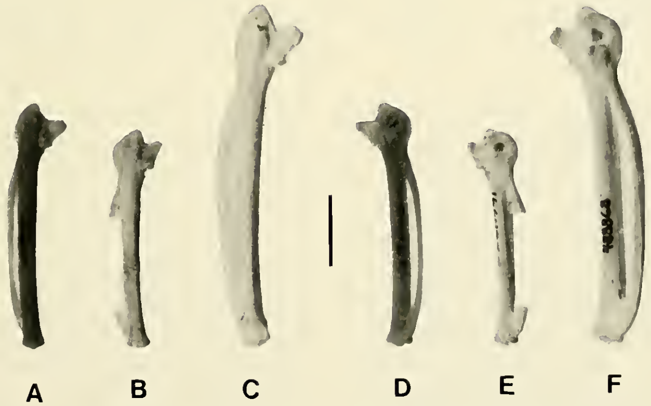

Fig. 4. The carpometacarpus of *Porphyrio* in dorsal (A–C) and ventral (D–F) aspects. A, D, *P. martinica,* USNM 501122, male; B, E, *P. paepae,* BPBM 166427, unsexed; C, F, *P. porphyrio,* USNM 488868, male. Scale bar = 10 mm.

Table 1.—Measurements (in mm) of the carpometacarpus of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown.

	Total length	Proximal width	Proximal depth	Least depth of shaft
Porphyrio paepae	29.3	6.8	3.6	2.1
Tahuata, Marquesas (U)	1	1	1	1
BPBM 166427				
Porphyrio porphyrio	45.2	9.5	4.8	3.0
Bechuanaland (M)	1	1	1	1
USNM 488868				
Porphyrio porphyrio	—	10.5	4.9	—
New Caledonia (M)		1	1	
USNM 561547				
Porphyrio porphyrio	47.1	10.0	4.8	3.6
New Caledonia (F)	47.0–47.2	9.9–10.0	4.8	3.5–3.7
USNM 561549, 561551	2	2	2	2
Porphyrio porphyrio	52.4	10.8	5.0	3.9
Captive (M) USNM	52.0–52.9	10.8–10.9	4.9–5.2	3.9
555504, 557529	2	2	2	2
Porphyrio poliocephalus	43.5	9.5	4.4	2.8
Thailand (F)	1	1	1	1
USNM 343212				
Porphyrio poliocephalus	54.5	11.5	5.3	3.6
Captive (M) USNM 491890	1	1	1	1
Porphyrio poliocephalus	43.5	10.0	4.3	3.4
Captive (F) USNM 347372	1	1	1	1
Porphyrio pulverulentus	47.0	10.0	4.7	3.4
Philippines (M, U)	46.5–47.4	9.9–10.2	4.6–4.8	3.3–3.5
USNM 200817, 226035	2	2	2	2
Porphyrio martinica	32.6	7.1	3.4	2.1
Florida (M)	31.6–33.1	6.8–7.5	3.2–3.5	2.0–2.2
USNM 501122, 501126,	5	5	5	5
501128, 501129, 501131				
Porphyrio martinica	30.8	6.6	3.2	2.1
Florida (F) USNM	30.6–31.3	6.3–6.9	3.0–3.4	2.0–2.3
501123–501125, 501130	4	4	4	4

oto, pers. comm.). Kirch (1986:25) reported a radiocarbon date of 1930 ± 80 yr B.P. for Hanatekua Shelter No. 2, although I am not sure how this date relates stratigraphically to the fossils of *P. paepae.* The chronology of the Hanamiai Site on Tahuata is currently being resolved and lies mainly in the range of 1500 to 800 yr B.P. (B. Rolett, pers. comm.). All bones of *P. paepae* from Hanamiai are associated with Polynesian artifacts from the lowest cultural levels.

The only other large rails from the Marquesas are extinct, undescribed, flightless species of *Gallirallus* from Ua Huka, Nuku Hiva, Hiva Oa, and Tahuata. The wing elements in these species are much smaller than those in any species of *Porphyrio,* including *P. paepae.* Based upon the size and morphology of the carpometacarpus, *P. paepae* had somewhat reduced powers of flight compared to congeners, yet probably was not flightless. A crude indication of volancy is presented in Table 5 by the ratio of the total lengths of the carpometacarpus and femur (the only wing or leg bones known in *P. paepae* for which the total length could

Table 2.—Measurements (in mm) of the femur of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown.

	Total length	Depth of proximal end	Least width of shaft	Least depth of shaft	Width of distal end	Depth of condylus medialis
Porphyrio paepae	52.5	7.7	3.9	4.0	9.5	7.0
Hiva Oa, Marquesas (U)	1	1	1	1	1	1
Holotype BPBM 165649						
Porphyrio paepae	51.7+	—	4.2	4.3	9.5+	—
Tahuata, Marquesas (U)	1		4.1–4.2	4.2–4.4	1	
BPBM 166430, 166434			2	2		
Porphyrio porphyrio	81.1	12.3	5.9	5.8	13.0	9.9
New Caledonia (M)	1	1	1	1	1	1
USNM 561547						
Porphyrio porphyrio	72.6	10.9	5.3	5.5	13.8	10.0
New Caledonia (F)	72.4–72.8	10.9	5.2–5.4	5.4–5.6	1	1
USNM 561549, 561551	2	2	2	2		
Porphyrio porphyrio	74.5	10.1	5.1	5.0	12.6	9.6
Bechuanaland (M)	1	1	1	1	12.3–12.9	9.6–9.7
USNM 488868					2	2
Porphyrio porphyrio	76.8	11.2	5.9	5.8	13.5	11.3
Captive (M)	73.8–79.8	11.0–11.4	5.8–6.0	5.7–6.0	13.3–13.7	11.2–11.4
USNM 555504, 557529	2	2	2	2	2	2
Porphyrio poliocephalus	68.8	9.3	4.8	4.3	11.7	9.8
Thailand (F)	1	1	1	1	1	1
USNM 343212						
Porphyrio poliocephalus	76.2	11.3	5.5	5.7	13.2	10.8
Captive (M) USNM	62.7–83.7	8.9–12.5	4.4–6.3	4.4–6.5	10.8–14.6	8.8–12.0
318498, 344474, 491890	3	3	3	3	3	3
Porphyrio poliocephalus	67.0	9.6	4.6	4.4	11.3	9.2
Captive (F) USNM	64.6–70.7	9.1–9.9	4.5–4.7	4.2–4.6	10.9–11.8	8.7–9.4
289454, 321151, 347372	3	3	3	3	3	3
Porphyrio poliocephalus	69.0	9.2	4.8	5.2	12.0	9.4
Captive (U)	61.2–76.8	1	4.4–5.1	4.6–5.7	10.8–13.3	8.1–10.8
USNM 19761, 227119	2		2	2	2	2
Porphyrio pulverulentus	78.2	11.2	5.2	5.9	13.8	11.1
Philippines (M)	77.9–78.4	11.0–11.4	5.1–5.3	2	13.4–14.2	10.5–11.7
USNM 226035, 292297	2	2	2		2	2
Porphyrio pulverulentus	75.4	10.8	5.1	5.6	13.4	10.8
Philippines (F)	1	1	1	1	1	1
USNM 292296						
Porphyrio martinica	54.2	7.0	3.6	3.8	8.5	7.0
Florida (M) USNM	52.8–55.4	6.7–7.2	3.4–3.7	3.6–3.9	8.1–8.7	6.7–7.2
501122, 501126, 501128,	4	5	5	5	5	4
501129, 501131						
Porphyrio martinica	50.7	6.6	3.4	3.5	7.9	6.6
Florida, Louisiana,	47.7–52.4	6.1–7.2	3.2–3.6	3.2–3.8	7.4–8.8	6.1–7.1
Dominican Republic (F)	6	6	6	6	6	6
USNM 288205, 499438,						
501123–501125, 501130						

Table 3.—Measurements (in mm) of the tibiotarsus of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown. PE = proximal end. PS = pons supratendineus.

	Least width of shaft	Width of shaft at PE of PS	Least depth of shaft	Distal width	Height of condylus medialis	Height of condylus lateralis	Depth of condylus medialis	Depth of condylus lateralis
Porphyrio paepae	4.0	6.4	3.4	9.8	5.8	8.2	9.6	8.9+
Hiva Oa (U) BPBM	3.7–4.2	6.1–6.7	3.3–3.5	1	1	1	1	1
165651, 165652,	3	2	4					
165654, 167496								
Porphyrio paepae	—	5.8	3.4	8.6+	5.4+	7.3	8.5+	8.3
Tahuata (U) BPBM		5.7–6.0	3.4	1	1	1	1	1
1664228, 166433		2	2					
Porphyrio porphyrio	5.1	7.2	3.8	10.2	6.0	9.1	10.5	10.2
Bechuanaland (M)	1	1	1	1	1	1	1	1
USNM 488868								
Porphyrio porphyrio	6.0	8.1	4.8	11.1	7.0	9.8	11.6	11.3
New Caledonia (M)	1	1	1	1	1	1	1	1
USNM 561547								
Porphyrio porphyrio	5.6	7.6	4.3	10.4	6.4	9.2	11.0	10.4
New Caledonia (F)	5.4–5.9	7.4–7.8	4.3	10.3–10.5	6.3–6.4	9.2–9.3	10.8–11.1	10.2–10.5
USNM 561549, 561551	2	2	2	2	2	2	2	2
Porphyrio porphyrio	—	7.7	—	10.6	6.3+	9.9	10.9+	10.6+
Tikopia, Solomon Is.		1		1	1	1	1	1
BPBM 166227, 166263								
Porphyrio porphyrio	5.7	8.6	4.6	11.6	6.8	10.2	12.0	11.2
Captive (M)	5.5–5.9	8.3–8.9	2	11.5–11.8	6.8–6.9	10.2–10.3	11.9–12.1	10.9–11.5
USNM 555504, 557529	2	2		2	2	2	2	2
Porphyrio poliocephalus	4.4	6.6	3.5	9.2	5.6	8.2	9.9	9.2
Thailand (F)	4.3–4.6	6.4–6.7	3.4–3.6	9.1–9.2	5.3–5.9	8.0–8.3	9.6–10.2	2
USNM 343212, 343213	2	2	2	2	2	2	2	
Porphyrio poliocephalus	5.2	7.6	4.0	10.6	6.2	9.0	11.1	10.0
Captive (M)	4.5–5.8	6.8–8.5	3.4–4.6	9.1–12.0	5.3—7.1	7.8–10.3	9.2–13.0	8.6–11.3
USNM 344474, 491890	2	2	2	2	2	2	2	2
Porphyrio poliocephalus	4.8	6.8	4.0	9.7	6.0	8.4	10.0	9.4
Captive (F)	4.7–4.9	6.5–7.1	3.6–4.3	1	2	8.1–8.6	1	9.3–9.4
USNM 321151, 347372	2	2	2			2		2
Porphyrio pulverulentus	5.5	7.8	4.2	11.2	6.5	10.0	11.4	10.7
Philippines (M, U)	5.4–5.6	7.7–7.9	4.1–4.4	2	6.3–6.7	9.9–10.1	11.0–11.8	10.5–10.9
USNM 200817, 226035	2	2	2		2	2	2	2
Porphyrio martinica	3.5	5.0	2.7	7.1	4.3	6.2	7.0	6.9
Florida (M)	3.3–3.7	4.8–5.4	2.6–2.9	6.9–7.5	4.1–4.7	6.1–6.4	6.9–7.3	6.8–7.1
USNM 501122, 501126,	5	5	5	5	5	5	5	5
501128, 501129, 501131								
Porphyrio martinica	3.4	4.9	2.6	6.8	4.2	6.0	6.7	6.6
Florida, Louisiana,	2.8–3.6	4.7–5.1	2.5–2.8	6.3–7.5	3.9–4.4	5.8–6.3	6.1–7.0	6.2–7.1
Dominican Republic (F)	6	6	6	6	6	6	6	6
USNM 288205, 499438,								
501123–501125, 501130								

be determined). Although the value of this ratio is less in *P. paepae* than in other congeners, the difference is small and might be of little significance, especially because the fossils are of unknown sex. Note also that the skeletons of captive individuals of *P. porphyrio* and *P. poliocephalus* have higher ratios than those of wild individuals. For

Table 4.—Measurements (in mm) of the tarsometatarsus of *Porphyrio,* with mean, range, and sample size. F = female. M = male. U = sex unknown.

	Minimum width of shaft	Minimum depth of shaft	Proximal width	Width of hypotarsus
Porphyrio paepae	4.9	2.9	—	—
Hiva Oa, Marquesas (U)	1	1		
BPBM 165650				
Porphyrio paepae	—	—	10.4	5.1
Tahuata, Marquesas (U)			1	1
BPBM 166425				
Porphyrio porphyrio	5.0	3.6	10.9	5.4
Bechuanaland (M)	1	1	1	1
USNM 488868				
Porphyrio porphyrio	—	3.9	11.8	5.8
New Caledonia (M)		1	1	1
USNM 561547				
Porphyrio porphyrio	5.5	3.6	10.9	5.4
New Caledonia (F)	5.4–5.6	3.6–3.7	10.8–11.0	5.3–5.5
USNM 561549, 561551	2	2	2	2
Porphyrio porphyrio	—	3.7	—	5.6
Tikopia, Solomon Is. (U)		1		1
BPBM 166228, 166230				
Porphyrio porphyrio	5.9	4.2	12.4	5.8
Captive (M)	5.7–6.1	4.1–4.2	12.3–12.5	5.8–5.9
USNM 555504, 557529	2	2	2	2
Porphyrio poliocephalus	4.6	3.2	9.9	4.7
Thailand (F) USNM 343212	1	1	1	1
Porphyrio poliocephalus	6.5	4.3	12.4	6.3
Captive (M) USNM 491890	1	1	1	1
Porphyrio poliocephalus	5.2	3.3	10.4	5.0
Captive (F) USNM 347372	1	1	1	1
Porphyrio pulverulentus	5.5	3.8	11.6	6.0
Philippines (M, U)	5.1–5.9	3.7–4.0	11.5–11.6	6.0–6.1
USNM 200817, 226035	2	2	2	2
Porphyrio martinica	3.8	2.5	7.6	4.0
Florida (M)	3.7–3.9	2.3–2.6	7.3–7.9	3.8–4.3
USNM 501122, 501126, 501128, 501129, 501131	5	5	4	4
Porphyrio martinica	3.6	2.5	7.0	3.6
Florida (F)	3.2–3.9	2.4–2.6	6.7–7.2	3.4–3.7
USNM 501123–501125, 501130	4	4	4	4

this and other reasons, I do not consider the captive individuals to be an absolutely accurate representation of either the quantitative (Tables 1–5) or qualitative characters of *P. porphyrio* or *P. poliocephalus*. The diagnosis is based only upon wild individuals. In all of the tables, the values for *P. martinica* provide the best assessment of the intraspecific variation of wild populations.

Balouet & Olson (in press) have described a flightless, extinct species of *Porphyrio* from late Holocene fossils from New Caledonia. This new species was much larger even than *P. porphyrio,* which is the only other congener in the Pacific, other than the large, flightless species on New Zealand ("*Notornis*") and the historically extinct *P. albus* of Lord Howe Island, which was similar in size

Table 5.—Ratio of total lengths: carpometacarpus divided by femur, expressed as a percentage. From data in Tables 1 and 2.

Porphyrio paepae	56.7 (−)
Tahuata, Marquesas (U)	1
BPBM 166427, 166434	
Porphyrio paepae	55.8
Tahuata and Hiva Oa, Marquesas (U)	1
BPBM 166427, 165649	
Porphyrio porphyrio	60.7
Bechuanaland (M)	1
USNM 488868	
Porphyrio porphyrio	64.8
New Caledonia (F)	64.6–65.1
USNM 561549, 561551	2
Porphyrio porphyrio	68.4
Captive (M)	66.3–70.5
USNM 555504, 557529	2
Porphyrio poliocephalus	63.2
Thailand (F) USNM 343212	1
Porphyrio poliocephalus	66.3
Captive (M) USNM 491890	1
Porphyrio pulverulentus	60.4
Philippines (M)	1
USNM 226035	
Porphyrio martinica	60.6
Florida (4M, 4F)	58.4–62.7
USNM 501122–501126,	8
501128, 501130, 501131	

to *P. porphyrio* but had smaller wings. In the Pacific, *P. porphyrio* occurs from the New Guinean region east through Melanesia to the western Polynesian islands of Tonga, Samoa, and Niue; it has not been recorded, either living or as a fossil, from eastern Polynesia. Thus *P. paepae* represents an eastward range extension of 3200 km for the genus. Because *Porphyrio* once inhabited the Marquesas Islands, at the northeast corner of Polynesia, it is likely that fossils of these gallinules will be discovered elsewhere in eastern Polynesia.

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NITOKRA SPHAEROMATA, A NEW HARPACTICOID COPEPOD CRUSTACEAN ASSOCIATED WITH THE WOOD-BORING ISOPOD, *SPHAEROMA PERUVIANUM,* IN COSTA RICA

Thomas E. Bowman

Abstract.—*Nitokra sphaeromata* is described from the pleopods of the marine flabelliferan isopod *Sphaeroma peruvianum,* collected from burrows in mangroves in the Gulf of Nicoya, Costa Rica. It is the fourth species of *Nitokra,* a genus with about 40 species, known to have commensal relationships. Other crustaceans associated with species of *Sphaeroma, Iais* spp. (Isopoda: Asellota), and *Microsyssistria* (Ostracoda: Entocytheridae) are listed. The commonly used spelling *Nitocra* is replaced by Boeck's correct original spelling *Nitokra.*

During an investigation of the effect of the wood-boring isopod, *Sphaeroma peruvianum* Richardson, 1910, on red mangroves of Pacific Costa Rica by Richard C. Brusca and Diane Perry, a harpacticoid copepod was found on the pleopods of the isopod. Specimens were sent to me for identification, and they proved to be the new species of *Nitokra* described below.

Nitokra sphaeromata, new species
Figs. 1–16

Material.—Costa Rica: Gulf of Nicoya, Punta Morales (ca. 10°04′N, 84°58′W), from pleopods of *Sphaeroma peruvianum* collected from its burrows in red mangroves: holotype ♀ USNM 234096; paratypes 4 ♀, 2 ♂, 1 juv. USNM 234097. Leg. Richard C. Brusca and Diane Perry, Feb 1984.

Etymology.—*Sphaeromata* = "of *Sphaeroma,*" the host genus.

Description.—Lengths of 4 ♀, 1.22, 1.24, 1.25, 1.26 mm; of 2 ♂, 1.10, 1.16 mm. Prosome (head + pedigers 1–4) subequal in length to urosome (pediger 5 thru caudal rami). Greatest body width at level of head. Rostrum oval, short. Urosomites 2–5 with submarginal row of spinules limited to lateral surface, except on anal somite where row is marginal and continues dorsally. Anal operculum with marginal spinules. Caudal ramus about as long as wide, without spinules; medial seta and inner of 2 lateral seta subequal in length; outer lateral seta half as long; dorsal seta reduced to short spine at base of inner terminal seta.

Antenna 1 of ♀ with row of setules on anterior margin of segment 1; in ♂ with 2 serrate spines on segment 4 and 2 clublike setae on penultimate segment. Antenna 2, outer seta of exopod longer than others. Mandibular palp, segment 1 with seta on produced distomedial corner; segment 2 with 1 marginal and 5 terminal setae. Maxilla 1 inner lobe with 3 terminal spines and 1 seta on medial margin; middle lobe with 3 terminal setae; outer lobe with 5 terminal setae and 2 long setae on basal swelling. Maxilla 2 proximal endite produced into curved process with flaring tip armed with close-set setules; middle endite with 2 terminal setae; distal endite produced into claw with 2 slender basal setae and 1 basal seta with broadened tip having concave terminal margin. Maxilliped segment 1 with 3 setae on posterior margin and 1 at anterodistal corner.

All rami of swimming legs 1–4 3-merous. Leg 1 exopod segments (Re 1–3) subequal in length; Re 1–3 with 1-1-5 outer and terminal spines (Se and St) and 0-1-0 inner setae (Si); endopod segments (Ri 1–3) with no Se, 1-1-0 Si, and 3 terminal setae. Ri 1 about 2 × as long as Ri 2 and Ri 3 combined and slightly longer than entire exopod. Inner spine on 2nd basipod modified to dumbbell shape in ♂.

Re 1–3 of legs 2–4 with 1-1-3 Se, those of leg 2 enlarged, 1 St, and 0-1-3 Si. Ri 1–3 of legs 2–4 with 1-1-3, 1-1-3, and 1-1-4 Si, and 1 St.

Leg 5 of ♀, proximal segment as long as broad, with 5 distal setae; next-to-outermost seta slightly more than 2 × length of segment, other setae subequal, as long as segment. Distal segment slightly longer than proximal segment, 2 × as long as wide, with 5 distal setae having proportionate lengths (medial to lateral) 24:20:10:18:28 = 100.

Leg 5 of ♂, proximal segment very short, with 4 distal setae; 3 medial setae about 3 × as long as segment, lateral seta about as long as segment. Distal segment about 2 × as long as wide, with 5 setae having proportionate lengths (medial to lateral) 14:13:38:5:30 = 100.

Leg 6 of ♂ a tiny lobe armed with 2 setae; medial seta nearly 2 × length of lateral seta.

Comparisons.—In Wells (1976) *Nitokra sphaeromata* keys to *N. mediterranea* Brian (1928) and *N. reunionensis* Bozik (1969), from Italy and Réunion Island (western Indian Ocean) respectively. These two species, however, are clearly distinct from *N. sphaeromata.*

Nitokra mediterranea is much smaller, 0.4 mm in length. In legs 2–4 the endopod is shorter than the first two exopod segments combined, whereas in *N. sphaeromata* the endopod of legs 2–4 is nearly as long as the exopod. In leg 1 the third exopod segment has four rather than five spines. In the ♀ leg 5 proximal segment the two lateral setae are subequal, and the distal segment has six rather than five setae. In the ♂ leg 5 proximal segment the two lateral setae are subequal. Finally, the anal operculum of *N. mediterranea* is unarmed.

Nitokra reunionensis is also smaller than *N. sphaeromata,* ♀ ca. 0.75 mm, ♂ 0.70 mm. It has a dorsal spine row on the preanal segment, and the spines of the anal operculum reach beyond the posterior margin of the anal segment. The rami of leg 1 are subequal in length. The ♀ leg 5 proximal segment has four rather than five setae. The ♂ leg 5 proximal segment has two rather than four setae, and the distal segment has six rather than five setae. There are also important differences in the armament of maxilla 1 and 2.

From the Pacific coast of the Americas the only *Nitokra*'s known are the two new taxa described from Monterey Bay, California, by Lang (1965), *N. spinipes armata* and *N. affinis* f. *californica,* and *N. lacustris columbianus* Reid (1988) from Bahía Solano, Colombia (6°17′N, 77°25′W). In both California forms the subterminal row of spines on the urosomites extends completely around them, whereas in *N. sphaeromata* the row is confined to the lateral surface. Also in both the endopod of leg 4 reaches barely beyond the proximal margin of the second exopod segment, and the ♂ leg 6 has three rather than two setae. In *Nitocra lacustris* the exopod of leg 1 is about as long

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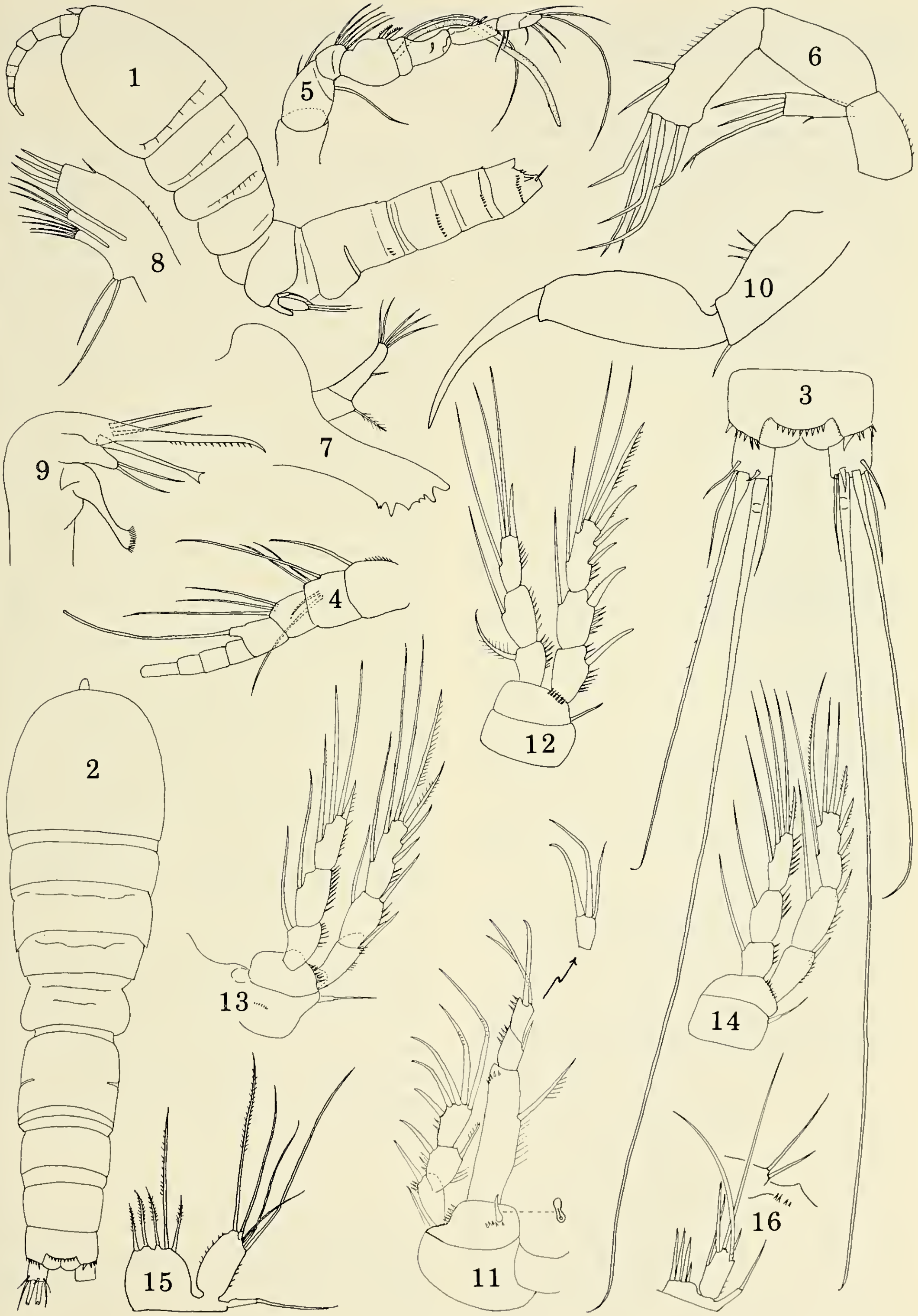
⟶

Figs. 1–16. *Nitokra sphaeromata*: 1, Female, lateral; 2, Female, dorsal; 3, Anal segment and caudal rami of female, dorsal; 4, Antenna 1, female, setae of distal segments omitted; 5, Antenna 1, male; 6, Antenna 2; 7, Mandible; 8, Maxilla 1; 9, Maxilla 2; 10, Maxilliped; 11, Leg 1, arrow points to endopod segment 3 in lateral view, dashed line leads to modified spine on 2nd basipod of male; 12, Leg 2; 13, Leg 3; 14, Leg 4; 15, Leg 5, female; 16, Legs 5 and 6, male.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as the endopod, whereas in *N. sphaeromata* the exopod is shorter than the 1st segment of the endopod.

Host relationship.—Nothing is known about the relationship of *Nitokra sphaeromata* with its host, *Sphaeroma peruvianum,* except that it occurs on the pleopods of the isopod. The copepods were discovered on preserved *Sphaeroma*'s long after the field work in Costa Rica had been completed.

Other crustaceans are associated with species of *Sphaeroma.* The asellote isopod *Iais californica* (Richardson) occurs on *Sphaeroma quoyanum* Milne Edwards (=*S. pentadon* Richardson) (Menzies & Barnard 1951, Hurley 1956, Rotramel 1972), and on *S. terebrans* Bate, as *I. singaporensis* Menzies & Barnard (Menzies & Barnard 1951, Pillai 1961). *Iais pubescens* (Dana) is associated with *S. walkeri* Stebbing (Stebbing 1917, Barnard 1920, 1955) and *S. annandalei* Stebbing (Barnard 1955). The recently introduced population of *S. walkeri* in San Diego Bay, California, is not infested with *Iais* (Carlton & Iverson 1981). The collections of the Division of Crustacea, Smithsonian Institution, contain associated specimens of *Sphaeroma peruvianum* and *Iais californica* from the Gulf of Guayaquil, Ecuador, donated in 1977 by Billy A. F. Hammond, then of the University of North Carolina, Wilmington.

Two species of the entocytherid ostracode genus *Microsyssitria* Hart, Nair, & Hart are associated with *Sphaeroma terebrans*: *M. indica* Hart, Nair, & Hart (1967) in Kerala State, India, and *M. nhlabane* Hart & Clark (1984) from Lake Nhlabane, South Africa.

Nitokra sphaeromata is the fourth species of *Nitokra* known to have commensal relationships. *Nitokra bdellurae* lives in the egg capsules of *Bdellura propinqua* and *B. candida,* flatworms which live upon the carapace of the horseshoe crab *Limulus* (Liddell 1912). *Nitokra divaricata* lives in the gill chambers of the crayfishes *Astacus fluviatilis* (see Chappuis 1926) and *A. leptodactylus* (see Jakubisiak 1939). *Nitokra medusaea* was found on the exumbrellar surface of an unidentified species of the scyphozoan genus *Aurelia* (Humes 1953).

Nitokra or *Nitocra*?

The correct spelling of the harpacticoid genus is *Nitokra,* Boeck's (1865) original spelling. Later authors, except Brady & Robertson (1873) have spelled the genus *Nitocra.* The first to use the latter spelling appears to have been Giesbrecht (1881), who did so without comment. It can be presumed that Giesbrecht considered *Nitocra* the correct Latin form, the Greek letter kappa being transliterated as "c," as given today in ICZN Appendix B. However, ICZN Article 11(b)(v) states that the letter "k" may be used in scientific names, hence *Nitokra* Boek, 1865 is clearly available. *Nitocra* is an "incorrect subsequent spelling" and not available [ICZN Article 33(c)]. *Nitokra* cannot be suppressed as an unused senior synonym [ICZN Article 79(c)], since *Nitocra* is not available and therefore not a synonym.

The choices available under the ICZN are two: (1) Return to the correct original spelling *Nitokra,* even though it has not been used for more than a century, and *Nitocra,* with about 40 species, has appeared in the zoological literature several hundred times. (2) Ask the Commission to use its plenary power to suppress *Nitokra* and validate *Nitocra,* in accordance with usage.

I have elected the first choice because the matter seems too trivial to submit to the Commission. Although well known among copepodologists, *Nitocra* is scarcely a familiar name among other zoologists. I am not replacing a long-standing name but returning to the original spelling, following the ICZN.

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POLYCHAETOUS ANNELIDS FROM THE INTERTIDAL ROCKY SUBSTRATUM OF A POLLUTED AREA OF THE RÍA DE PONTEVEDRA (GALICIA, SPAIN)
2. TAXONOMIC ASPECTS WITH THE DESCRIPTION OF *LUGIA ATLANTICA*, N. SP.

Antonio Villalba and José M. Viéitez

Abstract.—Some taxonomic aspects derived from a study of the taxocoenosis of polychaetes inhabiting the intertidal zone of an area in the ría de Pontevedra (NW of Spain), affected by industrial wastes, are presented. A new species, *Lugia atlantica* (Phyllodocidae), is described, and detailed descriptions of specimens of the genus *Micronereis* Claparède (Nereididae) and family Capitellidae with dubious taxonomic positions, are offered.

In a previous report (Villalba & Viéitez 1985), the taxocoenosis of polychaetous annelids inhabiting the intertidal zone of an area in the ría de Pontevedra was studied, and the effects of industrial wastes from Kraftpaper and chlorine-soda factories on these components of the benthic fauna were discussed. Among the sampled material, some specimens with interesting taxonomic implications were found. These are described and discussed below.

Three sampling stations were established on the southern side of the estuary (Fig. 1). The studied area, sampling stations, material and methods are described elsewhere (Villalba & Viéitez 1985).

Family Phyllodocidae Williams, 1851
Genus *Lugia* Quatrefages, 1865
Lugia atlantica, new species
Fig. 2

Lugia sp. Villalba & Viéitez, 1985:376.
Phyllodocidae ind. Villalba & Viéitez, 1985: 373–376.

Material examined.—Sta M (42°24′N, 05°00′W), lowest intertidal band, holotype and paratype. Sta A, intertidal band of *Ulva rigida* and *Fucus vesiculosus*, paratype. Sta B, intertidal band of *U. rigida* and *F. vesiculosus*, paratype. All specimens deposited in the collection of the Zoology Department of the University of Alcalá de Henares, Madrid.

Description of holotype.—Elongate body, tapering anteriorly and posteriorly, with constriction on segment 10, at level of end of inverted proboscis. Segments 25, 1.8 mm long and 0.4 mm wide. Prostomium round, slightly bilobed, about as wide as long; narrower anterior end with 4 cirriform antennae of equal length, slightly shorter than prostomium (Fig. 2A). Without median antennae or nuchal papilla. One pair of lensed eyes on posterior part of prostomium. Proboscis inverted; when observed through body wall it consisted of wider region with papillae and perhaps narrower bare region.

Segment 1 dorsally distinct from prostomium, with pair of tentacular cirri tapering gradually distally, longer than antennae. Segment 2 with pair of similar dorsal tentacular cirri but twice as long; setal lobes with aciculum and setae; pair of ventral cirri shorter than dorsal tentacular ones, but longer than following ventral cirri; similar in shape and size to remaining dorsal cirri. Tentacular formula: $1 + S\frac{1}{N} + S\frac{N}{N}$ (Fig. 2A).

Parapodia uniramous; from segment 3 consisting of lanceolate dorsal cirrus, setigerous lobe with aciculum and setae, and shorter, oval ventral cirrus. Setal lobes with 2 rounded presetal lobes of equal size. Aciculum with blunt tip and very slender extension protruding from setal lobe (Fig. 2D). Setae of 2 kinds: compound setae variable in number per parapodium, from 3 setae in 2nd segment to 9 in middle region of body. Compound setae consisting of smooth shaft with swollen joint bearing bundle of very small spines and 2 larger unequal spines; blades minutely serrated, with obliquely striated surface (Fig. 2B); simple setae, single one in parapodia of segments 20 to 23, with very finely serrated distal tip (Fig. 2C). Parapodia of posterior 2 segments very reduced, without setae, perhaps area of active growth. Anal cirri lacking.

Color in formalin light brown with darker spots.

Paratypes.—Segments from 25 to 28. One specimen with proboscis slightly everted, showing portion covered with fleshy papillae. Number of posterior segments bearing simple setae from 2 to 6. All of paratypes with 2 lanceolate anal cirri, slightly longer than dorsal cirri of middle region.

Remarks.—Quatrefages (1866:152) included *Eteone aurantiaca* Schmarda, 1861, and *E. pterophora* Ehlers, 1864, in his new genus *Lugia.* Bergstrom (1914:184) selected Ehlers's species as the type species and included a diagnosis for the genus. Bergstrom (1914:201) also retained Schmarda's species in *Eteone.* In her Catalogue, Hartman (1959: 154) incorrectly listed Schmarda's species as the type species of *Lugia*; this was followed by Fauchald (1977:49).

Uschakov (1958:204) added *Lugia rarica* from the Kurile-Kamchatka trench but later (1972:121, 1974:116), referred it to *Mystides rarica,* based on the lack of dorsal cirri on segment 3.

Uschakov (1972:116, 1974:113) added *Lugia abyssicola* from abyssal bottoms off Japan and the Pacific Ocean off California. Campoy & Alquézar (1982:123) and Alós, Campoy & Pereira (1982:143) added *Lugia incognita* from the Iberian Peninsula.

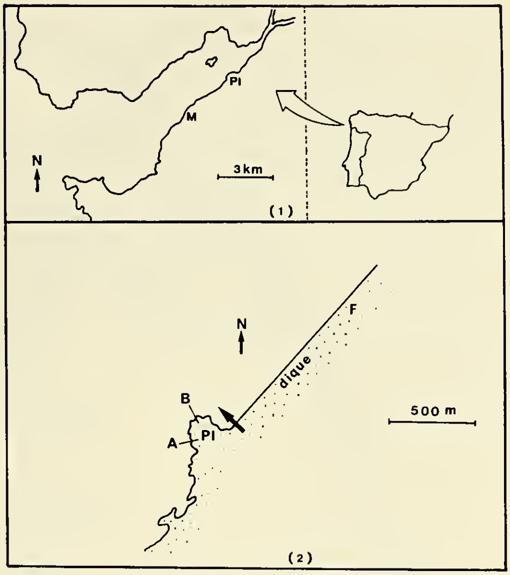

Fig. 1. (1) Map of the ría de Pontevedra showing the Península of Placeres, Pl (with two sampling stations) and Mogor, M (the third sampling station); (2) Detail of the Península of Placeres showing the location of two sampling stations, A and B, and the industrial complex, F. The location of the sewer is marked by the arrow. (Dique = Dike).

Lugia atlantica differs from *L. pterophora,* which is characterized by setae with smooth blades (without serrations and striations), lacking simple setae, and by the presence of a very elongate prostomium (Ehlers 1864:pl. 6, figs. 22–25; Fauvel 1923:fig. 63i).

There are ecological and morphological differences between *L. atlantica* and *L. abyssicola,* the later inhabiting the abyssal zone and lacking eyes and simple setae (Uschakov 1972, 1974:figs. 1–5).

Lugia atlantica differs from *L. incognita,* the latter having much shorter and rounded tentacular cirri with rounded tips, dorsal cirri, lacking simple setae and with fewer compound setae per parapodium (Campoy & Alquézar 1982:fig. 2A–F).

Etymology.—The name *atlantica* is pro-

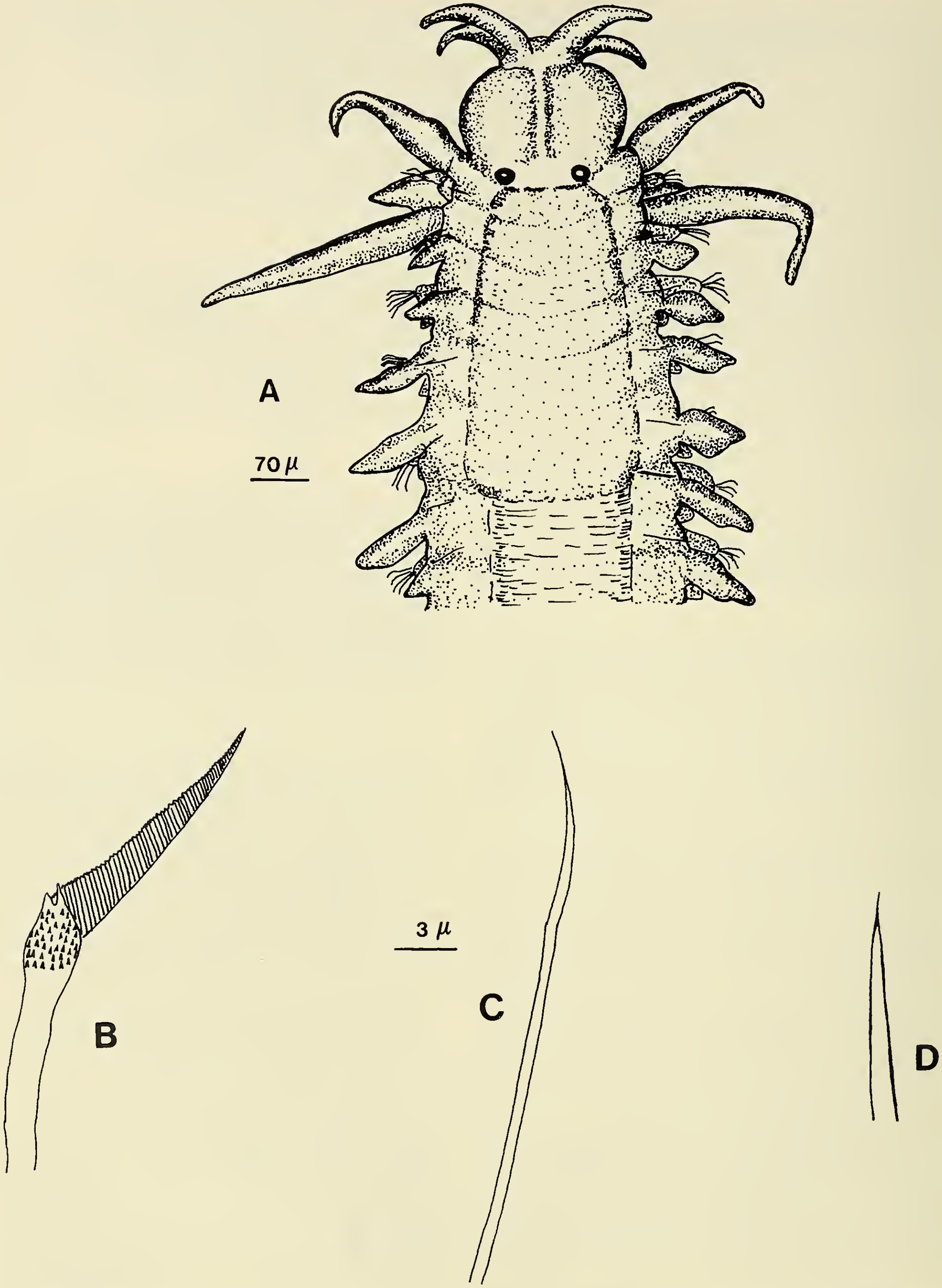

Fig. 2. *Lugia atlantica* holotype. A, Dorsal view of anterior region; B, Compound setae; C, Simple setae from posterior parapodium; D, Aciculum.

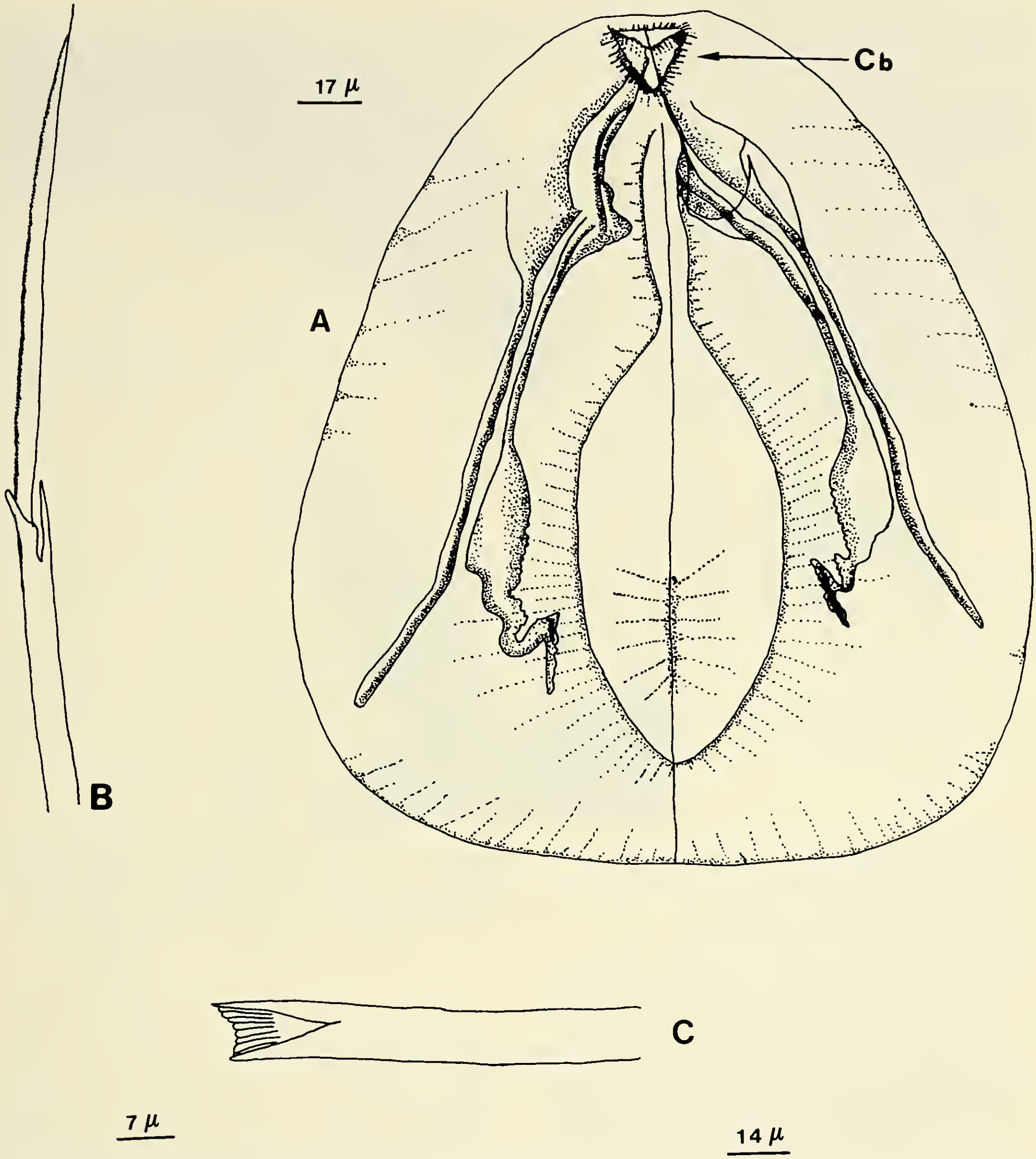

Fig. 3. *Micronereis* sp. A, Pharynx of male with jaws and buccal cavity (Cb); B, Compound homogomph setae; C, Shaft of compound setae showing articulation.

posed because this is the first time specimens of the genus *Lugia* have been found in the Atlantic Ocean. The others have been described from the Mediterranean Sea (*L. pterophora, L. incognita*) and the Sea of Japan and the Pacific Ocean (*L. abyssicola*).

Family Nereididae Johnston, 1845

Genus *Micronereis* Claparède, 1863

Micronereis sp.

Figs. 3, 4A.

Material examined.—Sta M. Lowest intertidal band, 1 male specimen.

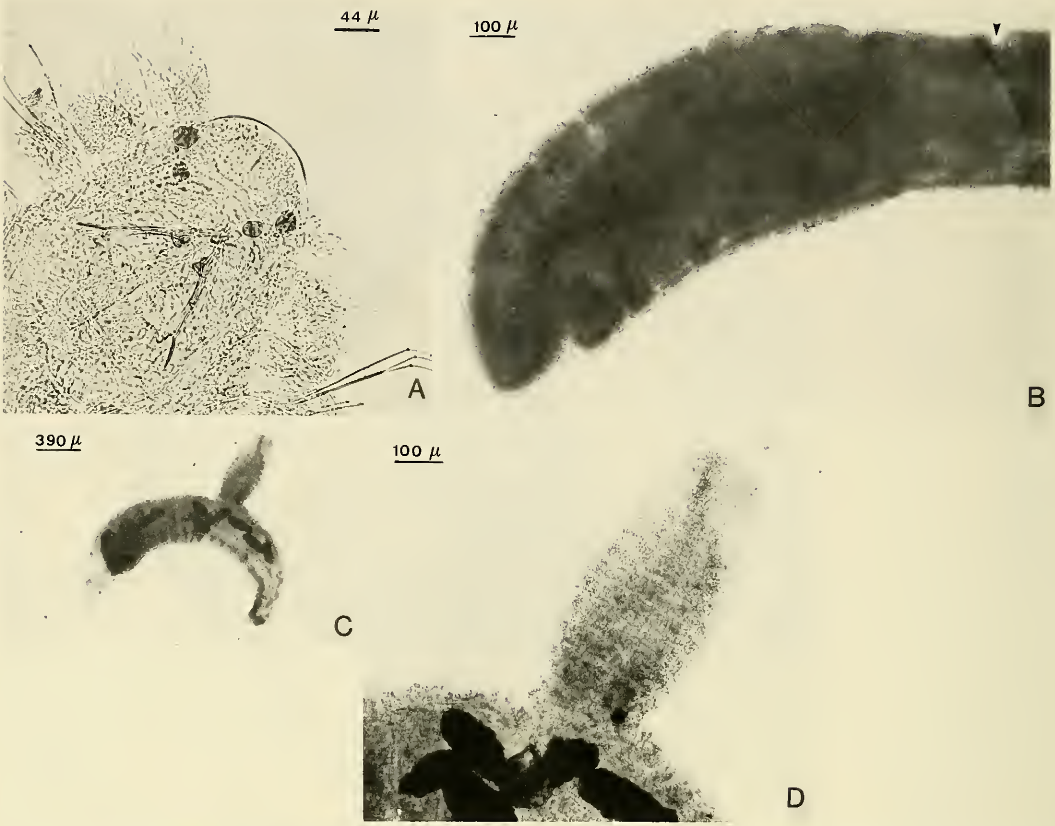

Fig. 4. A, *Micronereis* sp. Dorsal view of anterior end showing jaws, one of right tentacular cirri detached by manipulation; B, Capitellidae indet., thoracic region showing genital hook between setigers 9 and 10 (arrow); C, *Capitella capitata* (?), fragment of abdominal region with bud-like expansion; D, *Capitella capitata* (?), abdominal fragment, enlarged.

Description.—Body flat, 2 mm long and 0.6 mm wide excluding setae, with 16 setigerous segments. Prostomium broad, slightly bilobed, distinct from peristomium, with 2 pairs of eyes in trapezoidal arrangement, anterior pair slightly larger and laterally located along maximum width, posterior pair located in posterior portion of prostomium (Fig. 4A). Paired lobes located anteroventrally, called palps after Paxton (1983). Tentacular cirri 4 pairs with broad bases, gradually tapering distally. Anterior 2 pairs lateral to prostomium, of similar length; posterior 2 pairs slightly longer, lateral to peristomium, one pair anterior and ventral, other pair posterior and dorsal (Fig. 4A).

Pharynx with 2 yellow jaws extending from peristomium to setiger 2. Jaws of male consisting of 2 regions: base with 3 teeth, broadest of them with 8 denticles. Base continuing distally into slender prolongation ending in 2 round expansions and sharp tip; buccal cavity with circle of many rows of very small paragnaths (Fig. 3A).

Setigers 1 and 2 with uniramous parapodia, consisting of setigerous lobe, aciculum, fascicle of setae, and ventral cirrus; dorsal cirrus lacking. Parapodia of following setigers biramous, with divergent rami.

Dorsal and ventral cirri similar in length. Acicula sharp-pointed with straight tips. Compound setae with homogomph articulations, with joint slightly crenulate; smooth shafts without transverse septa and long blades slightly serrate, sharp-pointed. Each neuropodium of setiger 3 with pair of copulatory hooks. Anal cirri lacking.

Remarks.—The taxonomic status of this genus has been studied and changed in different reviews (Reish 1961, Banse 1977, Buzhinskaya 1981, Paxton 1983). Our specimen cannot be included with conviction in any of the valid species that Paxton (1983) considered. The specimen differs from *Micronereis nanaimoensis* Berkeley & Berkeley, 1953, *M. halei* Hartman, 1954, *M. eniwetokensis* Reish, 1961, and *M. bansei* (Hartmann-Schröder 1979) because all of them have shortened type of jaws. Our specimen also differs from *M. ochotensis* Buzhinskaya, 1981, with different kind of jaws, shafts of compound setae with septa and blades with much more conspicuous denticles. It differs from *M. minuta* (Knox & Cameron 1970), with accessory parapodial cirri and simple setae, lacking copulatory hooks, and blades of the compound setae very coarsely serrated. It differs from *M. piccola* Paxton, 1983, in having ocular spots on the segments, compound falcigers, and shafts with septa.

Our specimen does not completely agree with *M. variegata* Claparède, 1863. The main difference resides in the shape of the jaws, this character being the most useful for the diagnosis of this species (Amoureux et al. 1978). Paxton (1983) could not examine the holotype of the species. Based on specimens that she considered similar to the original, however, she offered a drawing of the jaws of a male, which differ from our specimen. Other characters established by this author, those related to number of setigers, length, and setae, are similar to our specimen. In spite of these differences, we consider that one specimen is not enough to establish a new taxon.

Family Capitellidae Grube, 1862
Capitellidae indet.
Fig. 4B

Material examined.—Sta A, intertidal band of *Ulva rigida,* complete specimen and one without abdominal region.

Description.—The external appearance agrees with *Capitella capitata* (Fabricius 1780), except for copulatory apparatus located between setigers 9 and 10, instead of 8 and 9 (Fig. 4B). Setigers 1 to 6 with capillary setae exclusively. Parapodial rami of segment 7 with hooded hooks, except right ventral ramus with capillary setae. Setiger 8 with hooded hooks exclusively. Setiger 9 and 10 with hooded hooks in ventral rami and genital hooks in dorsal.

Remarks.—We have not found in the literature any genus of this family with the copulatory apparatus between setigers 9 and 10. These specimens could lead to the establishment of a new genus, but we prefer to wait for new findings of specimens with this character, especially from unpolluted areas.

Genus *Capitella* Blainville, 1828
Capitella capitata (Fabricius 1780)
Fig. 4C, D

Material examined.—Sta A, intertidal band of *Ulva rigida,* fragment of the abdominal region of a specimen belonging very likely to *Capitella capitata.* It bears a lateral segmented bud-like expansion with hooded hooks in every segment, showing the typical arrangement for the species.

Remarks.—We have not found any reference in the literature pointing out the possibility of budding in this family. Using high levels of heavy metals in culture, Reish (1974, 1977) obtained larvae of this species with bifurcated abdomens. These abnormal specimens, however, never passed the 8-segmented metatrochophore stage. The fragment we are reporting belongs to an adult specimen. We do not discount the idea that the bud-like expansion may be a kind of anomaly caused by the industrial pollution of the area.

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THOONCHUS LONGISETOSUS AND *OXYONCHUS STRIATUS,* NEW SPECIES OF FREE-LIVING MARINE NEMATODES (NEMATODA: ENOPLIDA) FROM NORTHWEST FLORIDA, U.S.A.

Edwin J. Keppner

Abstract.—Two new species of free-living marine nematodes from the genera *Thoonchus* and *Oxyonchus* (Nematoda: Enoplida) are described from sediments off the Gulf of Mexico and St. Andrew Bay, Bay County, Florida, U.S.A. *Thoonchus longisetosus* is unique in the presence of distinct labial setae rather than labial papillae, in the size and shape of the amphid, the position of the excretory pore, and in the shape of the gubernaculum. *Oxyonchus striatus* is unique in the presence of distinct transverse striations of the cuticle and in the size and shape of the spicules and gubernaculum. Keys are provided to the species of each genus.

The two new species described here were recovered from sediment in a bayou and lagoon off St. Andrew Bay, and from sediment adjacent to a rock outcrop in the Gulf of Mexico, Bay County, Florida.

Sediment samples were obtained from the bay sites with a 4.5 cm diameter corer to a depth of 10 cm in the sediment. Sediment samples were obtained from the Gulf of Mexico with SCUBA equipment, and a 3.5 cm diameter corer to a depth of 5–10 cm. Nematodes were extracted by repeated washing of the sediment in seawater, allowing the heavier particles to settle for 15 sec and decanting the supernatant water and suspended material to a second container. The suspended material from four washings was allowed to settle for 15–20 min, and the supernatant water was decanted. Nematodes were removed alive from the remaining sediment, fixed in hot alcohol-formalin-acetic acid for 24 h, cleared in glycerine, and mounted in anhydrous glycerine on Cobb slides.

Measurements were made with a calibrated ocular micrometer. All measurements are given in μm unless othewise indicated, and the mean is followed by the range in parentheses. The taxonomic hierarchy is that of Gerlach & Riemann (1974).

Enchelidiidae Filipjev, 1918
Thoonchinae Gerlach & Riemann, 1974
Thoonchus Cobb, 1920
Thoonchus longisetosus, new species
Figs. 1–5, 10, 11

Diagnosis.—One male from Gulf of Mexico. Body slender; cuticle thin, smooth. Head with circle of 6 long slender labial setae and single circle of 10 (6 + 4) cephalic setae, 4 submedian setae about ⅔ length of other 6. Cervical setae long, slender; present from immediately posterior to amphid to level of nerve ring. Somatic setae not observed; caudal setae present. Stoma large with heavily cuticularized walls and 3 teeth, right subventral tooth largest; size and position of left subventral and dorsal teeth about equal. About 6 complete irregular circles of small round denticles present anterior to dorsal and left subventral teeth. Amphid posterior to base of stoma; wide with thickened lateral margins. Excretory pore posterior to base of stoma. Esophagus long, muscular; not expanded at junction with intestine. Tail conical, then cylindrical. Spinneret and caudal glands present; caudal gland cell bodies extend anterior to cloaca. Female unknown.

Male (n = 1): Length 2.62 mm, width at midbody 32. Head diameter 21 at level of cephalic setae. Labial setae 7 long, cephalic setae 12 and 8 long. Stoma 21 long, 19 wide at level of denticles. Amphid 18 wide. Esophagus 778 long; excretory pore 30 and nerve ring 202 from anterior end. Tail 86 long, 33 wide at cloaca. Two midventral areas of thickened cuticle 102 and 150 anterior to cloaca; each with central depression and small central sensilla. One pair small, subventral papillae present 78 anterior to cloaca. Single midventral, cuticular elevation with pore 22 anterior to cloaca. Two pairs subventral setae immediately anterior to cloaca. Spicules 35 long, arcuate with curved tip. Corpus of gubernaculum surrounding spicules; gubernacular apophysis 8 long, dorsally directed. a = 81.9; b = 3.37; c = 30.5.

Type specimen.—Holotype male, USNM 77137.

Type locality.—Sediments consisting of coarse sand, shell, and sponge spicules in Gulf of Mexico adjacent to exposed rock outcrop Bay County, Florida (30°12′45″N, 86°02′10″W).

Etymology.—The specific name is from the Latin *longus* for long and *seta* for bristle in reference to the long labial setae of this species.

Remarks.—The genus *Thoonchus* contains three species, *T. ferox* Cobb, 1920, *T. inermis* Gerlach, 1953, and *T. giganticus* Belogurova, Belogurov & Khamula, 1986. Cobb (1920) stated that *T. ferox* has labial papillae and the amphids are faint. He figured the amphids as small and located over the base of the stoma. Males of *T. ferox* have a single elevated precloacal supplementary organ and a pair of subventral papillae immediately anterior to the cloaca. Spicules are arcuate, the corpus of the gubernaculum does not surround the spicules, and the gubernaculum has a thin proximal extension parallel to the spicules.

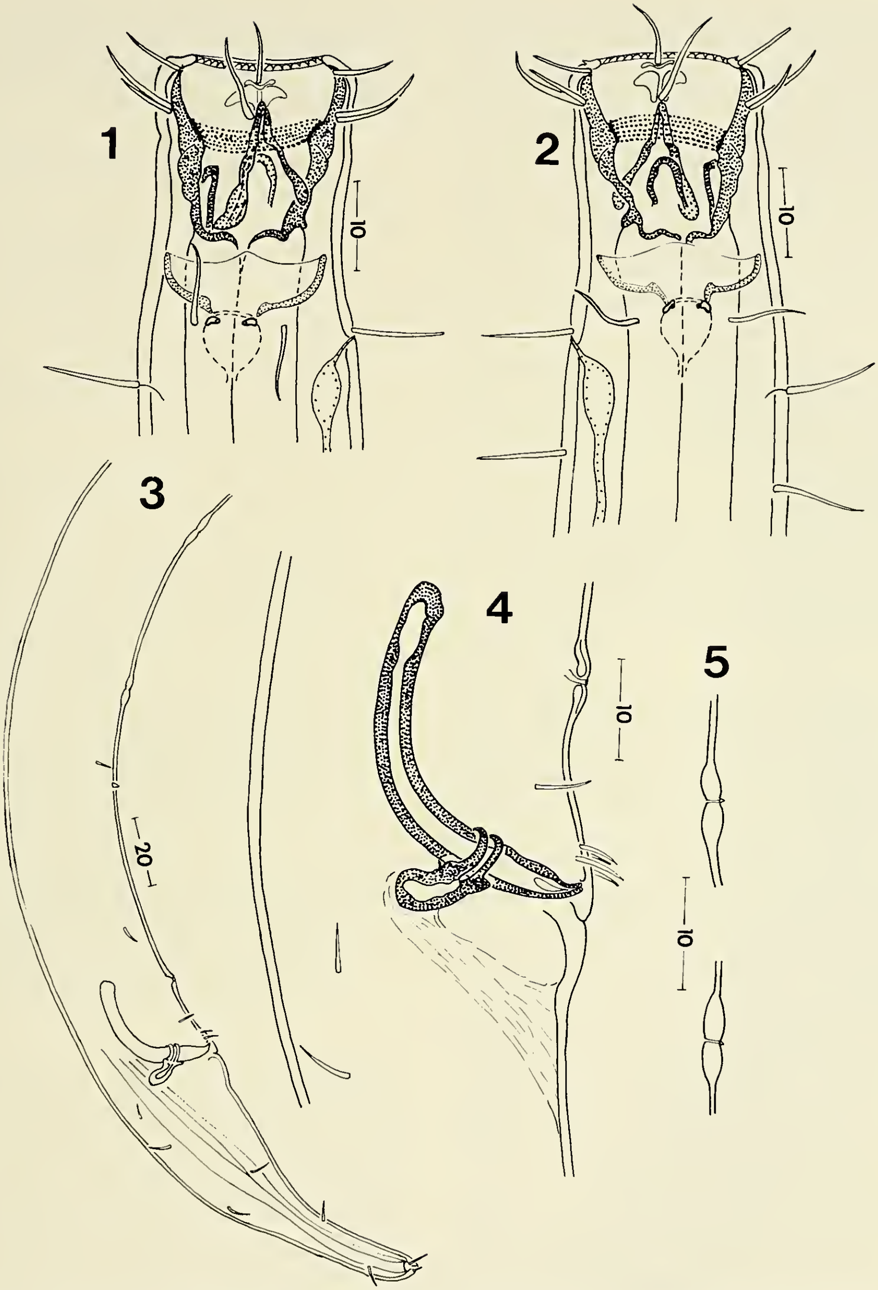
Chitwood (1960) described *T. ferox* as having labial papillae, an excretory pore anterior to the cephalic setae, and amphids located over the base of the stoma. Males have at least two subventral precloacal papilloid supplements and the spicules and gubernaculum are as described by Cobb (1920).

Gerlach (1953) described the male, and Gerlach (1954) described the female of *T. inermis. Thoonchus inermis* has labial papillae, the excretory pore is at the base of the stoma, amphids are located over the middle of the stoma, and the right subventral tooth is largest. Males do not have precloacal supplements or papillae and the gubernaculum has a pointed apophysis.

Thoonchus longisetosus can be distinguished from *T. ferox* by the presence of long labial setae rather than labial papillae, the amphid is posterior to the stoma and is large with thickened lateral margins rather than thin-walled and over the stoma, and the excretory pore is posterior to the stoma rather than anterior to the cephalic setae. The male genital apparatus of *T. longisetosus* differs from that of *T. ferox* in that the gubernaculum surrounds the spicules and the gubernaculum has a broad apophysis rather than a thin proximal extension parallel to the spicules.

Thoonchus longisetosus can be distinguished from *T. inermis* by the presence of long labial setae rather than papillae, the amphids are large and posterior to the stoma rather than over the middle of the stoma, and the excretory pore is posterior to the stoma rather than at the base of the stoma. The male genital apparatus of *T. longisetosus* differs from that of *T. inermis* in the presence of precloacal supplements and papillae, in the presence of a gubernaculum that surrounds the spicules, and the gubernaculum has a broad blunt apophysis rather than a pointed apophysis.

The three species of *Thoonchus* discussed



Figs. 1–5. *Thoonchus longisetosus*: 1, Male, head, right lateral view; 2, Male, head, left lateral view; 3, Male, posterior end, right lateral view; 4, Male, right spicule and gubernaculum, lateral view; 5, Male, precloacal supplements, right lateral view (anterior, top; posterior, bottom). Scales in μm.

above are quite similar in the presence of the oncholaimoid structure of the stoma. The stoma is 1.1–1.5 times as long as broad and the teeth are short, broad, and originate from a wide base at the posterior end of the stoma. The spicules are short and arcuate. The gubernaculum has an expanded corpus and an apophysis. Cobb (1920) and Chitwood (1960) emphasized the oncholaimoid shape of the stoma as characteristic of the genus *Thoonchus.* Wieser (1953) stated in reference to the genera of Thoonchinae (*Thoonchus* and *Ditlevsenella* Filipjev, 1925) "buccal cavity oncholaimoid i.e. the two subventral teeth strongly developed and with a broad base."

Belogurova et al. (1986) described a male nematode from the Tatar Strait as *Thoonchus giganticus.* They placed this species in *Thoonchus* based on the presence of three teeth in the stoma and the absence of supplements in the male. Examination of the drawings of *T. giganticus* reveals that the shape of the stoma and teeth differ significantly from the oncholaimoid type of stoma and teeth of the other species in the genus. The stoma is long and narrow (2.5 times as long as broad). The subventral teeth are figured as almost equal, narrow, and extend from a narrow base at the posterior end of the stoma to almost the anterior end of the stoma. The dorsal tooth is smaller and slightly posterior to the anterior terminus of the subventrals. The spicules of *T. giganticus* are elongate (chord = 558; arc = 360) and thin. The gubernaculum is a thin plate without apophysis or extension. The precloacal organs are papilloid.

The shape of the stoma, teeth, and male genital apparatus deviate significantly from that of *Thoonchus.* The shape of the these parts are more similar to those of certain genera in the Enchelidiinae rather than Thoonchinae. Based on the information available, it is not prudent to emend the genus *Thoonchus* to include this species. It is also difficult to place this species within the existing genera in the Enchelidiinae or erect a new genus for it. Therefore, *Thoonchus giganticus* Belogurova, Belogurov, & Khamula, 1986, is considered of doubtful generic assignment.

The following key differentiates the three species of *Thoonchus.*

1. Labial sensillae papilliform; amphid over stoma; excretory pore at level of base of stoma or anterior to cephalic setae 2
– Labial sensillae setiform; amphid posterior to stoma; excretory pore posterior to stoma .... *T. longisetosus* n. sp.
2(1). Excretory pore anterior to cephalic setae; male gubernaculum with thin proximal extension parallel to spicules; precloacal supplements and papillae present .... *T. ferox* Cobb, 1920
– Excretory pore at base of stoma; male gubernaculum with pointed apophysis; precloacal supplements and papillae absent .... *T. inermis* Gerlach, 1953

Enoplidae Dujardin, 1845
Oxyonchinae De Coninck, 1965
Oxyonchus Filipjev, 1927
Oxyonchus striatus, new species
Figs. 6–10, 13, 14

Diagnosis.—One male, one female, and one juvenile. Body long, slender. Cuticle thick with distinct transverse striations beginning at base of head and extending length of body. Head with 3 low lips, 6 labial setae, and single circle of 10 (6 + 4) cephalic setae; 4 submedian setae about 45% length of other 6 in male, 36% of other 6 in female. Cephalic organ not observed. Cephalic capsule thin, distinctly light refractive. Cervical setae of variable length, numerous to level of nerve ring; longest setae in dorsal, ventral, and lateral rows. Somatic setae short, sparse; caudal setae variable in length, numerous. Stoma with 2 large subventral teeth, left subventral longer, reaching just anterior to anterior margin of mandibles; dorsal tooth not observed. Mandibles complex, well-developed; each with two thick arched rods converging medially. Each rod with small tooth (denticle) at base of transverse bar. Rods connected by broad transverse bar with claws. A series of refractile rods or tubules extending radially from oral surface of each mandible, terminating at about posterior margin of transverse bar. Amphid near base of head, oblong with thickened anterior margin. Esophagus vesiculate-crenulate; excretory pore not observed. Tail cylindrical for first two-thirds, then narrower; tip slightly expanded. Caudal glands and spinneret present.

Male (n = 1): Length 3.41 mm, width at midbody 43. Head 38 long, 34 wide at level of cephalic setae. Labial setae 6 long; cephalic setae 33 and 15 long. Amphid 7 wide. Subventral teeth 26 and 23 long. Esophagus 590 long; nerve ring 135 from anterior end. Tail 115 long, 40 wide at cloaca. Single, midventral, tubular supplement 22 long, located 74 anterior to cloaca. One pair subventral, papillae 61 posterior to cloaca. Spicules 140 long, capitulum funnel-shaped then narrowed, then expanded and gradually narrowed to flattened tip. Gubernaculum bipartite, each lateral piece a narrow tube 28 long, apophysis absent. a = 79.3; b = 5.78; c = 29.7.

Female (n = 1): Length 4.44 mm, width 54 at midbody. Head 37 long, 37 wide at level of cephalic setae. Cephalic setae 30 and 11 long. Amphid 7 wide. Subventral teeth 30 and 28 long. Esophagus 683 long; nerve ring 150 from anterior end. Tail 112 long, 45 wide at anus. Reproductive system didelphic, amphidelphic, ovaries reflexed. Vulva 2.74 mm from anterior end. Two eggs present, 120 and 144 long. a = 82.2; b = 6.50; c = 39.6; V = 62%.

Type specimens.—Holotype male, USNM 77134; allotype female, USNM 77135; paratype juvenile, USNM 77136.

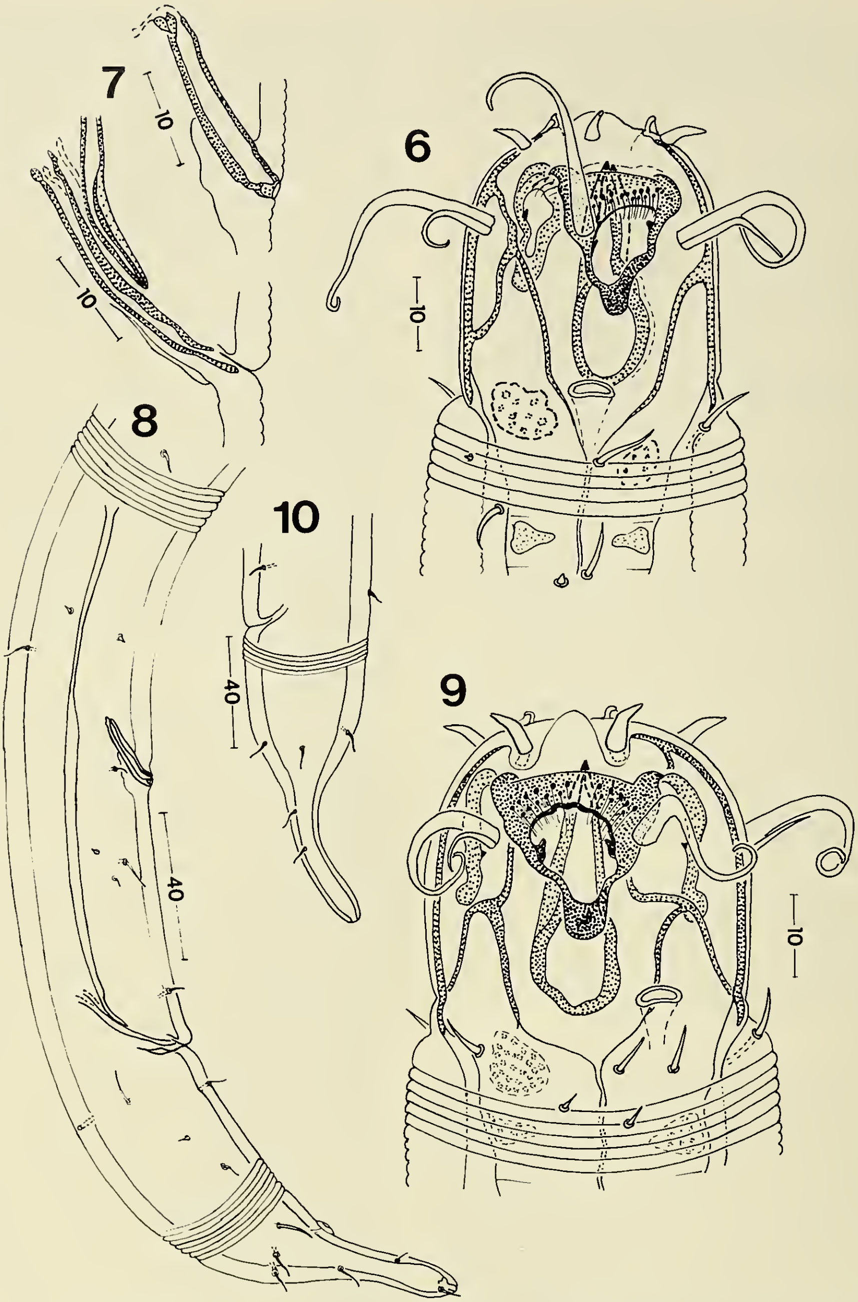
Type locality.—Holotype male from nonvegetated sediment consisting of fine sand and detritus from mouth of Freshwater Bayou off St. Andrew Bay, Bay County, Florida (85°39′00″W, 30°07′30″N). Allotype female from nonvegetated sediment consisting of fine sand and detritus from Grand Lagoon off St. Andrew Bay, Bay County, Florida (85°43′15″W, 30°07′50″N).

Etymology.—From the Latin *stria* for furrow in reference to the transverse striations in the cuticle of this species.

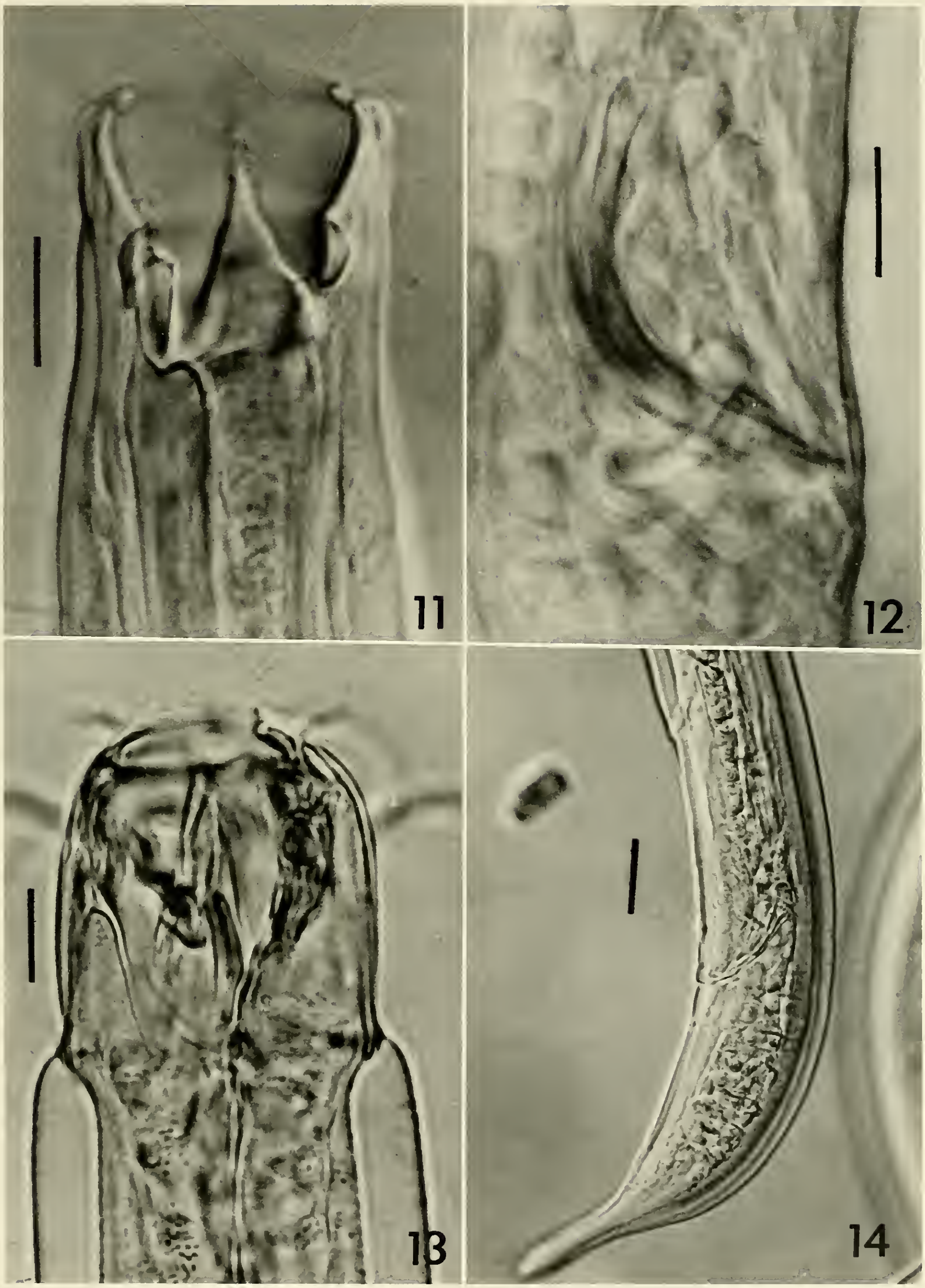
Remarks.—The genus *Oxyonchus* is characterized by the presence of two large subventral teeth in the stoma that extend to the anterior end of the mandibles. The dorsal tooth is reduced or absent. Mandibles are arch-shaped, well developed, and denticles can be present on the inner surface of the mandibular plate. Until now all species for which males are known have arcuate, relatively short spicules (1–1.9 cloacal diameters).

De Coninck & Stekhoven (1933) provided a key to the species of *Oxyonchus* and considered *O. stateni* Allgen, 1930 as insufficiently characterized and possibly a synonym of *O. australis* (De Man, 1904) Filipjev, 1927. Wieser (1953) revised the genus *Oxyonchus* and provided a key to the species. He considered *O. stateni* a synonym of *O. australis*. Species added to the genus *Oxyonchus* since 1953 are: *O. subantarcticus* Mawson, 1958; *O. culcitatus* Wieser, 1959; and *O. ditlevseni* Inglis, 1964.

Allgen (1959) described five new species of *Oxyonchus*; *O. brachysetosus, O. crassicolis, O. macrodon, O. notodentatus,* and *O. parastateni.* He disagreed with the position of Wieser (1953) regarding the synonymy of *O. stateni* and *O. australis* but did not provide additional figures or information to support the validity of *O. stateni.* The description, figures, and absence of figures for the new species of *Oxyonchus* provided by Allgen (1959) are insufficiently adequate to distinguish the species from others and to place these species in a key. Therefore, *O. brachysetosus, O. crassicolis, O. macrodon,*



Figs. 6–10. *Oxyonchus striatus*: 6, Male, head, left lateral view; 7, Male, precloacal supplement and gubernaculum, right lateral view; 8, Male, posterior end, right lateral view; 9, Female, head, left sublateral view; 10, Female tail, lateral view. Scales in μm.



Figs. 11–14. Figs. 11–12. *Thoonchus longisetosus*: 11, Male, head, lateral view; 12, Male posterior end, lateral view; Scale bars = 10 μm. Figs. 13–14. *Oxyonchus striatus*: 13, Male, head, lateral view; Scale bar = 10 μm; 14, Male, posterior end, lateral view; Scale bar = 20 μm.

O. notodentatus, and *O. parastateni* are considered *species dubia.*

Oxyonchus striatus, n. sp. differs from all other species of the genus in the presence of the distinctly striated cuticle, the length and shape of the spicules, and the shape of the gubernaculum.

The following key to the species of *Oxyonchus* is to a great extent based on the key developed by Wieser (1953). Wieser (1953) stated in the introductory remarks to his key that "as to the species described there are some problems which can not be cleared up from the records in the literature." The statement remains applicable, and some of the species included in the genus do not appear to belong in *Oxyonchus*. An examination of the type specimens for each species would be required in order to complete a thorough analysis of the genus.

Key to Species of *Oxyonchus* Filipjev, 1927

1\. Cuticle with transverse striations; spicules long, slender, not arcuate, 3.5 cloacal diameters long; gubernaculum without apophysis ...... *O. striatus*, n. sp.

– Cuticle without transverse striations; spicules arcuate, broad, 1–1.9 cloacal diameters long; gubernaculum with or without apophysis 2

2(1). Tail 9–10 cloacal diameters long .... *O. dubius* (Filipjev, 1918) De Coninck & Stekhoven, 1933

– Tail 7 cloacal diameters long or less 3

3(2). Longer cephalic setae 0.8 head diameter or less in length 4

– Longer cephalic setae 1 head diameter or more in length 8

4(3). Precloacal supplement absent in male 5

– Precloacal supplement present in male 6

5(4). Tail 7 cloacal diameters long; spicules 1.9 cloacal diameters long; gubernaculum with apophysis .... *O. problematicus* Filipjev, 1946

– Tail 4.2 cloacal diameters long; spicules 1 cloacal diameter long; gubernaculum without apophysis .... *O. pachylabiatus* Stekhoven, 1946

6(4). Mandibles each with 14–15 denticles; cephalic capsule 45–50 μm long ..... *O. acantholaimus* (Saveljev, 1912) Filipjev, 1927

– Mandibles with about 6 denticles; cephalic capsule less than 45 μm long 7

7(6). Spicules 1.5 cloacal diameters in length .... *O. hamatus* (Steiner, 1916) Filipjev, 1927

– Spicules 1.0 cloacal diameter in length .... *O. australis* (De Man, 1904) Filipjev, 1927

8(3). Tail 4–4.25 anal diameters in length 9

– Tail 5–6 anal diameters in length 11

9(8). Longer cephalic setae 2.7 head diameters in length .... *O. culcitatus* Wieser, 1959

– Longer cephalic setae about 1.0 head diameter in length 10

10(9). Mandibles each with 15–20 denticles; male precloacal supplement 2–2.5 cloacal diameters from cloaca .... *O. dentatus* (Ditlevsen, 1918) Filipjev, 1947

– Mandibles each with about 4 denticles; male precloacal supplement 3.8–4.2 cloacal diameters from cloaca .... *O. polaris* Filipjev, 1927

11(8). Precloacal supplement about 2.2 cloacal diameters from cloaca; gubernacular apophysis direct-

ed caudally ....
.... *O. ditlevseni* Inglis, 1964

– Precloacal supplement about 3.7 cloacal diameters from cloaca; gubernacular apophysis directed dorsally ....
.. *O. subantarcticus* Mawson, 1958

Acknowledgments

Sincere appreciation is expressed to Dr. W. Duane Hope of the National Museum of Natural History, Smithsonian Institution, for reviewing the manuscript, examining the specimens, and directing attention to the complex structures in the specimens. Appreciation is also expressed to Mr. & Mrs. William Fable, U.S. National Marine Fisheries Service, Panama City, Florida for collecting the sediment samples from the Gulf of Mexico.

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NEW SPECIES AND NEW RECORDS OF SCALED POLYCHAETES (POLYCHAETA: POLYNOIDAE) FROM HYDROTHERMAL VENTS OF THE NORTHEAST PACIFIC EXPLORER AND JUAN DE FUCA RIDGES

Marian H. Pettibone

Abstract.—The joint Canadian-American Seamount Expedition in the Northeast Pacific uncovered additional polynoid polychaetes associated with hydrothermal vents of the Explorer and Juan de Fuca Ridges. They included five species, two new, in three subfamilies of Polynoidae: Lepidonotopodinae: *Lepidonotopodium piscesae,* new species; Macellicephalinae: *Levensteiniella kincaidi* Pettibone: Branchinotogluminae: *Branchinotogluma grasslei* Pettibone, *P. sandersi* Pettibone, *Opisthotrochopodus tunnicliffeae,* new species. The diagnosis of *Opisthotrochopodus* is emended. Habitats of some species are discussed.

Among the unusual marine life discovered in August 1983 by the joint Canadian American Seamount Expedition (CASM) in the Northeast Pacific (Tunnicliffe & Juniper 1983, Harman 1984, Canadian American Seamount Expedition 1985) and later studies on the Axial Seamount of the Juan de Fuca Ridge (Tunnicliffe et al. 1985) and the Explorer Ridge (Tunnicliffe et al. 1986), were five species of polychaete worms belonging to three subfamilies of Polynoidae. The subfamilies were described earlier by me from hydrothermal vents of the Tropical East Pacific: the Galapagos Rift and 21°N (Pettibone 1983, 1984, 1985a, b), and three of the five species were previously described from these areas: *Levensteiniella kincaidi,* Macellicephalinae; *Branchinotogluma grasslei* and *B. sandersi,* Branchinotogluminae. The remaining two are new species: *Lepidonotopodium piscesae,* Lepidonotopodinae, and *Opisthotrochopodus tunnicliffeae,* Branchinotogluminae.

The polynoids were collected by the Canadian submersible DSRV *Pisces IV* in 1983, 1984, and 1986, and by DSRV *Alvin* in 1984, and sent to me for study by Verena Tunnicliffe. Additional specimens collected by DSRV *Alvin* in 1984 were provided by Meredith L. Jones. The specimens were obtained from four vent areas: Explorer Ridge (50°N); Endeavour segment of the Juan de Fuca Ridge (48°N); Axial Seamount of the Juan de Fuca Ridge (46°N); and Southern Juan de Fuca Ridge (45°N).

The Axial Seamount of the Juan de Fuca Ridge was described by Tunnicliffe & Juniper (1983), Harmon (1984), Canadian American Seamount Expedition (1985), and Tunnicliffe, Juniper, & de Burgh (1985). Axial Seamount is a volcanic feature formed by hydrothermal activity, 46° off the U.S.-Canadian border. The seamount is crossed by a fissure of about 1510 meters, within which is a system of vents with water temperatures up to 35°C. Dense thickets of vestimentiferan tubes overgrow the major vents and consist of deposits of sulfide-forming chimneys. Large quantities of mucus bind the tubes together and provide habitats for many organisms. Chemosynthetic bacteria are found in the mucous strands. The vents vary from diffuse flow through bacterial mats to large structures (over 2 meters high) built by the vestimentiferan tube worms. The minor vents are surrounded by bacterial mats, small prone vestimentiferans, and limpets. Colonial protozoans (folliculine ciliates) and bacterial mats cover most surfaces of the active fissures.

Associated animals of the Axial Seamount, in addition to the vestimentiferan *Ridgeia piscesae* Jones, with its large, soft collared tubes, were two species of alvinellid polychaetes: *Paralvinella palmiformis* Desbruyères & Laubier, the large "palm-worm" that wraps the caudal end around the *Ridgeia* tubes with the anterior end held upright; and *P. pandorae* Desbruyères & Laubier, the smaller "pandora-worm," that forms mucus-lined tubes on the bases of the vestimentiferans. The ampharetid *Amphisamytha galapagensis* Zottoli was also found living in small tubes of mineral fragments on the periphery of the vents. Two new polynoid polychaetes were tentatively identified as species A and B by D. Weston; they were examined and referred herein to *Lepidonotopodium piscesae,* n. sp. (species A) and *Branchinotogluma grasslei* Pettibone, 1985 (species B). The larger white polynoids (=*L. piscesae*) were observed crawling on vestimentiferan tubes and rocks and grazing on bacterial and protozoan mats; its white coloration was due to the filamentous bacteria attached to the elytra. The smaller red polynoids (=*B. grasslei*) were found closer to the water flow than the larger white species.

The extensive hydrothermal vents of the Explorer Ridge (50°N, 130°W, 1820 m) were described by Tunnicliffe et al. (1986). This is the most northern of the recently explored vent areas of the eastern Pacific. The vents are formed of large sulfide mounds projecting 2 to 20 meters in height through thick grey hydrothermal sediment. The mounds are covered with active chimneys and vent grey 'smoke' which is a fluid rich in hydrogen-sulfide and of a high temperature (25–310°C). Vestimentiferan tubes were the major habitat for other species; limpets were particularly abundant. Three polynoid species were listed (Pettibone, personal communication): *Branchinotogluma* sp. (=*B. grasslei, B. sandersi* Pettibone, 1985), *Lepidonotopodium* sp. (=*L. piscesae,* n. sp.), and *Levensteiniella* sp. (=*L. kincaidi* Pettibone, 1985).

Holotype, paratypes, and additional specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Paratypes and representative specimens are deposited in the National Museum of Natural Sciences, Ottawa, Canada (NMCA).

Family Polynoidae

Subfamily Lepidonotopodiinae
Pettibone, 1983

Lepidonotopodium Pettibone, 1983

The genus includes three previously described species: *L. fimbriatum* Pettibone, 1983, from off western Mexico at 21°N; *L. riftense* Pettibone, 1984, and *L. williamsae* Pettibone, 1984, both from the Galapagos Rift. A new species from the Explorer and Juan de Fuca Ridge systems is added.

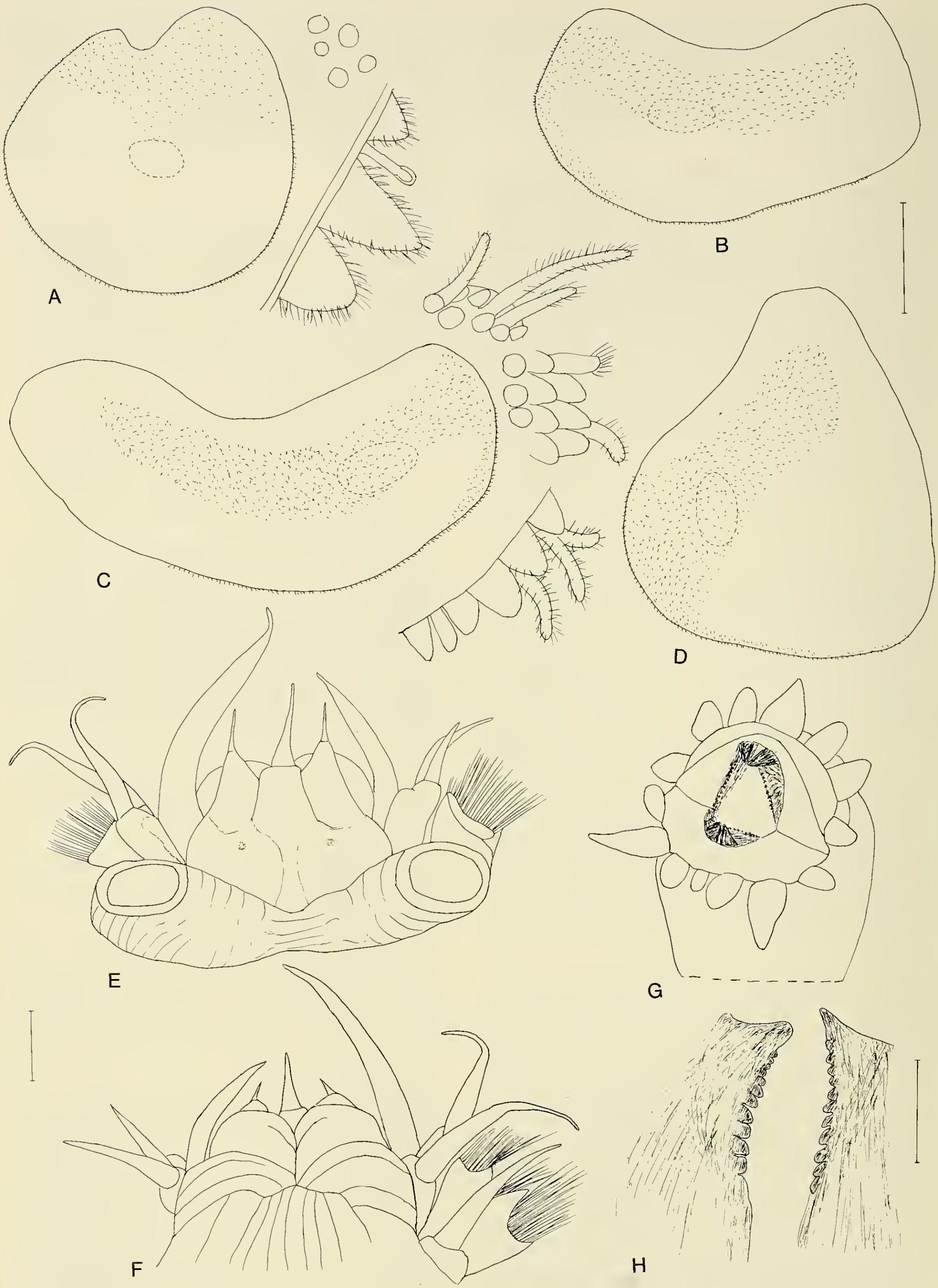
Lepidonotopodium piscesae, new species
Figs. 1–4

Large white polynoid, Tunnicliffe, Juniper, & de Burgh, 1985:454, 455, 459, fig. 4 (bottom left). [Axial Seamount]

Lepidonotopodium sp., Tunnicliffe et al., 1986:407. [Explorer Ridge]

Lepidonotopodium, n. sp. (A), Desbruyères et al., 1985:114. [Juan de Fuca, sulfide rocks]

Material.—Hydrothermal vents of Northeast Pacific, dives by DSRV *Pisces IV* (P) and DSRV *Alvin* (A): EXPLORER RIDGE, 49°45′N, 130°16′W, 1812–1823 m: P1494-600/605, Gulati and Gusher vents, 1 Jul 1984, 14 paratypes (8 small) (USNM 102883); P1497-611, Crab vent, 4 Jul 1984, 7 paratypes (USNM 102886); P1505-617, Buster Thruster vent, 19 Aug 1984, 8 para-


A
B
C
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H

types (USNM 102888).—ENDEAVOUR SEGMENT, JUAN DE FUCA RIDGE, 47°57'N, 129°06'W, 2208 m, A1452-621/641, 7 Sep 1984, 7 paratypes (USNM 102889).—AXIAL SEAMOUNT, JUAN DE FUCA RIDGE, 45°56–59'N, 130°01–03'W, 1546–1592 m: A1411, 16 Jul 1984, 2 young paratypes (USNM 102882); A1413, 18 Jul 1984, holotype (USNM 102878), 3 paratypes (USNM 102881), 23 paratypes (USNM 102887), 3 paratypes (NMCA1987-0449); P1327-639, 17 Aug 1983, Taylor's vent, paratype (USNM 102884); P1721-628, 17 Jul 1986, Embley's Inferno, 3 paratypes (USNM 102879); P1728-632, 29 Jul 1986, Demon vent, 3 small paratypes (USNM 102880).—SOUTHERN JUAN DE FUCA RIDGE, 24 Oct 1984, 44°39'N, 130°22'W, 2200 m: A1455-1B-616, 4 paratypes (USNM 102890); A1463-7B-615, paratype (USNM 102885).

Measurements.—Holotype from Endeavour Segment, Juan de Fuca Ridge, 28 mm long, 13 wide with setae, with 26 segments, last one small; additional paratypes 13–29 mm long, 8–12 mm wide, with 24–26 segments. Adult paratypes from Explorer Ridge 10–23 mm long, 6–11 mm wide, with 24–26 segments: young paratype 4 mm long, 3 mm wide, with 18 segments, last one small. Adult paratypes from Axial Seamount, Juan de Fuca Ridge, 11–28 mm long, 6–14 mm wide, with 24–28 segments, last one minute; young paratype 9 mm long, 7 mm wide, with 22 segments. Paratypes from Southern Juan de Fuca vent 19–29 mm long, 9–13 mm wide, with 25–26 segments.

Description.—Body sturdy, elongate-oval, rounded anteriorly and posteriorly, flattened ventrally and arched dorsally; color brownish to tan. Elytra 11 pairs, on segments 2, 4, 5, alternate segments to 21; with dorsal cirri on posterior segments. Elytra large, overlapping, covering dorsum, thick, stiff, opaque, attached eccentrically on prominent elytrophores. First pair oval, with anterolateral notch (for passage of dorsal tentacular cirrus), following ones subreniform, posterior pair (11th) subtriangular (Fig. 1A–D). Elytral surface thickly covered with opaque, rounded to conical microtubercles, especially thick on somewhat raised transverse areas in middle of elytra and along posterior and lateral borders, and with scattered globular and filiform micropapillae; both tubercles and papillae with bacterial "hairs" attached (Fig. 1A–D). Dorsal cirri on segments lacking elytra with large cylindrical cirrophores on posterior sides of notopodia, with styles long, tapered, extending beyond tips of neurosetae; dorsal tubercles on cirrigerous segment elongate, inflated (Fig. 2C). Surfaces of elytrophores, dorsal tubercles, and anterior sides of parapodia with numerous ciliated ridges (Figs. 1E, 2A–C).

Prostomium bilobed, with anterior lobes prominent, tapered, with rather long frontal filaments; wider on posterior half, whitish, with pair of tannish or dark spots, appearing as "eyes"; median antenna with large cylindrical ceratophore in anterior notch with style short tapered, about length of ceratophore; palps stout, smooth, tapering, about 1½ time length of prostomium (Fig. 1E). First or tentacular segment fused to prostomium, not visible dorsally; tentaculophores lateral to prostomium, without setae, each

←

Fig. 1. *Lepidonotopodium piscesae*, A–F, holotype; G, H, paratype, USNM 102890: A, Left 1st elytron, segment 2, with detail of microtubercles, micropapillae, and bacterial "hairs"; B, Left 2nd elytron, segment 4; C, Right middle elytron, with detail of A; D, Left 11th elytron, segment 21; E, Anterior end, dorsal view, palp, dorsal and ventral tentacular cirri of right side smaller, regenerating; F, Same, ventral view, right parapodium of segment 2 not shown; G, Extended pharynx, frontal view, showing border papillae and dark red jaws; H, Dorsal jaws removed. Scales = 2.0 mm for A–D; 1.0 mm for E–G; 0.5 mm for H.

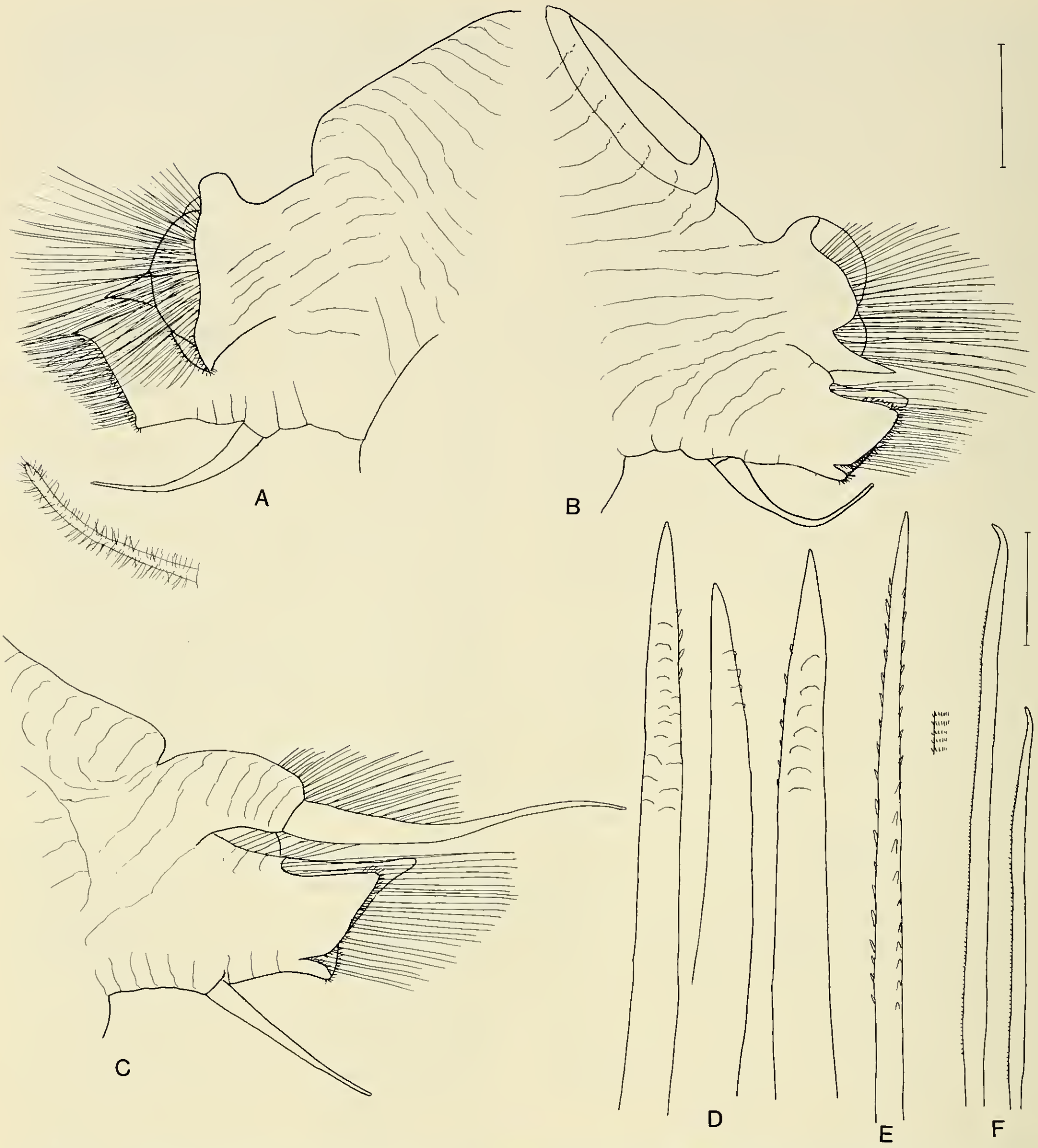

Fig. 2. *Lepidonotopodium piscesae,* holotype: A, right middle elytragerous parapodium, anterior view, with detail of neuropodial papillae with bacterial "hairs"; B, Same, posterior view; C, Right middle cirrigerous parapodium, posterior view; D, Notosetae; E, Supraacicular neuroseta; F, Upper and lower subacicular neurosetae, with detail of spinous rows. Scales = 1.0 mm for A–C; 0.1 mm for D–F.

with pair of tentacular cirri, subequal in length, slightly shorter than palps; without distinct facial tubercle (Fig. 1E, F).

Second or buccal segment with first pair of large elytrophores, biramous parapodia, and ventral buccal cirri attached basally on prominent cirrophores lateral to ventral mouth, with styles similar to tentacular cirri, larger than following ventral cirri (Fig. 1E, F). Ventral mouth enclosed in fleshy upper, lateral and posterior lips medial to parapodia of segments 1 and 2 (Fig. 1F).

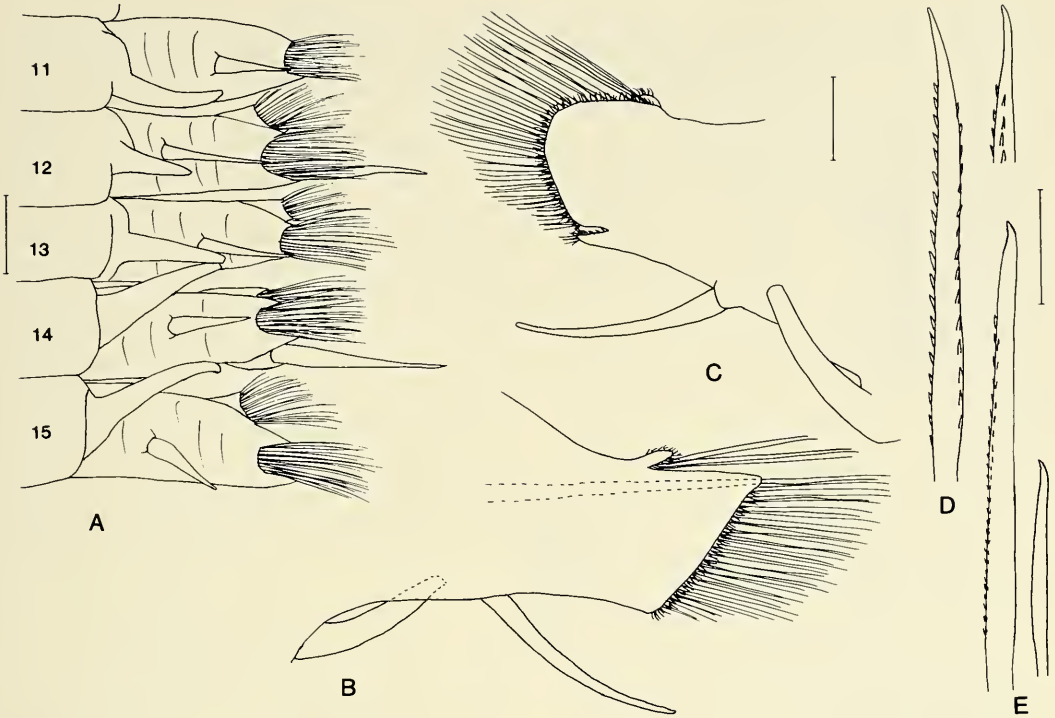

Fig. 3. *Lepidonotopodium piscesae,* paratypes, A, USNM 102887; B–E, USNM 102889: A, Ventral view of left side of segments 11–15, showing segmental papillae; B, Left neuropodium from segment 12, anterior view, separated from notopodium, neuroaciculum dotted; C, Same, posterior view; D, Supraacicular neurosetae from same; E, Upper and lower subacicular neurosetae from same. Scales = 1.0 mm for A; 0.5 mm for B, C; 0.1 mm for D, E.

Large muscular eversible pharynx with 7 pairs of border papillae and 2 pairs of strong, hooked, dark red jaws; dorsal row of papillae subequal in size, with middle one only slightly larger; ventral row with lateral pair and 3 medial papillae smaller, with next to lateral pair elongate and tapered (Fig. 1G). Jaws serrated on cutting edge, with up to 12 or so teeth (Fig. 1G, H).

Biramous parapodia with shorter notopodia on anterodorsal sides of longer neuropodia (Fig. 2A–C). Notopodium large, rounded, with projecting acicular lobe on posterior side, hidden by very numerous notosetae, and nearly enclosed by well-developed, large, flaring bract, attached to acicular lobe on posterior side; lower thinner part of bract bordered with papillae with attached bacterial "hairs" (Figs. 2A, B, 4A). Neuropodium diagonally truncate, with shallow notch on posterior lower side and deep notch on posterior upper side; upper part of presetal acicular lobe projecting beyond shorter postsetal lobe; distal borders of neuropodial lobes papillate with attached bacterial "hairs" (Figs. 2A–C, 3B, C). Notosetae very numerous, forming radiating bundles, varying in length from short to long, much stouter than neurosetae, distal part with 2 rows of spines and blunt tapered tips, most with numerous attached bacterial "hairs" (Figs. 2D, 4B). Neurosetae numerous, forming fan-shaped bundles. Upper, supraacicular neurosetae few (4 or so) emanating from upper posterior notch of neuropodium, stouter than lower neurosetae, with 2 rows of prominent, lateral spines and bare tapered tips (Figs. 2E, 3D). Very nu-

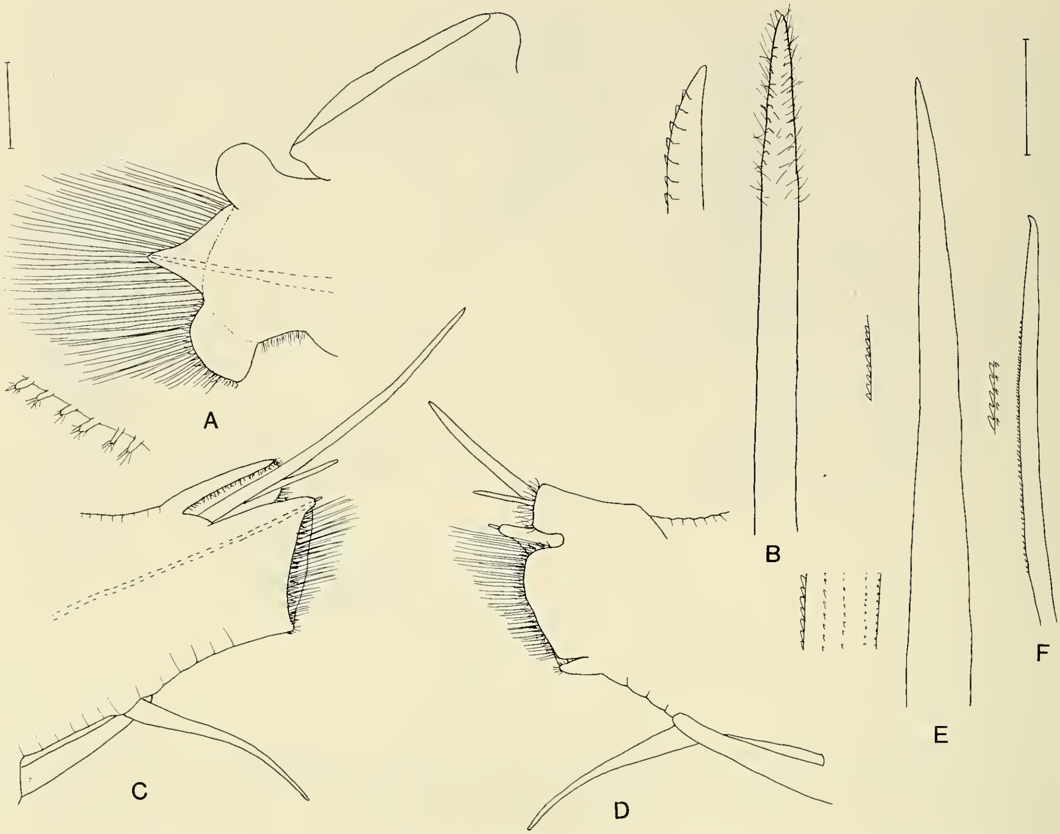

Fig. 4. *Lepidonotopodium piscesae,* paratype, USNM 102889: A, Left notopodium and elytrophore from segment 13, separated from neuropodium, posterior view, notoaciculum dotted, with detail of papillae on ventral part of bract; B, Short (left) and long (right) notosetae from same, with bacterial "hairs"; C, Left neuropodium from segment 13 anterior view, neuroaciculum dotted; D, Same, posterior view; E, Supraacicular neuroseta from same, with detail of fine spinous rows; F, Subacicular neuroseta from same, with detail of spinous rows. Scales = 0.5 mm for A, C, D; 0.1 mm for B, E, F.

merous subacicular neurosetae with slightly hooked tips and fine spinous rows on cutting edge (Figs. 2F, 3E, 4F). On 7 paratypes, neuropodia of segment 13 differing by presence of only 1–2 long, stout, reddish sabre-like supraacicular neurosetae, appearing smooth but with longitudinal rows of fine spines (Fig. 4C–E), with greater development of upper fimbriated bract (compare Figs. 3B–D and 4C–E). Ventral cirri attached on middle of neuropodia, tapering to slender tips, and extending to tips of neuropodia (Figs. 2A–C, 3B, C).

About half of adult paratypes with 5 pairs of elongate ventral papillae on segments 11 to 15, attached on middle bases of neuropodia, and extending to near bases of ventral cirri or beyond (Figs. 3A–C, 4C, D). Pygidium bulbous dorsal lobe between parapodia of posterior few smaller segments, with or without pair of anal cirri.

Etymology.—The species is named for the Canadian submersible DSRV *Pisces IV.*

Distribution.—Hydrothermal vents of Northeast Pacific, in 1546 to 2208 meters.

Biology.—*Lepidonotopodium piscesae* lives on the periphery of the vents, crawling on rocks and vestimentiferan tubes, grazing on protozoan and bacterial mats. One specimen was observed on time-lapse photography crawling to the top of a tube and groping around inside (V. Tunnicliffe, in litt.). The elytra are often coated with bacterial filaments, giving them a white color.

Lepidonotopodium piscesae is most closely related to *L. williamsae* from the Galapagos Rift. The two species differ from one another as follows: *L. piscesae* has 5 pairs of elongate segmental papillae on segments 11–15, instead of 4 pairs on segments 12–15; a pharynx with 7 pairs of unequal-sized border papillae, instead of subequal papillae, jaws with up to 12 basal teeth, instead of 7, and has 1–2 elongate sabre-like supraacicular neurosetae on segment 13 of a few specimens, instead of lacking them entirely.

Subfamily Macellicephalinae
Hartmann-Schroder, 1971,
emended Pettibone, 1976
Genus *Levensteiniella* Pettibone, 1985
Levensteiniella kincaidi Pettibone
Fig. 5

Levensteiniella kincaidi Pettibone, 1985b: 741, figs. 1–3.

Levensteiniella sp. Tunnicliffe et al., 1986: 407. [Explorer Ridge]

Material.—Hydrothermal vents of Northeast Pacific, dives by DSRV *Pisces IV* (P) and DSRV *Alvin* (A): EXPLORER RIDGE, 49°45′N, 130°16′W, 1818–1823 m: P1494-604/605, 1 Jul 1984, 5 specimens (USNM 102869), 1 specimen (NMCA 1987-0451); P1505-602, 19 Aug 1984, Busted Thruster vent, 1 specimen (USNM 102867).—ENDEAVOUR SEGMENT, JUAN DE FUCA RIDGE, 47°57′N, 129°04–06′W, 2208–2213 m A1418, 24 Jul 1984, 1 specimen (USNM 102868); A1447-614, 3 Sep 1984, 2 specimens (USNM 102870); A1452-621, 7 Sep 1984, Lt. Obo vent, 1 specimen (USNM 102871).—AXIAL SEAMOUNT, JUAN DE FUCA RIDGE, 45°56–57′N, 130°01′W, 1546–1553 m; A1411, 16 Jul 1984, residue from animal container, young specimen (USNM 102866); A1413, 18 Jul 1984, young specimen (USNM 102872).

Remarks.—The 12 specimens agree with previously described specimens from the Galapagos Rift and 21°N vent sites. Some specimens are larger than previously reported (12 mm long, 6 mm wide, with 25 segments). The largest specimen from Explorer Ridge is 16 mm long, 9 mm wide, for 25 segments, with the last one small; additional adult specimens are 12–15 mm long, 7–9 mm wide, for 25 segments: a small specimen is 7 mm long, 4 mm wide, for 23 segments, with the last 3 small. The largest specimen from the Endeavour Segment is 16 mm long, 9 mm wide, for 25 segments; a small specimen is 6 mm long, 5 mm wide, for 22 segments. Two young specimens from Axial Seamount are 1.2 mm long, 1.2 mm wide, for 11 segments.

Most of the elytra were missing. On a small specimen from Endeavour Segment, Juan de Fuca Ridge, three pairs of elytra remained on segments 2, 4, and 5; in addition to the usual filiform papillae on the surface, some papillae on the posterior and lateral borders were enlarged basally (Fig. 5A, B). Four of the larger specimens had long ventral papillae on segments 11 and 12, sometimes directed dorsally between the parapodia.

Distribution.—Hydrothermal vents of Tropical East Pacific: Galapagos Rift and East Pacific Rise at 21°N, in 2457–2633 m; Northeast Pacific: Explorer Ridge, Endeavour Segment and Axial Seamount, Juan de Fuca Ridge, in 1546–2213 m.

Subfamily Branchinotogluminae
Pettibone, 1985
Branchinotogluma Pettibone, 1985
Branchinotogluma grasslei Pettibone

Red polynoid polychaete, Tunnicliffe & Juniper, 1983:966. [Axial Seamount, Juan de Fuca Ridge]

Branchinotogluma grasslei Pettibone,

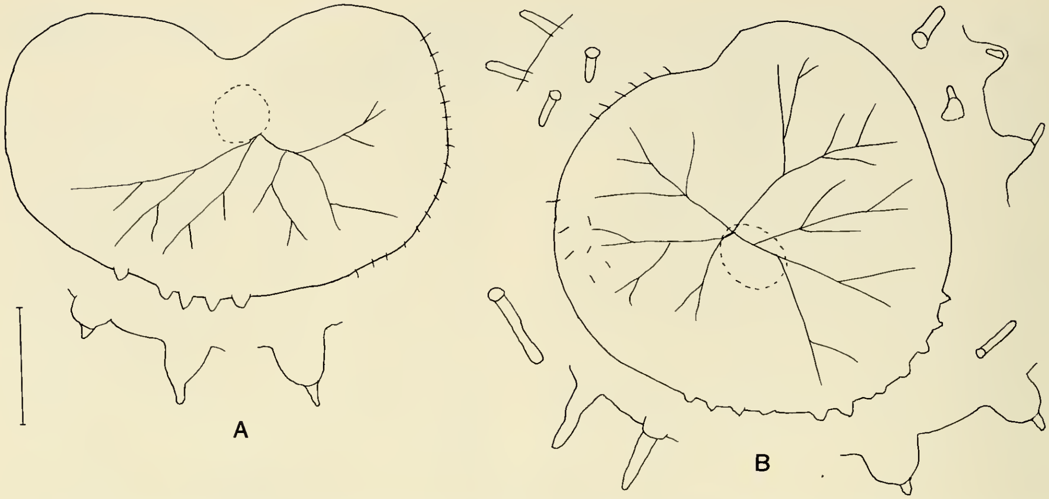

Fig. 5. *Levensteiniella kincaidi*, small specimen (6 × 5 mm, with 22 segments), USNM 102870: A, Left 1st elytron, segment 2, with detail of border papillae; B, Right 2nd elytron, segment 4, with detail of border and surface papillae. Scale = 0.5 mm.

1985a:457, figs. 5, 6.—Newman, 1985 (list).

Branchinotogluma sp., Tunnicliffe et al., 1986:407. [Explorer Ridge]

Material.—Hydrothermal vents of Northeast Pacific, dives by DSRV *Pisces IV* (P) and DSRV *Alvin* (A): EXPLORER RIDGE, 49°45′N, 130°16′W, 1818 m: P1494, 1 Jul 1984, 1 specimen (USNM 102864); P1495-606, 2 Jul 1984, Lunch Hour vent, 2 specimens (USNM 102861).—ENDEAVOUR SEGMENT, JUAN DE FUCA RIDGE, 47°57′N, 129°04–06′W, 2208 m: A1419, 25 Jul 1984, 13 specimens (USNM 102859), 2 specimens (NMCA 1987-0452); A1452.-21, Lt. Obo vent, 7 Sep 1984, 4 specimens (USNM 102865).—AXIAL SEAMOUNT, JUAN DE FUCA RIDGE, 45°59′N, 130°03′W, 1592 m: P1327, 17 Aug 1983, Taylor's vent, 2 specimens (USNM 102860); P1728-634, 29 Jul 1986, Demon vent no. 1, 6 specimens (USNM 102863).—SOUTHERN JUAN DE FUCA RIDGE, A1410, 15 Jul 1984, 45°13′N, 130°09′W, 2380 m, on chaleopyrite and sphalerite, 1 specimen (USNM 102862).

Remarks.—The 31 specimens from the four vent areas agree with the specimens previously described from the Galapagos Rift and 21°N vent sites. Specimens from the Explorer Ridge are 14–23 mm long, 7–10 mm wide with setae and have 21 segments. From Endeavour Segment, larger specimens are 13–31 mm long, 6–12 mm wide, and have 21 segments; small specimens are 5–7 mm long, 3–4 mm wide, and have 18–20 segments. From Axial Seamount, the larger specimens are 12–26 mm long, 6–11 mm wide and have 21 segments; the small specimen is 5 mm long, 3 mm wide, with 19 segments. Specimen from Southern Juan de Fuca Ridge is 25 mm long, 12 mm wide, and has 21 segments.

Distribution.—Hydrothermal vents of Tropical East Pacific: Galapagos Rift and East Pacific Rise at 21°N, in 2482–2633 m; Northeast Pacific: Explorer Ridge, Endeavour Segment and Axial Seamount, Juan de Fuca Ridge, and Southern Juan de Fuca Ridge, in 1495–2380 m.

Biology.—*Branchinotogluma grasslei* has been found living on rocks and the soft vestimentiferan tubes of *Ridgeia piscesae* Jones in the vicinity of very hot vents and high hydrogen-sulfide levels. They are bright red and very difficult to see in the shimmering hot water of the vents (V. Tunnicliffe, in litt.).

Branchinotogluma sandersi Pettibone

Branchinotogluma sandersi Pettibone, 1985a:453, figs. 3, 4.—Newman, 1985: 232 (list).

Branchinotogluma sp., Tunnicliffe et al., 1986:407. [Explorer Ridge]

Material.—Hydrothermal vents of Northeast Pacific, dives by DSRV *Pisces IV* (P) and DSRV *Alvin* (A): EXPLORER RIDGE, 49°45′N, 130°16′W, 1818 m, P1494, 1 Jul 1984, 2 specimens (USNM 102857).—ENDEAVOUR SEGMENT, JUAN DE FUCA RIDGE, 47°57′N, 129°04–06′W, 2208 m: A1419, 25 Jul 1984, 3 specimens (USNM 102853), 1 specimen (NMCA 1987-0453); A1452-621, Lt. Obo vent, 7 Sep 1984, 3 specimens (USNM 102856).—AXIAL SEAMOUNT, JUAN DE FUCA RIDGE, 45°59′N, 130°03′W, 1592 m: P1327-640, 17 Aug 1983, Taylor's vent, 1 specimen (USNM 102854): P1728-634, 29 Jul 1986, Demon vent no. 1 specimen (USNM 102855).

Remarks.—The 11 specimens from three vent areas agree with the previously described specimens from the Galapagos Rift and 21°N vent sites. Two specimens from Explorer Ridge are 8–12 mm long, 4–6 mm wide with setae, for 21 segments. Larger specimens from Endeavour Segment measure 12–15 mm long, 6–8 mm wide, for 21 segments; smaller specimens are 8–9 mm long, 5–6 mm wide, for 21 segments, with the posterior 3 segments not fully developed. A large specimen from Axial Seamount is 21 mm long, 11 mm wide, for 21 segments.

One specimen from Endeavour Segment (USNM 102856) was observed with groups of very long white filaments emerging from the body on the left side between parapodia of segments 12–13 and 13–14, possibly indicative of a parasite.

Distribution.—Hydrothermal vents of Tropical East Pacific: Galapagos Rift and East Pacific Rise at 21°N, in 2451–2633 m; Northeast Pacific: Explorer Ridge, Endeavour Segment and Axial Seamount, Juan de Fuca Ridge, in 1592–2208 m.

Branchinotogluma sp. B

Branchinotogluma sp. B, Pettibone, 1985a: 466.

Material.—Explorer Ridge, 49°45.6′N, 130°16.1′W, 1818 m, P1494, 1 Jul 1984, 2 young specimens (USNM 102858).

Remarks.—The two young specimens, 4–6 mm long, 2–3 mm wide with setae, and having 16–17 segments, may be juveniles of *B. grasslei, B. sandersi,* or *Opisthotrochopodus tunnicliffeae*; all three species were found at the same station.

Opisthotrochopodus Pettibone, 1985, emended

Type species.—*Opisthotrochopodus alvinus* Pettibone, 1985a; by original designation. Gender: masculine.

Opisthotrochopodus is emended to include the new species *O. tunnicliffeae.*

Diagnosis.—Body short, with 21 segments, first achaetous. Elytra 10 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19. Dorsal cirri with short cirrophores and long styles, and dorsal tubercles, in line with elytrophores, on segments 3, 6, 8, 10, 12, 14, 16, 18, 20, and 21. Arborescent branchiae 4 per segment, attached to lateral sides of elytrophores, dorsal tubercles, and dorsal sides of notopodia, beginning on segment 3 and continuing to segment 17 or 18. Prostomium bilobed with triangular anterior lobes bearing frontal filaments, with ceratophore of median antenna in anterior notch, with paired ventral palps, without lateral antennae or eyes. First or tentacular segment not visible dorsally; tentaculophores

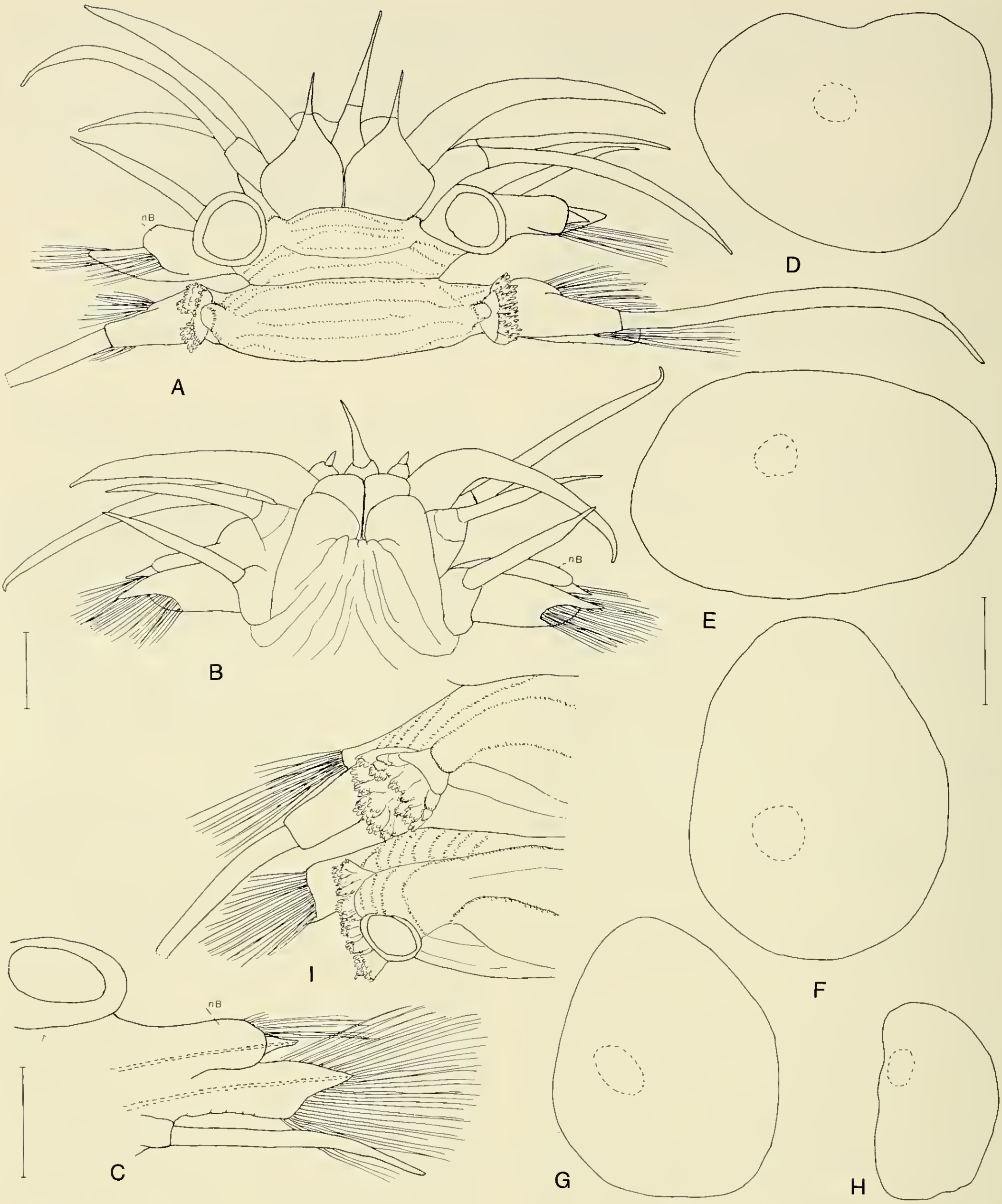

Fig. 6. *Opisthotrochopodus tunnicliffeae*, A–H, holotype; I, paratype, USNM 102874: A, Anterior end, dorsal view; B, Same, ventral view; C, Left elytragerous parapodium of segment 2, anterior view, acicula dotted; D, Left 1st elytron, segment 2; E, Left 2nd elytron, segment 4; F, Left 8th elytron, segment 15; G, Left 9th elytron, segment 17; H, Left 10th elytron, segment 19; I, Dorsal view left side of segments 8 (cirrigerous) and 9 (elytragerous), showing only base of dorsal cirrus. nB, notopodial bract. Scales = 1.0 mm for A, B, I; 1.0 mm for C; 2.0 mm for D–H.

lateral to prostomium, each with dorsal and ventral tentacular cirri, without setae. Second or buccal segment with first pair of elytra, biramous parapodia, and ventral or buccal cirri attached to basal parts of parapodia lateral to mouth; styles longer than following ventral cirri. Parapodia biramous, with notopodia shorter than neuropodia. Notopodia of elytragerous segments 2–17 with prominent rounded bracts enclosing conical acicular lobes and notosetae, or only on segment 2. Neuropodia with longer, flattened, conical presetal and shorter, rounded postsetal lobes. Notoseta stouter than neurosetae, straight, acicular, smooth or with spines. Neurosetae long, slender, finely spinous, with slightly hooked tips. Ventral cirri short, tapered. Posterior 4 segments (18–21) compressed; parapodia directed posteriorly and greatly modified, with expanded delicate lamellae; elongated cylindrical notopodia fused with dorsal cirrophores and distal styles on segments 20 and 21; with unique neuropodial wheel organs on segment 20, including stout acicular neurosetae. Pharynx with 5 border papillae, 3 dorsal and 2 ventral; 2 pairs of dorsal and ventral hooked jaws, each with row of numerous, minute teeth along edge. Segmental ventral papillae or lamellae on segments 12–17. Pygidium with or without pair of anal cirri.

Opisthotrochopodus tunnicliffeae, new species

Figs. 6–9

Material.—Hydrothermal vents of Northeast Pacific, dives by DSRV *Pisces IV* (P) and DSRV *Alvin* (A): EXPLORER RIDGE, 49°45′N, 130°16′W, 1818 m: P1494, 1 Jul 1984, paratype (NMCA 1987-0450): P1495-606, 2 Jul 1984, Lunch Hour vent, paratype (USNM 102877).—AXIAL SEAMOUNT, JUAN DE FUCA RIDGE, 16 Jul 1984, 45°57′N, 130°01′W, 1553 m, A1411, residue from animal container, holotype (USNM 102873), 4 paratypes, 2 young (USNM 102874-6).

Description.—Length of holotype 25 mm, width with setae 11 mm, segments 21. Length of largest paratype (USNM 102874) 30 mm, width 12 mm, segments 21. Two smaller paratypes 15–17 mm long, 7–9 mm wide, with 21 segments. Two young paratypes (USNM 102876) 2–2.5 mm long, 2–2.5 mm wide, with 14–17 segments, last ones minute. Body flattened ventrally, arched dorsally, slightly tapered anteriorly and posteriorly, with parapodia longer than body width; posterior few segments (18–21) compressed, with parapodia modified (Fig. 8B, C). Elytra large, overlapping, covering dorsum; round to oval, posterior pair smaller, elongate-oval, enclosing posterior modified segments (Fig. 6D–H). Elytra smooth, stiff, somewhat vaulted around place of attachment to elytrophores. Elytrophores large, projecting posteriorly, with arborescent branchiae attached on lateral sides (Figs. 6I, 7B, 8C, D). Dorsal tubercles elongate, projecting posteriorly with arborescent branchiae on distal part (Figs. 6I, 7A, 8C).

Prostomium bilobed, without eyes or lateral antennae; anterior lobes subtriangular, with rather long frontal filaments; median antenna with bulbous ceratophore in anterior notch, subulate style with long slender tip, shorter than tentacular cirri; palps stout, tapered, smooth (Fig. 6A, B). First or tentacular segment forming upper and lateral lips of mouth; tentaculopores lateral to prostomium, without setae, each with pair of tentacular cirri, dorsal tentacular cirrus longer than palp, ventral one shorter than dorsal (Fig. 6A, B). Second or buccal segment forming posterior lip of mouth, bearing biramous parapodia and first pair of elytrophores; notopodia with hood or bract (nB) on anterodorsal side encircling small bundle of notosetae and conical acicular lobe; ventral buccal cirri similar to tentacular cirri, longer than following ventral cirri (Fig. 6A–C). Muscular pharynx observed cut open, showing usual pattern in genus: 5 papillae around opening, 3 dorsal and 2 ventral; 2 pairs of amber-colored jaws minutely den-

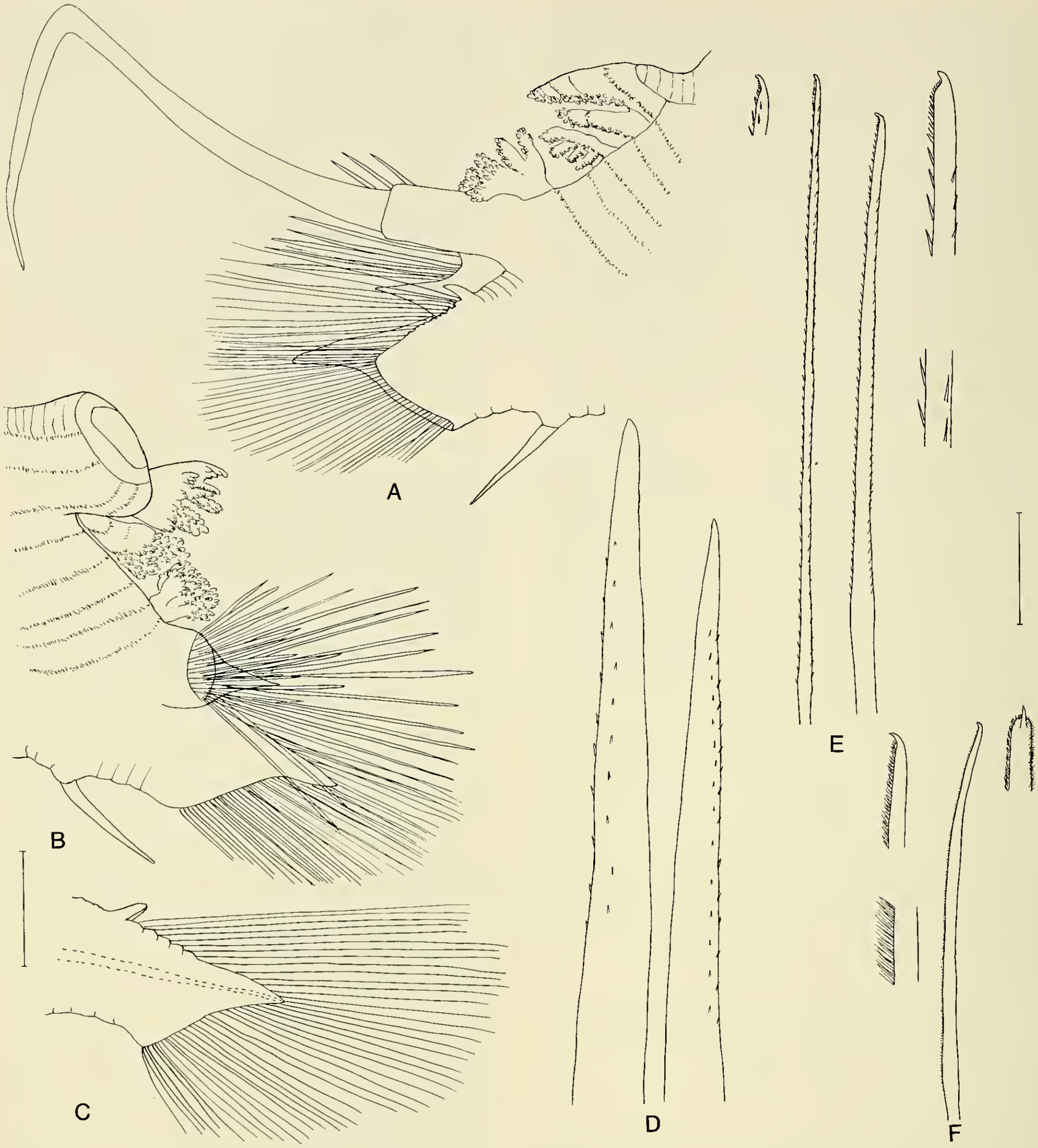

Fig. 7. *Opisthotrochopodus tunnicliffeae,* holotype: A, Left middle cirrigerous parapodium, posterior view; B, Left middle elytragerous parapodium, anterior view; C, Left middle neuropodium, anterior view, notopodium cut off, neuroaciculum dotted; D, Notosetae from same; E, Supraacicular neurosetae from same, with detail magnified; F, Subacicular neuroseta from same, with detail magnified, one view of tip turned. Scales = 1.0 mm for A–C; 0.1 mm for D, F.

ticled on inner border (see Pettibone 1985a: fig. 8H, I).

Biramous parapodia of segments 3–17 similar, with smaller notopodium on anterodorsal side of larger neuropodium; notopodium rounded, with projecting, tapered acicular lobe and radiating bundle of numerous notosetae; neuropodium with presetal lobe long, subconical, with projecting acicular lobe; postsetal lobe shorter,

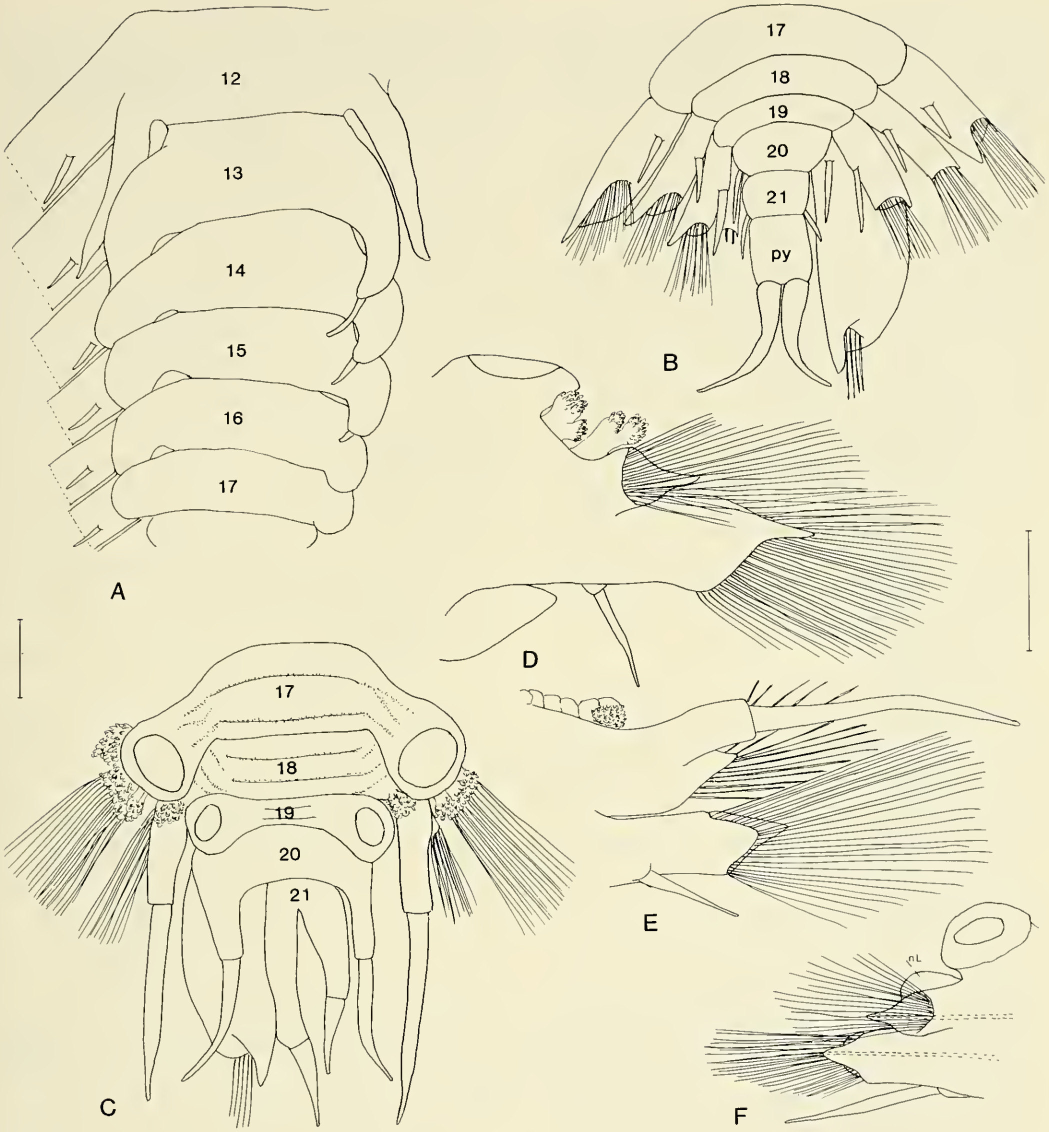

Fig. 8. *Opisthotrochopodus tunnicliffeae,* holotype: A, Ventral view of segments 12–17, showing ventral papillae on segments 12–15 and ventral lamellae on segments 16 and 17, parapodia incompletely shown; B, Ventral view of posterior end, including segments 17–21 and pygidium, wheel organ of segment 20 withdrawn on right side; C, Dorsal view of same; D, Left elytragerous parapodium from segment 17, anterior view; E, Right cirrigerous parapodium from segment 18, posterior view; F, Right elytragerous parapodium from segment 19, anterior view, acicula dotted. nL, notopodial lamella. Scales = 1.0 mm for A–C; 1.0 mm for D–F.

rounded; lobes widely separated on dorsal side, with projecting small lobe on dorsal base (hidden from view by anterior notopodium), with fan-shaped bundle of very numerous neurosetae (Figs. 7A–C, 8D). Notosetae stouter than neurosetae, long, straight, tapered, acicular, with 2 rows of spines; shorter notosetae mostly smooth (Fig. 7D). Neurosetae long, slender, slightly wider basally, with slightly hooked tips; supraacicular neurosetae with widely spaced spines extending to near tips, finely spinous distally (Fig. 7E): subacicular neurosetae finely spinous (Fig. 7F). Dorsal cirrus on cirrigerous segments on posterodorsal side of notopodium, with cylindrical cirrophore and long style extending far beyond setae; dorsal tubercle extending laterally, with arborescent branchia distally; additional branchia on dorsal base of notopodium (Figs. 6I, 7A). Elytragerous segments with large, bulbous elytrophore extending posterolaterally, with large arborescent branchia on lateral base and additional branchia on dorsal base of notopodium (Figs. 7B, 8C, D). Ciliated bands on dorsum, extending onto elytrophores and dorsal tubercles, as well as on anterior and posterior sides of parapodia (Figs. 6A, I, 7A, B). Ventral cirri on middle of neuropodia tapering to slender tips (Fig. 7A, B).

Cirrigerous parapodium of segment 18 much smaller than preceding parapodium, with long dorsal cirrus projecting posteriorly and single, small arborescent branchia projecting from dorsal tubercle (Fig. 8B–E).

Segment 19 with smaller elytrophores approaching medially, usually without branchiae (small one on under side of left elytrophore of holotype), with small parapodia wedged between adjacent parapodia and hidden from view dorsally; notopodium with delicate lamella (nL) on dorsal side; notosetae stout, acicular, with 2 rows of spines; neurosetae slender, minutely spinous, with capillary tips (Fig. 8B, C, F).

Segment 20 with parapodia greatly modified. Neuropodium enlarged (corresponding to wheel organ of *O. alvinus*), inflated, with projecting, conical acicular lobe, with neurosetae projecting from wide opening and ventral cirrus attached near base (Figs. 8B, C, 9A, B, F). Neurosetae consisting of up to 4 stout, acicular, harpoon setae (Fig. 9E) and long slender setae with 2 rows of long spines on basal half, tapering to slender, bare tips (Fig. 9D). Neuropodium on holotype inflated and extended on left side but retracted and wrinkled on right side (Figs. 8B, C, 9A, F); largest paratype (USNM 102874) with modified neuropodia extended on both sides. Notopodium with acicular lobe fused to cirrophore of dorsal cirrus, with style extending posteriorly; basal part of notopodium compressed against inflated neuropodium and hidden from view until separated, with row of about 13 short, spinous notosetae enclosed in delicate lamella (nL) (Fig. 9A–C). Small paratype of 17 × 9 mm (USNM 102877) with both neuropodia inflated, each with 2–3 harpoon neurosetae. Slightly smaller paratype of 15 × 7 mm (NMCA 1987-0450) with right neuropodium long, inflated, with 3 harpoon neurosetae; left side short, slightly inflated, without harpoon setae. Small paratype of 17 × 9 mm (USNM 102875) with neuropodia only slightly inflated and neurosetae only slender, spinous; notosetae short curved, smooth (Fig. 9H, J).

Segment 21 with elongate cirrophores fused medially with each other and laterally with notopodial lobe containing stout notoaciculum: dorsal cirrus short; notosetae absent (Figs. 8C, 9G). Neuropodium with small conical acicular lobe containing slender neuroaciculum, with small bundle of smooth capillary neurosetae; ventral cirrus longer than neuropodium, attached on lateral side of segment (Figs. 8B, 9G).

Pygidium rectangular, posterior to segment 21, with pair of stout anal cirri (Fig. 8B). Anal cirri sometimes broken off.

Ventral segmental papillae long, tapered on segment 12, shorter and thicker with slender distal part on segments 13–15, reduced to rounded lamellae on 16 and 17; papillae directed dorsally between parapodia, sometimes with yellowish secretion inside and pushed to outside (Fig. 8A, D).

Etymology.—The species is named for Verena Tunnicliffe, who sent me the polynoid specimens for study and furnished valuable information.

Distribution.—Hydrothermal vents of Northeast Pacific: Explorer Ridge and Axial

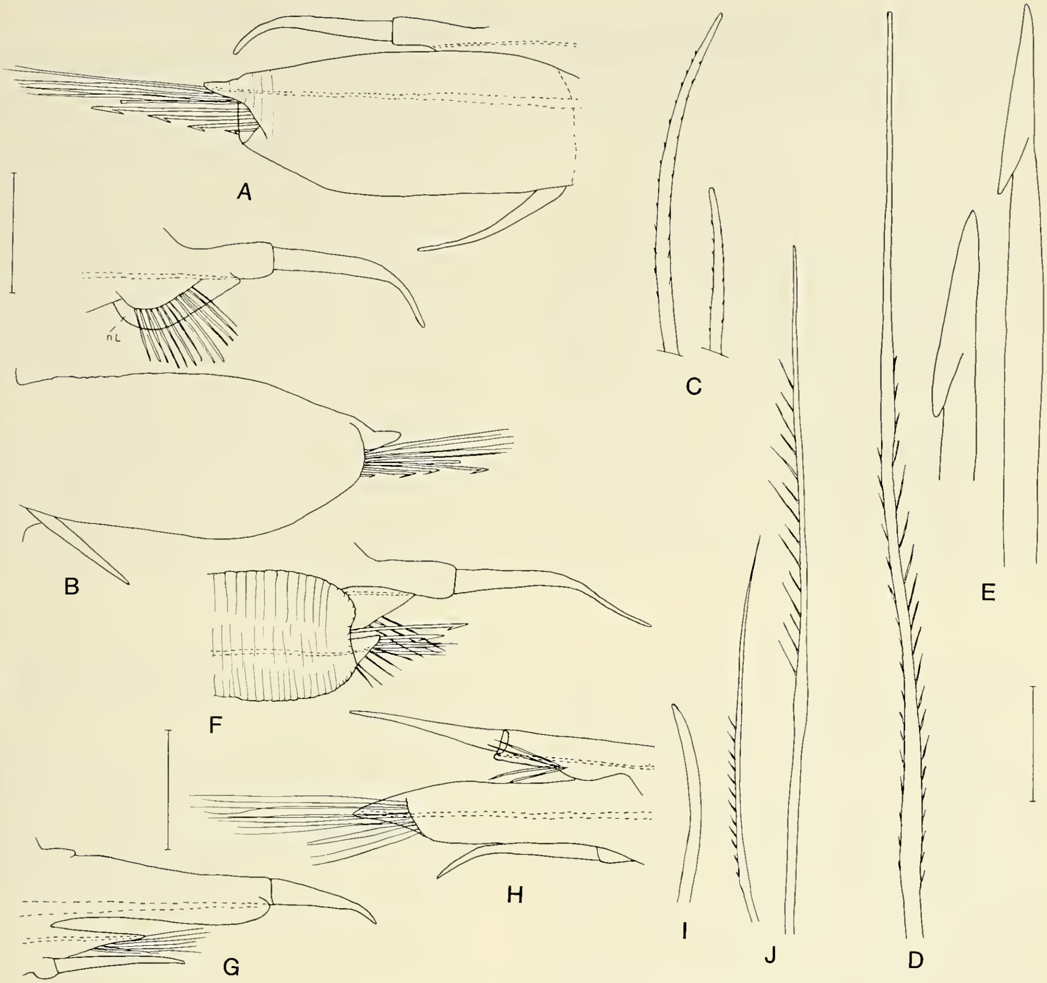

Fig. 9. *Opisthotrochopodus tunnicliffeae,* A–G, holotype; H–J, small paratype, USNM 102875: A, Left cirrigerous parapodium from segment 20, anterior view, acicula dotted; B, Notopodium and neuropodium of same, separated, posterior views; C, Notosetae from same; D, Slender neuroseta from same; E, Stout harpoon neurosetae from same; F, Right cirrigerous parapodium from segment 20, posterior view, basal part not shown, acicula dotted; G, Left cirrigerous parapodium from segment 21, anterior view, acicula dotted; H, Right parapodium from segment 20, anterior view, acicula dotted; I, Notoseta from same; J, Neurosetae from same. nL, notopodial lamella. Scales = 1.0 mm for A, B, F, G; 0.1 mm for C–E, I, J; 0.5 mm for H.

Seamount, Juan de Fuca Ridge, in 1818–1553 m.

Differential diagnosis.—*Opisthotrochopodus tunnicliffeae* differs from *O. alvinus* in having notopodial bracts only on segment 2, instead of on all elytragerous segments of 2–17, and agrees with *Brachinotogluma sandersi* and *B. grasslei* in this regard. The posterior modified segments differ in the two species: in *O. alvinus,* specialized neuropodia of segment 20 flare out and have several types of neurosetae appearing like spokes of a wheel, thus the name wheel organ; whereas in the new species, neuropodia are inflated and have stout, harpoon neurosetae, with "balloon organ" a more appropriate name. In *O. alvinus,* parapodia of segments 18–21 are more modified, lacking neurosetae on segments 18 and 19, ventral cirri on segments 20 and 21, and anal cirri; whereas these structures are present in *O. tunnicliffeae.*

Acknowledgments

I wish to thank the members of the joint Canadian American Seamount Expedition for the interesting material on which this study is based, and particularly Verena Tunnicliffe of the University of Victoria for sending me the specimens and for providing helpful information in correspondence as well as important literature. Meredith Jones of the Smithsonian Institution contributed additional specimens. The manuscript benefitted from the reviews of Thomas H. Perkins and James A. Blake.

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NOTES ON THE FROG GENUS *THOROPA* (AMPHIBIA: LEPTODACTYLIDAE) WITH A DESCRIPTION OF A NEW SPECIES (*THOROPA SAXATILIS*)

Reginald B. Cocroft and W. Ronald Heyer

Abstract.—A new species of *Thoropa* (*T. saxatilis*) is described from the State of Santa Catarina, Brazil. This species and the two other large *Thoropa* occur allopatrically in the middle and southern Atlantic Forest Domain and campos rupestres of Brazil. The ranges of the two small *Thoropa* species overlap with each other and with *T. miliaris* in the middle Atlantic Forest region. Immunological microcomplement fixation albumin distances indicate that the large forms share a similar ancestral morphology and that distributions cannot be explained on the basis of recent allopatric speciation of a widespread ancestor. Adult male *Thoropa* have clusters of dark spines or a pad on the hand, and males of four out of five species either show scarring on the dorsum indicative of male combat or are reported to be territorial.

While preparing a description for a new species of *Thoropa,* we found considerable previously unpublished data on localities, natural history, and nomenclature of this genus. The purpose of this paper is to summarize these findings in addition to describing the new species.

Nomenclature

While reviewing previously proposed names for *Thoropa* to verify that the new species was undescribed, we encountered one locality citation and one synonymy worthy of comment.

As Cochran's work (1955) often serves as a starting reference for those interested in the frogs of southeast Brazil, an error in a type locality is worth pointing out. Cochran (1955:293) gives the type locality of *Cystignathus missiessii* Eydoux & Souleyet, 1842 (the type species of *Thoropa* Cope), as "Eijouja." The locality as it appears in Eydoux & Souleyet (1842:149) is ". . . Tijouka, aux environs de Rio-Janeiro." Bokermann (1966:33) gives the type locality correctly as Tijuca, Rio de Janeiro, without comment.

Cochran (1955:297) stated that "In Vienna I examined Fitzinger's type of *Eupsophus fuliginosus,* from Rio de Janeiro taken by the Novara Expedition, 1857–1859; it appears to be a young *E. miliaris.*" She also presented a photograph of the type (plate 25, fig. E), for which the original photographs are still available (in our files). We disagree that *E. fuliginosus* is a synonym of *T. miliaris. Thoropa miliaris* typically has dark squarish or oblong dorsal blotches and distinct light markings on the posterior surface of the thigh (shown in Cochran's [1955] photograph of *T. miliaris,* plate 25, fig. F). The holotype of *E. fuliginosus* has a dark inverted V-shaped mark on the dorsum and the posterior surfaces of the thighs are almost uniformly dark, lacking distinct light marks. The dorsal pattern of the holotype of *E. fuliginosus* is the same as that found in individuals of *Thoropa lutzi* and *T. petropolitana* and differs from the dorsal patterns of both the new species and *T. megatympanum.* The finger tips of the holotype of *E. fuliginosus* are not swollen or expanded, as are those of *T. miliaris, T. lutzi,* and the new species. The second finger is longer than the first in the holotype of *E. fuliginosus* and in *T. petropolitana*; the first finger is longer than the second in all but the smallest *T. miliaris* (15 mm SVL). The holotype of *E. fuliginosus* (23 mm SVL) is in poor condition and does not have any nuptial spines or pads on the thumb. Drs. Grillitsch and Tiedemann (pers. comm.) kindly examined the holotype for us and stated that they are "sure that this specimen is a male." As adult male *Thoropa* have either thumb pads or spines, their absence in the holotype suggests that they have fallen off, apparently due to preservation problems (this condition is seen, albeit rarely, in other *Thoropa* specimens). The pattern of the posterior surface of the thigh in the holotype (almost uniformly dark with a few light specks) does not match the pattern found in most *T. petropolitana* (mottled, with dark cross bars dorsally). Fitzinger (1861:414) gave the type locality of *E. fuliginosus* as "Brazilien." Gans (1955) indicated that the "Novara Reise" was only in the region of Rio de Janeiro in Brazil, but included Rio de Janeiro, Corcovado, Tijuca, and Petrópolis, localities from which *T. lutzi, miliaris,* and *petropolitana* have been collected.

In summary, the following characteristics of the holotype of *E. fuliginosus* argue for or are consistent with the synonymy of *T. petropolitana* with *E. fuliginosus*: locality, adult size, dorsal pattern, relative first and second finger lengths, and finger-tip condition. The following two features argue against the synonymy of *T. petropolitana* with *E. fuliginosus*: lack of thumb spines, and the pattern on the posterior thigh. In our opinion, *E. fuliginosus* is definitely not the same species as either *T. lutzi, megatympanum, miliaris,* or the new species. The relationship of *E. fuliginosus* to *T. petropolitana* will not be settled until the holotype of *E. fuliginosus* is examined by someone familiar with variation in all *Thoropa*. Since we are unable to examine the holotype, we cannot resolve the question of the potential synonymy of *T. petropolitana* with *E. fuliginosus*; we consider *E. fuliginosus* a nomen dubium. We are certain, however, that neither *E. fuliginosus* nor any other name proposed for a *Thoropa* species applies to the new species, proposed as:

Thoropa saxatilis, new species

Fig. 1

Holotype.—MZUSP (Museu de Zoologia, Universidade de São Paulo) 64778, adult male, 23 Nov 1979, 20 km E of Bom Jardin on the road to Lauro Müller, State of Santa Catarina, Brazil, W. Ronald Heyer, Frances Irish, and Francisca C. do Val.

Paratopotypes.—MZÚSP 35478–96 (juveniles), Gertrude Rita Kloss, between 25 Oct and 14 Dec 1970.

Description of holotype.—Snout rounded in profile, nearly rounded from above; nostrils lateral, near tip of snout; canthus rostralis indistinct; loreal obtuse; tympanum distinct, rounded, just larger than eye; prominent annular ring hidden dorsally by supratympanic fold, fold extending halfway down posterior edge of tympanum; tongue elongate with slight emargination on anterior edge; vomerine teeth forming an obtuse angle between anterior portion of choanae, separated by less than one choanal diameter; vocal slits and sac absent; finger lengths III > IV > II = I; fingers unwebbed but with lateral ridges; tips of fingers flattened, expanded, disk shaped, wider than long (disk on finger III 2.4 mm wide), finger disks much more pronounced than toe disks; palmar tubercle large, cordate; thenar tubercle large, merging with prepollex, forming a rounded triangle with apex on palm, separated from thumb subarticular tubercle by about one length of subarticular tubercle; one rounded subarticular tubercle on finger II, two on fingers III and IV; no supernumerary tubercles on fingers; several small, accessory palmar tubercles; cluster of dark spines on distal surface of prepollex, and on dorsal surface of thumb above second joint, extending nearly to disk; row of 11–12 spines

Fig. 1. Dorsal and ventral views of holotype of *Thoropa saxatilis.*

dorsally on inner side of finger II, and row of 4–6 spines on finger III; dorsal texture smooth (weakly crenulate under magnification), upper eyelid granular, numerous scattered, low warts on flanks; venter smooth, under surface of thighs granular; tips of toes slightly expanded, flattened; toes unwebbed but with lateral ridges, ridges most pronounced on outer edges and on toe III; elongate inner metatarsal tubercle larger than rounded, pungent, outer metatarsal tubercle; weak tarsal fold extending length of tarsus.

SVL 57.5 mm; head length 21.7 mm; head width 23.9 mm; horizontal tympanum diameter 6.5 mm (including annulus); eye diameter 6.1 mm; distance from eye to posterior edge of naris 6.2 mm; thigh length 30.5 mm; shank length 33.9 mm; foot length 33.1 mm.

In preservative, dorsal basal color dark brown, with scattered, small light brown patches and irregular, longitudinal light brown patches; flanks indistinctly mottled gray and brown with scattered, low, light-pigmented warts; light gray-brown interocular line with wavy margins; upper lip light brown at base, brown in places extending upward and merging with gray loreal color. Dark brown, relatively broad canthal stripe from in front of naris to eye; upper surfaces of limbs barred; posterior surface of thigh almost uniform light brown with a few scattered light flecks; venter cream with light brown wash, wash more concentrated on throat and pectoral region.

Variation in adult specimens (n = 2 males, USNM [collections in National Museum of Natural History, Smithsonian Institution] 245972–73).—In preservative, the dorsal color ranges from a dark and light brown mottle in one specimen to light gray mottled with indistinct, rounded dark gray patches, a light central blotch, and light flecking on flanks and behind eyes in the other. The loreal color ranges from light brown to gray, the upper lip from dark brown to gray. The dorsal texture is smooth with numerous low warts on flanks and/or posteriorly on dorsum. One or two light interocular bars (dark bordered in one specimen) are present. Asperities are present on thumb and finger II

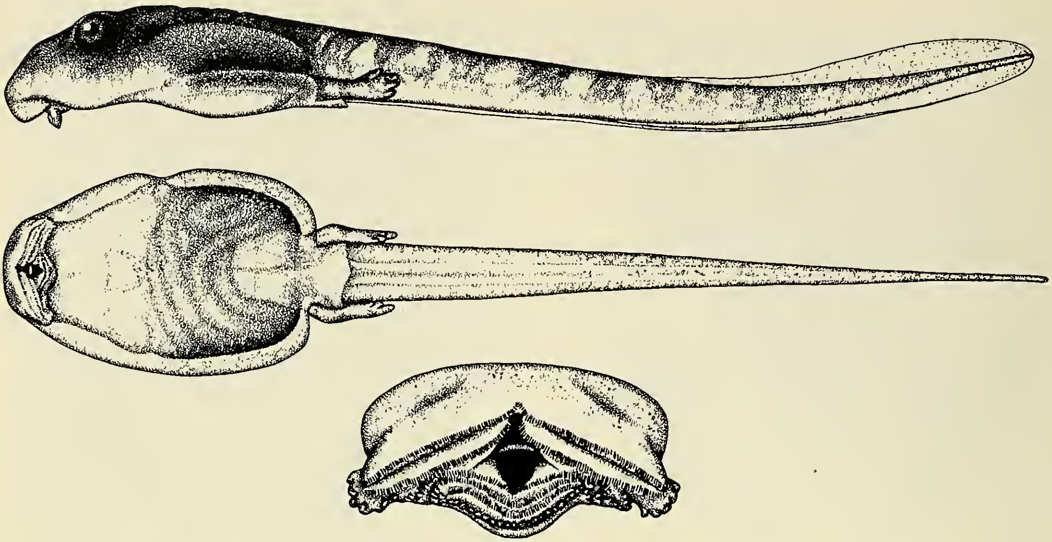

Fig. 2. Lateral, ventral, and mouthpart views of larval *Thoropa saxatilis,* stage 37.

or fingers II and III; the tympanum is just larger than the eye in one specimen and just smaller than the eye in the other. The disk on finger III is slightly more than twice the width of the finger at its narrowest point in one specimen, slightly less than twice the finger width in the other specimen.

Description of the larvae.—In addition to the specimen (stage 37) described and illustrated (Fig. 2), 10 other specimens (stages 29–39) were examined. The ranges of variation for these specimens appear in parentheses. Terminology follows Altig (1970).

Larvae elongate, depressed; tail fin low; dorsal fin present only on posterior 45% (35–60%) tail; ventral fin flattened and broadened, forming a concave strip narrowing posteriorly; depth of ventral fin increasing posteriorly, becoming just shallower than dorsal fin on posterior 40% of tail. Venter flattened, ventral skin forming a shelf extending slightly from the sides of the body, with a posterior flap projecting under the tail; spiracle sinistral, very small; anus median; eye moderately large, 15% (14–17%) head–body length; oral disk broad, 36% (34–41%) head–body length; oral disk laterally indented; oral papillae in single row, continuous posteriorly, but with anterior gap almost width of disk; tooth row formula 2(2)/3(1); upper tooth row adjacent to beaks consisting of two separate rows abutting medially; beaks laterally compressed, with deep central cusps.

Total length 28.5 mm (16.9–33.9 mm); head–body length 29% (29–33%) total length.

Dorsal color brown, lightening posteriorly; tail barred dorsally with lighter brown. Gut visible through peritoneum and ventral skin, ventral surfaces unpigmented except for few scattered melanophores on belly and posterior tail.

Habitat.—Two adult males and all juveniles collected by Heyer and associates were taken in January, from 2000–2215, along roadcuts where a thin film of water trickled over steeply inclined or vertical rock faces; larvae were collected from the same habitat. One adult male (the holotype) was collected in November, between 2100 and 2215 hr, on a rock near a waterfall in a ½–1 m wide stream. All collecting sites were in primary or secondary forest.

Advertisement call.—The call of this species is unknown. Although *Thoropa* lack vocal slits or sacs, calls have been recorded or reported for the other four species in the genus.

Etymology.—*Saxatilis* is a Latin word meaning "found among rocks."

Distribution (Fig. 4).—Southernmost extent of the Atlantic Forest and adjacent derivatives in the States of Santa Catarina and Rio Grande do Sul.

Referred specimens.—Brazil: Santa Catarina; Timbe do Sul (16 km from on road to Bom Jesus), USNM 245975–77, MZUSP 64786–93; Timbe do Sul (13 km from on road to Bom Jesus), USNM 245978–83; Itaimbezinho (10 km from on road to Praia Grande), USNM 245968–73, 245974 (larvae), MZUSP 64779–84, 64785 (larvae). Due to the high degree of local genetic differentiation of certain other Atlantic Forest frogs (e.g. Maxson & Heyer 1982), we feel it more prudent to consider other material we have examined from nearby localities as referred specimens, rather than type material.

Key to Adult *Thoropa* species

1. Finger disks markedly expanded, width of disk on finger III about twice width of finger at its narrowest point 2
– Finger disks not or only slightly expanded 3
2. Tympanum in adults about 60% size of eye, annulus and supratympanic fold low and indistinct; adult SVL 22–28 mm (males), 30 mm (females); asperities in males two dense, rounded patches of minute spines on thumb .... *T. lutzi*
– Tympanum in adults about 110% size of eye, annulus and supratympanic fold raised and distinct; adult SVL 41–58 mm (males); asperities in males in two patches of scattered spines on thumb and 1–2 rows on fingers II and III .... *T. saxatilis*
3. Posterior surface of thigh dark brown with contrasting, irregular, elongate white patches; dorsum often with 1–3 large, dark brown blotches (often with light borders) between eyes and sacrum .... *T. miliaris*
– Posterior surface of thigh uniform brown with light flecks or light and dark brown mottle; dorsum mottled light and dark brown 4
4. Tympanum in adults 100–110% size of eye, annulus and supratympanic fold pronounced; finger I longer than finger II; adult SVL 32–51 mm (males), 38–49 mm (females); males with two patches of spines on thumb, 1–2 rows of spines on fingers II and III .... *T. megatympanum*
– Tympanum in adults 60–70% size of eye, annulus and supratympanic fold low and indistinct; finger II longer than finger I; adult SVL 18–24 mm (males), 22–27 mm (females); males with a single patch of spines on thumb ..... *T. petropolitana*

Key to Larval *Thoropa* species

1. Skin on belly forming a ventrolateral shelf or ridge extending out from sides of body 2
– Skin on belly not forming a ventrolateral shelf or ridge extending out from sides of body *T. megatympanum*
2. Ventral skin shelf ending at posterior end of body, with posterior projection under tail 3
– Ventral skin shelf extending, entire, past posterior end of body 4
3. Tail fin near tip of tail deeper than tail musculature, tip of tail rounded .... *T. saxatilis*
– Tail fins near tip of tail less than or equal to depth of tail musculature, tip of tail tapering to a point .... *T. miliaris*
4. Belly transparent, viscera not or only

slightly obscured by ventral musculature .... *T. lutzi*

– Belly opaque, viscera obscured by sheet of ventral musculature .... *T. petropolitana*

Distribution

The known distribution of the genus *Thoropa* is concentrated in the middle and southern extent of the Atlantic Forests and the campos rupestres of the serras of Minas Gerais, with a few notable outliers (Fig. 3). One literature record not mapped (Fig. 3) is the type locality of *T. miliaris,* "fluminis Amazonum," which has been considered as erroneous by several authors (e.g., Bokermann 1965). There are two other localities that may well be in error. The first is the type locality of *Hylodes brieni,* Itaeté, Bahia (de Witte 1930) (Fig. 3, northernmost triangle). We have not examined the holotype, but the photographs accompanying the original description are good and there is no reason to question the identity of the specimen as anything but *Thoropa miliaris.* Itaeté is far removed geographically from the nearest *T. miliaris* locality (Fig. 3) and although we are not familiar with the environs of Itaeté, it is unlikely that characteristic *Thoropa* habitat is found there. A similar problem of apparent locality error has been noted for *Melanophryniscus* from the same expedition (see Frost 1985:68). Two adult specimens of *T. miliaris* from the Museu Nacional (Rio de Janeiro) collection (41a, b) have the locality data of São Paulo, Cachoeira de Itú (=Salto, 23°12′S, 47°17′W, P. E. Vanzolini, pers. comm.) (Fig. 3, southernmost triangle). This locality is outside of the Atlantic Forests in the State of São Paulo. There are no specimens of *Thoropa* from the area around Salto in the MZUSP collections, which increases the likelihood that this locality is in error. As there is considerable doubt about these two *T. miliaris* localities, we exclude them from further analysis. The remaining problematic locality (Fig. 3, remaining triangle in the State of Bahia) is a problem of identification. Miguel T. Rodrigues recently collected three very small *Thoropa* from Itajimirim, Bahia. The specimens clearly are *Thoropa,* but we are unable to assign them unequivocally to a species. They may represent a new species. If not, they are morphologically most similar to *T. megatympanum*; in any case, additional material is needed to clarify the identification. One additional noteworthy feature in the overall distribution of members of the genus *Thoropa* is the hiatus in the southeastern portion of the State of São Paulo, eastern Paraná, and north and central eastern Santa Catarina (Fig. 3). Within the middle and southern Atlantic Forests, *Thoropa* often share the same general habitat and usually are collected with members of the genus *Cycloramphus. Cycloramphus* species have been collected throughout the region of the distributional hiatus of *Thoropa* (Heyer 1983), so we believe this hiatus to be real and not an artifact of collecting.

The three large species of *Thoropa* are allopatrically distributed with respect to each other (Fig. 4). *Thoropa megatympanum* is now known from several localities in the State of Minas Gerais where campo rupestre vegetation is characteristic (see Giulietti & Pirani, 1988, for a discussion of campo rupestre) (Fig. 4, triangles). Morphologically, all populations appear similar. *Thoropa miliaris* is known from the Atlantic Forest and Atlantic Forest derivative vegetation in the States of Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo (Fig. 4). The question mark indicates a juvenile *Thoropa* (MZUSP 27250) with the locality "Serra da Bocaina." The individual is a *Thoropa,* probably *miliaris,* but positive identification is precluded by the condition of the specimen. It is curious that this specimen represents the only *Thoropa* record from the Serra da Bocaina, where extensive frog collections have been made. There is morphological variation within the species recognized in this paper as *T. miliaris,* most

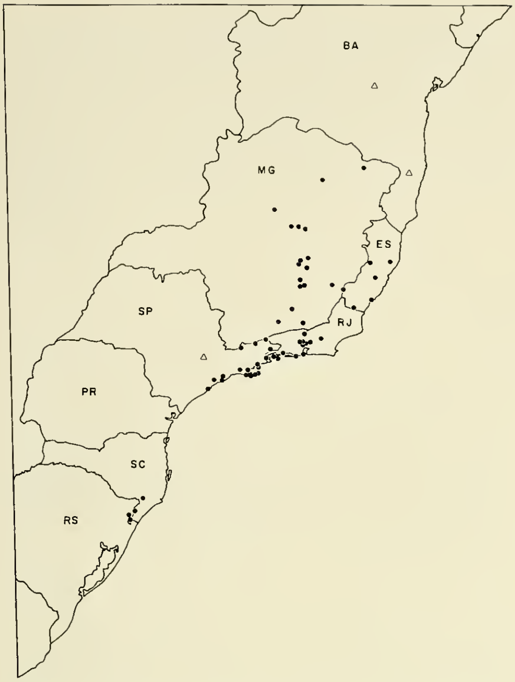

Fig. 3. Map of portion of eastern Brazil bounded by 10° and 55° W showing known and reported *Thoropa* localities. Triangles indicate questions of locality and identification (see text). State symbols: BA = Bahia; ES = Espírito Santo; MG = Minas Gerais; PR = Paraná; RJ = Rio de Janeiro; RS = Rio Grande do Sul.

Fig. 4. Distribution of large species of *Thoropa.* Open symbols indicate literature records for which we have not examined specimens. Triangles = *T. megatympanum,* circles = *T. miliaris,* squares = *T. saxatilis.* Question mark indicates possible *T. miliaris* locality in Serra da Bocaina (see text). State symbols as in Fig. 3.

notably in size; adults of the northern populations are notably smaller than those of the southern populations. Some of the variation is undoubtedly due to the presence of at least two cryptic species (see following section). *Thoropa saxatilis* is known from the southernmost extent of the Atlantic Forests in the State of Santa Catarina and possibly from a nearby locality in the State of Rio Grande do Sul. Braun & Braun (1980) record *Thoropa miliaris* from Cambará do Sul. Although we have not examined the specimen(s) in question, this record most likely refers to *T. saxatilis.* Bokermann (1965) tentatively included São Francisco de Paula, Rio Grande do Sul, as a *T. miliaris* locality, based on Hensel's (1867) report. Hensel (1867) used the name *Hylodes abbreviatus.* We concur with Bokermann (1965) that Hensel likely had a *Thoropa* in hand (other authors have considered *Hyla abbreviata* Spix to be a *Thoropa,* but as Hoogmoed & Gruber (1983:359–361) point out, *H. abbreviata* is a synonym of *Eleutherodactylus binotatus*). Hensel did not give a specific locality for his *Hylodes abbreviatus* (=*Thoropa miliaris*) although he did state that the specimens came from sandstone holes in primary forest in Rio Grande do Sul. As no other *Thoropa* have been collected from anywhere near São Francisco de Paula (Braun & Braun 1980), we do not include this locality in the distribution of *T. saxatilis.*

The two small species of *Thoropa* are known from the same general areas in the States of Espírito Santo and Rio de Janeiro (Figs. 5, 6). The two species occur sympatrically at two localities: Santa Teresa, Espírito Santo, and Petrópolis, Rio de Janeiro. Three Museu Nacional specimens (3578) are

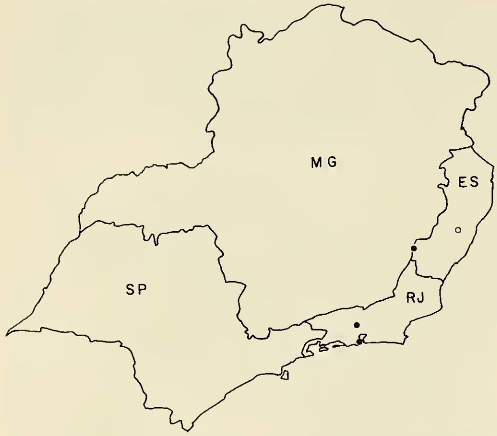

Fig. 5. Distribution of *Thoropa lutzi*. Open symbol indicates literature record for which we have not examined specimens. State symbols as in Fig. 3.

Fig. 6. Distribution of *Thoropa petropolitana*. Open circle indicates literature record for which we have not examined specimens. Triangle indicates questionable locality (see text). State symbol as in Fig. 3.

unquestionably *T. petropolitana* with the questionable locality data "Alto Serra de Cubatão ou Paranapiacaba, prope S. Paulo," collected by Hoge and B. Lutz, 17 December 1959. We also question this locality (Fig. 6, triangle) as these are the only specimens of *T. petropolitana* from the Cubatão–Paranapiacaba area, where extensive frog collections have been made, including large series of *T. miliaris.*

Thoropa megatympanum and *T. saxatilis* are not known to occur sympatrically with any other *Thoropa* species. In contrast, at all localities where *T. lutzi* and/or *petropolitana* have been collected, *T. miliaris* has also been taken.

Relationships

Morphologically, the three large species (*T. megatympanum, miliaris,* and *saxatilis*) are the most similar, not only in size but also in overall habitus and expression of male thumb and finger asperities. The distributions of these three species suggest recent allopatric speciation of a geographically widespread ancestor. However, the available data on estimates of genetic relatedness do not agree with this scenario. Maxson & Heyer (1982) reported immunological microcomplement fixation albumin distance values (IDs) for certain *Thoropa.* Antisera were prepared for *T. miliaris* from Boracéia, São Paulo, and all distances are in reference to this population. *Thoropa miliaris* was closer to *T. lutzi* (ID = 16) and *petropolitana* (ID = 48) than to *megatympanum* (ID = 60, listed as *T.* sp. in Maxson & Heyer 1982: table 3). Dr. Maxson kindly provided two additional values for inclusion in this paper. The available series of specimens of *T. miliaris* from Caparaó, on the state border of Espírito Santo and Minas Gerais, displays more pattern variation than typical *T. miliaris,* although some individuals do have patterns that are characteristic of *T. miliaris* elsewhere. Surprisingly, the ID value between the Boracéia and Caparaó samples is 37. The magnitude of this difference clearly indicates that the samples represent distinct species. We do not believe that presently available materials are adequate to separate the composite *T. miliaris,* however, and refrain from doing so.

The second value Dr. Maxson provided was between (Boracéia) *T. miliaris* and *T. saxatilis,* an ID value of 58. Although only one-way values are available, the data suggest that the overall similarities found among the large *Thoropa* species are due to shared ancestral morphology, and that the speciation events among the larger species predate those leading to the smaller species. The available data suggest that detailed analyses of genetic estimates among *Thoropa* would be scientifically rewarding.

Territoriality and Male Combat in *Thoropa*

Shine (1979) suggested that where sexually dimorphic development of spines occurs in male anurans, it is an adaptation to combat between males, rather than to maintaining contact with females during amplexus. One of the most striking aspects of mature male *Thoropa* is the presence of clusters of dark spines on the inner portions of the hand. While examining specimens of *T. miliaris* from Boracéia we noted that most mature males had series of close-set, raking scratches on the dorsum, particularly behind the eyes and above the tympanum (Fig. 7). The configuration of the scratches is congruent with that of the spines on the thumb, prepollex, and fingers of adult male *T. miliaris* (see Bokermann 1965, fig. 5). Furthermore, these scratches occur on seven out of nine adult males but on none of the eight adult females or 23 juveniles examined in detail. We interpret this as evidence of male combat (see Kluge 1981, for a discussion of male combat and scarring from prepollical spines in *Hyla rosenbergi*). Although some scratches could have occurred in the bag after the specimens were collected, it seems unlikely that contact after capture played more than a minor role. Two of the males with extensive scratches were collected alone or with juveniles, so any scratches clearly occurred before capture. The remaining five males with scratches were collected in a series, so more than one male may have been in a single collecting bag. However, the scratches occur on five out of the six males and on none of three females in the series, and we were unable to detect any differences in apparent age or placement of the marks between these males and the two mentioned above. Thus, we conclude that the scarring observed on these males resulted from face-to-face wrestling with other males at some point before they were collected.

Bokermann (1965) described the general ecology of three species of *Thoropa*. He reported that *T. miliaris* males show a marked tendency to occur in certain areas within their habitat on wet rock faces and to occupy a territory in which they feed and call. Females apparently are more wide-ranging, especially on rainy nights (Bokermann 1965).

Egg clutches of *T. miliaris* are deposited on wet rock faces near where males call and where the subaerial tadpoles subsequently develop (Myers 1946, Lutz 1954, Heyer & Crombie 1979). The length of the breeding season has not been reported for *T. miliaris*, but it appears to be a prolonged breeder in the sense of Wells (1977), with males calling for one to several months during the year (Heyer, pers. obs.). Where calling males occur, their density is low (Bokermann 1965; Heyer, pers. obs.). Non-breeding adults may feed in other habitats (Heyer, pers. obs.), so the territoriality of males on rock faces is probably primarily associated with reproduction. Suitable habitat for reproduction is available in man-made habitats such as quarry walls and road cuts, as well as natural rock outcrops. Even with the presence of man-made habitats, appropriate breeding habitat is probably a limited resource, as it almost certainly was in the forests where *Thoropa* evolved. Thus, it would be advantageous for a male to exclude other males from an area that would serve as a calling site, a potential egg deposition site, and suitable larval habitat.

The two other large species of *Thoropa* are *T. megatympanum* and *T. saxatilis*. Adult males of both species have spines very similar to those of *T. miliaris* (see Caramaschi & Sazima 1984:fig. 4, for *T. megatympanum*). Three out of four adult male *T. megatympanum* in the USNM collection

Fig. 7. Male *Thoropa miliaris* (USNM 209326) showing scratches on dorsal shoulder region.

have scratches similar to those found in *T. miliaris* (the remaining specimens, a male, two females, and a juvenile, lack scratches). *Thoropa megatympanum* breeds during the rainy season in the Serra do Cipó; males call from October to January and tadpoles have been found from November to February (Caramaschi & Sazima 1984). This species is found on inclined or vertical moist rock surfaces, under rocks, or in crevices on rocky, sandstone hillsides, and males call from hidden sites among the rocks (Caramaschi & Sazima 1984; Crombie, unpubl. data). Caramaschi & Sazima (1984) state that males are more "sedentary" than females; in conjunction with the evidence of male combat given above, this suggests that males are territorial and perhaps defend calling sites.

No information is available on the breeding behavior of *T. saxatilis.* All adults, juveniles, and tadpoles were collected on roadcut rock walls with water seeping over the rocks or on a rock face near a waterfall. The largest of the three adult males collected shows, under a light microscope, two rake-like scratches on the dorsum, similar to those found in males of the other two large species. Given this evidence of male fighting and the similarities in habitat with *miliaris* and *megatympanum,* we predict that *T. saxatilis* is a prolonged-breeding species with territorial males.

Heyer & Crombie (1979) reported reproductive behavior in *T. petropolitana,* the smallest species in the genus. This species breeds for a month or longer (Bokermann 1965; Heyer, unpub. data) in areas where a film of water trickles over inclined or vertical rock faces. Males are territorial and defend calling and egg deposition sites against other males, with territorial calls, jerky posturing motions, and wrestling (Heyer & Crombie 1979). Although males have a cluster of spines on the thumb which potentially could cause injury or scarring (see Bokermann 1965:fig. 7), we could find no corresponding marks on preserved specimens. Heyer & Crombie (1979) conclude that males are defending access to those limited sites providing appropriate conditions for egg deposition.

Few observations have been reported on the reproductive behavior of *T. lutzi,* the other small species in the genus. Males call on suitable wet rock wall habitat. Reproductive activity was recorded in January and February 1964 (Bokermann 1965), which suggests that this species also is a prolonged breeder. Males have two pads of minute spines on the thumb (see Bokermann 1965: fig. 6), but aggressive or territorial behavior has not been reported. However, since all the other members of the genus appear to be territorial, and since *T. lutzi* apparently is a prolonged breeder occurring in a limited breeding habitat, territoriality would not be unexpected.

Shine (1979) suggested that male combat was a selective pressure which could lead to large male size in frogs. Male combat apparently occurs in at least four of the five described species of *Thoropa.* However, females are larger than males in *T. miliaris* (Heyer et al., in press; Bokermann [1965] lists a snout–vent length of 78 mm for the largest male in his sample and 70 for the largest female, but does not provide means); *T. lutzi* (Bokermann 1965; Cocroft & Heyer, unpub. data); and *T. petropolitana* (Bokermann 1965; Cocroft & Heyer, unpub. data). Caramaschi & Sazima (1984) report that males are slightly larger than females in *T. megatympanum,* although data from 15 males and seven females in the MZUSP and USNM collections indicate that females are larger; in any case, the difference in size between the sexes is slight. No adult female *T. saxatilis* are available. Apparently, any selection pressure for large male size in *Thoropa* is balanced by pressures for large female size (see Woolbright 1983, Sullivan 1984).

Shine (1979) also suggested that combat is more likely to occur in the larger species within a group, since in large species males may face less risk of predation than in small species (we have encountered no evidence of toxicity in *Thoropa,* which could confer additional immunity from predation). However, it seems clear that male combat in *Thoropa* has arisen from life history traits unrelated to size, since it occurs in both large and small species. In *Thoropa,* male combat apparently has arisen as a means of territorial defense, giving males direct access to limited breeding sites occurring in the specialized habitat where the genus occurs.

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101(1), 1988, pp. 221–226

TULUMELLA UNIDENS, A NEW GENUS AND SPECIES OF THERMOSBAENACEAN CRUSTACEAN FROM THE YUCATAN PENINSULA, MEXICO

Thomas E. Bowman and Thomas M. Iliffe

Abstract.—*Tulumella,* new genus, the sixth genus of Thermosbaenacea, with type species *T. unidens,* new species, is reported from Najaron Cave, near Tulúm, Quintana Roo, Mexico. It is characterized by having small non-functional eyestalks, a scale on antenna 2, mandibles that may lack a lacinia mobilis and have reduced molars, a biramous pereopod 1, and a reduced pleopod 2. The family Monodellidae is recognized as valid, and a key is given to the families and genera of Thermosbaenacea.

In November 1986 the second author made collections in nine caves and cenotes on the Yucatan Peninsula, Mexico, mostly in the vicinity of the ancient Mayan city of Tulúm. From one of these caves he obtained three specimens of the new thermosbaenacean described below.

Order Thermosbaenacea Monod, 1927
Family Monodellidae Taramelli, 1954

Telson separate from pleonite 6. Seven pairs of pereopods present. Maxilliped of ♂ with or without endopod.

Tulumella, new genus

Diagnosis.—Small eyestalks present, without visual elements. Antenna 1 long, with up to 18 flagellar segments. Antenna 2 with scale (exopod). Right or both mandibles without lacinia mobilis; molar slender, cylindrical; chewing surface divided into a few slender spiniform teeth. Maxilla 2 with 2 broad basal endites armed with spoon-shaped setae; exopod setose, inserted well lateral to endopod. Maxilliped with broad endopod and exopod, both with several marginal setae. Pereopod 1 biramous, endopod 5-segmented (including basis); pereopods 2–7 with 2-segmented exopod and 6-segmented endopod. Pleopod 1 a small pyriform unarticulated lobe; pleopod 2 articulated, elongate. Uropod exopod slightly longer than endopod; 1st segment slightly longer than 2nd.

Type species.—*Tulumella unidens,* new species.

Etymology.—From the ancient Mayan city of Tulúm, with the diminutive Latin suffix "ella."

Tulumella unidens, new species
Figs. 1–2

Material.—Mexico: Quintana Roo, near ruins of Mayan city of Tulúm: Najaron (Naharon) Cave, leg. T. M. Iliffe 11 Nov 1986 (collection no. 86-106), 3 specimens: holotype, 2.9 mm, USNM 233394; paratypes, 3.0 and 1.8 mm, USNM 233395.

Etymology.—From the Latin "uni-" (one) + "dens" (tooth), referring to the lack of a lacinia mobilis in both mandibles.

Diagnosis.—As for the genus.

Description.—Length up to about 3 mm (the 3 mm paratype is in 2 pieces; hence its measurement is approximate). Carapace covering pereonites 1–6. Eyestalks oval, close together, partly covered by carapace.

Fig. 1. *Tulumella unidens*: A, Habitus; B, Antenna 1; C, Antenna 2; D, Right mandible; E, Left mandible; F, Right mandible; G, Maxilla 1; H, Maxilla 2; I, Maxilliped; J, Pereopod 1.

Telson linguiform, ⅓ longer than wide; posterior margin with medial pair of short spines flanked by 2 pairs of distinctly longer spines.

Antenna 1 nearly ¾ length of body. Peduncle segments progressively shorter, armed medially with long setae; segment 1 with lateral flange produced distally into blunt process bearing 2 long setae, segment 3 with median distal process bearing 3 apical setae. Outer flagellum 18-segmented, segments 4–15 each with 1 or 2 long esthetes and 1 or 2 shorter curved setae. Inner flagellum about 0.7 length of outer flagellum, 14-segmented, each segment with several distal setae of varying lengths. Antenna 2 scale about 3.5× as long as wide, with 10 marginal setae; flagellum about half as long as inner flagellum of antennae 1, 10-segmented.

Incisor of mandible slender with long neck, left 6-cuspate, right 4-cuspate. Left spine-row with 8 spines, right with 6, gaps between spines decreasing toward molar. Segment 2 of mandibular palp with single row of 4 pectinate spines on distal half, segment 3 with double row of 3 pectinate spines (6 in all) and pair of longer naked apical spines.

Maxilla 1, coxal endite with 15 plumose setae; basal endite with 9 apical spines with denticulate medial margins; endopod (palp) 2-segmented, distal margin of 2nd segment armed with 2 tricuspid spines, 2 spatulate apically ciliate spines, and 1 naked seta. Maxilla 2 coxa with row of about 22 long setae on medial margin; coxal endite with about 9 marginal setae; basal endites with 11 and 6 spoon-shaped setae respectively; endopod subequal in length to basal endites but much narrower, armed with 1 seta on medial margin, 1 subapical seta, and 3 apical setae; exopod oval, with 4 marginal setae.

Coxa of maxilliped not produced into endite; distal margin with 2 long setae reaching distal margin of basal endite and lateral to them a seta about ⅓ as long. Basal endite with 13 setae on apical margin as shown in Fig. 1I and 1 surface seta near medial margin. Endopod a broad shallow lobe with 5 marginal setae. Exopod oval, with narrow base and 3 setae on apical margin.

Pereopod 1 basis expanded anteriorly, with row of long setae on anterior margin. Ischium ¾ length of basis, expanded anteriorly with 1 long seta on anterior margin. Merus and carpus with long setae on posterior (flexor) margin. Propus broadening distally; distal margin with 3 spiniform and 1 slender setae, largest (anterior) spiniform seta interpreted as dactyl.

Pereopods 2–7 of uniform structure (Fig. 2A). Flexor margin of dactyl with row of delicate peg-shaped spines on proximal half and minutely serrate apex.

Pleopod 1 a short pyriform lobe with very long apical seta. Right and left pleopods separated by distance equal to ⅔ length of apical seta. Near lateral margin of pleonite 1, a second pyriform lobe with 2 setae at apex, 1 on lateral margin, and 1 at base of medial margin. Posterior margin of pleonite 1 between 2 lobes armed with 4 short setae with swollen bases (Fig. 2C). It is not known whether pleopod 1 is represented by the medial lobe only or by both lobes plus the intervening setae.

Pleopod 2 a pair of elongate rami nearly 8× as long as wide inserted close together in an emarginate medial part of pleonite 2. Apex of ramus with apical seta more than 1.5× length of ramus; lateral margin with 5 setae, penultimate of which nearly as long as ramus.

Exopod of uropod about ¼ longer than endopod, 1st segment slightly longer than 2nd. Medial margin of 1st segment and both margins of 2nd and of endopod armed with plumose setae. Distolateral corner of 1st segment of exopod with 3 spines increasing in size distally and several setae as shown in detail of Fig. 2E. Telson about 1.4 as long as wide; posterior margin armed with 3 pairs of spines with lengths (anterior to posterior) 2 > 1 > 3.

Comparisons.—The presence of a scale

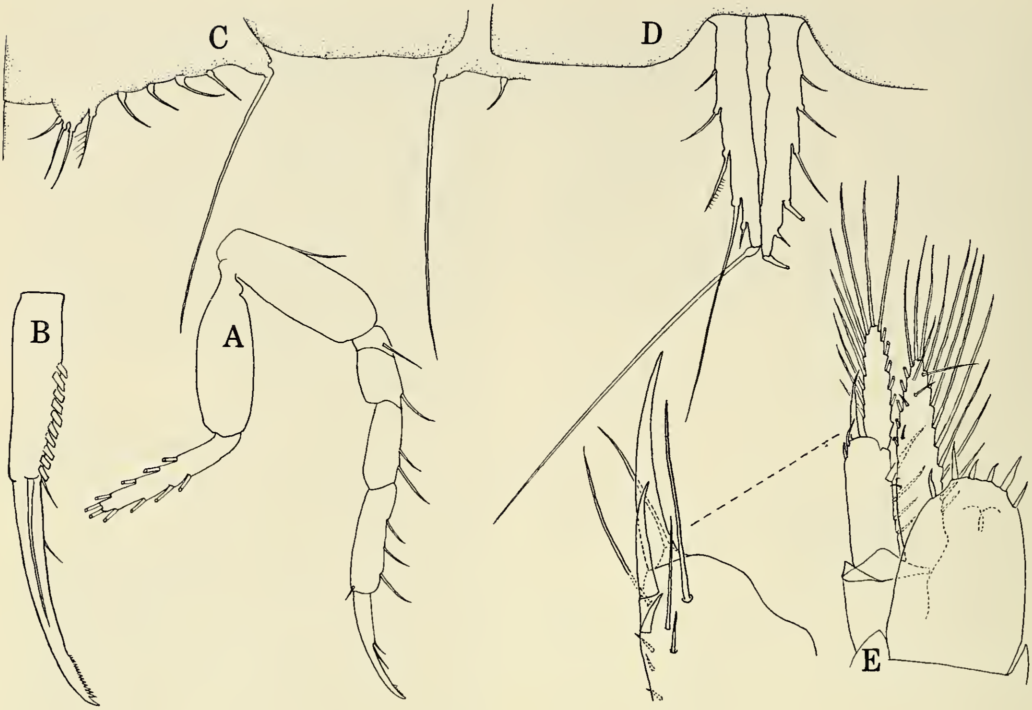

Fig. 2. *Tulumella unidens*: A, Pereopod 2; B, Pereopod 4 dactyl; C, Pleopod 1; D, Pleopod 2; E, Telson and uropod, dorsal.

on antenna 2 and the absence of a lacinia mobilis from both mandibles are unique features for *Tulumella*; the other features given in the diagnosis are shared with one or more of the other genera. However, undescribed species of *Tulumella* from the Bahamas have a lacinia mobilis on the left mandible (J. Yager, pers. comm.).

It is surprising that the family Monodellidae, proposed by Taramelli (1954), has not been recognized in subsequent works except those of Barker (1959) and McLaughlin (1980). Indeed, the family was overlooked by Bowman and Abele (1982) and Bowman and Iliffe (1986). In a recent list of all known Thermosbaenacea, Stock (1986) recognizes only one family, Thermosbaenidae Monod, 1927. However, we are convinced that the differences, given in the following key, are sufficient to merit the recognition of two families.

Key to the Families and Genera of Thermosbaenacea

1. Telson fused with pleonite 6. Maxilliped of ♂ without endopod. 5 pairs of pereopods .... Thermosbaenidae Monod, 1927, *Thermosbaena* Monod, 1927

– Telson separate from pleonite 6. Maxilliped of ♂ with or without endopod. 7 pairs of pereopods ..... Monodellidae Taramelli, 1954 ... 2

2. Eyestalks lacking. Exopod of pereopod 6 and 7 1-segmented. Pleopods 1 and 2 with basal articulation, nearly as long as their pleonites .. .. *Monodella* Ruffo, 1949

– Eyestalks present. Exopod of pereopod 6 1- or 2-segmented. Pleopod 1 a small unarticulated lobe or absent 3

3. Antenna 2 with scale. Lacinia mobilis present in left mandible or lacking in both mandibles. Pereopod 7 exopod 2-segmented .... *Tulumella,* new genus
– Antenna 2 without scale. Lacinia mobilis present in left mandible. Pereopod 7 exopod 1- or 2-segmented 4
4. Pereopod 7 exopod 2-segmented .. .. *Halosbaena* Stock, 1976
– Pereopod 7 exopod 1-segmented .. 5
5. Pereopod 1 endopod ending in long acute spine, flanked by 2 short spines. Flagella of antenna 1 with 3 and 4 segments .... *Limnosbaena* Stock, 1976
– Pereopod 1 endopod ending in 3 digitiform spines. Flagella of antenna 1 with 14 and 29 segments .... *Theosbaena* Cals and Boutin, 1985

Habitat.—Najaron (Naharon) Cave is a completely underwater limestone cenote cave located about 8 km inland from the Caribbean Sea on the eastern coast of the Yucatan Peninsula (Coke & de Groot 1987). The spacious underwater entrance to the upstream, spring cave opens from the far side of a large open spring/siphon pool. The walls of the cave are stained black, as are the numerous underwater stalactites and stalagmites. Cave passages are primarily developed at the depth of the halocline, about −15 m. At the halocline, a highly reactive geochemical zone is produced by the mixing of fresh ground water with subterranean Caribbean seawater, thus enhancing carbonate dissolution and formation of cave passages (Back et al. 1986). Salinities at the water surface in the open cenote and at just above the halocline at −14 m were 1.5‰, while those just below the halocline at −15 m and at the bottom at −20 m were 32.5 and 35‰, respectively. Water temperature was 24°C in November 1986. Water currents are localized to the upper fresher water layers in the cave. The spring cave consists of two main passages, each about 700 m in length. All biological collections were made from the Halocline System or East Side of the cave complex. Most animals were observed just above the halocline in oligohaline waters. Collecting was done with a plankton net and suction bottle from the water column in −10 to −18 m depths using scuba. In addition to *Tulumella unidens,* specimens of copepods, amphipods, shrimp, and remipedes—all still under study—were also collected from the cave.

Acknowledgments

Cave collections in Yucatan by T. M. Iliffe were supported by National Science Foundation Grants BSR-8215672 and BSR-8417494. We thank James Coke, Dinah Drago, Juan Jose Fucat, and Michael Madden for assistance with cave diving collections and Dr. John Markham for logistical and collecting aid. We thank Jill Yager for reviewing the manuscript. This publication is Contribution No. 1130 of the Bermuda Biological Station for Research.

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(TEB) Department of Invertebrate Zoology, National Museum of Natural History, NHB-163, Smithsonian Institution, Washington, D.C. 28560; (TMI) Bermuda Biological Station for Research, Inc., Ferry Reach 1-15, Bermuda..

Note added in proof.—Monod & Cals (1988: Comptes Rendus de l'Académie des Sciences, Paris 306 (Série III):99–108) recently rearranged the classification of the Thermosbaenacea, dividing the order into two families: 1. Thermosbaenidea, with the subfamilies Thermosbaeninae and Monodellinae; 2. Halosbaenidae, new, with the subfamilies Halosbaeninae, new, and Limnosbaenin, new. Under this scheme *Tulumella* would go into the Halosbaeninae.

ADDENDUM

The following entries were omitted from the Table of Contents and the Index to New Taxa, respectively, in the Proceedings of the Biological Society of Washington, volume 100, part 4:

CHORDATA

Aves

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Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

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CONTENTS

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TURRITOPSOIDES BREHMERI, A NEW GENUS AND SPECIES OF ATHECATE HYDROID FROM BELIZE (HYDROZOA: CLAVIDAE)

Dale R. Calder

Abstract.—*Turritopsoides brehmeri,* n. gen., n. sp., is described from specimens collected on turtlegrass (*Thalassia*) in a mangrove system at Twin Cays, Belize, Central America. The colony form of *T. brehmeri* is stolonal, with well developed hydranth pedicels having a distinct sheath of perisarc enclosing a narrower tube of coenosarc. Hydranths are cylindrical and elongate, with numerous scattered filiform tentacles at the distal end. This newly-discovered hydroid differs from other representatives of the family Clavidae in colony form and in the location and characteristics of the gonophores, which are fixed sporosacs arising singly from the hydrorhiza and pedicels.

Field studies of the hydroid fauna of a Caribbean mangrove system were conducted at Twin Cays, a pair of mangrove islands 15 km east of Dangriga, Belize, during winter 1987. Amongst material collected in a small cove, known as "The Lair," were specimens at first thought to be the common and widespread athecate species *Turritopsis nutricula* McCrady, 1859a. Unlike *T. nutricula,* however, the gonophores of this hydroid are fixed sporosacs instead of free medusae; moreover, they arise from the hydrorhiza or hydranth pedicels instead of from a well-developed hydrocaulus. The hydroid cannot be assigned to any presently known genus or species, and is described and named here.

Family Clavidae McCrady, 1859b
Turritopsoides, new genus

Diagnosis.—Hydroid colonies mostly stolonal, infrequently with an irregular branch given off from a hydranth pedicel. Branch, when present, adnate to pedicel over part of its length. Perisarc of moderate thickness on hydrorhiza and pedicel, extending up over basal third of hydranth as a thin film. Hydranths elongate, tubular to clavate, monomorphic. Tentacles filiform, numerous, scattered. Hypostome proboscis-like to dome-shaped. Nematophores absent.

Gonophores fixed sporosacs, covered with sheath of perisarc, arising via short stalks from hydrorhiza or hydranth pedicel; male gonophores pyriform; female gonophores almost spherical, spadix branched, clasping embryos.

Type species.—*Turritopsoides brehmeri,* n. sp., designated herein.

Etymology.—The generic name, derived from a combination of the generic name *Turritopsis* and the Greek suffix *-oides* (like), reflects the superficial resemblance of the genus to *Turritopsis.* The gender of the name is masculine.

Turritopsoides brehmeri, new species
Figs. 1, 2

Material examined.—Belize: "The Lair" at Twin Cays, on *Thalassia testudinum,* depth 2 m, water temperature 24°C, 8 Feb 1987.—Holotype: one colony with female gonophores, Royal Ontario Museum, Invertebrate Zoology (ROMIZ), ROMIZ B930.—Paratypes: one colony with male gonophores, ROMIZ B931; one colony without gonophores, ROMIZ B932.

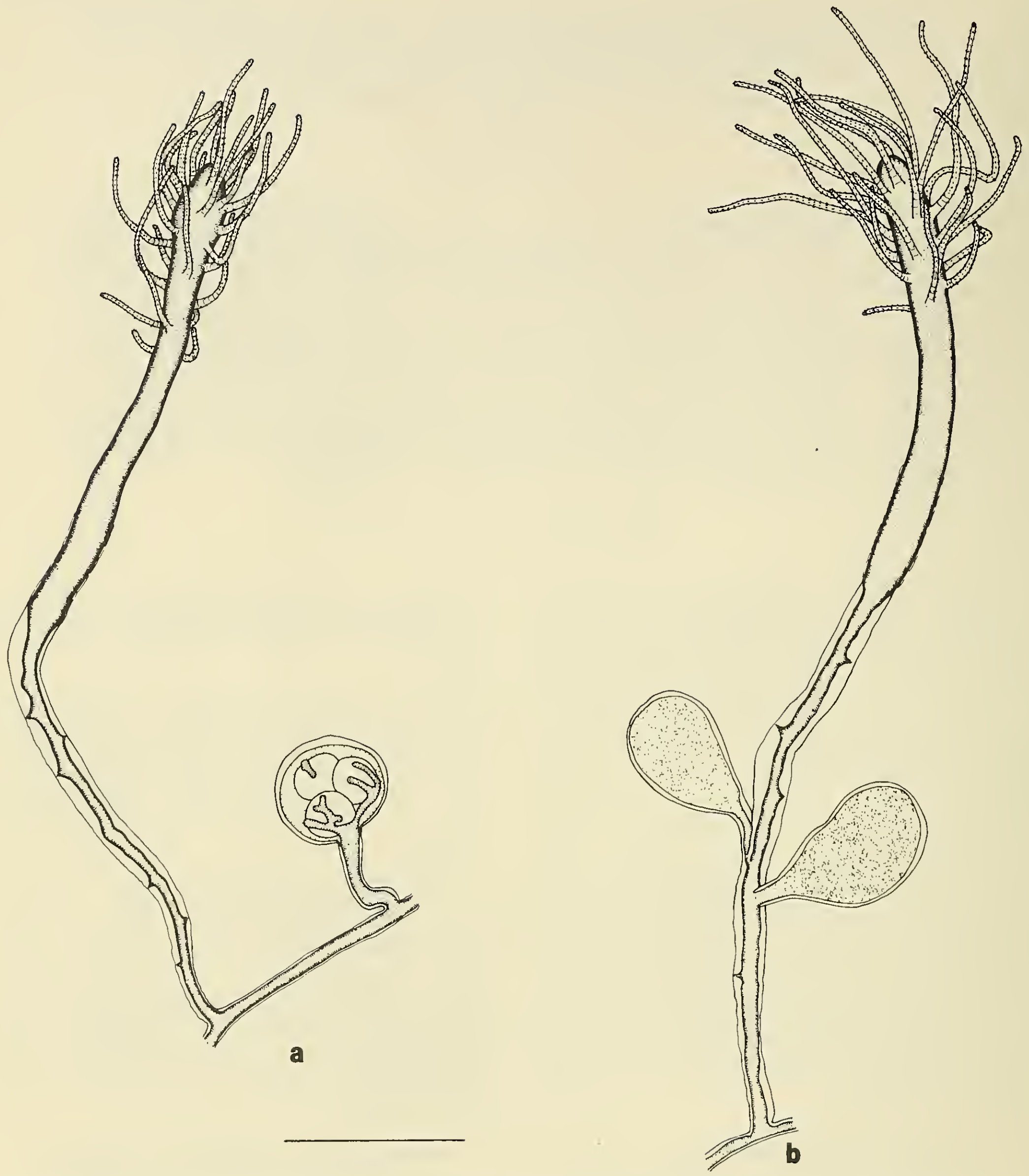

Fig. 1. *Turritopsoides brehmeri,* n. gen., n. sp.: a, Holotype, with female gonophore, ROMIZ B390; b, Paratype, with male gonophores, ROMIZ B391. Scale line equals 1 mm.

Description.—Colonies stolonal, or infrequently with a branch arising from the primary pedicel; arising from a creeping, reticular hydrorhiza. When present, branch adnate to pedicel for a short distance at origin, curved outwards and becoming free distally. Pedicels short, up to 4 mm high from insertion with hydrorhiza to hydranth base. Perisarc of moderate thickness on hydrorhiza and pedicel; clear to straw-colored; occasionally creased and wrinkled but with no distinct annulations; increasing gradually in diameter distally, diameter about 0.1 mm at proximal end, 0.2 mm at distal end,

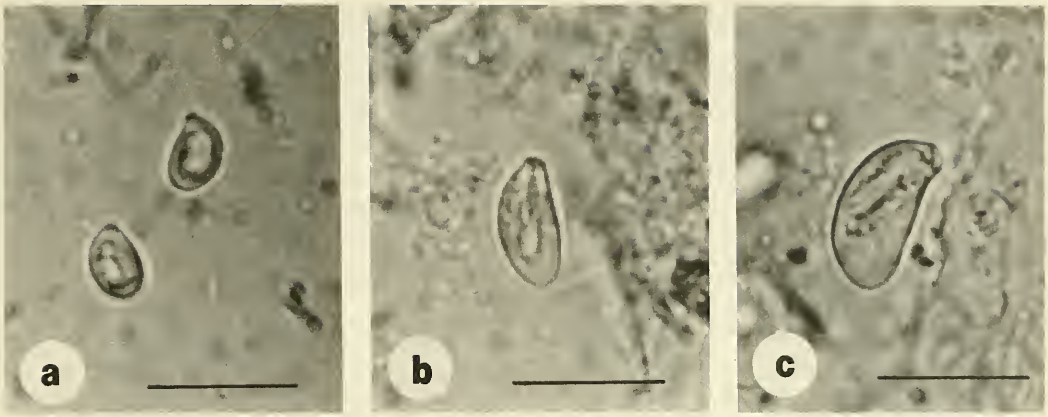

Fig. 2. Preserved nematocysts of *Turritopsoides brehmeri,* n. gen., n. sp.: a, Desmonemes; b, Small heterotrichous microbasic eurytele; c, Large heterotrichous microbasic eurytele. Scale lines equal 10 μm.

enclosing a much narrower tube of coenosarc up to base of hydranth; extending upward over proximal third of hydranth base as a thin, closely adhering film. Hydranths elongate, tubular to clavate, occasionally somewhat dilated distally, reaching 4 mm long from base to tip of hypostome, about 0.3 mm wide when expanded. Tentacles filiform, up to 35 or more, scattered over distal ⅓–½ of extended hydranth, those at distal end longer and stouter than those more proximal. Hypostome prominent, proboscis-like to dome-shaped. Nematophores absent. Living hydranths white, with red endoderm.

Gonophores fixed sporosacs, arising via short stalks from hydrorhiza or hydranth pedicels, covered with smooth, thin perisarc. Female gonophores nearly spherical, about 0.6 mm high and wide, with branched spadix curving over embryos, each gonophore with three developing embryos. Male gonophores pyriform, 0.8–0.9 mm high, 0.5 mm wide, containing dense mass of spermatogenic tissue and sperm.

Nematocysts—

desmonemes (on hydranths, female gonophores): 5.4–5.7 μm × 3.7–3.8 μm (undischarged)
small heterotrichous microbasic euryteles (on hydranths, male gonophores, female gonophores): 8.5–9.4 μm × 4.0–4.5 μm (undischarged)
large heterotrichous microbasic euryteles (on hydranths, male gonophores, female gonophores): 10.4–11.3 μm × 4.8–5.6 μm (undischarged)

Etymology.—The specific name honors Dr. Morris L. Brehmer, a mentor who kindly made it possible for me to pursue my interest in the taxonomy of hydrozoans two decades ago in Virginia.

Discussion.—In having elongate and generally clavate hydranths with scattered filiform tentacles, and branches (when present) adnate to the pedicels for a varying distance basally, *Turritopsoides* is related to a group of genera, including *Corydendrium* Van Beneden, 1844, *Turritopsis* McCrady, 1859a, and possibly *Tubiclava* Allman, 1863, in the family Clavidae McCrady, 1859b.

Turritopsoides, and its single species *T. brehmeri,* can be distinguished from other taxa in the Clavidae (see Bouillon 1985, Calder 1988) by the location and morphology of the gonophores and by colony form. Unlike *Turritopsis* McCrady, 1859a, gonophores are fixed sporosacs rather than free medusae. Gonophores are not enclosed within the perisarc of the hydrocaulus and branches, as in *Corydendrium* Van Beneden, 1844. In *Hataia* Hirai & Yamada, 1965, gonophores occur among the tentacles of solitary, naked hydranths. Gonophores occur only on the hydrorhiza in *Rhizogeton* L. Agassiz, 1862, in clusters on large hydranths in *Clava* Gmelin, 1790, presumably in clusters on the hydranths in *Tubiclava* Allman, 1863, and on the hydrocaulus and branches in *Cordylophora* Allman, 1844. *Merona* Norman, 1865, is the only clavid genus having gonophores on gonozooids; furthermore, it is the only known representative of the Clavidae to have nematophores. The nominal genus *Oceania* Péron & Lesueur, 1810, customarily included in the Clavidae, is of uncertain identity. *Oceania* originally included species of medusae now referred to several different families, and attempts to redefine and restrict the genus according to the useage of Kölliker (1853) are not in accordance with provisions of the International Code of Zoological Nomenclature. *Oceania armata* Kölliker, 1853, was designated type species of the genus by Mayer (1910), but the designation is invalid because *O. armata* was not one of the originally included species. In any event, *Turritopsoides* differs from *Oceania* sensu Kölliker in having fixed sporosacs instead of free medusae.

Turritopsis, Corydendrium, and *Cordylophora* also differ from *Turritopsoides* in having colonies with a distinct, typically branched hydrocaulus. Unlike *Cordylophora,* there are no distinct annulations in the perisarc of the pedicels, hydrocaulus, or branches of *T. brehmeri,* and its hydranths are elongate and clavate rather than fusiform.

Among those clavids with stolonal colonies, *Turritopsoides brehmeri* most closely resembles species of *Tubiclava* and *Rhizogeton.* It differs from *Tubiclava* in gonophore location, and from *Rhizogeton* in having hydranths arising from well developed pedicels instead of from the hydrorhiza. Although similar to *Rhizogeton ezoense* Yamada, 1964, from Japan in general appearance, hydranths of the latter ". . . are not clearly separated from hydrocaulus" (Yamada 1964). Gonophores also appear to be restricted to the hydrorhiza in *R. ezoense,* instead of occurring on hydrorhiza and pedicels. In addition, Yamada (1964) noted that the female gonophores of *R. ezoense* bear 10–13 eggs (or embryos), whereas three are present in *Turritopsoides brehmeri.*

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NOMENCLATURE AND BIOLOGY OF *ASTRANGIA POCULATA* (=*A. DANAE*, =*A. ASTREIFORMIS*) (CNIDARIA: ANTHOZOA)

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Walter C. Jaap, Judith C. Lang, Carol E. (Cummings) Vasleski, and
Lauren St. Pierre Gollahon

Abstract.—The encrusting to ramose northern star coral, *Astrangia poculata,* is a common inhabitant of rocky shorelines, jetties, and pilings along the northwest Atlantic and Gulf of Mexico coastlines of the United States. Despite its popularity as an experimental laboratory animal, there has been considerable confusion as to the number of species which may exist and the proper name(s) of the species. A reexamination of material from throughout this range confirms that there is only one species, the correct name of which is *Astrangia poculata* (Ellis & Solander, 1786). A neotype has been deposited in the National Museum of Natural History. The same neotype is also deposited as the type of *A. michelinii* Milne Edwards & Haime 1849, type species of *Astrangia.*

The genus *Astrangia* includes over 30 Recent nominal species within the family Rhizangiidae, and is represented by 20 fossil species, some of which lived as early as the Middle Cretaceous, approximately 100 million years ago (Wells 1956). Members of the genus are all relatively small and are usually insignificant components of the fauna where they occur. The various species of *Astrangia,* however, collectively occupy a vast geographic range, possibly broader than that of any other genus of coral.

Unfortunately, the genus *Astrangia* has never been completely reviewed. It is probable that many species names are synonyms, and also that a number of yet undiscovered species may exist (Pilson 1975). The confusion that exists within this genus became evident when a group of scientists at the University of Rhode Island began a series of studies on the ecology, physiology, and life history of the coral found in Narragansett Bay. Whereas several previous studies had referred to the northern star coral as *Astrangia danae,* a number of other papers had been published on the very similar *Astrangia astreiformis* from the southeastern coasts of the United States. However, other texts suggested that only one species of *Astrangia* existed along the entire North Atlantic and Gulf coasts of North America (Hyman 1940, Wells 1956, for reviews see Cummings 1983, and Jaap, in prep.). *A. astreiformis* was also reported to occur off the west coast of Africa (Thiel 1928, Chevalier 1966).

Throughout its range, the northern star coral appears remarkably tolerant of a wide range of environmental conditions. Colonies of *Astrangia* are generally considered to be ahermatypic (non-reef-building) and hence azooxanthellate (=asymbiotic, i.e., lacking zooxanthellae), but some colonies of the northern star coral contain these algal cells abundantly within their tissues (Boschma 1925a). These two factors, adaptability and variability in algal symbiosis, have contributed to the increasing popularity of this coral as an experimental laboratory animal. Therefore, in order to aid future researchers, we were motivated to clarify the taxonomic status of this coral.

Family Rhizangiidae d'Orbigny, 1851

Genus *Astrangia* Milne Edwards & Haime, 1848a

Diagnosis.—Colonial, usually azooxanthellate. Colonies encrusting or subplocoid, formed by extratentacular budding from edge zone; corallites united basally by thin coenosteum; septa dentate; columella papillary. [Type species: *A. michelinii* Milne Edwards & Haime, 1848b, by monotypy (=*A. poculata* Ellis & Solander, 1786).]

Astrangia poculata (Ellis & Solander, 1786) Figs. 1–6

"Stony coral found on the shore near New York.": Ellis, 1755:84, pl. 32, figs. A.1, A.3.

?*Madrepora calycularis* Pallas, var. *β*, 1766: 319 note 186B.—Esper, 1790:283.

Madrepora poculata Ellis & Solander, 1786: 165.—Gmélin, 1791:3766.—Esper, 1790: 283 (=*M. calycularis β*). [Original type locality "near New York." Type specimen lost (P. F. S. Cornelius, pers. comm.).Type locality (neotype) "off Atlantic City, New Jersey." Neotype deposited in the National Museum of Natural History USNM 80350.]

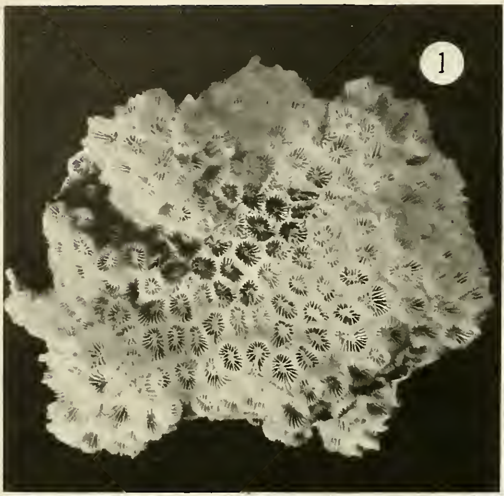
Madrepora porculata: Turton, 1806:623 [Misspelling of *poculata*].

Astrangia michelinii Milne Edwards & Haime (ME & H), 1848b:320, pl. 7, fig. 5, 5a; 1857:614. [Type of the genus. Original type locality unknown. Type specimen last seen by Wells in 1934, Coll. Michelin No. 412. Type lost (Chevalier, 1966). Type locality (neotype) "off Atlantic City, New Jersey." Neotype deposited in the USNM, USNM 80350.]

Astrangia michelini: ME & H, 1849:181; 1850:xliv (cited as the type species).—Verrill, 1866a:324.—Vaughan, 1901: 299.—Vaughan & Wells, 1943:177.—Alloiteau, 1952:623 (=*A. danae* Agassiz 1850).—Chevalier, 1966:930 (=?*A. astraeiformis* ME & H 1849).—Wells, 1986:6 (cited as the type species). [Emended spelling of *A. michelinii.*]

Astrangia danae ME & H, 1849:180.—Verrill, 1863:40; 1864:47 (*not A. danae* Agassiz 1850); 1866a:324 (=*A. edwardsii*); 1866b:335; 1872:432–438; 1874:446 (geography).—Pearse & Wharton, 1938: 636.—Cairns, 1979:207.—Jacques & Pilson, 1980:167–178 (physiology, symbionts, Rhode Island).—Szmant-Froelich, 1980a:1–191 (natural history, biochemistry, Rhode Island).—Szmant-Froelich & Pilson, 1980:85–97 (feeding frequency, biochemistry, Rhode Island).—Szmant-Froelich, 1981:133–144 (nutrition, Rhode Island).—Cummings, 1983:1–147 (physiology, morphology, Rhode Island, Florida).—Peters, 1984:61–63, figs. 6b, c, d, 10d, e, 13g, 17a, b, 22h, 26f, g (histology, Rhode Island).—Wiseman, 1984:1–75 (biochemistry).—Peters & Pilson, 1985:215–230 (sedimentation stress, histopathology, Rhode Island). [Type locality unknown. Type specimen last seen by Wells in 1934, now missing from Coll. Michelin (Cairns 1981).]

Astrangia astreiformis ME & H, 1849:181.—Verrill, 1864:47; 1866a:324.—Vaughan, 1901:300, pl. II, figs. 2, 2a, 2b (Puerto Rico).—Whitten et al., 1950:75 (Texas channels).—Parker, 1959:2130, 2131, fig. 19a; 1960:317, 334, pl. 3, fig. 23 (inlet and deep channel assemblage, common on shell, Texas).—Richmond, 1962:69 (Mississippi).—Wells et al., 1964:566, 581 (on scallop shells, North Carolina).—Macintyre & Pilkey, 1969:374–375 (off North Carolina).—Macintyre, 1970: 178.—Pampe, 1971:399, pl. 2, fig. 7.—Defenbaugh, 1976:27, 37, pl. 5f, fig. 53.—Cairns, 1977:5; 1978:10 (east, west and southwestern Gulf of Mexico, 10–29 m); 1981:10, fig. 12 (systematics: =*A. danae* Agassiz 1850 *not A. danae* ME & H 1849).—Cooley, 1978:8, 86 (Pensacola, Florida, estuary).—Fotheringham et al., 1980:17, 103, fig. 2.25.—Brunet, 1982:1–150 (feeding behavior, growth and sur-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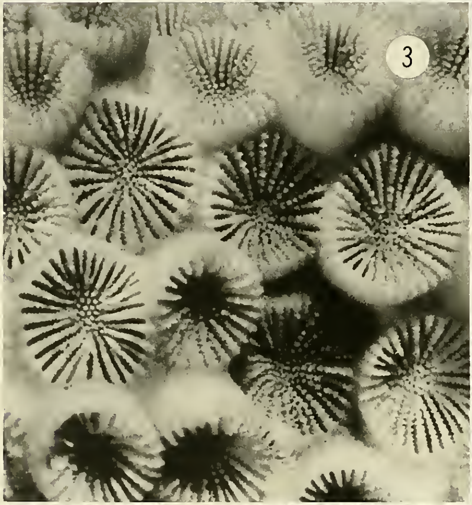
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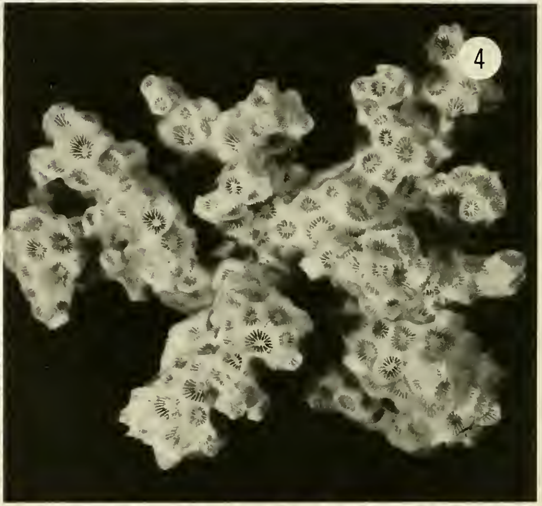
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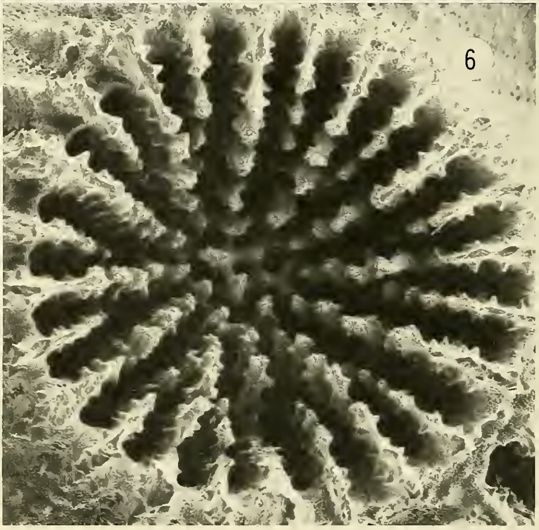
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vival, Texas).—St. Pierre, 1986:1–55 (reproduction, Texas). [Type locality "United States." Type found by Wells in Paris in Coll. Michelin in 1934, but not found by Chevalier in 1980 (Cairns 1981).]

Astrangia danae Agassiz, 1850:68–77, pl. I, fig. 7 (feeding behavior, digestion, colony growth, new polyp formation, nematocyst function, Massachusetts).—Verrill, 1863:40 (North Carolina); 1864:47 (=*A. astreiformis* in Leidy, 1855, *not A. danae* ME & H 1849); 1866a:324 (*not A. danae* ME & H 1849); 1866b:335; 1872:436, 437 (=*A. astraeiformis* ME & H 1849); 1873: 408; 1874:446 (Vineyard Sound and adjacent waters).—Agassiz & Agassiz, 1865: 16, figs. 16–20.—Pourtalès, 1871:80.—Dana, 1872, 1890:67–68, figured p. 68, a, b, c.—Damon, 1882:221.—Fewkes, 1889: 7–10, pls. 1–5 (natural history illustrations); 1891:53.—Hargitt, 1914:250, pl. 43, fig. 9 (natural history, Casco Bay, Maine).—Boschma, 1925a:65–67 (zooxanthellae symbiosis); 1925b:407–439 (feeding behavior, digestion, zooxanthellae symbiosis).—Cowles, 1930:333 (Chesapeake Bay, Cape Henry, Cape Charles).—Pratt, 1935:159, fig. 239.—Pearse, 1936:178.—Richards & Harbison, 1942:178, pl. 22, figs. 2 & 3 (Miocene, New Jersey).—Vaughan & Wells, 1943:177 (see footnote 52: =?*A. michelini* ME & H 1848).—Field, 1949:6, 18, pl. I, fig. 7.—Waterman, 1950:127–131, fig. pp. 120–121 (structure of corallum and polyps, zooxanthellae, feeding, reproduction).—Alloiteau, 1952:623, fig. 74 (=*A. michelini* ME & H 1848).—Hand, 1964: 25, pl. 3, fig. 4 (description).—Driscoll, 1967:633–641.—Robertson et al., 1970: 55–65.—Calder, 1972:101 (Chesapeake Bay, Hog Island and Eastern Shore).—Sassaman & Mangum, 1973:1313–1319 (anerobic metabolism).—Jacques et al., 1977:455–461 (physiology, calcification, Rhode Island).—Hayes & Goreau, 1977: 26–40 (calcification, histology).—Bachand, 1978:283–284 (habitat, life history).—Calder & Hester, 1978:93 (Charleston, South Carolina).—Weston, 1980:1–93 (zooxanthellae distribution, Chesapeake Bay). [Type locality "Massachusetts." Deposition unknown.]

Astrangia astraeformis: ME & H: Leidy, 1855:139–140, pl. 10, figs. 9–16 (synonymy, nematocysts, Rhode Island). [Misspelling of *A. astreiformis* ME & H 1849].

Astrangia astraeiformis: ME & H: ME & H, 1857:614.—Verrill, 1863:39; 1866a:324; 1866b:335; 1872:436 (=*A. danae* Agassiz 1850).—Pourtalès, 1871:80.—*not* Thiel, 1928:283–285, pl. 2, fig. 22 (=*A. mercatoris* Thiel 1941, West Coast of Africa).—Thiel, 1941:5, 15, pl. 1, figs. 5–6 (Martinique).—Pearse & Williams, 1951: 136 (incorrectly attributed to Leidy, 1855, Maine to Florida and the West Indies).—Chevalier, 1966:926–930, pl. 3, figs. 2–3, pl. 4, fig. 6 (synonymy, description, Sierra Leone, Africa). [Misspelling (or corrected spelling) of *A. astreiformis* ME & H 1849.]

Astrangia danai: ME & H, 1857:614. [Misspelling (or corrected gender) of *A. danae* ME & H 1849.]

Astrangia edwardsii Verrill, 1866a:324 (=nom. nov. for *A. danae* ME & H 1849, see Remarks); 1866b:335.

not *Astrangia mercatoris* Thiel, 1941:16–17, pl. 2, fig. 1 (=*A. astraeiformis* Thiel, 1928:283–285, pl. 2, fig. 22; Angola, Bay of Elephants, West Coast of Africa).—

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Figs. 1–6. *Astrangia poculata*: 1, Neotype colony (off Atlantic City, New Jersey, USNM 80350), × 0.88; 2–3, Colony from off Jacksonville, Florida, 15 m, USNM 78509, ×1.20, ×3.40, respectively; 4, Deep-water branched colony (off Western Dry Rocks, Sand Key, Florida, 263 m, USNM 78508), ×0.86; 5, SEM of coenosteum adjacent to calice showing lines of perforations constituting intercostal striae and coenosteal granules, ×49; 6, SEM of calice with 24 septa, ×23 (5–6, R/V Gerda station 1002, USNM 78507).

Chevalier, 1966:929–930 (discusses synonymy, see Remarks).

Astrangia astraeiformis: no authority cited: Hedgpeth, 1953:164 (Texas). [Misspelling of *A. astreiformis*.]

not *Astrangia astraeformis*: no authority cited: Buchanan, 1954:85–86 (=*A. astraeiformis* Thiel 1928 =*A. mercatoris* Thiel 1941, Ivory Coast, French Congo, Angola, Africa). [Misspelling of *A. astreiformis*.]

Astrangea danae: no authority cited: Goreau & Bowen, 1955:1188 (calcification). [Misspelling of *Astrangia danae*.]

Astrangia astreformis: Milne Edwards & Haines (sic): Pampe, 1971:399, pl. 2, fig. 7 (Pleistocene, Texas). [Misspelling, spelled *A. astreiformis* later on same page.]

Astrangia asteriformis: no authority cited: Rudloe, 1971:154–157, 167, 172–174, figured on p. 174 (natural history, hardiness in aquarium, Florida). [Misspelling.]

Astrangia astreiformis: no authority cited: Ladd, 1951:137, 139, 149 (Texas coastal waters).—Stephenson & Stephenson, 1952:35 (distribution, taxonomy).—Hedgpeth, 1953:164 (Texas).—Gunter & Geyer, 1955:40, 44, 45, 56, 57, 65 (Texas, Louisiana).—Parker, 1956:310, 315, 329, 354, 370 (dead specimens collected in east Mississippi delta region).—Courtney & Edmond, 1974:63 (Marco Island, Florida).—Fotheringham & Brunenmeister, 1975:36, 161, fig. 2.24 (natural history).

Astrangia danae: no authority cited: Wilson, 1900:350 (North Carolina).—Allee, 1923:176 (Woods Hole, Buzzards Bay, and Vineyard Sound, Massachusetts).—Hyman, 1940:610–611 (morphology, natural history).—Storer, 1951, figured on p. 321.—Stephenson & Stephenson, 1952: 35 (distribution, taxonomy).—Blake, 1953:23 (Pleistocene, Maryland).—Zinn, 1964:15 (Rhode Island).—Goreau et al., 1971:254.—Williams & Murdoch, 1973: 551–563 (effects of gamma radiation on).—Cummings, 1976:1–115 (physiology, Rhode Island).—Szmant-Froelich & Pilson, 1977:417–424 (nitrogen excretion, symbiosis, Rhode Island).—Hoffman et al., 1978:165–170.—Jacques, 1978:1–169 (calcification).—Gosner, 1979:93–94,fig. 20.—Storer et al., 1979, figured on p. 320, 372, 390.—Szmant-Froelich, 1980b:1–3 (popular account).—Szmant-Froelich et al., 1980:257–269 (reproduction, Rhode Island).—Meinkoth, 1981:391.—Cummings & McCarty, 1982:1125–1129 (calcification, stable carbon isotopes, Rhode Island).—Jacques et al., 1983:135–148 (ecology, metabolism, Rhode Island).—Swart, 1983:72 (stable carbon isotopes).—Szmant-Froelich & Pilson, 1984:153–162 (feeding frequency, nitrogen metabolism, respiration, Rhode Island).

Astrangia sp.: Ferguson, 1948:17 (salinity tolerance, Louisiana).—Keith & Weber, 1965:500 (isotopic composition, calcification, in part: Woods Hole, Massachusetts).—*not* Rabalais, 1978:62 (= *Oculina diffusa*, Gulf of Mexico).

Diagnosis.—Encrusting, massive, or ramose irregularly shaped colonies. Corallum cerioid to plocoid, new polyps produced by extratentacular budding, having corallites united basally by thin peritheca (vesicular coenosteum). Corallites round, irregular, or polygonal; tightly packed or spaced several millimeters apart, highly variable even within a single specimen. Calices 1–7 mm in diameter, with distinct equal costae on many corallites. Septa hexamerally arranged in 4 cycles, however, complete fourth cycle (48 septa) only attained in very large calices. Most calices have 24 septa, the S_3 merging basally with the S_2 about ¾ distance to columella. With increase in calicular diameter, pairs of S_4 form flanking some S_3, often with one pair per system (the space between two S_1) resulting in 36 septa. Complete fourth cycle (48 septa) attained only in calices over 6 mm in diameter. Septa strongly dentate, particularly S_3 at region of S_4 fusion, and slope gradually toward columella. Fossa shallow. Columella trabecular or papillose.

Polyps up to 1 cm tall and translucent white (azooxanthellate = asymbiotic) to brown (zooxanthellate = symbiotic, see Schuhmacher & Zibrowius 1985, for review of this terminology). Numerous nematocyst batteries on surface of tentacles; tip of tentacle rounded. Directive mesenteries present. Corallum often invaded by endolithic red or green boring algae, burrowing polychaetes, or sponges (e.g., *Cliona celata* Grant, see Cummings 1983).

Cnidocyst batteries principally composed of spirocysts. Terminal knob packed with large microbasic-p-mastigophore nematocysts (about 29 μm long × 8 μm in diameter in fixed, paraffin embedded sections) and spirocysts. Occasional small microbasic-p-mastigophores scattered in epidermis (about 20 μm long × 7 μm in diameter). Cnidoglandular band of mesenterial filaments possesses large microbasic-p-mastigophores (about 40 μm long × 7 μm in diameter), holotrichous isorhizas (about 45 μm long × 15 μm in diameter), and small microbasic mastigophores (?) (about 11 μm long × 5 μm in diameter). The distribution of these nematocysts varies with location on the filament (ECP, unpublished). Histologically distinguished by well-developed longitudinal retractor muscles along the mesogleal pleats. Gastrodermis lining calicoblastic epidermis features large cells with basophilic globules (osmiophilic, non-PAS positive, non-mucin) up to 4 μm in diameter, which increase in number and density towards base of the polyps. Calicoblastic epidermis thickened with fine eosinophilic granules (Peters 1984). Colonies gonochoric (=dioecious), gametes spawned annually (Szmant-Froelich et al. 1980, St. Pierre 1986).

Remarks.—Madrepora poculata was described by Ellis & Solander (1786), based on the illustration of a specimen from "near New York" figured by Ellis (1755). Another reference to this "American" coral appeared in Pallas (1766) under the name *Madrepora calycularis*, var. β. Typical *M. calycularis* Pallas (1766) is now known as *Astroides calycularis* (Pallas, 1766), found only in the Mediterranean (Zibrowius 1980). Therefore, the name *calycularis*, even if applied to a specimen of western Atlantic *Astrangia* as form β, is preoccupied by the Mediterranean species. Esper (1790:283) equated *M. poculata* with the *M. calycularis* β of Pallas, describing a corallum encrusting an American gastropod, which may have been the same as the astrangid-encrusted specimen of *Conus spurius* from the West Indies, figured by Seba (1758:152, pl. 55, figs. 11, 12). The last known reference to *M. poculata* was Turton (1806).

ME & H (1848b) described *Astrangia michelinii* as an illustration found in Memoire 4, Monographie des Astreides; this is a valid "indication" (International Code of Zoological Nomenclature (ICZN) 1985: Article 16, vii), and therefore it is a valid species and the type species of *Astrangia* by monotypy. It was described without a type locality.

In 1849, ME & H described (in order) 3 types in the Muséum National d'Histoire Naturelle, Paris, (MNHNP), *Astrangia danae, Astrangia michelini*, and *Astrangia astreiformis*. The descriptions of the type specimens were very similar. They noted that *A. michelini* was closely related to *A. danae*. Unfortunately, only the type locality of one of the 3 species, *A. astreiformis*, was given, as from the "United States."

Agassiz (1850) described the same species from the United States and used one of the same names used by ME & H, *Astrangia danae*, in a paper presented before the American Association for the Advancement of Science meeting in 1849, but it was not published until 1850. He made no comparisons and apparently did not know that the name had already been used for a species in the previous year (ME & H 1849), and therefore was a junior primary homonym. It is curious that Dana (1872, 1890) referred to *A. danae* Agassiz, suggesting that he had not been in correspondence with ME & H in the late 1800's. Dana noted that he himself had proposed the name *Pleiadia* for the genus, alluding to the crowd of stars (the appearance of the corallum), in his report on Zoophytes (Dana 1846:722, Wells 1986: 50, nom. nud.). However, Agassiz (1850: 69) made no reference to this particular report. That he chose to call his species *Astrangia* presumably means that he had seen the figure (if not the specimen on one of his European trips) of *A. michelinii* published in 1848.

Later authors, who had compared the type specimens and descriptions, commented on the relations of these species. Vaughan (1901:300) noted that the specimen of *Astrangia astreiformis* (corallites free above their bases), which he had collected in Puerto Rico, was not typical of the specimens of *A. astreiformis* then in the USNM, and observed that the figure of *A. michelini* ME & H "suggests great similarity to the specimen from Puerto Rico." Alloiteau (1952) believed that *A. michelini* ME & H was the same species as *A. danae* Agassiz. Chevalier (1966) observed that *A. astraeiformis* ME & H was similar to *A. michelini* of ME & H. Thus, *A. michelinii* Milne Edwards & Haime is "similar" to *A. danae* Agassiz (Vaughan & Wells 1943, Alloiteau 1952), *A. astreiformis* ME & H (Vaughan 1901, Chevalier 1966), and *A. danae* ME & H (Milne Edwards & Haime 1849).

Leidy (1855) considered *Astrangia astreiformis* ME & H to be the same as *A. danae* Agassiz. In 1863, Verrill recorded that *A. danae* Agassiz was equal to the *A. astreiformis* described by Leidy in 1855, and noted that *A. danae* Agassiz was not the same as *A. danae* ME & H. Verrill (1866a) reported that *A. bella* E. & H. [ME & H], known from the Miocene formations in Maryland, was very similar to both *A. danae* Agassiz and *A. astreiformis* ME & H, and noted that some authors would unite all three species. Pourtalès (1871:80) remarked "The differences between these two species (*A. astreiformis* M. E. & H. and *A. danae* Ag.) are of the slightest character, being chiefly derived from the mode of grouping, which is denser in the first than in the second. I am strongly inclined to believe that they will ultimately be united." In 1872, Verrill united *A. astreiformis* ME & H with *A. danae* Agassiz. Cummings (1983) and Jaap (in prep.) united *A. astreiformis* ME & H with *A. danae* Agassiz, noting the great variability in specimens collected from throughout its range along the coastline of the eastern United States. Only Vaughan (1901) felt that there were sufficient distinctions based on the skeletal structures to maintain *A. astreiformis* ME & H and *A. danae* Agassiz as separate species.

Thus, these observations link *Astrangia astreiformis* ME & H with *A. danae* Agassiz. Although *A. danae* ME & H appeared to be very similar to *A. astreiformis* ME & H (Leidy 1855, Chevalier 1966) and *A. michelini* ME & H (Milne Edwards & Haime 1849), subsequent authors (Verrill 1863, 1866a) did not connect *A. danae* ME & H with *A. danae* Agassiz. Verrill (1866a:324) stated again that *A. danae* ME & H ("the corallites being scattered and connected only at the base") was different from *A. danae* Agassiz, and therefore proposed the name *A. edwardsii* as a replacement name for *A. danae* ME & H. He erroneously thought that the date for Agassiz's name was 1849 and the date of ME & H's was 1850, because this latter date was cited in error by ME & H (1857:614). A number of later references attributed the publication date of Agassiz's name to 1847 (e.g., Calder 1972) or 1848 (e.g., Field 1949), further adding to the confusion. Fewkes (1889:8) noted that "The polypdom of *A. Danae* (sic) M. E. & H., is held by Prof. Joseph Leidy to be different from that of our New England species of *Astrangia* and more like *A. astraeformis* of the same authors . . . . It is not possible to determine from the description of *A. Danae* given by Milne Edwards & Haime whether our species differs from that which they describe under that name or not."

J. W. Wells examined the type specimens in the MNHNP in 1934. Of *Astrangia michelini* ME & H 1848 (No. 412, Michelin Coll.), he noted "Does not look like the figure but has M.E. & H.'s label on the wooden base. Very like *A. danae* [no authority cited] except for smaller [corallites] (2.5–3.0 mm). It is attached to a bit of igneous rock. This is the type species of *Astrangia* by monotypy. No loc." (JWW notes, February, 1934). He also observed that in the Paris collection "Specimens labeled *A. danae* [ME & H 1849] are from St. Thomas and are *A. solitaria,* coll. Duchassaing ca. 1846, *except* for one that appears to be the type. It encrusts a *Tellina* and fits the description well and is evidently conspecific with *A. michelini* as latter was figured in 1848 by M.E.&H. Has M.E.&H.'s label. No loc." Wells noted that the type of *A. astreiformis* ME & H 1849 was in the Paris collection in 1934, with the locality designated "Etats-Unis," but did not make any other observations on this specimen (JWW notes, February, 1934). From all indications (Cairns 1981), all of the types are now missing from the collections of the MNHNP.

Wells considered *Astrangia danae* ME & H 1849 to be the proper name for the American northern star coral (pers. comm. to A. Szmant-Froelich, 13 December 1977), noting that "Over the years I have examined many specimens from throughout this range [Massachusetts to Texas] and although there is much variation in skeletal morphology, the variation seems not be geographical or provincial, for specimens from one locality frequently show the full range of variation in compactness or isolation of corallites, size of corallites, equality of septa, etc." Although the names *A. danae* Agassiz and *A. astreiformis* ME & H had been used nominally to separate specimens from north of Cape Hatteras to New England from those specimens collected from south of Cape Hatteras into the eastern and western Gulf of Mexico, respectively, Wells observed that *A. danae* ME & H had priority as the senior synonym.

Cairns (1981) argued that *Astrangia astreiformis* was the appropriate name for the American species. He noted that ME & H described both *A. danae* and *A. astreiformis* in the same paper. Although *danae* had page priority, the type was lost, the description poor, and the type locality not given. He could not confirm that *A. danae* ME & H was the same as *A. danae* Agassiz and *A. astreiformis* ME & H, hence, he considered *A. danae* ME & H to be a nomen dubium. The locality for *A. astreiformis* was given as "United States." Although the type of *A. astreiformis* was also lost, it at least had a type locality, which is why Cairns considered it as the senior synonym. Because Agassiz's description of the same species, which he named *A. danae,* was not published until 1850, Cairns also considered this name a junior synonym of *A. astreiformis* and junior homonym of *A. danae* ME & H 1849.

Based on our present examinations of specimens and recent biological data (see below), we concur that there is only one species of star coral of the genus *Astrangia* along the Atlantic and Gulf coasts of North America. Although the type specimens are now missing from the Michelin collection, earlier observations by Leidy, Verrill, Pourtalès, Fewkes, Wells, Alloiteau, and Chevalier suggest that the *Astrangia* types established by ME & H were very similar. The latter four authors thought that these types were probably only morphological variants of the colonial northern star coral. There is no doubt that this species is the same as the *Madrepora poculata* described by Ellis & Solander over 200 years ago. Although the names *A. danae* and *A. astreiformis* have been used widely in the recent literature (73 and 41 references, respectively), these names must be considered junior subjective synonyms. We conclude that the correct name, based on the Principle of Priority (ICZN 1985), is *Astrangia poculata* (Ellis & Solander, 1786).

The type specimen of *Madrepora poculata* is not present at the Glasgow or the British Museum (Natural History) and is believed to be lost (P. F. S. Cornelius, pers. comm.). In order to help clarify the complex nomenclatural issues concerning the names *Astrangia poculata, A. michelinii* ME & H 1848, *A. danae* ME & H 1849, *A. astreiformis* ME & H 1849, and *A. danae* Agassiz 1850, a neotype is chosen for *M. poculata.* It is deposited at the USNM (USNM 80350) and was collected from New Jersey, relatively close to the original type locality of "off New York."

As mentioned before, there is no type specimen of the type species *Astrangia michelinii* (see Chevalier 1966). Furthermore, it was described without a type locality and its original description and figures do not reliably distinguish it from the other approximately 30 Recent species in the genus. Subsequent references to *A. michelinii* have always been in its capacity as the type species of the genus, not as a new record. Therefore, in order to redefine *A. michelinii,* and the genus *Astrangia* by virtue of its status as the type species of the genus, a neotype is chosen for *A. michelinii.* Because several authors (e.g., Vaughan 1901, Alloiteau 1952, Chevalier 1966) have suggested that *A. michelinii* is synonymous with the United States east coast species, the neotype chosen for *A. michelinii* is a specimen of *A. poculata,* in fact the same specimen chosen as the neotype of *M. poculata,* a specimen from New Jersey (USNM 80350). *A. michelinii* thus becomes a junior objective synonym of *A. poculata.*

Thiel (1928) described a colonial *Astrangia* from the Atlantic coast of Africa, and identified it as *A. astraeiformis* ME & H. In 1941, Thiel doubted the existence of the American species on the west coast of Africa, and established the species *A. mercatoris* as the African species. Buchanan (1954) reported *A. astreiformis* from the Ivory Coast and Gulf of Guinea off western Africa. Buchanan (1954:86) remarked that his specimens agreed well with Thiel's (1928) description of *A. astreiformis* from Africa. Chevalier (1966), however, believed that the American and African specimens that he examined were sufficiently similar to merit recognition as the same species. Unfortunately, as we know nothing of the African *Astrangia,* Thiel's (1928) specimens may indeed represent a different species.

Material examined.—From the USNM, 85 lots, the specimens representing the following localities: Martha's Vineyard Sound, Buzzards Bay, Woods Hole, Massachusetts; Newport, Rhode Island; 19 lots from R/V *Gosnold* collected off northeastern Florida and Georgia (13–54 m); Chesapeake Bay, Virginia Beach, Virginia; Cape Henry, North Carolina; Myrtle Beach, South Carolina; Nassau County, Florida; northeastern coast of Florida; Dry Tortugas, Western Dry Rocks off Sand Key, Florida; Marco, Gulf coast of Florida; Rockport, Galveston, Port Aransas, Texas.

Specimens from the Texas coast deposited in the Texas Memorial Museum, Austin, Texas (Numbers 1568–1573, 1753).

Specimens from the Hourglass Cruises, deposited in the collection of the Department of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida (Numbers FSBC I 10027, 11360, 17984, 19858–19862) and 49 other cataloged specimens (various numbers from FSBC I 10028–31954, eastern Gulf of Mexico and Florida east coast), as well as specimens on loan from Texas A&M University (College Station, Texas), and Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts), representing locations from New England to Florida, Louisiana, and Texas.

Geologic and geographic distribution.—*Astrangia poculata* is recorded from the Miocene (Richards & Harbison 1942), Pleistocene (Blake 1953, Pampe 1971) and Recent (Alloiteau 1952, Wells 1956). It occurs at depths from 0 to 263 m. It has been reported off Maine (Hargitt 1914) and from Cape Cod south along the eastern United States, around the Gulf coast of Florida to the southern Gulf coast of Texas and Mexico (E. Jordan pers. comm. to WCJ). It is very rare in the coastal region from south of Palm Beach to the Ten Thousand Islands, Florida, and is disjunct in the Mississippi delta region. It is also noted from Puerto Rico (Vaughan 1901) and Martinique (Thiel 1941). Thiel (1928) and Buchanan (1954) reported it from the Ivory Coast, French Congo, Angola, Africa, (although its existence off Africa based on these reports has been questioned, see Remarks), and Chevalier (1966) reported it from the Bight of Biafra, Freetown, Sierra Leone, Konakry, Guinea, Dakar and Senegal (Gulf of Guinea), Africa.

Discussion.—Coral species traditionally have been determined on the basis of their skeletal morphologies (since these are preserved most easily, and appear in the fossil record). Veron (1982) stated that biological species in corals are "the sum of a series of forms of variation which differ in relative importance from species to species." Recent attempts to determine the range of variation which may exist within a single species have revealed the relative influence of phenotypic and genotypic variation in skeletal development, and the contributions of each may vary between species or genera (see reviews by Wijsman-Best 1974; Foster 1979, 1980). Lang (1984) reviewed the utility of non-skeletal characters to aid in the differentiation of species when skeletal characters are ambiguous or environmentally variable.

Recent studies have revealed a wide range of variation in the types of skeletal structures produced by colonies of *Astrangia poculata.* Field (1949) reported that branching forms might be found when the colonies were located in a protected spot. Cummings (1983) investigated patterns of morphological variability in colonies of *A. poculata* from Rhode Island and the Gulf coast of Florida and found a high degree of morphologic plasticity. She noted that the parameters measured (height/length, branching, and polyp density) were correlated with exposure (light and wave action), and did not differ significantly between zooxanthellate and azooxanthellate colonies. Colonies from Panacea, Florida were, however, more branched than those from Fort Wetherill, Rhode Island, and contained more zooxanthellae per unit area of tissue. The Fort Wetherill colonies possessed more corallites per unit area and were smaller than elsewhere. As depth increased, colonies became taller and more branched, and polyp density decreased. Brunet (1982) described colonies from various sites off the Texas coast. Encrusting, mound and digitate colonies were found at the Port Aransas jetty on the channel at the end of the barrier island. Mostly mounding and a few encrusting colonies, only rarely with early digitate morphologies, were present on the pilings of the nearshore oil rigs he examined. He suggested that the digitate growth form was a response to sedimentation, to allow the polyps to extend above the substratum. He also noted that the appearance of filamentous algae growing on dead portions of the corallum might force adjacent polyps to continue growing and overtop the algae to form characteristic knobby branches. The large expansive polyps of the star coral are well-suited to removing sediment particles that may fall on its surface (Peters 1984). However, we (ECP, CEV, LSG) have observed that during periods of cold weather (in both Rhode Island and Texas corals) the coenosarc tissues of *A. poculata* often contract and expose the coenosteum (as the polyps contract and forego feeding), which may be covered with sediment or colonized by algae. These lesions may contribute to the formation of digitate colonies when the coral resumes skeletal deposition in the spring, although this has not been confirmed experimentally. St. Pierre (1986) also observed high variability in colony morphology from encrusting to ramose or both types on the same colony, at the Port Aransas jetty. Jaap (in prep.) noted that substratum may also control colony morphology, with encrusting forms found on mollusk fragments or shells and thicker or branching forms on igneous rock bases. As for other skeletal characters, Jaap (in prep.) reported that Gulf of Mexico specimens generally had smaller corallite diameters and there were reduced numbers of septa in specimens taken from Texas or the western Gulf sites. He observed a minimum annual growth rate (basal diameter) of 38.4 to 46.8 mm for two clusters of *Astrangia* which attached to a stone crab trap between April and September 1977 (Jaap, in prep.). The largest branching specimen in the USNM (USNM 78508, Fig. 4) was collected from 263 m depth off Western Dry Rocks, Sand Key, Florida.

The cellular composition and structure of *Astrangia poculata* are distinctive, particularly in the development of the mesogleal pleats and the granules in the cells of the aboral gastrodermis and calicoblast epidermis, and differ from other members of this and closely-related families, such as the Oculinidae (see Peters 1984). *A. poculata* is one of the few subtropical to temperate corals that may possess symbiotic dinoflagellate algae known as zooxanthellae within its gastrodermal tissues, and is the only member of the genus reported to do so. Cummings (1976), Jacques et al. (1977), and Szmant-Froelich (1980a) showed that zooxanthellae densities in some colonies from Narragansett Bay may be equal to or greater than those reported to occur in tropical reef corals. In Narragansett Bay, colonies with zooxanthellae are found directly adjacent to those without, and there are colonies that are only partially pigmented (spotted) brown by the algae. All varieties are found throughout the year. Colonies which appear to lack zooxanthellae usually possess small populations of the algae (less than 1×10^5 cells per polyp). Hence, Swart's (1983:72) arguments that colonies of *A. danae* (=*A. poculata*) that lack zooxanthellae might be a different species, or might be found under stress conditions, appear to be invalid.

Algal populations do vary seasonally with changes in light intensity and temperature (Cummings 1983), and under sedimentation stress (Peters & Pilson 1985). The algal populations also increase under conditions of high light and temperature in the laboratory (Cummings & McCarty 1982, Cummings 1983, Peters & Pilson 1985). Cummings (1976, 1983) suggested that this change was caused by differences in physiological tolerances between zooxanthellate and azooxanthellate colonies, with the former better adapted to summer (high temperature and light) and the latter better adapted to winter (low temperature and light) conditions. Possibly, because of the seasonal fluctuations of these conditions, fully zooxanthellate colonies are not numerically dominant in Narragansett Bay. Jacques (1978) observed that at high light and temperature conditions, the zooxanthellate colonies calcified significantly faster than azooxanthellate ones. Peters & Pilson (1985) found that the tissues of zooxanthellate colonies were more easily damaged by combined sedimentation and starvation stress than azooxanthellate colonies, and suggested that genetic as well as environmental factors influence the symbiosis. Weston (1980) found only zooxanthellate colonies in the relatively well-illuminated surface waters of Chesapeake Bay and azooxanthellate colonies deeper. Both kinds were found inhabiting a transition zone, the depth of which correlated with 89 to 95% attenuation of surface incident light. He also sugested that both genetic and environmental factors might influence the symbiosis. The colonies which Brunet (1982) found on shallow substrata (less than 2 m water depth) at the Port Aransas, Texas, jetty site contained zooxanthellae. At depths greater than

2 m, and at the oil rig and the Liberty ship, specimens of *Astrangia* always lacked zooxanthellae.

Colonies of *Astrangia poculata* tolerate a wide variety of environmental conditions. In nature, populations have been found in salinities ranging from oceanic (36‰) seawater (Cummings 1976) to salinities of 16–19‰ in Texas bays (Ladd 1951). Experimentally, this coral can adapt to salinities ranging from 10 to 40‰ (Ferguson 1948, Cummings 1976) and can survive for more than six days under low oxygen conditions (Sassaman & Mangum 1973). In Naragansett Bay, Rhode Island, *A. poculata* survives an annual temperature range of −1.5°C to 22°C, and up to 35°C under experimental conditions in the laboratory (Cummings 1976, Jacques 1978, Peters & Pilson 1985). St. Pierre (1986) observed annual temperature fluctuations from 17°C to 30°C during a study of *Astrangia* from Port Aransas, Texas. The unusual hardiness of *A. poculata* is illustrated by the fact that MEQP (unpublished) often kept colonies in small containers in his office. In one case a small colony was maintained for more than three years in a one-liter container, often without feeding it or changing the water for months.

The sexual reproduction of *A. poculata* in Narragansett Bay, Rhode Island, was examined by Szmant-Froelich et al. (1980). They demonstrated that each colony is dioecious, with a 1:1 male : female sex ratio for the population. Fertilization is external, with development of planktonic planula larvae, and zooxanthellae are not passed on in the eggs or sperm but must be acquired after settlement. An annual reproductive cycle appeared to be tied to the seasonal maximum temperature. Well-fed colonies, experimentally maintained year-round under high light and temperature (20–22°C or 26°C) conditions continuously produced gametes (Szmant-Froelich 1981, Peters & Pilson 1985). St. Pierre (1986) studied the reproductive cycle of a population of *Astrangia* from a jetty off Port Aransas, Texas. She also found a 1:1 sex ratio. Gametogenesis began in February, with spawning occurring in late August to September, corresponding to the maximum water temperatures at this Gulf of Mexico site. Another cycle of gametogenesis appeared to begin in November. Similarly, a second cycle was reported for the Rhode Island colonies beginning in October. Because the reproductive cycle of this coral appears to be essentially the same throughout its range, St. Pierre supported the synonymy of *A. danae* with *A. astreiformis* (St. Pierre 1986).

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MIROSTENELLA ARTICULATA, A REMARKABLE NEW GENUS AND SPECIES OF PRIMNOID OCTOCORAL (GORGONACEA) WITH UNCALCIFIED AXIAL NODES

Frederick M. Bayer

Abstract.—A new genus and species are established for a primnoid octocoral having flexible organic nodes at the bifurcations of the heavily calcified axis. Its significance in the relationship of the Primnoidae to the Isididae is discussed and the need for further study is stressed.

Kükenthal (1915:144) considered the Primnoidae to be the most thoroughly investigated family of the order Gorgonacea thanks to the work of Studer (1878), Studer & Wright (1887), and Versluys (1906). After repeating that statement in his account of the gorgonians of the Valdivia Expedition, he presented a new treatment of the family based on 138 species distributed among 12 genera (Kükenthal 1919:311). Since that time, several new species have been described, and four new genera have been established, five elevated from subgeneric to generic rank, and one revalidated from synonymy.

Molander (1929) created a new subfamily Lycurinae for his *Lycurus antarcticus,* which Carlgren (1943) later reassigned to the genus *Ainigmaptilon* Dean, simultaneously renaming the subfamily Ainigmaptiloninae and elevating it to full family rank. Subsequently this family has been submerged within the Primnoidae (Bayer 1981:946).

Based upon such thorough investigation and comprehensive material, the diagnosis of the family Primnoidae as set forth by Kükenthal (1919:309; 1924:252) has subsequently undergone no substantial modification. Although the specifications regarding the development of the distalmost polyp sclerites as opercular scales do not fit some species precisely, the significant array of characters shared by all members of the Primnoidae has remained unchanged until now.

At station 1536 off South Georgia, USNS *Eltanin* obtained one of the richest hauls of gorgonian corals taken during the U.S. Antarctic Research Program. The gorgonian community at that locality was dominated by primnoids, among which were collected several specimens of a gorgonian of predominantly primnoid appearance but having a calcified axis with organic nodes suggestive of the Isididae. This species, not referable to any genus and species heretofore known, contradicts one of the basic diagnostic characters of the Primnoidae and raises some fundamental questions about the relationships of the families of holaxonian gorgonians having heavily calcified axes without a cross-chambered hollow core.

In his paper on the classification and phylogeny of the Primnoidae, Kükenthal (1915:154) remarked that we know next to nothing about the relationships of the primnoids to the other families of Gorgonacea. This equivocal new species will necessitate a review of the gorgonian families and their relationships as well as a redefinition of the family Primnoidae.

Mirostenella, new genus

Diagnosis.—Dichotomously branched primnoid with polyps arranged in pairs or whorls of 3–4, with 8 complete rows of body scales, operculars aligned with marginals. Calcified axis interrupted by organic nodes at points of bifurcation.

Type species.—*Mirostenella articulata*, new species, here designated.

Etymology.—Latin *mirus*, extraordinary, wonderful, from *miror*, to be astonished at + *Stenella*, name applied to a genus of primnoid gorgonians by J. E. Gray; in allusion to the similar arrangement of the polyps.

Mirostenella articulata, new species
Figs. 1–3

Material.—Off South Georgia: 54°29′S, 39°22′W to 54°31′S, 39°19′W, 659–686 m. *Eltanin* cruise 22, sta 1536, 8 Feb 1966. Holotype, USNM 79959; paratypes, USNM 79960; BM(NH) 1987.9.17.1; SMF 5687.

Diagnosis.—Dichotomously branched primnoid with calcified axis interrupted by organic nodes at points of bifurcation. Polyps in pairs or whorls of 3–4; marginal scales with smooth apical thorn or spine, longitudinally aligned with opercular scales.

Description.—Colonies (Fig. 1a–c) reach a height of about 8 cm and a width of about 10 cm, dichotomously branched mostly in one plane but with occasional strays out of the principal plane, attached by a small discoidal holdfast. As in other dichotomous primnoids examined, the bifurcations are not true dichotomies as in *Chelidonisis* and *Melithaea* because they originate as lateral branchlets from the primary axis of terminal twigs. The axis between bifurcations is of typical primnoid aspect, opaque straw yellow with metallic iridescence, and marked by conspicous longitudinal ridges and grooves; oval depressions, shallower than in most isidids but similar to those of other primnoids, mark the locations of desmocytes in the axis epithelium. At the points of bifurcation the axial material is translucent dark brown, smooth but without iridescence, forming flexible organic nodes between the rigid, heavily mineralized internodes. Sharp reduction of calcium at the nodes was verified by energy-dispersive X-ray analysis. The nodes are not so abruptly delimited from the internodes as in the Isididae; strands of pale calcified material extend from the internodes into the darker, translucent nodal substance. The bifurcations enclose angles of roughly 45°, often a little more or less; the internodes, including the basal one, range between 4 mm and 15 mm in length, and the unbranched terminal twigs may be as long as 3.5 cm, but most are shorter. The trunk of the largest colony is slightly over 1 mm in diameter including the coenenchyme; thereafter the internodes diminish in diameter distad, tapering to 0.04 mm (without coenenchyme) at the apex.

The polyps (Fig. 2) are arranged in widely spaced pairs or whorls of 3 or 4, of which 3 or 4 occur in 1 cm of branch length. The polyps are directed slightly upward, either straight or with a weak upward curvature, about 2 mm tall and 0.6 mm in diameter proximally, widening to 0.8–0.9 mm distally.

The sclerites of the polyps are thin scales of the usual primnoid type, nearly smooth on the outer surface but covered with small, complicated tubercles on the inner, with radial orientation of the component microcrystals resulting in a cruciform extinction pattern when viewed under crossed Nicols. Those of the distalmost circle (Fig. 3a) are 8 narrowly triangular sclerites about 0.4–0.5 mm tall, without a prominent keel on the inner surface of the apex. They close over the withdrawn tentacles and oral region as a low, conical operculum. The 8 marginal scales (Fig. 3b) surrounding the operculum are ellipsoidal, mostly 0.4–0.5 × 0.22–0.3 mm, their upper edge prolonged into a smooth, narrow spine 0.075–0.3 mm long; they are incapable of folding inward, hence are not a "circumoperculum" in the sense of Kükenthal (1919:329), but together they surround the operculum like a spiny diadem. The body sclerites (Fig. 3c) are thin, oval, squarish, or elongate scales about 0.3–0.35 mm in greatest dimension, placed in 8 longitudinal rows that may be somewhat disrupted by breakage; they diminish to

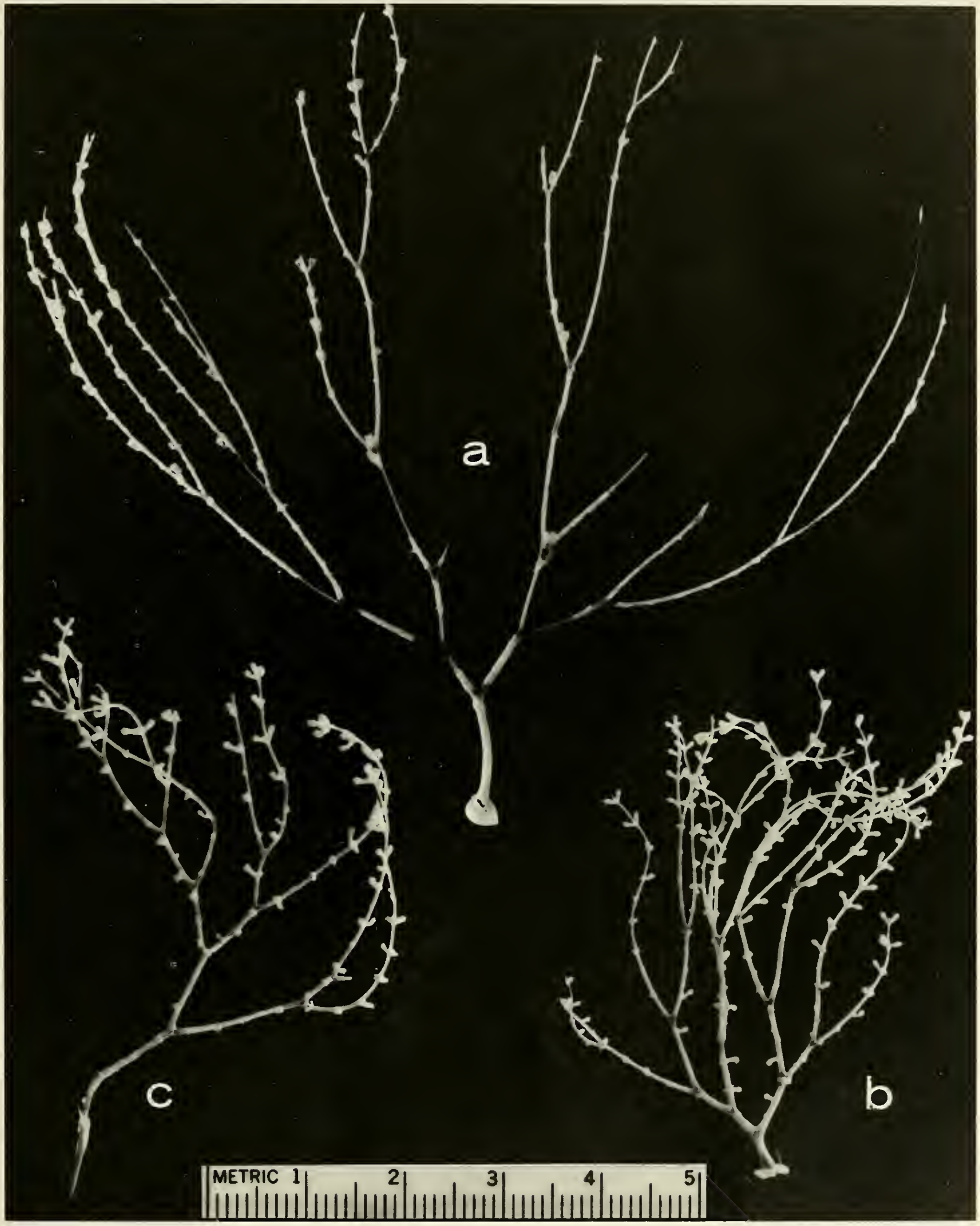

Fig. 1. *Mirostenella articulata*: a, c, Paratypes, USNM 79960; b, Holotype, UNSM 79959.

about 0.1 mm in diameter toward the base of the polyps, where they are discoidal in outline (Fig. 3d) and irregular in arrangement. The sclerites of the coenenchyme (Fig. 3e) are thick platelets up to 0.4 mm in length, of very irregular outline and covered with conspicuous bluntly conical projections.

Comparisons.—No primnoid so far de-

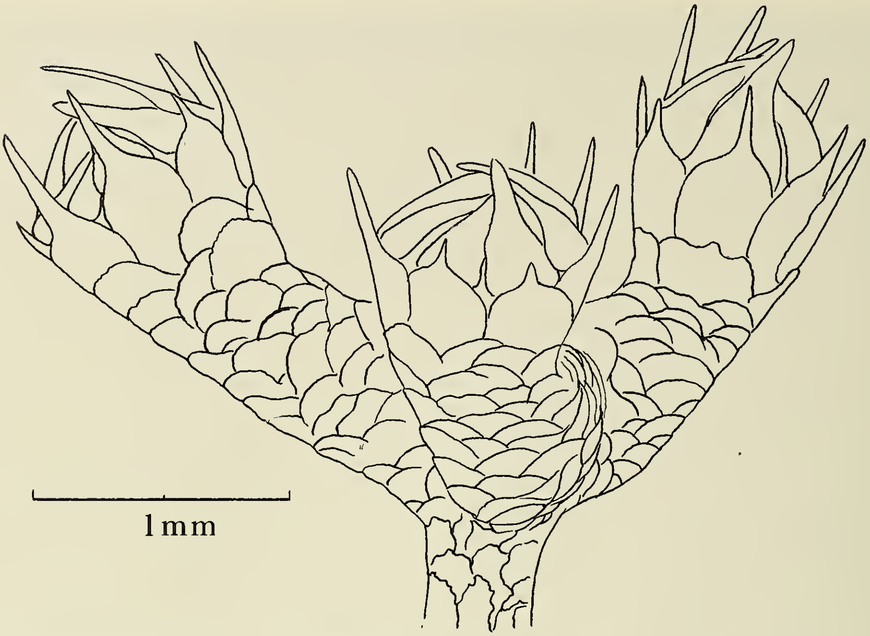

Fig. 2. *Mirostenella articulata*: Terminal whorl of three polyps.

scribed has organic nodes at the points of ramification of the calcified axis. The arrangement in pairs or whorls of the almost vertically placed polyps most closely resembles the condition in *Candidella, Parastenella,* and *Pterostenella,* but in the first of those there are only four marginal scales, in the second six, and in the last eight which alternate with the opercular scales, not in line with them as in the present case. In shape the polyps most closely resemble those of a few species of *Plumarella,* but in that genus the polyps are always isolated, never in whorls, and moderately to strongly recurved toward the axis.

Taxonomic implications.—The unequivocal presence of axial articulation in a primnoid species blurs the distinction of the family Primnoidae from the Isididae at the practical level. Before the significance of this axial feature can be evaluated, closer investigation of the structure in *Mirostenella articulata* is essential for comparison with isidid axial structure. Preliminary examination of the axis shows that it is formed on an organic matrix with a mineralized core, increasing in diameter proximad by the addition of concentric layers of mineralized tissue, presumably secreted by an axis epithelium as in other gorgonians. At the points of bifurcation, the layers of secondary thickening around the core fail to mineralize, resulting in purely organic nodes. This condition is certainly analogous with that of the isidid axis, and may well be homologous.

Kükenthal (1915:124; 1919:634, 712) considered the family Isididae to be polyphyletic, with the articulated axis arising independently four different times. He derived the subfamily Mopseinae from the primnoid stem partly on the basis of the similarity of the undulated concentric lamellae of the axis (Kükenthal 1919:712) and the scale-like form of the sclerites (Kükenthal 1919:637) to those of primnoids; the Isidinae from the Plexauridae; the Ceratoisidinae from the Gorgonellidae [=Ellisellidae]; and the Muricellisidinae from the Muriceidae [=Paramuriceidae].

Fig. 3. *Mirostenella articulata,* sclerites: a, Operculars; b, Marginals; c, Of polyp body; d, From base of polyp; e, Of coenenchyme.

Now the discovery of an otherwise "typical" primnoid having a clear manifestation of axial articulation lends weight to a relationship of the isidids to the primnoids, but the other similarities may not be as significant as Kükenthal thought. The scales of Mopseinae such as *Primnoisis* are structurally more similar to those of chrysogorgiids than to those of primnoids, as the component microcrystals are oriented longitudinally rather than radially and thus do not yield a cruciform extinction pattern under crossed Nicols. Moreover, the undulate concentric lamellae of gorgonian axes are a reflection of the longitudinal grooving of the axial surface marking the course of coenenchymal stem canals, as is the case also in the Isidinae (e.g., *Isis hippuris*; Simpson, 1906:430). Both primnoids and isidids vary in this respect, and its phylogenetic significance would appear negligible.

At the present time it is premature to speculate upon the position of *Mirostenella articulata* relative to other primnoids, and its significance in the relationships of the gorgonacean families with calcified axes. The species is here placed on record to call attention to the complexities of phylogenetic speculation in the absence of a useful fossil record, and to stimulate further interest in the taxonomic and phylogenetic problems of the Octocorallia.

Abbreviations.—BM(NH) = British Museum (Natural History), London; SMF = Natur-Museum Senckenberg, Frankfurt; USNM = National Museum of Natural History (Department of Invertebrate Zoology), Smithsonian Institution, Washington, D.C.

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A NEW SPECIES OF *CHRYSOGORGIA* (OCTOCORALLIA: GORGONACEA) FROM NEW CALEDONIA, WITH DESCRIPTIONS OF SOME OTHER SPECIES FROM THE WESTERN PACIFIC

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Abstract.—A new species of the gorgonacean genus *Chrysogorgia* from New Caledonia is described and illustrated, along with five additional new species from the Philippines, Celebes, Paumotus and Hawaii. *Chrysogorgia stellata* Nutting from Hawaii is redescribed and illustrated and tentatively recorded from the Molucca Passage on the basis of fragmentary material. A key to the species of the group "Squamosae aberrantes" of *Chrysogorgia* is presented.

Among the many novelties included among the octocorals collected in New Caledonian waters by M. Georges Bargibant is a species of *Chrysogorgia* unlike any heretofore described. It is similar in many respects to another species, also new, trawled in the Philippine Islands by the U.S. Fish Commission steamer *Albatross* during the Philippine Cruise of 1906–1910. Investigation of these specimens has necessitated the review of other Pacific chrysogorgiid material in the collections of NMNH and reemphasizes the inadequacy of present knowledge about this distinctive family of Gorgonacea.

The admirable treatment of the Chrysogorgiidae of the Siboga-Expedition by J. Versluys (1902) has yet to be surpassed in its careful detail of observation and critical evaluation of taxonomic characters. Unfortunately, the Siboga collection of these corals was limited, and even though Versluys reexamined the *Challenger* material, the only other significant collection obtained up to that time, his results suffered from an insufficiency of basic data. This insufficiency still exists. Additional material has, of course, been obtained subsequently, but specimens more often than not are unique and localities widely scattered. As a result there still is little useful information about individual and geographical variation and, consequently, about the significance and reliability of the morphological characters now used in classification.

Family Chrysogorgiidae

Diagnosis.—Gorgonacea with scleroproteinous axis containing non-spicular crystalline calcification, core not hollow and cross-chambered, concentric layers not conspicuously undulate. Polyps contractile but not retractile into common coenenchyme, forming prominent verrucae not set in pairs or whorls. Sclerites predominantly flat scales or plates, usually smooth or nearly so, in many cases accompanied by rods or spindles with more or less conspicuous thorny sculpture. Scales viewed under crossed nicols often show concentric bands of interference colors but never a cross-shaped extinction figure.

Remarks.—Most members are easily recognized as belonging to this family by either the scalelike sclerites that show no trace of a cruciform extinction figure under crossed Nicols, or the angular, dichotomous manner of branching, or by both. In most species the axis has a noticeable to brilliant metallic luster. Therefore it is difficult to understand why so perceptive an investigator as Versluys placed the ellisellid genus *Riisea* in this family, as its sclerites are so similar to those of *Ellisella,* its axis lacks metallic gloss and is structurally like that of other ellisellids. Conversely, Nutting (1910) assigned his new genus *Isidoides* to the Gorgonellidae (i.e., Ellisellidae) in spite of its chrysogorgiid scales, finding instead a resemblance to isidid sclerites.

So far, no species of the Chrysogorgiidae has been taken in the lagoon or on the reefs of New Caledonia, even though the genus *Stephanogorgia* is known from the Philippines and the Palau Islands (Bayer 1974, Bayer & Muzik 1976). The delicate, feathery growth form of the colonies resembles that of certain hydroids so closely that collectors may not have recognized them as gorgonians.

Key to the Genera of Chrysogorgiidae

1(7). Colonies unbranched, flagelliform, in some cases spirally twisted.
2(3). Polyps arranged uniserially along the stem .... *Radicipes* Stearns, 1883
3(6). Polyps arranged biserially along the stem.
4(5). Distal sclerites of polyps differentiated to form an operculum consisting of 8 triangular scales; abaxial body scales transverse .... *Chalcogorgia* Bayer, 1949
5(4). Distal sclerites not in the form of an operculum consisting of 8 triangular scales; abaxial body scales longitudinal .... *Distichogorgia* Bayer, 1979
6(2). Polyps arranged multiserially along the stem, crowded but leaving a longitudinal tract free of polyps .... *Simpsonella* Stiasny, 1940
7(1). Colonies repeatedly branched.
8(13). Terminal branches long, slender, whiplike, originating directly from the main stem or after a few bifurcations of primary branches.
9(10). Terminal branches simple, arising around the outside of the spirally coiled main stem; colonies not flabellate .... *Iridogorgia* Verrill, 1883
10(9). Terminal branches arising in one plane, colonies more or less distinctly lyrate.
11(12). Terminal branches flexible, slender. Sclerites exclusively in the form of small scales, or completely absent .... *Trichogorgia* Hickson, 1905
12(11). Terminal branches stiff, rather stout and brittle. Sclerites include unilaterally developed spheroids and thick plates with closely set, stout, rounded projections on the outer surface .... *Pleurogorgia* Versluys, 1902
13(8). Terminal branches short, the last of several subdivisions of the primary branches.
14(17). Branching in one plane.
15(16). Branching profuse, pinnate, producing flabellate, more or less plumose colonies; polyps small, coenenchyme extremely thin, sclerites small, up to 0.15 mm in length .... *Stephanogorgia* Bayer & Muzik, 1976
16(15). Branching sparse, lateral or openly pinnate, producing loose, open colonies; polyps large, coenenchyme thick, sclerites large, up to 0.45 mm in length .... *Isidoides* Nutting, 1910
17(14). Branching not in one plane.
18(19). Branches subdividing irregularly, originating on all sides of the main stem but not in a regular spiral around it, forming

bottle-brush shaped colonies. Axis weakly calcified, without metallic luster .... *Xenogorgia* Bayer & Muzik, 1976

19(20). Colonies sympodial, branches subdividing dichotomously, originating in a regular spiral around the main axis, or forming 2 parallel fans at the top of a short trunk. Axis strongly calcified, with brilliant metallic luster .... *Chrysogorgia* Duchassaing & Michelotti, 1864

20(19). Colonies monopodial, dichotomously subdivided branches arising from the top of a tall, upright main stem. Axis strongly calcified, with metallic luster most conspicuous on the secondary branches, the main trunk glossy but almost black .... *Metallogorgia* Versluys, 1902

Chrysogorgia Duchassaing & Michelotti, 1864

Chrysogorgia Duchassaing & Michelotti, 1864:13.—Duchassaing, 1870:17.—Gray, 1870:45.—Verrill, 1883:21.—Studer [& Wright], 1887:41.—Wright & Studer, 1889:23.—Versluys, 1902:17.—Kükenthal, 1909:40.—Kinoshita, 1913:2.—Kükenthal, 1919:505; 1924:388.—Thomson, 1927:21.—Deichmann, 1936:227.—Bayer, 1956:F216; 1981:940 (in key only).

Dasygorgia Verrill, 1883:21.—Studer [& Wright], 1887:41.—Wright & Studer, 1889:23.

Diagnosis.—Sympodial chrysogorgiids with branches repeatedly subdividing dichotomously, either arising in a regular spiral around the main stem or forming 2 parallel uniplanar fans from a short main trunk. Axis with brilliant metallic luster.

Remarks.—In his masterful treatment of the Chrysogorgiidae of the Siboga Expedition, Versluys (1902) divided the genus *Chrysogorgia* into three groups called "Spiculosae," "Squamosae aberrantes," and "Squamosae typicae" on the basis of differences in spiculation.

All of the species under consideration here can be assigned to the group "Squamosae aberrantes," in which the polyps have spindles, rods, or thick, irregular sclerites longitudinally placed in the back of the tentacles, in addition to the usual chrysogorgiid scales in the body of the polyps and in the coenenchyme.

Key to species of Squamosae aberrantes

1(9). Sclerites in proximal part of tentacles are rods, more or less pointed and more or less bent (i.e., "typical spicules" in the sense of Versluys), with coarse, granular sculpture but not conspicuously irregular.

2(5). Polyps 1.8–3.0 mm tall.

3(4). Polyps 1.8–2.0 mm tall; body scales up to 0.43 mm, coenenchymal scales to 0.13 mm; colonial form and branching sequence unknown ..... *intermedia*

4(3). Polyps 2–3 mm tall; body scales may exceed 1 mm in length, coenenchymal scales to 0.5 mm.; colony flabellate .. .. *stellata*

5(2). Polyps at most 1.5 mm tall.

6(7). Branching sequence 1/4R; polyps up to 1.5 mm tall; body scales up to 0.5 mm, coenenchymal scales to 0.45 mm .. .. *calypso* n. sp.

7(8). Branching sequence 1/6R; polyps up to 1.2 mm tall but mostly 1 mm or less; body scales up to 0.2 mm, coenenchymals to 0.08 mm .... *bracteata* n. sp.

8(6). Branching sequence 1/7R; polyps up to 1.5 mm tall; body scales up to 0.3 mm, coenenchymal scales to 0.12 mm .... *admete* n. sp.

9(1). Sclerites in proximal part of tentacles are irregularly shaped, often with one end marginally lobed.

10(13). Colonies with a distinct and persistent main axis that gives rise in regular spiral sequence to dichotomously subdivided lateral branches.

11(12). Polyps 1.75 mm tall; coenenchyme with nematozooids .... *expansa*

12(11). Polyps up to 2.5 mm tall; coenenchyme without nematozooids .... *octagonos*

13(10). Colonies in the form of two to several more or less planar fans arising from the upper end of a short main trunk, without a distinct axis that persists throughout the height of the colony.

14(15). Base of tentacles covered by coarse, irregular sclerites with dentate projections at one or both ends; no naked area *curvata*

15(14). Base of tentacles with a naked area not completely covered by sclerites.

16(17). Proximal sclerites of tentacles are coarse, blunt roads up to 0.3 mm long, often with lobed ends; body scales terete, tapering smoothly toward pointed ends; coenenchymal scales with conspicuously lobed margins .... *chryseis* n. sp.

17(16). Proximal sclerites of tentacles are flat scales with one end pointed and the other broad, with more or less distinct lobes.

18(19). Polyps 2.75 mm tall, with distinct points beneath the tentacles; margins of body scales with low, broad lobes; coenenchymal scales are slipper-shaped up to about 0.33 mm long .... *scintillans* n. sp.

19(18). Polyps 1.75–2 mm tall, with only low, inconspicuous projections beneath the tentacles; margins of body scales often with narrow, prominent lobes; coenenchyme with narrow, tapered scales often with prominent marginal lobes .... *electra* n. sp.

Chrysogorgia admete, new species
Figs. 1, 2

Material examined.—New Caledonia: 22°49′S, 167°12′E, 390 m. Dredge no. 1, 13 Apr 1978; HGP-14. Two specimens, one dry (paratype, USNM 80433), one in alcohol (holotype, MNHN OCT.A.1988.2 Paris).

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with counterclockwise spiral branching in 1/7 sequence.

Description.—The colony is 10 cm high, 6.5 cm wide, arising from a calcareous holdfast that had been attached to solid substrate. The stout main stem is slightly curved, ascending in a smooth counterclockwise spiral giving off from its outside dichotomously subdivided branches. The branches of the first 5 turns of the main stem are broken off leaving only short stumps, so the first complete branch occurs 2.5 cm above the holdfast. The branching sequence is 1/7, so the main branches are aligned in 7 regular longitudinal rows. The main stem ascends about 5 mm with each turn of its spiral, i.e., the distance from one branch to the one aligned vertically above it (the 8th). The branches arise at such short intervals that their bases are nearly in contact; the stem internodes thus are extremely short. The branches arise at decreasing angles from the base upward, the lowest at about 60° from the vertical, those at mid-height at about 45°, and the uppermost even less. They subdivide dichotomously at angles from about 25° to 45°. The first bifurcation occurs

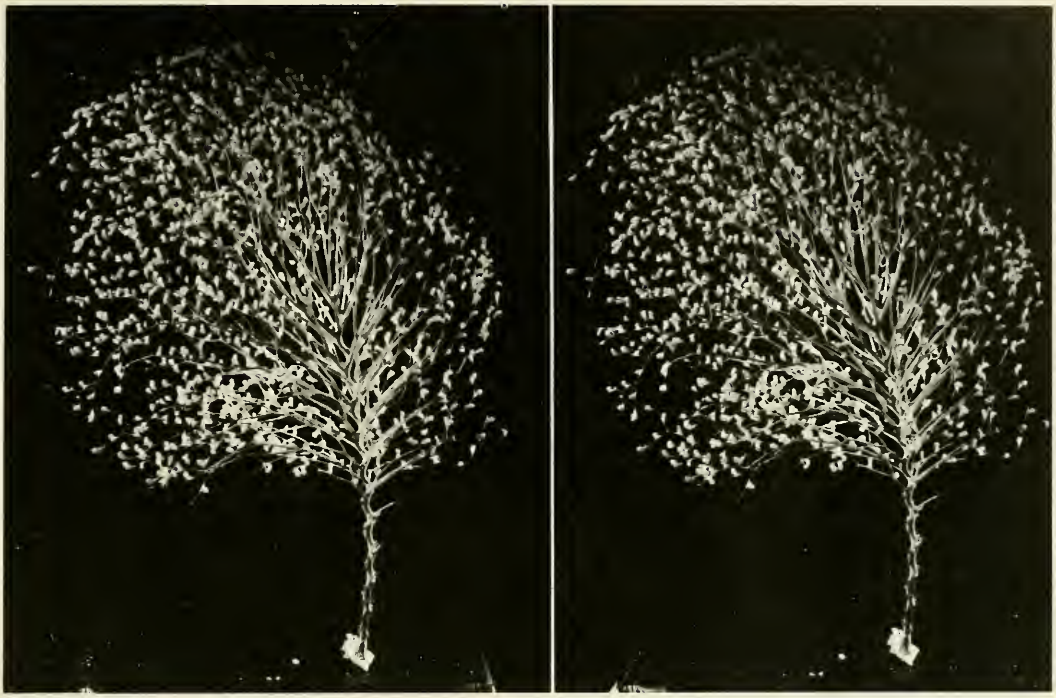

Fig. 1. *Chrysogorgia admete,* holotype colony; height 10 cm. Stereoscopic pair.

at about 5 mm from the main stem, the second from as little as 5 or 6 mm to as much as 20 mm, usually more or less unequal, and the third at 6–10 mm; some of the uppermost branches may have a fourth and sometimes a fifth bifurcation, also at 6–10 mm, sometimes unilaterally. The internodes commonly are 5 mm long, but on the more distal branches the second internode may be as much as 15 mm long. Polyps are situated 1 to 5 per internode, commonly 2, especially on the more distal internodes; only infrequently is a polyp located at a node. In most cases the first internode of the branches is devoid of polyps, as is often the second.

The polyps (Fig. 2a) are about 1.5 mm tall except the distalmost ones on each branchlet, which tend to be somewhat shorter. They are of the general type illustrated by Versluys (1902:64, fig. 98) for *C. expansa* and by Kinoshita (1913:26, fig. 24) for *C. versluysi,* having at the base of each tentacle an area free of sclerites that permits the unimpeded outfolding of the tentacles when extended. The body is at most about 1 mm high and often is less, especially in the apical polyps, and about 0.8 mm wide toward the base but only 0.6 mm at the conspicuous constriction below the tentacular crown. The body wall is filled with a dense layer of thin scales with finely serrate edges, mostly of rounded or oval outline but not uncommonly irregularly lobate, the largest about 0.3 mm in greatest diameter (Fig. 2b). Above the neck-like constriction the body wall flares outward, forming a projecting shelf beneath the tentacle bases. The backs of the tentacles are filled with longitudinally placed irregular rods with granular sculpture, more or less curved and rather flattened, up to 0.3 mm long (Fig. 2c); those approaching and surrounding the naked space of the tentacle bases are somewhat thinner. The thin coenenchyme is filled with scales similar to those of the polyps but at

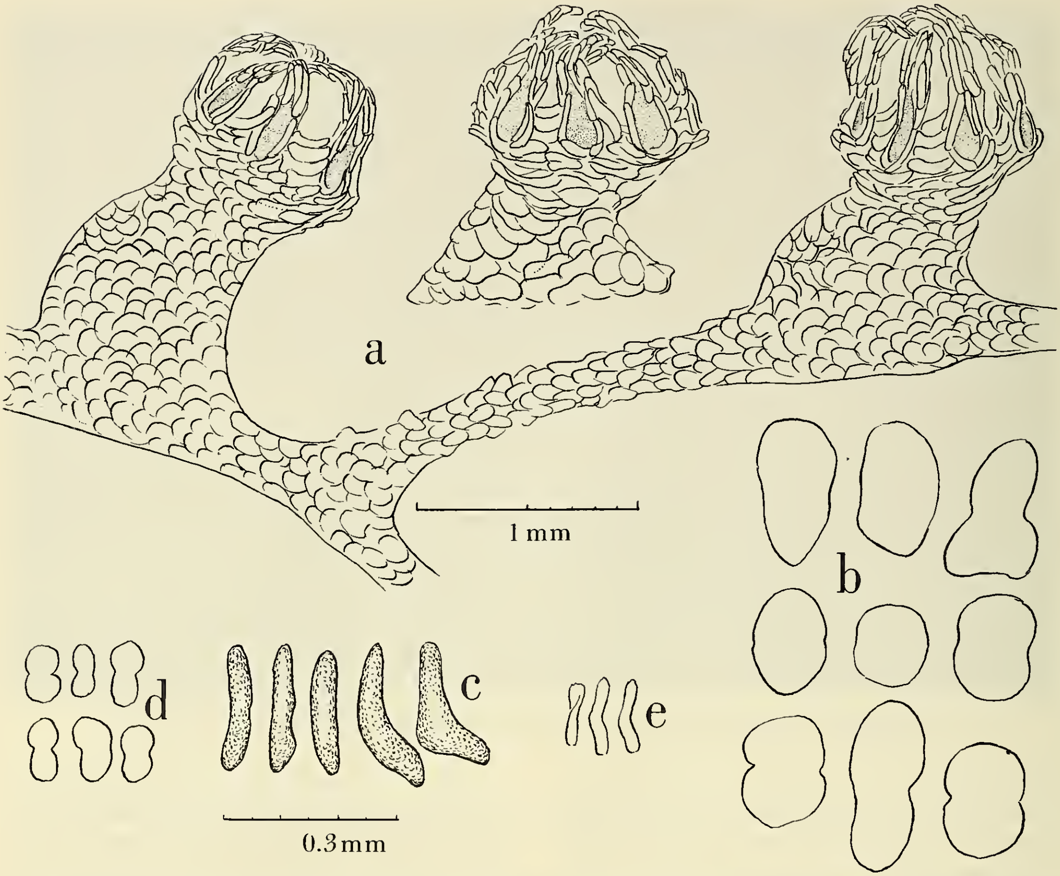

Fig. 2. *Chrysogorgia admete*: a, Polyps; b, Body scales; c, Sclerites from tentacle base; d, Coenenchymal scales; e, Pinnular sclerites. 0.3 mm scale applies to all sclerites.

most only 0.12 mm long; blunt-conical projections resembling nematozooids are widely scattered over its surface but true nematozooids are not present. The conical projections are formed by the protruding edge of some of the larger coenenchymal scales, which are longer than the diameter of the axis but not curved to conform to its shape.

The axis is heavily calcified, brown in the main stem, becoming lighter on the branches until it is pale straw-color in the distal branchlets, with only weak metallic reflections. The holdfast is a white calcareous expansion attached to solid substrate.

Etymology.—Admete, one of the oceanids, descendant of Oceanus.

Discussion.—As this species has only thin scale-like sclerites in the body of the polyps, and rod-like forms longitudinally arranged in the backs of the tentacles, it fits subgroup B_2 of the group "Squamosae aberrantes" proposed by Versluys (1902:61). Several species have similar polyps with the upper part of the body flared to form a ring beneath the bases of the tentacles, and with an oval space without sclerites at the base of each tentacle. These are *C. expansa* Versluys, *octagonos* Versluys, *versluysi* Kinoshita, *stellata* Nutting, and *scintillans* (=*curvata* Nutting not Versluys).

This species differs in its counterclockwise 1/7 branching sequence from all species of *Chrysogorgia* that have been adequately described up to the present time. It differs

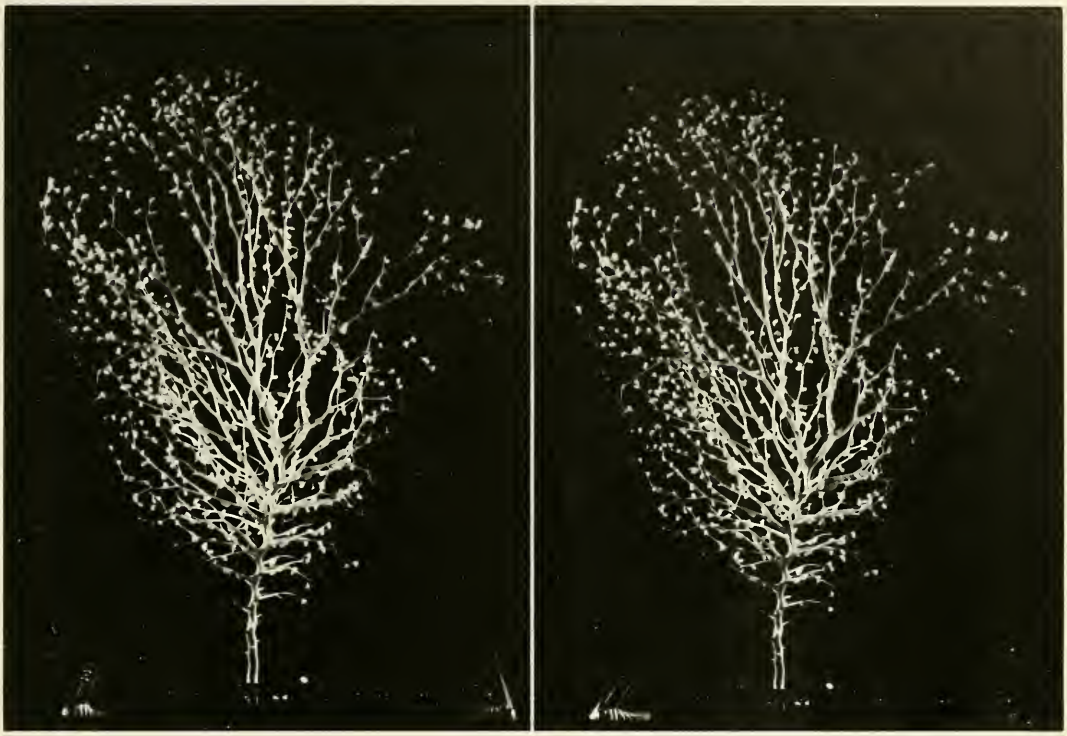

Fig. 3. *Chrysogorgia bracteata,* holotype colony; height 10 cm. Stereoscopic pair.

from species having similar polyps but unknown branching sequence in its much smaller polyps (*admete*: 1.5 mm tall; *versluysi*: 2–4 mm tall; *stellata*: 2–3 mm tall; *scintillans*: 2.75 mm tall). *C. versluysi* differs further in having elongate, narrow rather than broadly oval body scales, and prominent points formed by converging sclerites beneath each tentacle; *C. stellata* has even narrower acute body scales and more prominent points beneath the tentacles; *C. scintillans* has larger, often irregular body scales as much as 0.5 mm in greatest dimension.

Chrysogorgia bracteata, new species
Figs. 3, 4

Material.—Philippine Islands, Verde Island Passage: 13°34′37″N, 121°07′30″E (Malabrigo Light N 81°E, 8 miles), 180 fath., USFC steamer *Albatross,* sta. D-5367, 22 Feb 1909. Four incomplete colonies, in alcohol. Holotype, USNM 80432; paratypes, USNM 49973.

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with counterclockwise spiral branching in 1/6 sequence.

Description.—The colony is 10 cm high, 7.5 cm wide, the main stem broken off just above the holdfast. The stout main stem ascends in a smooth counterclockwise spiral giving off from its outside dichotomously subdivided branches. The branches of the first 3 turns of the main stem are broken off leaving only short stumps, so the first complete branch occurs 14 mm above the holdfast. The branching sequence is 1/6, so the branches are aligned in 6 longitudinal rows. The main stem ascends about 4.5–5 mm with each turn of its spiral, i.e., the distance from one branch to the one aligned vertically above it (the 7th). The branches arise at short intervals, the stem internodes being about 1 mm long. The branches arise at

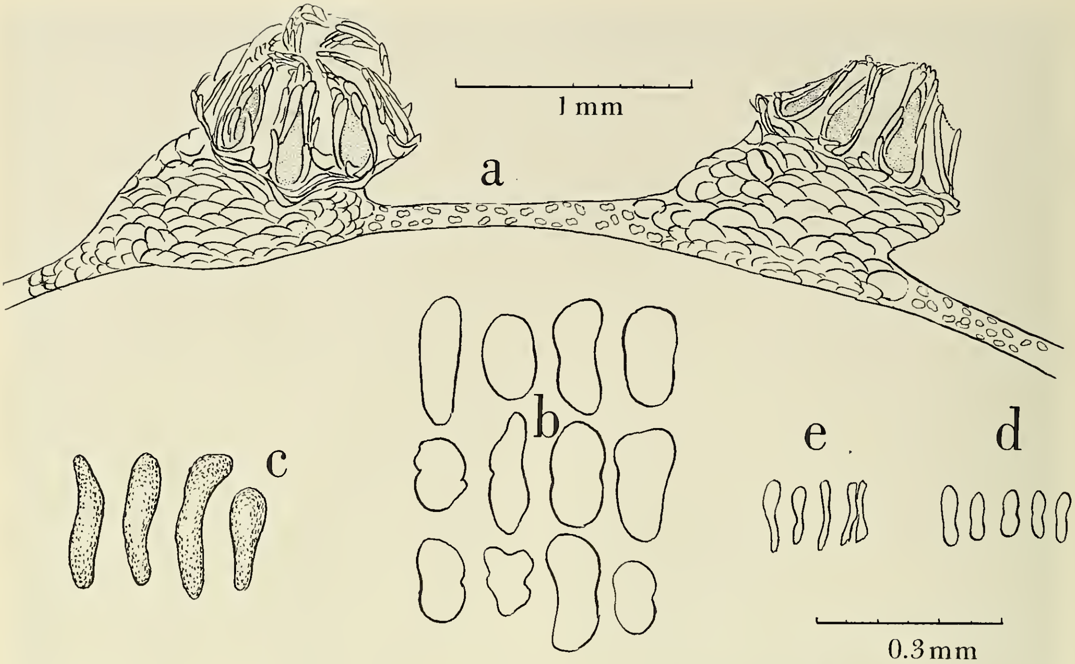

Fig. 4. *Chrysogorgia bracteata*: a, Polyps; b, Body scales; c, Sclerites from tentacle base; d, Coenenchymal scales; e, Pinnular sclerites. 0.3 mm scale applies to all sclerites.

gradually decreasing angles from the base upward, the lowest at about 75° from the vertical, those of the eighth turn at about 65°. The dichotomous bifurcations diverge at an angle of about 50°. The branch internodes are mostly about 5 mm long, the bifurcations usually about equal; the lower branches have 3 bifurcations but the uppermost branches have as many as 9, spreading almost in a single plane. Polyps are situated 1 or 2 per internode, commonly 2, but the terminal twigs may have 3 or 4.

The polyps are at most about 1.2 mm tall, generally only 1 mm or even less, the body up to the tentacle bases 0.5–0.9 mm; they are about 0.7 mm wide basally but only 0.4 mm at the constriction below the tentacles. They are similar in form to those of *C. admete,* the body tapering upward to a constriction just below the tentacles. Above the neck-like constriction the body wall flares outward, forming a projecting shelf beneath the tentacle bases. The body wall is filled with a dense layer of thin scales with the edges extremely finely serrate, most oval in outline with median constriction, occasionally irregularly lobate, the largest about 0.2 mm in greatest dimension. The backs of the tentacles are filled with longitudinally placed irregular rods with granular sculpture, rather flattened and up to 0.24 mm long, those approaching and surrounding the naked space of the tentacle bases somewhat thinner and curved. The pinnules contain narrow, thin scales about 0.1 mm long, slightly bent in the middle and with the twist characteristic of pinnular scales. The thin coenenchyme contains widely scattered slipper-shaped scales up to 0.08 mm in length.

The axis is heavily calcified, brown in the main stem, becoming lighter on the branches until it is pale straw-color in the distal branchlets, with only weak metallic reflections.

Etymology.—Latin *bracteata,* gilt or glittering like gold, in allusion to the metallic luster of the axis.

Comparisons.—*Chrysogorgia bracteata*

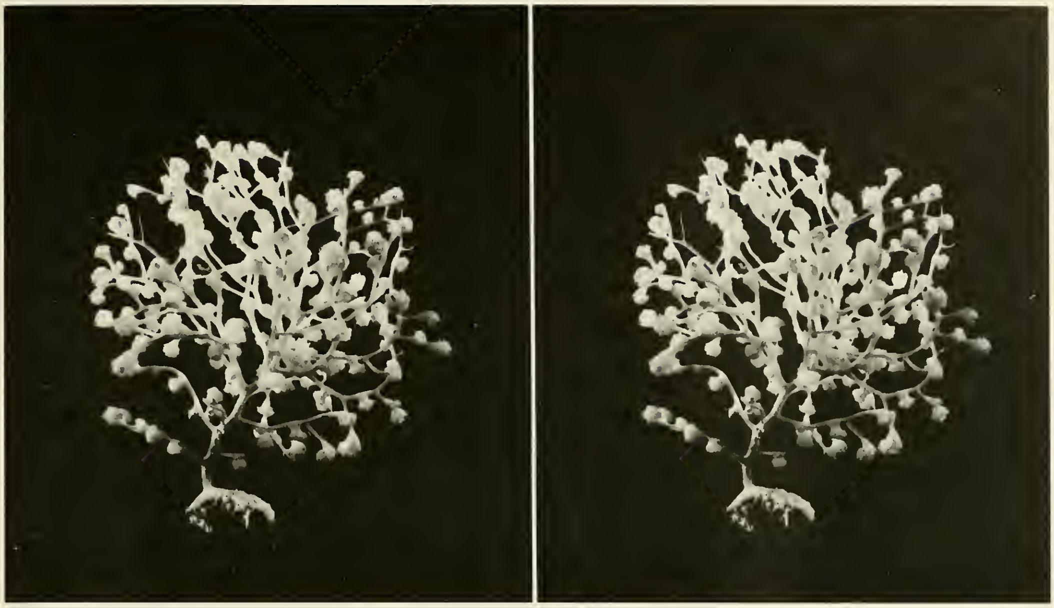

Fig. 5. *Chrysogorgia calypso,* holotype colony; height 3 cm. Stereoscopic pair.

closely resembles *Chrysogorgia admete.* Although it is possible that the two are subspecies, or even merely geographical variants, of a single species, the differences between them warrant recognition at species level until additional material is available to clarify their status. As branching sequence ("Aststand") has traditionally been treated as a character of major importance, the difference between a counterclockwise 1/6 and 1/7 is here considered significant; this coupled with the smaller size of the polyps and the smaller and differently shaped sclerites justifies maintaining the Philippine material as distinct from *C. admete.*

Chrysogorgia calypso, new species
Figs. 5, 6

Material.—Celebes: off Kapoposang Light, 4°43′22″S, 118°53′18″E, 400 fath., USFC steamer *Albatross* sta. 5564, 28 Dec 1909. One colony with holdfast, USNM 50019 (holotype).

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with counterclockwise spiral branching in 1/4 sequence; polyps 1.5 mm tall, tentacle bases with bent, granulate rods.

Description.—The holotype is a colony 3 cm tall, complete with holdfast attached to a small pebble. The main stem is distinctly developed and gives off dichotomously subdivided lateral branches in a counterclockwise 1/4 spiral at intervals of about 1 mm. The internodes of the branches mostly are about 2 mm long save the terminal ones, which are as long as 7 mm; all the internodes have a single polyp except the distalmost, which may have 2 or even 3. No nematozooids could be found on stem or branches. The axis is calcified, smooth, basally bronze colored gradually paling distad to light golden yellow with metallic iridescence.

The polyps are up to 1.5 mm tall, the terminal ones usually the largest, distally expanded around the tentacles, below each of which a prominent point is formed by converging body scales. Above the projecting points an oval area at the base of each tentacle is without sclerites; coarsely granulated rods up to 0.4 mm long, more or less curved and sharper at one end than the oth-

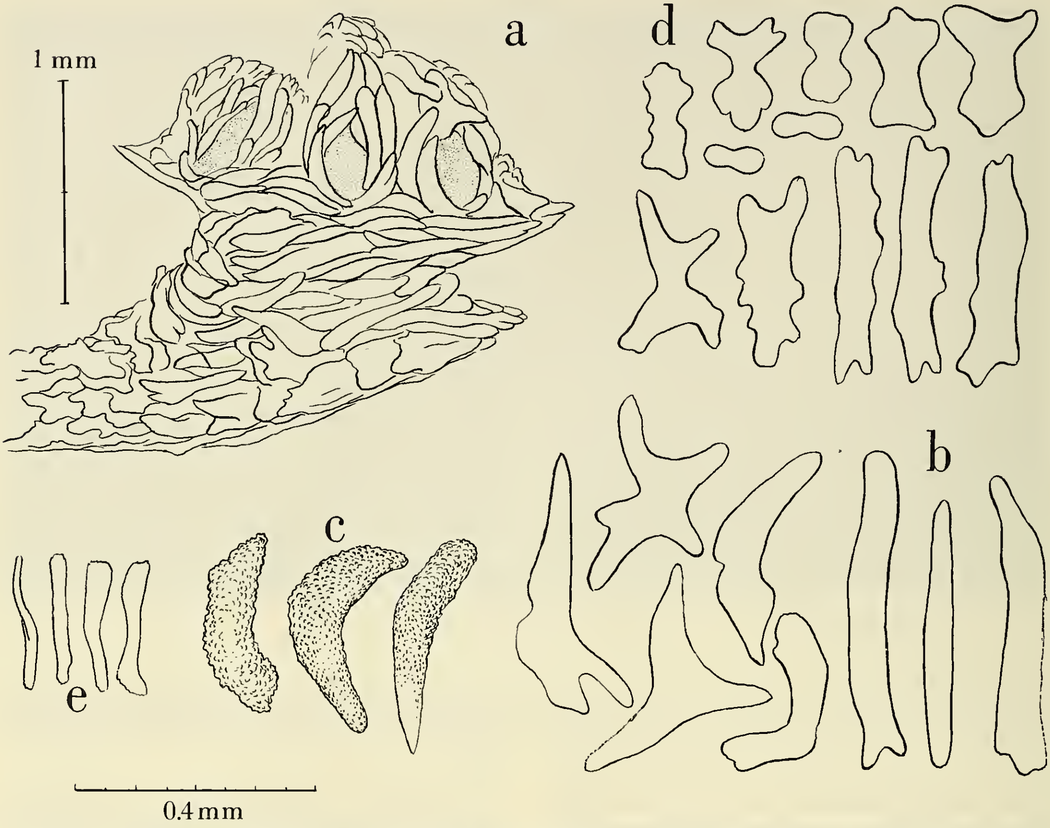

Fig. 6. *Chrysogorgia calypso*: a, Polyp; b, Body scales; c, Sclerites from tentacle base; d, Coenenchymal scales; e, Pinnular sclerites. 0.4 mm scale applies to all sclerites.

er border the naked space and extend longitudinally along the backs of the tentacles. The pinnules are supported by narrow, concave scales reaching 0.23 mm in length. Below the 8 projections the body sclerites are transversely arranged, narrow, elongate scales up to 0.5 mm in length. Proximad, the body scales become irregularly lobed and merge with the coenenchymal scales, many of which are long, narrow, and marginally somewhat lobed, reaching a length of 0.45 mm, interspersed with numerous smaller, lobed scales with a constricted waist.

Etymology.—Greek Καλυψώ, daughter of Oceanus and Tethys.

Comparisons.—Among Squamosae aberrantes, two other species have counterclockwise branching in 1/4 sequence: *C. expansa* (Wright & Studer) and *C. octagonos* Versluys. *C. calypso* differs from *C. expansa* (1) by lacking nematozooids, (2) by having bent, granulate rods in the tentacle bases instead of elongate flattened forms, and (3) by having narrow flat scales and irregularly lobed forms in the coenenchyme instead of oval and slipper-shaped scales. The polyps of *C. calypso* are much smaller (1.5 mm) than those of *C. octagonos* (2.5 mm), the sclerites of the tentacle bases are typical spindles and rods rather than coarse, irregular forms, and its coenenchymal sclerites are narrow, flat scales up to 0.45 mm long mixed with smaller lobed scales, rather than slipper-shaped scales up to 0.25 mm long.

Among the species with biplanar colonies, *C. calypso* is closer to *C. chryseis* than to any other, but its polyps have a conspicuous naked area at the base of each tentacle,

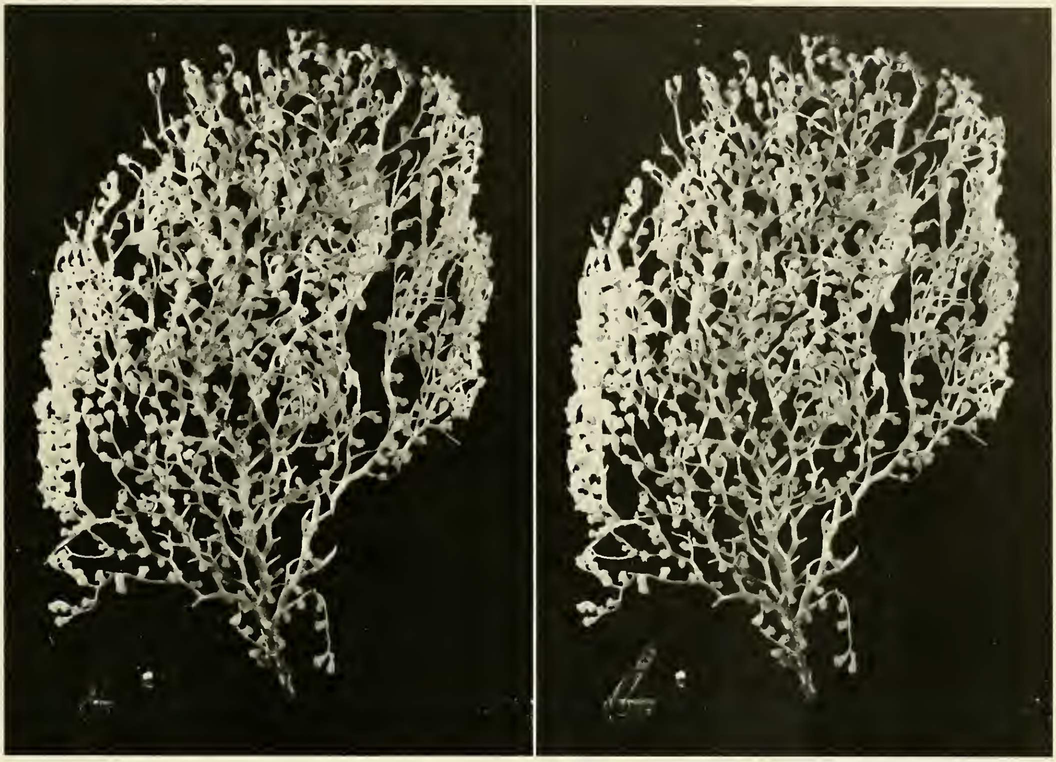

Fig. 7. *Chrysogorgia chryseis,* holotype colony; height 10 cm. Stereoscopic pair.

its body scales are much smaller, and the sclerites of the tentacle bases are more regular spindles and rods.

Remarks.—Even though the spiral deployment of the lateral branches in a counterclockwise 1/4 sequence around the main axis is distinct, the small size of this specimen leaves a question whether with maturity the main axis would persist, as is the case in *C. octagonos,* or would yield to planar development of two of the lateral branches, resulting in a biplanar or multiplanar colony. Nevertheless, it differs sufficiently from all species now on record to be considered distinct.

Chrysogorgia chryseis, new species
Figs. 7, 8

Material.—Ceram Sea: 1°53′30″S, 127°39′00″E (Gomomo Island (E.) N 14°W, 2.5 miles), 400 fath., USFC steamer *Albatross* sta. D-5635, 3 Dec 1909. One colony lacking holdfast. Holotype, USNM 49967.

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with planar branching producing a biflabellate colony; polyps with distinct projecting points beneath each tentacle, bases of tentacles with small naked area followed by coarse blunt rods to 0.3 mm in length; body scales narrow, terete, with weak marginal lobes or none; no nemtozooids.

Description.—The holotype is a colony 10 cm tall, in the form of 2 parallel uniplanar fans arising from a short trunk broken off from its holdfast. The branching is regularly dichotomous, with internodes mostly about 5 mm long, even the terminal ones. Anastomoses occur irregularly where the course of neighboring branches coincided during the course of growth. Nematozooids are not discernible even on the stem and large branches, and are therefore presumed to be

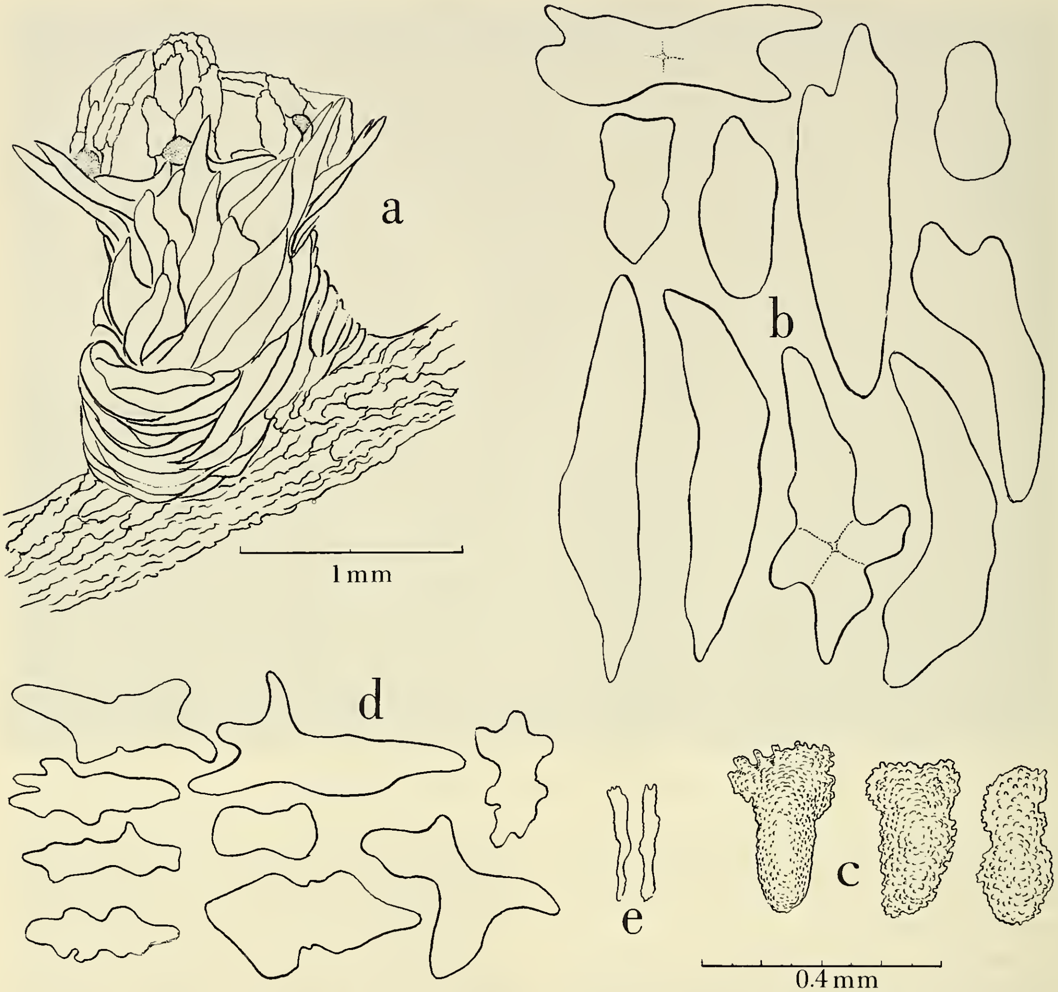

Fig. 8. *Chrysogorgia chryseis*: a, Polyp; b, Body scales; c, Sclerites from tentacle base; d, Coenenchymal scales; e, Pinnular sclerites. 0.4 mm scale applies to all sclerites.

absent. The axis is strongly calcified and smooth; the short main trunk is bronze in color, fading distad to pale gold with bright metallic luster. Usually each internode bears a single polyp except the terminal ones, which commonly have 2.

The polyps are directed generally upward and outward, so they appear uniserial on any given length of axis. They are up to 2 mm tall, with 8 projecting points below the base of the tentacles. The body of the polyps is covered by a layer of overlapping, obliquely or transversely placed, elongate, narrow scales that reach a length of about 0.7 mm, tapered to a blunt point at each end and with at most only weak marginal lobes. Numerous smaller, oval scales with a median waist lie mostly beneath the large scales, forming with them a multiple layer of sclerites. The distalmost large body scales converge to form the 8 projecting points beneath the tentacles. The tentacles have an inconspicuous naked area at the base, above which they are armed with thick, blunt, coarsely granulate rods up to 0.3 mm long, many of which are broader and more or less lobed at one end. Thin, narrow scales about 0.2 mm long extend into the pinnules, usually in pairs.

The coenenchyme contains many elongate, marginally lobed scales of diverse shape, up to about 0.5 mm in length.

Etymology.—Chryseis, one of the oceanids, descendant of Oceanus.

Discussion.—The growth form of *C. chryseis* corresponds closely with that of *C. stellata* Nutting, and probably also with those of *C. scintillans* and *electra.* Its polyps are smaller than those of *stellata* and the proximal sclerites of its tentacles are quite different; its body scales and proximal sclerites of its tentacles are different from those of *scintillans*; and its polyps have much stronger points below the tentacles than do those of *electra.*

Chrysogorgia electra, new species
Figs. 9, 10

Material.—Paumotu Islands: NW face Hao Atoll, E 2 miles, 812 fathoms; bottom temperature 37.6°F; USFC steamer *Albatross* sta. 3690, 29 Oct 1899. One incomplete colony in alcohol, USNM 49632 (holotype).

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with planar branching; polyps with weak projections beneath the tentacles, bases of tentacles with naked area followed by flat scales pointed at one end and broadly lobed at the other; some body scales narrow and terete, others wide, blunt and lobate.

Description.—Branching of the complete colony unknown. The specimen consists of one major branch that bifurcates twice in planes approximately at right angles and thereafter in one plane. This results in 2 approximately parallel planar branches dichotomously subidivided at angles of roughly 60°–65°, with always the same half of each bifurcation dominating so that each branch has a regularly curved principal axis from the convex side of which the subordinate dichotomous branchings originate; branchlets whose courses intersect may anastomose. The complete colony therefore probably had a form similar to that of *C. stellata.* The internodes are commonly 8–10 mm long, but a few are as short as 6 mm and as long as 12 mm. Each internode has a single polyp except for the terminal ones, some of which have 2; in a few cases the polyp occurs so near the distal end of the internode that it approaches the point of bifurcation and may even be directly on the node.

The polyps are generally 1.75–2.0 mm tall and 1 mm in diameter at the narrowest point below the flared distal part of the body. The body of the polyps has a dense covering of obliquely or transversely placed, elongate smooth scales with finely serrate edges, many of them irregularly lobed, reaching a length of about 0.6 mm. Beneath each tentacle the uppermost body scales form an inconspicuous shelf-like projection, above which the tentacle bases are devoid of sclerites in a rather narrow oval tract. Proximally the backs of the tentacles contain flat scales pointed at one end and broad at the other, the wide end with several marginal lobes; distally the scales are shorter and squarish or polygonal. The pinnules contain slightly bent, narrow gutter-like scales often slightly expanded at the ends.

The coenenchyme contains elongate scales, many of them irregularly lobed, slightly exceeding 0.6 mm in length. Nematozooids are not present.

Etymology.—Elektra, one of the oceanids, descendant of Oceanus.

Discussion.—In growth form, this species resembles most closely *Chrysogorgia scintillans, C. stellata* Nutting, and *C. chryseis.* From the first of these it differs in the shape of the sclerites of the tentacle backs as well as those of the polyp body and coenenchyme. From *stellata* and *chryseis* it differs not only in the shape of the sclerites of the polyps but also in the minimal development of the subtentacular projections formed by

Fig. 9. *Chrysogorgia electra,* holotype branch; height 9 cm. Stereoscopic pair.

the body scales; from *chryseis* it differs further in the form of sclerites of the tentacle backs and the much larger sclerite free area at the base of each tentacle.

Like *C. scintillans* and *C. stellata,* 49632 is infested with parasitic copepods that form conspicuous blister-like tunnels along the coenenchyme of the larger branches.

Chrysogorgia scintillans,
new species
Figs. 11, 12

Chrysogorgia curvata.—Nutting, 1908:591, pl. 45, fig. 9.

Not *Chrysogorgia curvata* Versluys, 1902: 67, figs. 104–108.

Material.—Hawaiian Islands, between Kauai and Moku Manu (Bird Island): center of Moku Manu S 12°W, 9.7 miles, 962–1059 fath., bottom temp. 37°F; U.S.F.C. steamer *Albatross* sta. 4153, 5 Aug 1902. One specimen in alcohol, USNM 25371.

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with planar branching; polyps up to 2.75 mm tall, body scales broadly lobed, thin, up to 0.6 mm long; proximal sclerites of tentacles flat, often wider and lobed at one end.

Description.—Branching pattern of the complete colony unknown; as the specimen consists of a major branch with a principal bifurcation each half of which dichotomously subdivides in an unequal manner producing 2 large, curved secondary branches that give rise to subordinate branchlets from their convex sides, forming 2 roughly parallel, almost uniplanar components, the intact colony was probably similar to that of *C. stellata.* It is probable

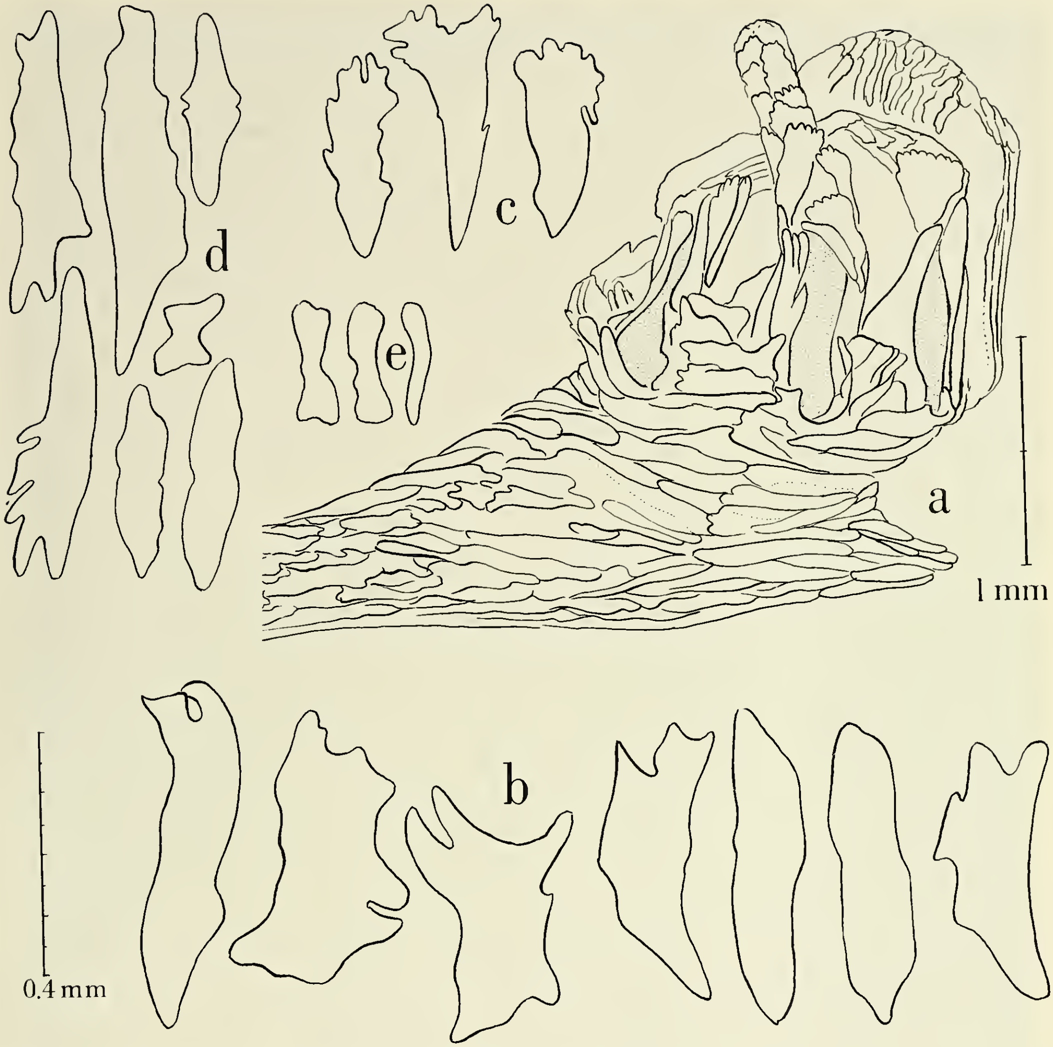

Fig. 10. *Chrysogorgia electra*: a, Polyp; b, Body scales; c, Sclerites from tentacle base; d, Coenenchymal scales; e, Pinnular sclerites. 0.4 mm scale applies to all sclerites.

that the spiral of the main axis is irregular, and the lateral branches are bifurcated practically in one plane. Lateral branches stout, the internodes about 7 mm long, each with one polyp except the last, which sometimes has 2.

The polyps are about 2.75 mm tall by 1.5 mm wide, distally flared, and have 8 blunt points below the tentacles. The body wall is filled with thin scales of various shapes: double discs, slipper shapes, elongate and irregular forms up to 0.6 mm long, mostly arranged with their long axes transverse; the tentacle bases have elongate, twisted, flat sclerites, often lobed, arranged around an oval naked tract above each sub-tentacular point; tentacle backs with flat, bilobed or multilobed scales decreasing in size distally.

The coenenchyme is thin and has no nematozooids; it is filled with scales of predominantly slipper-shape smaller than those of the body, commonly 0.3–0.4 mm.

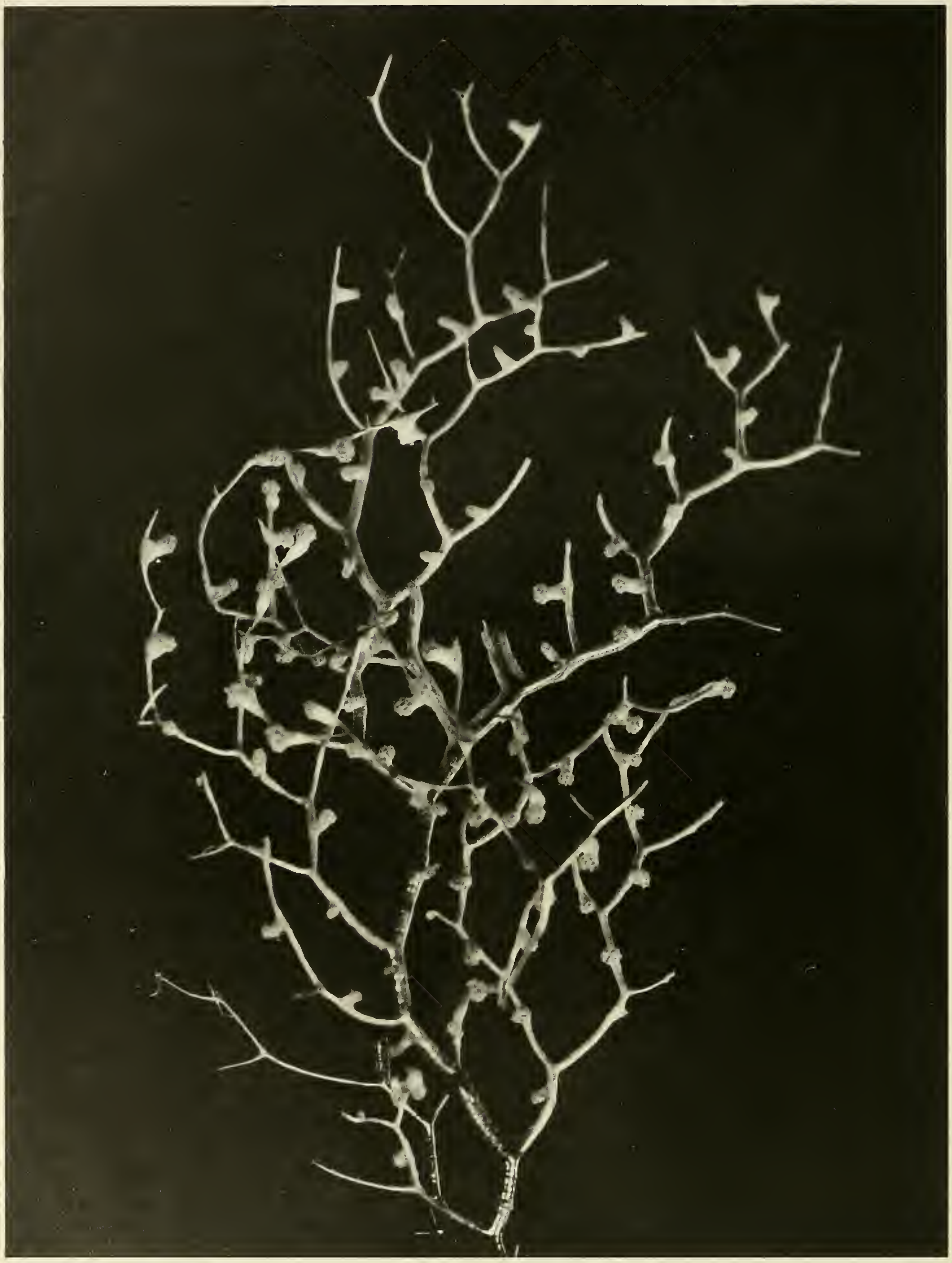

Fig. 11. *Chrysogorgia scintillans,* holotype branch; height 10 cm.

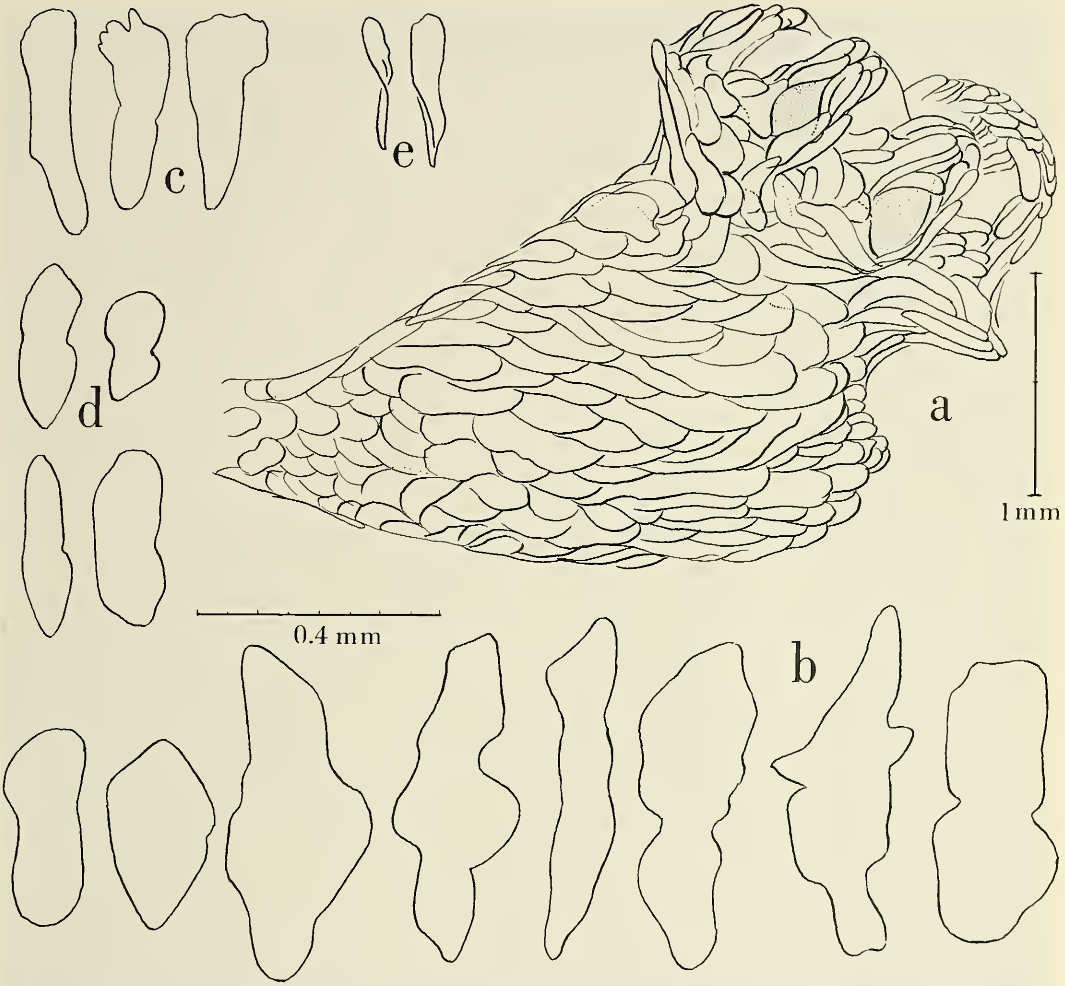

Fig. 12. *Chrysogorgia scintillans*: a, Polyp; b, Body scales; c, Sclerites from tentacle base; d, Coenenchymal scales; e, Pinnular sclerites. 0.4 mm scale applies to all sclerites.

Etymology.—From Latin *scintillo,* to sparkle or gleam, in allusion to the brillant golden reflections of the axis.

Discussion.—The polyps of *Chrysogorgia scintillans* are similar to those of some other "Squamosae aberrantes" in having the body scales converging as a projecting process beneath each tentacle. Together with *C. stellata,* it forms a group distinct in manner of branching from *C. expansa, octagonos,* and *versluysi.* From *C. stellata* it is at once distinguishable by its thin, broadly lobed body scales, shorter and blunter sub-tentacular processes, and flat, smooth sclerites of the tentacle bases.

Although originally identified by Nutting (1908:591) as *Chrysogorgia curvata* Versluys, this species has rather thin, smooth scales in the tentacle bases rather than the "dickere Scleriten, welche an den Enden zahnartige Höcker tragen" reported by Versluys (1902:68, fig. 108a) for *curvata,* as well as regular slipper-shaped scales in the coenenchyme rather than the irregularly lobed

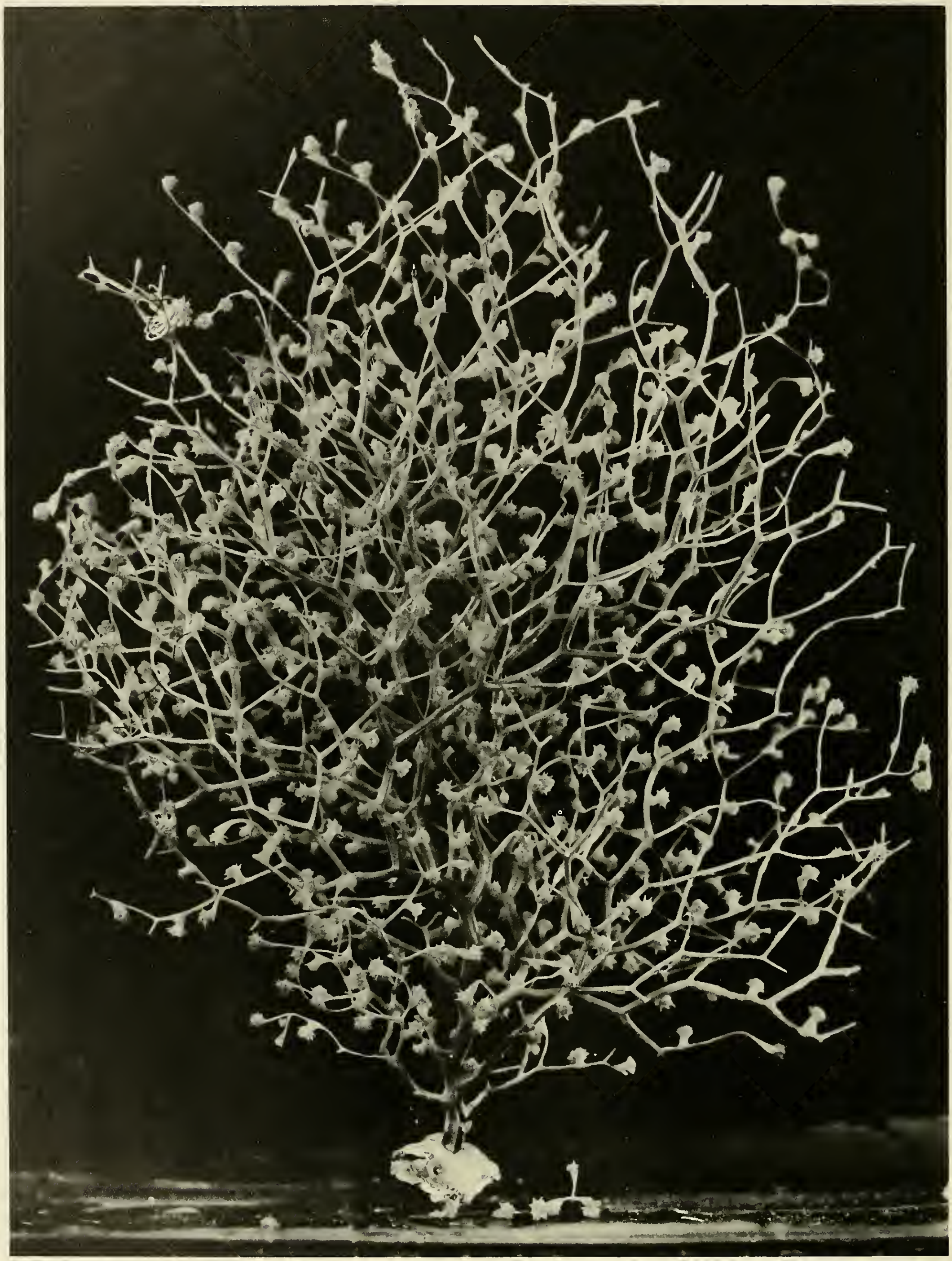

Fig. 13. *Chrysogorgia stellata,* holotype colony; height 13.5 cm.

Fig. 14. *Chrysogorgia stellata,* polyps.

forms illustrated by Versluys (1902:67, fig. 105). In view of these differences it is preferable to treat the present material from Hawaii as a separate species.

This specimen is parasitized by copepods of the family Lamippidae. The coenenchyme of almost all the large branches is raised, blister-like, along one side, forming

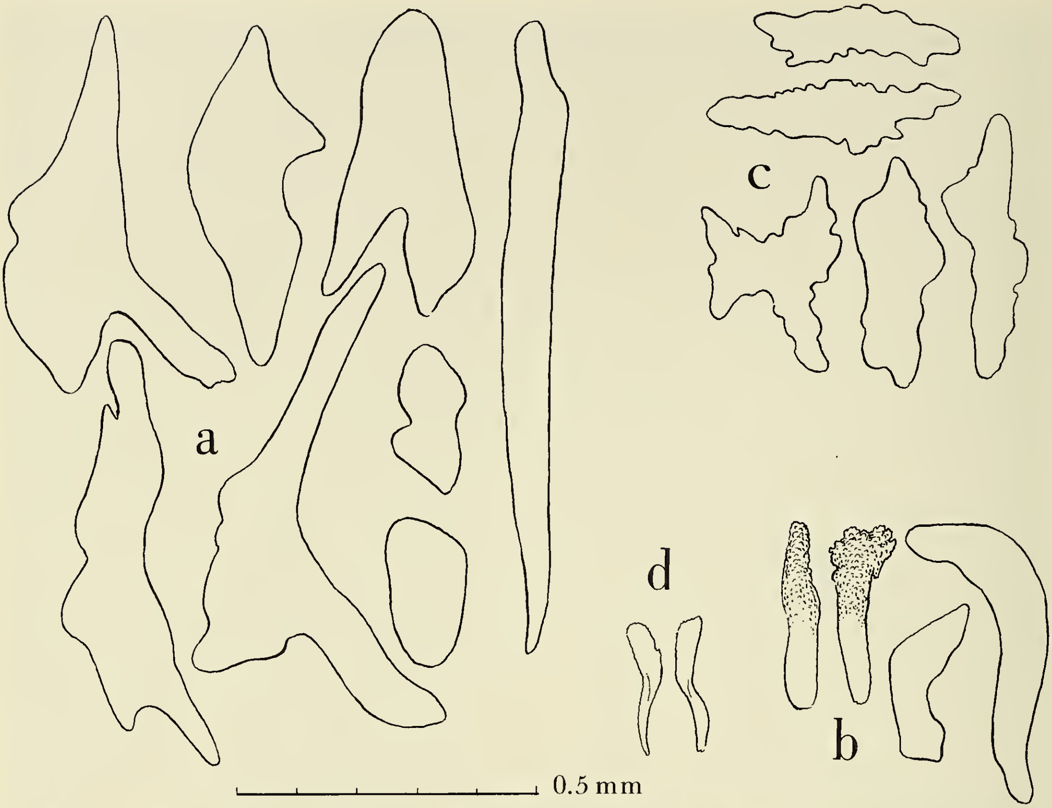

Fig. 15. *Chrysogorgia stellata*: a, Body scales; b, Sclerites from tentacle base; c, Coenenchymal scales; d, Pinnular sclerites.

long tunnels in which the copepods live. The sclerites over these tunnels are arranged crosswise, whereas elsewhere they are more or less clearly longitudinal. The type specimen of *C. stellata* is similarly parasitized.

Chrysogorgia stellata Nutting, 1908
Figs. 13–15

Chrysogorgia stellata Nutting, 1908:592, pl. 46, fig. 3; pl. 50, fig. 3.—Kükenthal, 1919: 538; 1924:408.

Material.—Hawaiian Islands, south coast of Molokai: Lae-o Ka Lau Light, N 46°, W, 9.2 miles; 371 fathoms; USFC steamer *Albatross* sta. 3826, 1 Apr 1902. Holotype, USNM 25380.

Diagnosis.—*Chrysogorgia* (group Squamosae aberrantes) with multiplanar flabellate colonies; polyps 2 mm or more in height; smooth, terete body scales exceeding 1 mm in length; proximal sclerites of tentacles in the form of coarsely granular blunt rods up to 0.5 mm long, more or less curved and sometimes with one end lobed; coenenchymal scales elongate oval with median waist and more or less lobed margins.

Description.—The holotype colony is 13.5 cm tall, upright and rather compressed, arising from a disk-like calcareous holdfast. The main stem irregularly gives off several small branches before undergoing a major division 16 mm from the base, where the stem divides into 2 large branches, each of which produces branchlets only from the upper side. These branchlets subdivide dichotomously almost in one plane, so that the entire colony is composed of several parallel

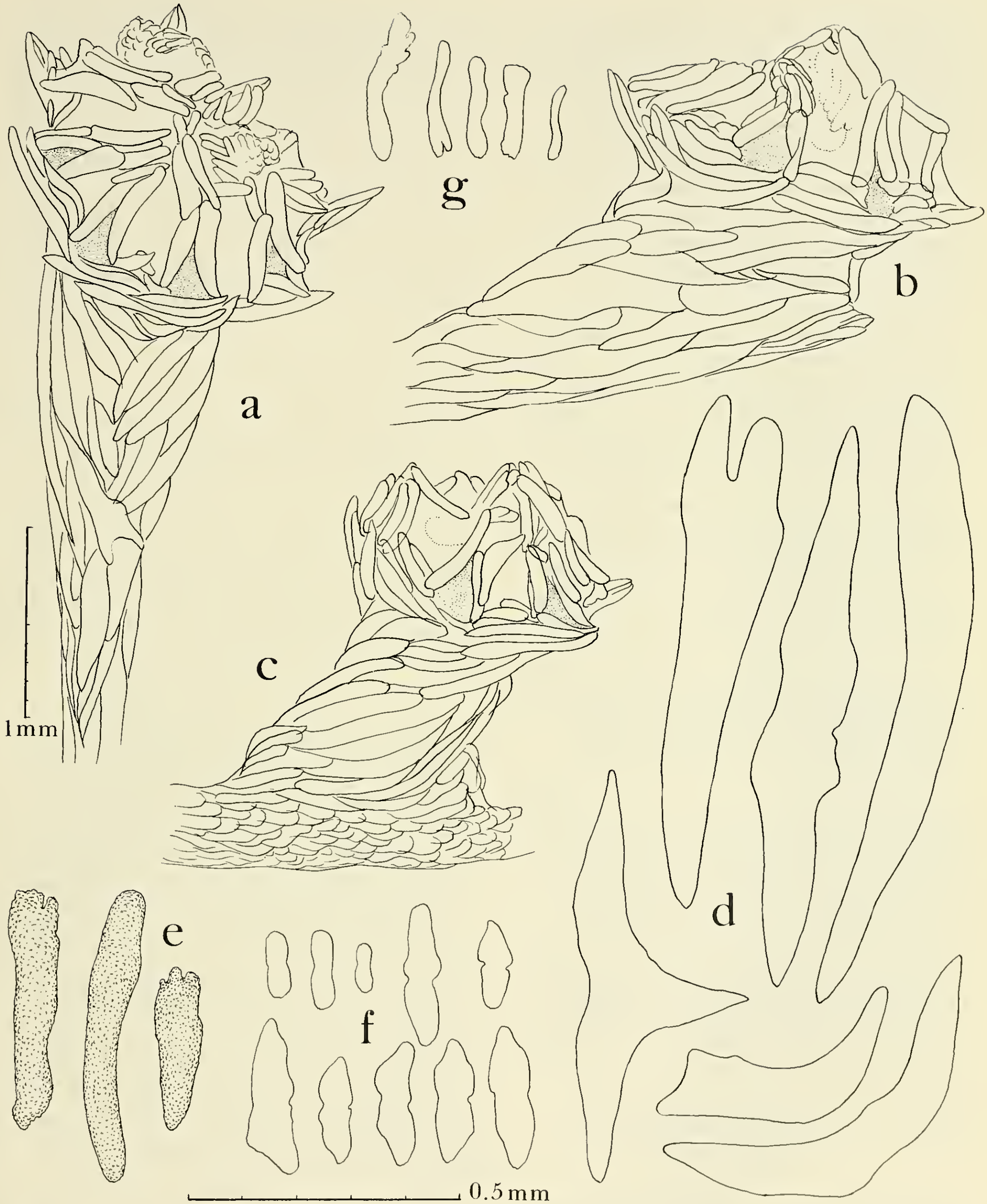

Fig. 16. *Chrysogorgia* sp. cf. *stellata*: a–c, Polyps; d, Body scales; e, Sclerites from tentacle base; f, Coenenchymal scales; g, Pinnular sclerites. 0.4 mm scale applies to all sclerites.

flabellate parts. The internodes of the stem and largest branches are unequal in length but those of the smaller branches are mostly about 8–10 mm long. Nematozooids are conspicuous on the stem and large branches but become less noticeable on the smaller branches and twigs, where they are easily overlooked. The axis is light pinkish brown with brilliant golden sheen, covered by translucent white coenenchyme.

The polyps are 2–3 mm high, sometimes perpendicular to the axis but generally inclined at a moderate angle toward the branch tips. Each internode bears a single polyp except the terminal ones, which may have 2 or 3. The polyps are covered with almost smooth, flat, lobed plates up to about 0.8 mm long arranged transversely in the basal part of the body; in the upper part, long, thick, narrow scales up to 1.1 mm long are arranged in 8 multiple rows, the uppermost of which converge beneath the tentacles to form 8 prominent points. Between the tentacle bases the distal body scales are transversely placed, the uppermost extending up into the naked intertentacular space. The tentacles have an oval area without sclerites immediately above each of the marginal points; above this naked area the backs of the tentacles contain longitudinally arranged thick, irregular rods followed distally by irregular flat scales transversely arranged. Each pinnule contains a pair of elongated, trough-like scales. The coenenchyme contains numerous elongate, smooth scales with lobed margins, up to 0.45 mm in greatest dimension.

Chrysogorgia sp. cf. *stellata* Nutting
Fig. 16

Material.—Molucca Passage, Tifore Island (C.) N 40°W, 35 miles: 0°32′30″N, 126°31′30″E, 1021 fathoms; USFC steamer *Albatross* sta. D-5615, 22 Nov 1909.

Several detached branches obtained by the *Albatross* in the Molucca Passage have much the same aspect as the branches of the type specimen of *C. stellata* and, as measurements agree in general with those of that species, we at first were inclined to consider them conspecific. However, direct visual comparison demonstrated so many inconsistencies that we cannot maintain that position. Although the polyps (1) are similar to those of *stellata* in size and form, with prominent points beneath the tentacles, they are slightly smaller and the points are not so long and sharp (Fig. 16a–c); (2) the body sclerites are of nearly the same size (up to 1.2 mm), but are of more regular terete outline (Fig. 16d); (3) the proximal sclerites of the tentacles are coarsely granular rods sometimes with lobes at one end, but are larger (Fig. 16e); and (4) the coenenchymal scales are smaller, more regular slipper shapes with little or no marginal lobing (Fig. 16f). No nematozooids were found, but this could be attributed to the small size of the branches, since those structures are obscure also on the smaller branches of *stellata*.

The occurrence in the Moluccas of a species previously known only from Hawaii would not be surprising, as species of *Callogorgia* and *Fanellia* have been shown to have a similar distribution (Bayer, 1982). The differences between the two specimens could be attributed to either individual or geographical variation but, as nothing is known of the variation in *C. stellata*, and the growth form of the Moluccan material is unknown, we cannot consider them conspecific. Therefore, we report the occurrence of this form in the Moluccas without assigning it to any known species in order to bring it to the attention of investigators who in the future may obtain better specimens.

Acknowledgments

We are grateful to Dr. Bertrand Richer de Forges and Mr. Georges Bargibant for the opportunity to study the important collection of gorgonians assembled by the expeditions conducted in New Caledonian waters by ORSTOM, which obtained one of the new species described herein. The other specimens included in this paper were taken by the U.S. Fish Commission steamer *Albatross*. This manuscript has benefitted from the helpful suggestions of Dr. Manfred Grasshoff of the Forschungsinstitut Senckenberg, Frankfurt, and Dr. Thomas E. Bowman, Department of Invertebrate Zoology, Smithsonian Institution.

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THE SYSTEMATICS OF THE SOUTHERN HEMISPHERE CHITON GENERA *RADSIA* GRAY, 1847, AND *SYPHAROCHITON* THIELE, 1893 (MOLLUSCA: POLYPLACOPHORA: CHITONIDAE)

Robert C. Bullock

Abstract.—The name *Radsia* Gray, 1847, which has generally been considered to be a junior synonym of *Chiton* Linnaeus, 1758, should be used as a genus-group *nomen* for its originally designated type species, *Chiton barnesii* Gray, 1828, and the South African *Chiton nigrovirescens* Blainville, 1825. Although *Radsia* was at first characterized by its multiple-slit insertion plate, which is not always a reliable taxonomic character, it appears useful to employ the name *Radsia* for these two species that exhibit ancestral shell, radular, and reproductive features reminiscent of certain members of the Ischnochitonidae. *Sypharochiton* is used for a single species, *S. pelliserpentis* (Quoy & Gaimard, 1835), from southeastern Australia and New Zealand. *Sypharochiton pelliserpentis* exhibits great variation not only in shell and girdle scale morphology, but in the conspicuously polymorphic denticle cap of the major lateral tooth of the radula.

During a study of the polyplacophoran subfamily Chitoninae, it became evident that some members of this group exhibit shell and radular features that suggest ischnochitonid affinities. Conspicuous among this group are species that have at times been placed in the genus *Sypharochiton* Thiele, 1893, and those that have proved to belong to the genus *Radsia* Gray, 1847. The present report utilizes scanning electron microscopy of the girdle scales and dorsal shell surface that has provided information about the usefulness of these phylogenetic characters and the taxonomic status of the species involved.

Methods and Materials

Specimens of *Radsia* and *Sypharochiton* housed in most major museums of the U.S. East Coast and Europe were examined. Selected specimens were used for light and scanning electron microscopic (hereafter SEM) studies of shell surfaces, girdle scales, and radulae. Specimens were prepared for the SEM following the procedures presented by Bullock (1985). The valves were cleaned thoroughly in a heated 2 N solution of KOH, washed several times in distilled water, mounted on aluminum specimen stubs, coated with carbon and gold/palladium in a Denton DV-502 vacuum evaporator, and examined using an ISI MSM-3 SEM located in the Department of Zoology at the University of Rhode Island. Radulae used for light microscopic studies were cleaned, mounted on microslides in Canada balsam, and observed using compound and dissecting microscopes.

Abbreviations

ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History), London
DMNH	Delaware Museum of Natural History, Greenville

IRSN	Institut royal des Sciences naturelles de Belgique, Brussels
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHNP	Muséum national d'Histoire Naturelle, Paris
NMB	Naturhistorisches Museum, Bern
NRS	Naturhistoriska Riksmuseet, Stockholm
RCB	Collection of R. C. Bullock
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
USNM	National Museum of Natural History, Washington, D.C.
ZMA	Zoölogisch Museum, Amsterdam
ZMHU	Zoologischen Museum, Humboldt-Universität, Berlin
ZMK	Universitetets Zoologiske Museum, Copenhagen

Genus *Radsia* Gray, 1847

Radsia Gray, 1847b:126. Type species by monotypy: *Chiton barnesii* Gray, 1828.
Radsiella Thiele, 1893:368 [in part].

Description.—Animal reaching 35 mm in length. Lateral triangle with radial sculpture, directed forward. Central areas with numerous longitudinal, beaded, rarely smooth, ribs. Insertion teeth deeply grooved to highly pectinate. Jugal sinus wide. Primary slit-ray consisting of a band of numerous pores; additional pores scattered in posterior depression. Denticle cap of radula elongate, with evidence of 2 cusps, one much more prominent than other; small crystal-like nodules in medial area of larger cusp; central tooth rather broad. Scales dull in appearance, often tan, somewhat squarish, with numerous, fine, irregular striations. Young brooded in branchial groove of female.

Remarks.—The genus *Radsia* and its relationship to other groups of the Chitoninae which exhibit ancestral characteristics present some of the most interesting and perplexing systematic problems among the Chitonidae. Gray (1847b) first separated *Chiton barnesii* Gray, 1828, from *Chiton* when he introduced the genus *Radsia,* which he characterized by its possession of two slits on each insertion plate, although he had previously described another species, *Chiton capensis* Gray, 1828 [=*Chiton nigrovirescens* Blainville, 1825], which is herein placed in *Radsia.* Earlier in 1847, Gray (1847a) presented a classification of the chitons which provoked the notable conchologist Reeve (1847: pl. 28), but Gray's studies contributed to a much better classification with more natural groupings. But concerning the genus *Radsia,* Gray proposed a useful name for the wrong reason, i.e., two slits on each side of the insertion plate of each intermediate valve. Even Gray (1847b:127) noted that in *Chiton bowenii,* which he evidently considered to be *Chiton* s.s., he found one valve with two slits on one side and "the normal single one of the genus on the other." Unfortunately, the multiple slitting of the insertion plate was considered by conchologists to be the primary characteristic of *Radsia,* and a number of Panamic *Chiton* were placed in *Radsia* by various authors. The natural affinities of *Chiton barnesii* were overlooked because all Panamic species of *Chiton* until now have been placed in *Chiton* s.s.

The recognition of *Radsia* as a natural grouping aids greatly in an evolutionary treatment of the Chitoninae because one can begin to understand the derivation of some shell and radular characteristics intermediate between some *Ischnochiton* groups (family Ischnochitonidae) and species traditionally placed within the Chitonidae. For example, the shovel-like denticle cap of typical chitonid species has an accessory cusp in *Radsia,* an obvious reduction of the second cusp of a bi-cusped, ischnochitonid ancestor. It should be noted that if one were to classify the Polyplacophora solely on the basis of the radula, *Radsia* would be placed in the Ischnochitonidae. In fact, Thiele (1893, 1909), who emphasized the radula as a phylogenetic tool, placed *R. nigrovirescens* in the genus *Ischnochiton.*

An *Ischnochiton* origin of *Radsia* is evidenced not only by radular characters, but by certain morphological features of the shell. A comparison between *Radsia barnesii* (Gray), the type species of *Radsia,* and *Ischnochiton australis* (Sowerby), the type species of the ischnochitonid subgenus *Ischnoradsia,* illustrates this point. Both species have similar tegmental sculpture, especially since the several "species" of *Ischnoradsia,* which vary greatly in this regard, may in fact be a single species (Leloup 1959). Both *R. barnesii* and *Ischnoradsia* have intermediate valves with a rather thin, multiple-slit insertion plate, and both exhibit a field of pores in the posterior depression on the ventral surface. *Ischnoradsia,* however, has a typical ischnochitonid radula, while that of *R. barnesii,* though not typically chitonid, is similar in some respects to other species of Chitoninae.

An examination of external esthete morphology also confirms the belief that *Radsia* forms a very distinct genus within the Chitoninae. In both *R. barnesii* and *R. nigrovirescens* one finds megalopore-micropore structure unlike other Chitoninae, especially with regard to the collar-like fold surrounding the pores (Figs. 9–12).

In summary, the exact systematic position of *Radsia* is unclear and needs more attention. The species included here have pectinate insertion teeth and a nearly chitonid-like radula, or a radula with a reduced secondary cusp. Excluded species include those with a "definite" *Ischnochiton* radula and/or species with a "definite" *Ischnochiton* insertion plate. There are obvious flaws to such a treatment, but so little material of the questionable species was available for study that such an arrangement was necessary. In any case, the *Radsia* problem poses important questions concerning the validity of nearly all of the phylogenetic characters presently used by polyplacophoran systematists.

Radsia barnesii (Gray, 1828)

Figs. 2, 4, 6, 7, 11–13, 15, 31, 32

Chiton barnesii Gray, 1828:5 (Coquimbo; type BMNH 1951-1-23.1).—Reeve, 1847: pl. 1, sp. 1.—Pearse, 1979:75, 77 [reproduction].

Radsia barnesii (Gray).—Gray, 1847b:126; 1847c:168.

Chiton (*Radsia*) *barnesii* Gray.—Pilsbry, 1893:190, pl. 29, figs. 10–12.—Dall, 1909: 247.—Thiele, 1929:29.—Van Belle, 1978: 20.

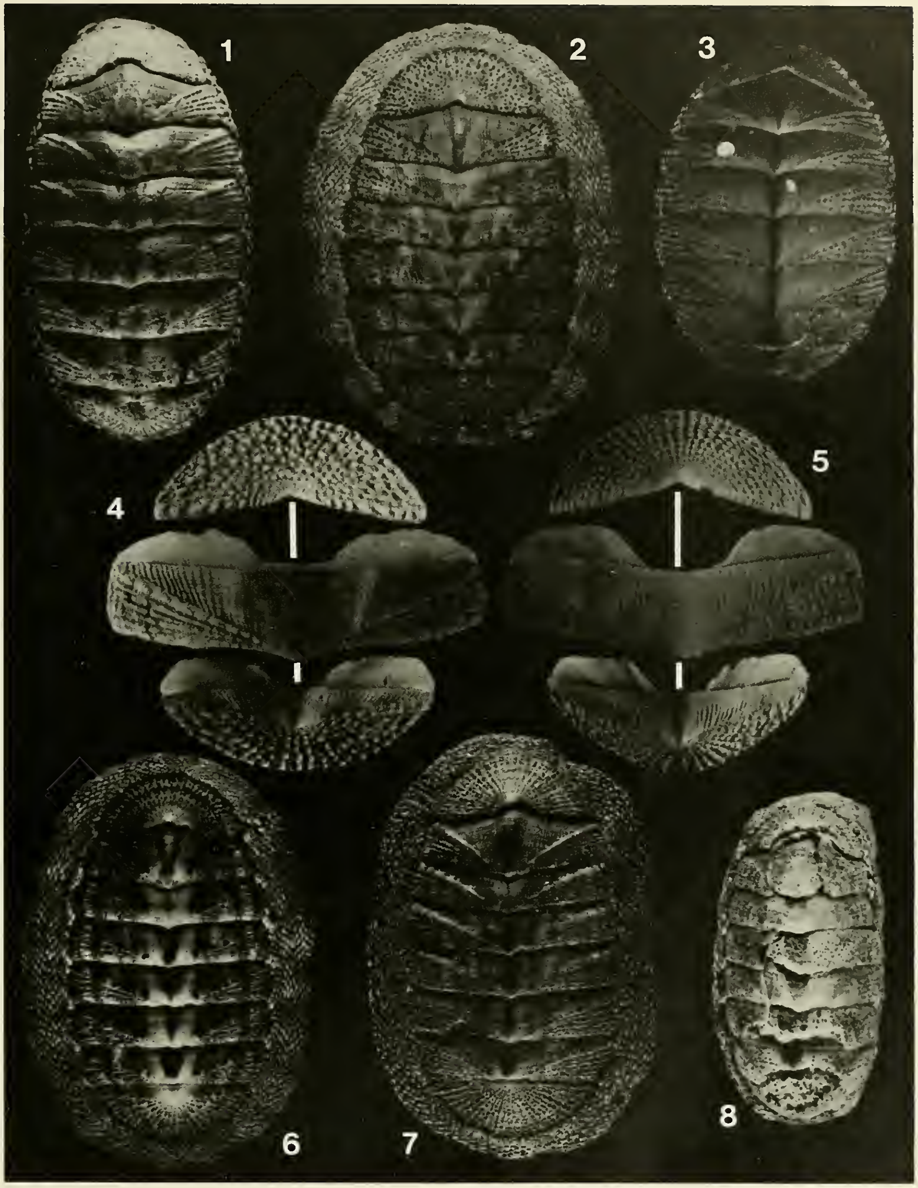
Chiton barnesi Gray.—Plate, 1899:59, pl. 4, fig. 191 [anatomy].—Leloup, 1956:46 [habitat].

Chiton (*Radsia*) *barnesi* Gray.—Kaas & Van Belle, 1980:14.

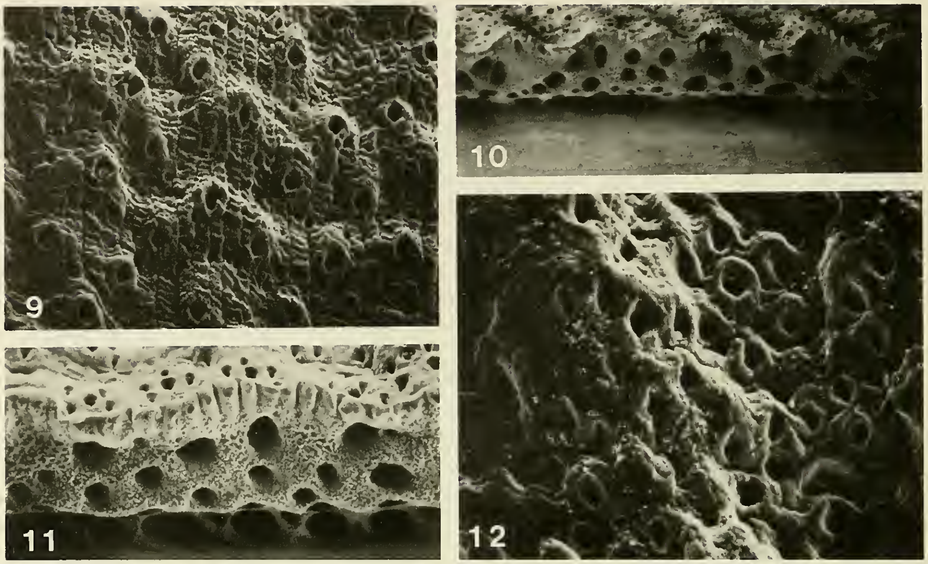
Description.—Animal reaching a length of 35 mm, a width of 26 mm. Valves quite flat, angle about 130°. Anterior valve straight; post-mucral slope of posterior valve straight to slightly concave. Mucro somewhat pointed, anteriorly acentric on posterior valve. Jugal region smooth; central area with numerous uneven longitudinal ribs. Lateral triangle barely raised, with 5–7 irregular nodules. Shell color cream white with reddish brown splotches on central areas, irregular longitudinal dark reddish brown bands on lateral triangles, and occasional dark reddish brown on jugum. Girdle light greenish brown with faint trace of alternating lighter bands in some specimens. Interior of valves white; brownish tegmental color visible in jugal region.

Insertion plates: Apophyses broad, moderately and evenly extended. Intermediate valves multi-slitted, with 2–4 slits per side; insertion teeth deeply pectinate. Anterior valve with 16 teeth; posterior valve with 19–20 teeth.

Tegmentum: Upper layer of suprategmentum thin; lower portion of suprateg-



Figs. 1–8. Shells of *Radsia barnesii* (Gray) and *R. nigrovirescens* (Blainville): 1, Lectotype of *Chiton capensis* Gray [=*R. nigrovirescens*], Cape of Good Hope, 19 mm (BMNH 1951.2.1.9); 2, Holotype of *Chiton barnesii* Gray, Coquimbo, Chile, 35 mm (BMNH 1951.1.23.1); 3, *Radsia nigrovirescens,* Buffels Bay, Cape Point, Port Alfred, South Africa, 14.5 mm (DMNH 16078); 4, *Radsia barnesii,* Cape Choros, Chile, width of intermediate valve 14.3 mm (MCZ 204337); 5, *Radsia nigrovirescens* Buffels Bay, Cape Point, Port Alfred, South Africa, width of intermediate valve 10.3 mm (DMNH 16078); 6, Paratype of *Chiton barnesii* Gray, Coquimbo, Chile, 32 mm (BMNH 1951.1.23.2); 7, *Radsia barnesii,* Cape Choros, Chile, 28.5 mm (MCZ 204337); 8, Syntype of *Chiton nigrovirescens* Blainville, Baie de la Table, 16 mm (MNHNP).



Figs. 9–12. Scanning electron micrographs of esthete pore morphology and anterior tegmental innervation in the genus *Radsia*: 9, 10, *Radsia nigrovirescens* (Blainville), Buffels Bay, Cape Point, Port Alfred, South Africa, 126×, 63×, respectively (DMNH 16078); 11, 12, *Radsia barnesii* (Gray), Cape Choros, Chile, 126×, 252×, respectively (MCZ 204337).

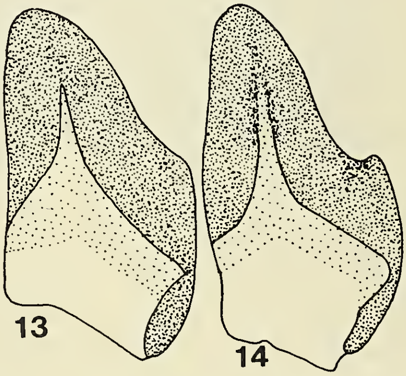
mentum enlarged and separated from subtegmentum by thin, esthete-pierced ridge. Suprategmentum and subtegmentum structurally identical, with small to medium, non-close-packed canals. Close to jugum, subtegmentum differentiated somewhat, composed of slightly larger canals. Suprategmentum alone on jugum (Fig. 11).

Esthete pores: Megalopores round to ovate, usually situated within a surrounding collar; micropores somewhat smaller, about half diameter of megalopores, more slit-like; most pores connected linearly by obscure anteroposterior crevices (Fig. 12).

Hypostracum: Central depression with few elongate slits, at times more numerous along lateral margins of jugal tract. Primary slit-rays prominent; slits oval to elongate, occasionally a few per longitudinal row. Secondary slit-ray present as field of small esthete holes.

Girdle scales: Moderate in size, roundly triangular, occasionally somewhat pointed; irregular basal reticulations proceed apically as somewhat irregular, variably pronounced ribs, which inturn obliquely and form elongate nodules near apex (Figs. 31, 32).

Radula: Central tooth moderately broad, very concave distally, tapering slightly midway toward base, but widening near base. Pad on centrolateral tooth lacking. Wing of



Figs. 13, 14. Denticle caps of *Radsia*: 13, *Radsia barnesii* (Gray), Cape Choros, Chile (MCZ 204337); 14, *Radsia nigrovirescens*, Buffels Bay, Cape Point, Port Alfred, South Africa (DMNH 16078).

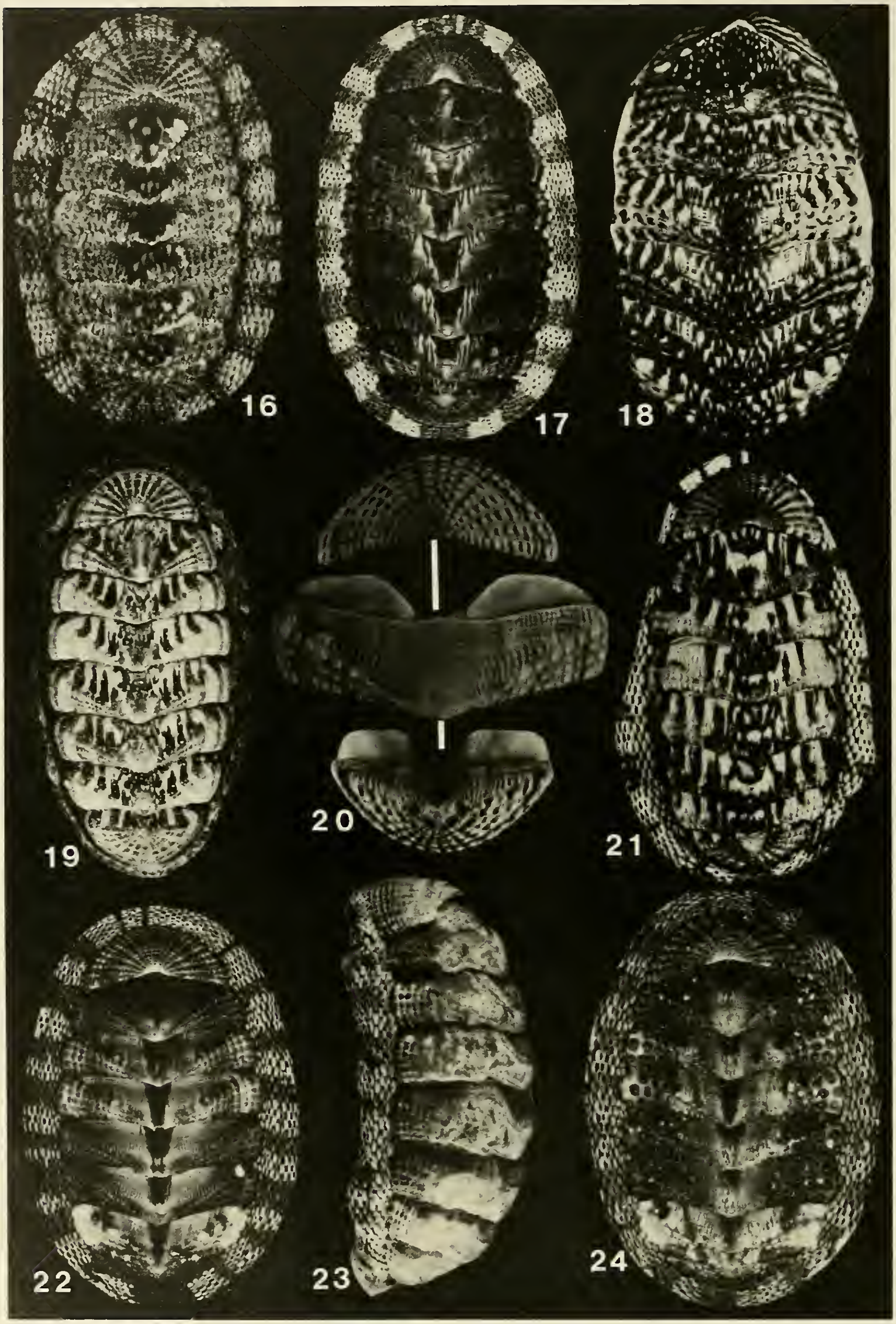
Fig. 15. Known distribution of *Radsia*: *Radsia barnesii* (Gray) (●); *Radsia nigrovirescens* (Blainville) (▲).

major lateral tooth large, broad, cup-like, with thickened distal edges. Denticle cap elongate, back completely black except for poorly developed channel which extends midway; secondary cusp greatly reduced; primary cusp with black crystal-like nodules coalesced to form elongate black streak beginning at base of channel, widening somewhat as it proceeds distally, and stopping short of tip, except for slight ridge proceeding distally to thin peripheral lip (Fig. 13).

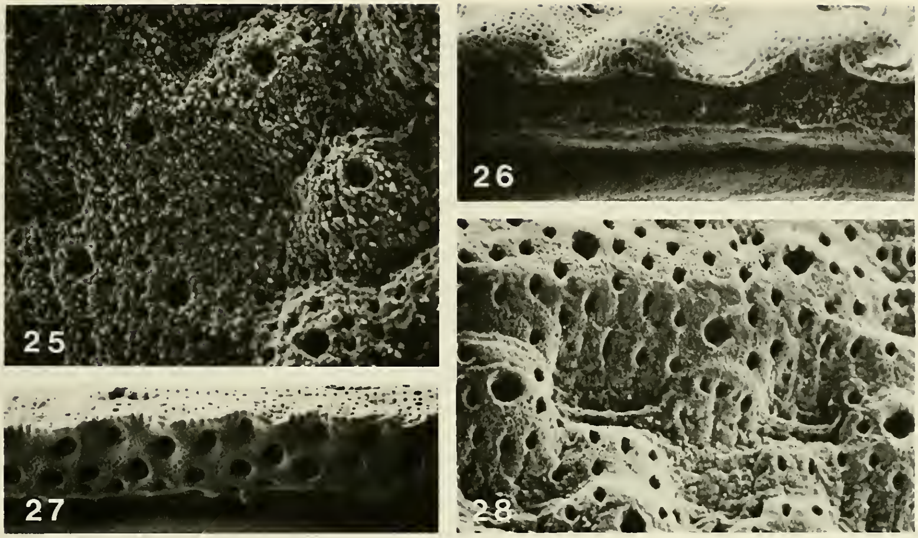
Remarks.—*Radsia barnesii* is closely related to *R. nigrovirescens,* but may be distinguished from the latter by its greenish-brown girdle, which nearly lacks evidence of banding, and shell color pattern, which is often brown speckled with light tan. *Radsia nigrovirescens* is characteristically solid brown, with alternating brown and tan bands on the girdle. The central areas of both species have numerous, narrow longitudinal ribs; *R. nigrovirescens* differs, though, by having these ribs reduced or lacking at the center of the valves. The girdle scales also serve to differentiate these two closely related species: those of *R. nigrovirescens* exhibit a fine reticular pattern over much of the surface; in *R. barnesii* irregular longitudinal ribs are often evident and the reticular sculpture is reduced to the lower ventrolateral area. The radular denticle cap has a greatly reduced secondary cusp which is not as prominent as the secondary cusp in *R. nigrovirescens.*

Radsia barnesii may be confused with *Chiton stokesii* Broderip, 1832, but the lateral triangle of *C. stokesii* is not projected forward as much, and the longitudinal ribbing of the central areas is more prominent. The girdle scales differ significantly: in *C. stokesii* the scales have conspicuous reticular sculpture ventrolaterally and numerous pustules are present apically. *Radsia barnesii* lacks this sculpture. Also, in *C. stokesii* the radular denticle cap differs by lacking any evidence of a secondary cusp and by having a prominent, elongate black tab distally on the back surface.

Aspects of the reproductive biology of both *R. barnesii* and *R. nigrovirescens* afford



Figs. 16–24. Shells of *Sypharochiton pelliserpentis* (Quoy & Gaimard): 16, Kawhia Harbour, New Zealand, 14 mm (ZMK); 17, South Tasmania, 34 mm (MCZ 23160); 18, Little Manly, Auckland, New Zealand, 20.5 mm (USNM 681354); 19, Mt. Manganui, Bay of Plenty, New Zealand, 32.5 mm (DMNH 275511); 20, Tamarama, Sydney, New South Wales, Australia, width of intermediate valve, 12.5 mm (RCB); 21, Little Manly, Auckland, New Zealand, 17.5 mm (USNM 681354); 22, Shellharbour, New South Wales, Australia, 28 mm (MCZ 204350); 23, Syntype of *Chiton pelliserpentis* Quoy & Gaimard, New Zealand, 34 mm (MNHNP); 24, Shellharbour, New South Wales, Australia, 22.6 mm (MCZ 204350).



Figs. 25–28. Scanning electron micrographs of esthete pore morphology and anterior tegmental innervation in *Sypharochiton pelliserpentis*: 25, 26, "*sinclairi*" form, Little Manly, Auckland, New Zealand, 262×, 66×, respectively (USNM 681354); 27, 28, Tamarama, Sydney, Australia, 262×, 66×, respectively (RCB).

evidence that the translocation of only one individual could lead to successful colonization. *Radsia barnesii* is known to retain its eggs within the branchial groove until at least the trochophore larval stage (Plate 1897, 1898, 1901). *Radsia nigrovirescens* has been reported to harbor its young in the branchial groove until the final stage of metamorphosis (Thiele 1910, Barnard in Ashby 1931, A. G. Smith 1966). It is interesting to note that these two *Radsia* may be the only Chitoninae known to have nonpelagic larval development. Bullock (in Pearse 1979) reported that "*Chiton*" *torri* Suter, 1907, from Stewart Island, New Zealand, also broods its young. Although Johns (1960, unpublished) examined the type specimen of *C. torri* and stated it to be a juvenile specimen of *Sypharochiton pelliserpentis* (Quoy & Gaimard), the identity of Suter's species needs to be investigated. *Sypharochiton pelliserpentis* does not brood its young (Johns 1960, unpubl. data) and it is unlikely that *Chiton torri* Suter is conspecific with the former species.

Distribution.—*Radsia barnesii* occurs along the Chilean coast from Coquimbo south to the Chonos Archipelago (Fig. 15).

Material examined.—Chile: (IRSN, NMB); Coquimbo (numerous records); Valparaiso (USNM); Chonos Archipelago (ANSP).

Radsia nigrovirescens (Blainville, 1825)
Figs. 1, 3, 5, 8–10, 14, 15, 29, 30

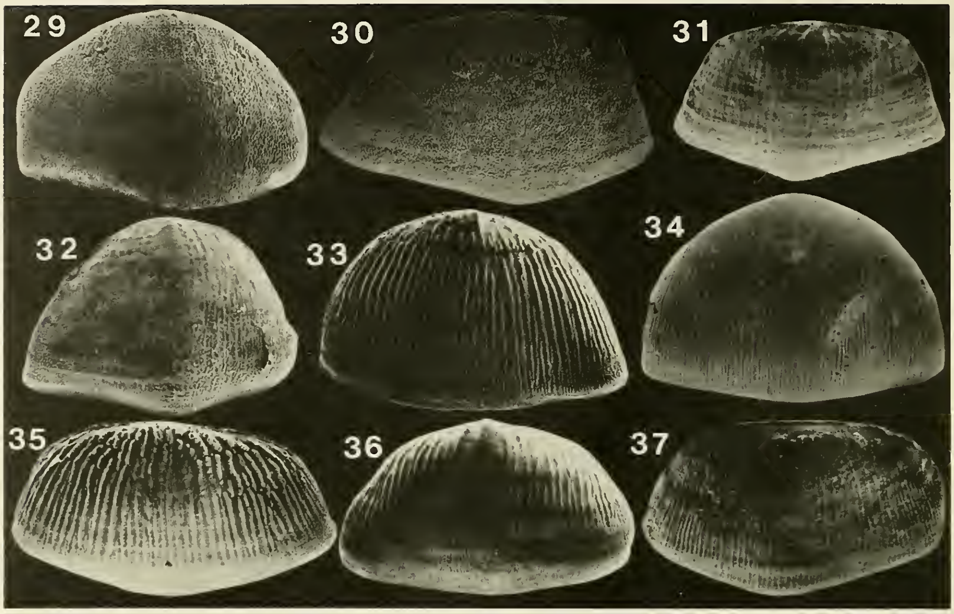
Chiton nigrovirescens Blainville, 1825:538 (Des mers du cap de Bonne-Esperance; type in MNHNP).—Krauss, 1848:38.—Haddon, 1886:22.—Sowerby, 1892:51.—Barnard, 1963:342.—Pearse, 1979:75, 77 [reproduction].—Kaas & Van Belle, 1980: 90.

Chiton capensis Wood, 1828:1, pl. 1, fig. 11 (locality unknown; type in BMNH? [not found]). Non Schroter, 1801; nec Gray, 1828.

Chiton capensis Gray, 1828:5 (Cape of Good Hope; type BMNH 1951.2.1.9) [reference to Wood (1828:pl. 1, fig. 11)].—Reeve, 1847:pl. 22, sp. 151.—Krauss, 1848:37.—Sowerby, 1892:51. Non Schroter, 1801; nec Wood, 1828.

Radsiella capensis (Gray).—Thiele, 1893: 369, pl. 30, fig. 20 [radula].

Chiton nigrovirens [sic] Blainville.—Pilsbry, 1893:187, pl. 31, figs. 41–42.—Sykes,



Figs. 29–37. Scanning electron micrographs of girdle scales of *Radsia* and *Sypharochiton*: 29, 30, *Radsia nigrovirescens* Blainville, Buffels Bay, Cape Point, Port Alfred, South Africa, 73×, 85×, respectively (DMNH 16078); 31, 32, *Radsia barnesii* (Gray), Coquimbo, Chile, 37×, 45×, respectively (BMNH); 33, *Sypharochiton pelliserpentis* (Quoy & Gaimard), Island Bay, Wellington, New Zealand, 42× (MCZ 278394); 34, *S. pelliserpentis*, "*sinclairi*" form, Little Manly, North Auckland, New Zealand, 49× (USNM 681354); 35, *S. pelliserpentis*, Shellharbour, New South Wales, Australia, 43× (MCZ 204350); 36, *S. pelliserpentis*, South Tasmania, 35× (MCZ 23160); 37, *S. pelliserpentis*, "*sinclairi*" form, Island Bay, Wellington, New Zealand, 53× (MCZ 278394).

1894:134.—Nierstrasz, 1906:503, figs. 44–49.—Bergenhayn, 1930:29 [shell structure].—Fischer, 1978:46.

Chiton (*Lophyrus*) *capensis* Gray.—Clessin, 1904:97, pl. 34, fig. 7 [poor figure].

Ischnochiton nigrovirens [sic] (Blainville).—Thiele, 1909:2; 1910:112.

Chiton (*Sypharochiton*) *nigrovirens* [sic] Blainville.—Ashby, 1928:91, pl. 7, fig. 17; 1931:47, pl. 7, figs. 78–81.

Sypharochiton nigrovirens [sic] (Blainville).—Dell, 1962: 513 [brooding behavior]; 1964:121.

Non Georgus nigrovirenscens [sic] 'Blainville' Thiele, 1893: 367 [=*Chiton angusticostatus* Quoy & Gaimard, fide Thiele (1909)].

Description.—Animal moderately small, attaining a length of 25 mm, a width of 15 mm. Valves flattened, angle about 120°. Anterior valve straight to slightly convex. Posterior valve mucro rather blunt, centrally located; post-mucral slope straight. Jugal region granular; central areas granular with numerous irregular longitudinal ribs. Lateral triangle barely raised, with 6–7 uneven, irregularly nodulose, radiating ribs. Terminal areas with numerous such ribs. Shell color dark brown with lighter areas near each mucro. Girdle alternately banded dark brown and reddish tan. Interior of valves light blue, with dull green near apophyses and posterior depression.

Insertion plates: Apophyses moderately extended, slightly more so medially. Jugal sinus broad, trapezoidal; 6–13 irregular, branching jugal teeth, located entirely beneath tegmentum. Intermediate valves with 1–2 slits per side; insertion teeth deeply pectinate. Anterior valve with 16 teeth; posterior valve with 19 teeth.

Tegmentum: Suprategmentum brown, thick, porous, with medium-sized canals; subtegmentum yellowish white, nearly hidden beneath suprategmental overhang, composed of one row of fairly close-packed, larger sized canals (Fig. 10).

Esthete pores: Megalopores round to ovate, located with surrounding collar; micropores about one-third diameter of megalopores, more slit-like; all pores conspicuously connected by anteroposterior crevices (Fig. 9).

Hypostracum: Central depression with number of transverse slits. Primary slit-ray a row of irregular holes. Secondary slit-ray partially developed laterally.

Girdle scales: Relatively moderate in size, roundly triangular, basal reticular sculpture extending dorsally; no trace of lateral ribs except near apex, where some nodes may be present (Figs. 29, 30).

Radula: Central tooth of moderate width, becoming wider basally. Pad on centrolateral tooth not evident. Wing of major lateral tooth large, very conspicuous, with thickened distal edges, cup-like. Denticle cap elongate, back completely black except for poorly developed channel extending midway toward apex; secondary cusp distinctly evident. Back of primary cusp with small, crystal-like nodules medially; distal end smooth, with peripheral swelling forming slight lip, perhaps with low nodule (Fig. 14).

Remarks.—On the basis of the radula and shell morphology, *R. nigrovirescens* is most closely related to *R. barnesii* (Gray) from the west coast of South America, and the two species are herein considered the sole members of the genus *Radsia*. Convincing evidence of this relationship is afforded by the fact that both species have a radular denticle cap that exhibits an obsolete, but still evident, second cusp (Fig. 14; see comparative remarks under *R. barnesii*).

The systematic position of *Radsia nigrovirescens* has not been discussed fully. Ashby (1928, 1931), who first placed *R. nigrovirescens* in *Sypharochiton*, considered the latter nomen as meriting only subgeneric rank within *Chiton*. Dell (1962, 1964) referred to this species as *Sypharochiton nigrovirens* [sic], because by this time *Sypharochiton* had been raised to full generic rank by Iredale and Hull (1926, 1927) and others, and the subfamily Sypharochitoninae had been mentioned. I believe that *Sypharochiton* should only be used as the genus-group nomen for the type species, *Sypharochiton pelliserpentis* (Quoy & Gaimard). Pilsbry (1893), who stressed shell morphology, placed *R. nigrovirescens* in the genus *Chiton*. On the basis of radular studies, Thiele (1909, 1910) considered *R. nigrovirescens* to be an *Ischnochiton*.

As Barnard (1963) noted, Nierstrasz (1906) questioned the identity of Thiele's *Georgus nigrovirescens* (Blainville), because he observed differences between the radulae of his own specimens and the illustration given by Thiele (1893). Thiele (1909), however, corrected himself, pointing out that his *Georgus nigrovirescens* was, in fact, *Chiton angusticostatus* [=*Rhyssoplax mauritiana* (Quoy & Gaimard), fide Bullock (1972)].

Although a number of authors have "corrected" the spelling of the specific name to "*nigrovirens*," the correct spelling is actually "*nigrovirescens*," as Tomlin (1931) pointed out. It should be noted, however, that both Haddon (1886) and Sowerby (1892) had correctly spelled the name of this species.

Distribution.—*Radsia nigrovirescens* occurs along the South African coast from Saldanha Bay east to Muizenberg (Fig. 15). The Durban locality is highly suspect.

Material examined.—South Africa: Saldanha Bay (ANSP, DMNH, ZMHU); Hoetjes Bay, Saldanha Bay (ANSP); Dassen Is. (RNHL); Robben Is. (ZMHU); Table Bay (IRSN, MNHNP, ZMHU); Cape Town (IRSN, NRS); Sea Point, Cape Town (ANSP, BMNH, DMNH, ZMA); Oudekraal (BMNH, ZMHU); Muizenberg (ZMA); Durban [Port Natal] (NRS).

Genus *Sypharochiton* Thiele, 1893

Sypharochiton Thiele, 1893:365. Type species by monotypy: *Sypharochiton pellisserpentis* [sic] (Quoy & Gaimard) [=*Chiton pelliserpentis* Quoy & Gaimard, 1835].

Triboplax Thiele, 1893:366. Type species, to be declared by the ICZN: *Chiton pelliserpentis* Quoy & Gaimard [=*Triboplax scabricula* 'Sowerby' Thiele, non Sowerby, fide Thiele, 1909].

Sympharochiton 'Thiele' Oliver, 1915:558 [spelling error].

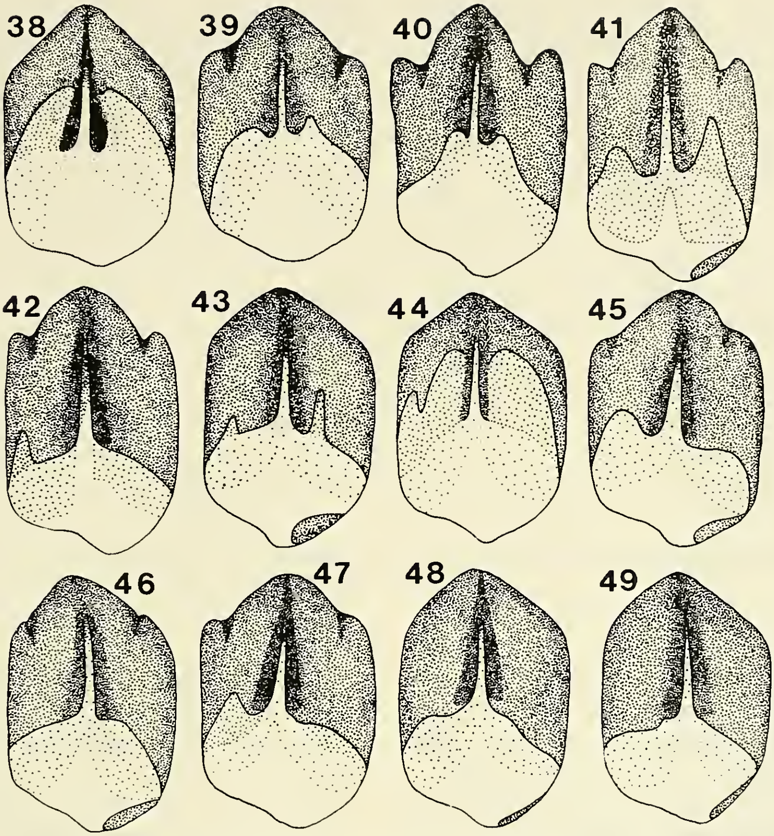
Description.—Animal medium to large, reaching a length of 63 mm, valves elevated. Jugal and central regions with numerous incised lines, ribs, or rows of granules; occasionally smooth. Lateral triangle and terminal areas with radiating nodular ribs. Interior of valves yellowish white to blue-green; muscle scars often dark blue-green. Insertion plate of intermediate valves with single slit per side; insertion teeth grooved dorsally. Central depression with a few scattered slits. Denticle cap of major lateral shovel-like, at times with evidence of one secondary cusp on either side of broad central cusp (Figs. 38–49).

Remarks.—*Sypharochiton* is distinguished from *Radsia* by its more elevated valves and more pronounced radial rows of nodes on the lateral triangle and terminal areas. *Chondroplax,* a subgenus of *Chiton* which has a shell that could be confused with that of *Sypharochiton,* differs from the latter by having widely spaced nodes on the terminal areas and by lacking the conspicuous transverse grooves in the central depression. Each group has distinctly different radular morphology.

As mentioned under the remarks section of *Radsia,* a number of species placed in *Sypharochiton* by Iredale & Hull (1926, 1927) have been excluded from the present study because of their definite ischnochitonid affinities. "*Chiton*" *torri* Suter, 1907, broods its young (Bullock in Pearse 1979) and it is unlikely to be conspecific with *S. pelliserpentis* as Johns (1960, unpublished) stated [see remarks under *Radsia*]. Some may properly belong in the Chitoninae, and if so they would be placed in *Radsia.* Davis et al. (1979) published an annotation of an ANSP label for *Chiton iatricus* Winckworth [=*Rhyssoplax peregrina* Thiele] that suggests that this species should be included in *Sypharochiton.* The results of the present study indicate that this is not the case.

The complete acceptance of *Sypharochiton* as a genus-group nomen is not evident in the latest biological literature. Most recent Australian and New Zealand biologists have placed *Chiton pelliserpentis* in the genus *Sypharochiton* (Boyle 1970, 1976; Murdoch & Shumway 1980; Horn 1982; Sakker 1984). However, in an extensive study Johns (1960) utilized *Sypharochiton* at the subgeneric level, and Kaas & Van Belle (1980) did not use *Sypharochiton* in their Catalogue of Living Chitons. The use of *Sypharochiton* is necessary because of the morphological differences between *Sypharochiton pelliserpentis,* the monotypic representative of the genus, and other chitonid genera including *Chiton* and *Radsia.* Radular morphology in particular supports the usefulness of this separation.

There could be some question regarding the type species of *Triboplax* Thiele. *Chiton scabriculus* Sowerby, the name used by Thiele, is not a member of the Chitonidae; Thiele (1909) recognized his mistake and clearly stated that he was working with *Chiton pelliserpentis* at the time that he instituted *Triboplax.* In spite of the obvious solution to this problem, namely to designate *Chiton pelliserpentis* as the type species, the International Code of Zoological Nomenclature stipulates that this situation be referred to the Commission (Art. 70b).



Figs. 38–49. Denticle caps of *Sypharochiton pelliserpentis* (Quoy and Gaimard): 38–40, Tamarama, Sydney, New South Wales, Australia (RCB); 41, Shelly Beach, Manly, Sydney, New South Wales, Australia (RCB); 42, Twofold Bay, Eden, New South Wales, Australia (RCB); 43, 45, Stanley, Tasmania (RCB); 44, Hobart, Tasmania (MCZ 98905); 46–48, Near marine lab, Portobello, Otago Harbour, South Id., New Zealand (RCB); 49, "*sinclairi*" form, Island Bay, Wellington, New Zealand (MCZ 278394).

Sypharochiton pelliserpentis
(Quoy & Gaimard, 1835)
Figs. 16–28, 33–37, 38–50

Chiton pelliserpentis Quoy & Gaimard, 1835:381, pl. 74, figs. 17–22 (Astrolabe Bay, New Zealand; type in MNHNP).—Pilsbry, 1894:85.—Pearse, 1979:63 [reproduction].

Chiton pellis-serpentis [sic] Quoy & Gaimard.—Gray, 1843:246.—Reeve, 1847: *Chiton* pl. 22, sp. 143.—Hutton, 1873:40; 1880:111; 1882:129, pl. 17, fig. 1 [radula].—Haddon, 1886:22.—Cox, 1894: 428.—Suter, 1897:195.—Nierstrasz, 1905:86.—Suter, 1913:33, Atlas pl. 2, fig. 12; pl. 4, fig. 6.

Chiton sinclairi Gray, 1843:263 (Great Barrier Island, North Island; type in BMNH).—Reeve, 1847:pl. 22, sp. 143.—Hutton, 1872:176; 1873:40; 1880:111.—Pilsbry, 1893:174, pl. 36, figs. 1–3.—Suter, 1897:195.—Wissel, 1904:627, pl. 23, figs. 38–44; pl. 24, figs. 45–58 [anatomy].—Suter, 1913:35, Atlas pl. 2, fig. 14; pl. 4, fig. 7.—Iredale & May, 1916:115.—Kaas & Van Belle, 1980:120.

Chiton (*Lophyrus*) *pellis-serpentis* [sic] Quoy & Gaimard.—von Martens, 1873:36.

Fig. 50. Known distribution of *Sypharochiton pelliserpentis* (Quoy & Gaimard).

Chiton (*Lophyrus*) *sinclairi* Gray.—von Martens, 1873:36.

Chiton (*Leptochiton*) *sinclairi* Gray.—E. A. Smith, 1874:pl. 1, fig. 17 [type fig'd.].

Sypharochiton pellis-serpentis (Quoy & Gaimard).—Thiele, 1893:366, pl. 30, fig. 12 [radula].—Ashby, 1918:86.—May, 1921:33.—Ashby, 1922:21.—May, 1923: 37, fig. 12.—Iredale, 1924:214.—Allan, 1950:238, text-fig. 55, fig. 14a.

Triboplax scabricula (Sowerby).—Thiele, 1893:366, pl. 30, fig. 13 [radula]. Non *Chiton scabriculus* Sowerby, fide Thiele (1909).

Chiton pellisserpentis [sic] Quoy & Gaimard.—Pilsbry, 1893:173, figs. 14–18.—Leloup, 1952:31, text-fig. 12; pl. 4, fig. 2.—Kaas & Van Belle, 1980:97.

Chiton (*Lophyrus*) *pellis serpentis* [sic] Quoy & Gaimard.—Clessin, 1903:5, pl. 4, fig. 5.

Chiton (*Lophyrus*) *sinclairi* Gray.—Clessin, 1903:5, pl. 20, fig. 6.

Chiton squamosus Linnaeus.—Wissel, 1904: 619, text-fig. F. Non *Chiton squamosus* Linnaeus.

Chiton (*Sypharochiton*) *pellisserpentis* [sic] Quoy & Gaimard.—Thiele, 1909:2.

Sypharochiton sinclairi (Gray).—Iredale, 1915:426.—Iredale & Hull, 1932:153, pl. 10, figs. 1, 2.—Powell, 1937:93, pl. 13, fig. 23.

Sypharochiton maugeanus Iredale & May, 1916:114, pl. 5, fig. 6 (Port Arthur, Southern Tasmania; type in Tasmanian Museum, fide Cotton, 1964 [not seen]).—Iredale, 1924:214.—Iredale & Hull, 1926: 258, pl. 37, fig. 3; 1927:121, pl. 15, fig. 3.—Cotton & Weeding, 1939:199.—Cotton & Godfrey, 1940:563, fig. 569 [holotype fig'd.].—Allan, 1950:238, text-fig. 55, fig. 14a.—Cotton, 1964:97, fig. 109 [holotype fig'd.].

Sypharochiton pelli-serpentis maugenaus [sic] Iredale & May.—Ashby, 1918:86 [spelling error].

Sypharochiton pellis-serpentis [sic] *maugeanus* Iredale & May.—Ashby, 1920: 579.

Sypharochiton pellis-serpentis [sic], var. *sinclairi* (Gray).—Ashby, 1922:579.

Sypharochiton (*Chiton*) *pellis-serpentis* [sic] (Quoy & Gaimard).—Ashby, 1922:579.

Sypharochiton pellis-serpentis [sic] *septentriones* Ashby, 1924:321 (New South

Wales; type in Ashby collection [presumed lost]).

Sypharochiton (*Chiton*) *sinclairi* (Gray).—Ashby, 1924:331.

Sypharochiton septentriones Ashby.—Iredale & Hull, 1926:257, pl. 37, figs. 2, 4, 29; 1927:120, pl. 15, figs. 2, 4, 29.—Allan, 1950:238.—Selwood, 1968:71 [reproduction]; 1970:178 [reproduction].

Sypharochiton pelliserpentis (Quoy & Gaimard).—Iredale and Hull, 1926:257; 1927:120; 1932:152, pl. 9, fig. 21.—Powell, 1937:93.—Fleming, 1966:86.—Boyle, 1970:364–384 [ecology].—Luckens, 1974: 637–654 [ecology].—Boyle, 1976:382 [esthetes].—Murdoch & Shumway, 1980: 128 [oxygen consumption].—Horn, 1982: 253 [ecology].—Sakker, 1984:111 [sperm morphology, spermatogenesis, spermiogenesis].

Chiton (*Sypharochiton*) *pellis-serpentis* [sic] Quoy & Gaimard.—Ashby, 1927:108; 1931:47.

Chiton (*Sypharochiton*) *pelliserpentis* Quoy & Gaimard.—Johns, 1960:27 [extensive synonymy].

Description.—Animal medium to large in size, reaching a length of 63 mm, a width of 35 mm. Angle of valves variable, 95–110°. Anterior valve and postmucral slope of posterior valve convex. Mucro blunt, centrally located on posterior valve. Jugal and central regions with numerous longitudinal incised lines, ribs, or rows of granules which may not reach preceding valve; at times entire central area smooth. Lateral triangle slightly raised, extending forward, with 3–8 nodular, radiating ribs. End valves with 10–15 nodular, radiating ribs each of which may bifurcate. Shell color variable, often buff or yellowish white with various portions, particularly radial sculpture, dark greenish brown or purplish black. Occasionally some or all valves light or dark. Central areas often with light bluish white or tan. Interior of valves yellowish white to blue-green.

Insertion plates: Apophyses broad, moderately and rather evenly extended. Jugal sinus broad; jugal plate not prominent, grooved dorsally to form varying teeth. Insertion plate of intermediate valves with single slit per side; insertion teeth grooved dorsally, not deeply pectinate. Anterior valve with 13 teeth; posterior valve with 12–16 teeth.

Tegmentum: Suprategmentum overhanging subtegmentum, composed dorsally of pigmented zone, ventrally of layer of non-close-packed, small, horizontal canals. Subtegmentum of numerous, irregular, small to medium close-packed canals, and fully continuous over jugum. Immature specimens with thick, very porous suprategmentum and thin subtegmentum composed of single layer of small, non-close-packed canals (Figs. 26, 27).

Esthete pores: Megalopores moderately large, round, about 2–3 times as large as ovate micropores; megalopores often situated individually on mound with surrounding micropores (Figs. 25, 28).

Hypostracum: Central depression with few scattered slits in jugal tract. Posterior portion of central depression and anterior slope of callus with faint grooves, apparently with no slits. Callus developed. Primary slit-ray with numerous small holes, irregularly arranged; mature specimens often with perforated ridge. Posterior depression dull, with numerous scattered small holes, mostly in jugal tract region. Secondary slit-ray similar to primary slit-ray.

Girdle scales: Moderate in size, roundly triangular to nearly rectangular; basal reticular sculpture reduced, somewhat granular; lateral ribs of varying thickness, but constant in single specimen, proceeding apically where they become obsolete or form irregular nodules near apex (Figs. 33–37).

Radula: Central tooth moderately broad; centrolateral tooth with conspicuous lateral pad. Major lateral tooth with squarish wing. Denticle cap of major lateral tooth somewhat ovate, back quite black, especially at margins and broad area on either side of distinct medial channel. Secondary cusp, sometimes very pronounced, may be visible on each side. Primary cusp broad; channel, bordered laterally by ridges, not reaching distal end. Nodules present on back surface on either side of channel, rarely within; distal lip not well formed, formed only at apex (Figs. 38–49).

Remarks.—Sypharochiton pelliserpentis most closely resembles *Chiton* (*Chondroplax*) *granosus* Frembly, 1827, from Chile, but in *C. granosus* the nodes on the terminal areas of the shell-plates are rather widely spaced, while in *S. pelliserpentis* they are closer together. The radula has a number of significant differences.

Sypharochiton pelliserpentis is a very common species, "often found above neap high water mark" (Iredale & Hull 1927:120). The species exhibits much intraspecific variation. According to previous work by Australian and New Zealand workers, the *S. pelliserpentis* group is composed of two to four species. In addition to *S. pelliserpentis* (Quoy & Gaimard), the names used in the literature of the past few decades include: *S. sinclairi* (Gray, 1843), *S. maugeanus* Iredale & May, 1916, and *S. septentriones* Ashby, 1924. Even a preliminary examination of these so-called species indicates that the taxonomy of this group is confusing and that the use of some of the names is inadvisable. Cotton & Godfrey (1940:563) and Cotton (1964:97) stated of *S. maugeanus*: "This is the Tasmanian representative of the New Zealand shell *Sypharochiton pelliserpentis* Quoy & Gaimard, and depends upon the geographical locality for status." Leloup (1952) considered all the forms conspecific, but erroneously included in his synonymy a reference to *Chiton angusticostatus* Quoy & Gaimard because of a comment by Pilsbry, who was uncertain of the latter species' identity [=*Rhyssoplax mauritiana* (Quoy & Gaimard), a Mascarene islands species (Bullock 1972)].

A rather thorough study by Johns (1960 unpubl. data), published in part by Knox (1963a, 1963b), did not really clarify the entire taxonomic situation. In his study of the ecology and behavioral biology of various populations, Johns found that there is clinal variation in the presence of a black second valve, considered a diagnostic characteristic of Iredale and May's *Sypharochiton maugeanus*, which is now recognized as a junior synonym of *S. pelliserpentis*. The black valve is present in the population at a frequency of 25–40 per cent in the northern portion of its range as compared to 80–90 percent in the south.

The part of Johns' study that dealt with New Zealand populations proved even more interesting. According to Johns, two forms are observed among the young specimens, which are always found subtidally; these forms are purported to differ in color, sculpture, and the radular ratio. As these animals mature, one form (*S. pelliserpentis*) migrates high into the intertidal zone while the other form (*S. sinclairi*) remains subtidal. The *pelliserpentis* form exhibits homing behavior, certainly an advantageous adaptation for a chiton living in such a habitat, while the *sinclairi* form has not been observed to exhibit homing (Johns in Knox 1963b). Luckens (1974) also observed this difference in homing behavior. Horn (1982: 259) corroborated Johns' results with regard to the radular ratio and noted that "variations in radular ratios are unlikely to be genetically determined."

In spite of these differences, which at first suggest that two separate species may be involved, I have concluded that only a single species exists. An examination of the shell and girdle scale morphology of individuals from many populations revealed that morphologically intermediate examples occur. Boyle (1970) arrived at the same conclusion and stated that the two forms are not likely to be reproductively isolated. The differences noted in homing behavior are not unexpected, because there is a general tendency for homing behavior in limpets and chitons to be much more pronounced in individuals that live in the intertidal zone. Also, this behavior seems to be totally absent in subtidal populations. Brian & Owen (1952) found that within a population of *Patella vulgata* Linnaeus a difference in the radular ratio obtains, depending on the position in the intertidal zone.

Previous workers have overlooked one intriguing aspect of *S. pelliserpentis* radular morphology. According to Johns (1960:19 unpublished), within the *S. pelliserpentis* group "no differentiation may be made between the species on the form and disposition of the radular teeth." I concur with Johns' conclusion. However, a study of denticle cap morphology, made possible by collections of *S. pelliserpentis* from Australia and New Zealand provided me by Dr. Ruth D. Turner of Harvard University, revealed that the denticle cap of the major lateral tooth of this species is polymorphic (Figs. 38–49). Two extreme forms may occur: one with a prominent secondary cusp on either side of a large, central cusp (Figs. 40–42), the other with no evidence of these secondary cusps (Figs. 38, 43, 48, 49). Various intermediate examples have been found (Figs. 39, 45–47). This polymorphism is found in both Australian and New Zealand localities and is not correlated with the size or sex of the individuals. Although relatively few examples of the *sinclairi* form were available for study, it appears that the radular differences observed do not aid in the separation of these forms.

The genetic basis of denticle cap polymorphism in *S. pelliserpentis* might possibly be an example of paedomorphosis. As noted in the discussion of *Radsia* radular morphology, one likely origin of the broad, single-cusped denticle cap of most chitonids would be a loss of all but the central cusp. O'Neill (1984) observed that in the chitonid *Onithochiton neglectus* Rochebrune the small juveniles (1.5 mm) have a tricuspid denticle cap, but that with increasing age, the caps quickly assume the typical single-cusped state. Perhaps in *Sypharochiton pelliserpentis* we see varying degrees of retention of a juvenile character; however, radulae of very small *S. pelliserpentis* have not been examined. Other important questions remain, including the relationship between denticle cap form, food sources, and feeding behavior.

The differences in shell morphology, radula, and behavioral ecology of *S. pelliserpentis* may be differentiated into those differences that are environmentally induced (homing behavior, radular ratio), and those that have primarily a genetic basis (shell and girdle scale morphology, denticle cap polymorphism). The present expression of these genetic differences might be explained by secondary intergradation or introgression. Given the geographic isolation of New Zealand and the possibility that gene flow between New Zealand and Australia is greatly restricted (judging from the speciation patterns of the Polyplacophora), one can surmise that incipient speciation could occur in isolated populations of *S. pelliserpentis*. However, this isolation has not been complete, perhaps due to the distances involved, changes in ocean currents, or unknowing translocation of individuals by commercial shipping. Regardless of the origin of this intraspecific variation, it is apparent that individuals of many populations exhibit polymorphic characters and morphological variation, and that the degree of these differences differs from population to population.

Luckens (1974) noted that *S. pelliserpentis* characteristically clears the algae from some areas, while leaving other regions untouched. According to Murray (in Luckens 1974:646): "*Sypharochiton* is an indiscriminate rasping form, and the gut contents include algae, rock particles, crushed barnacle shell and the remains of small crustaceans."

Luckens found that their activity kept the cleared areas devoid of settling barnacles. Most larger intertidal specimens live in a depression in the rock surface to which they exhibit homing behavior (Boyle 1970).

Distribution.—Sypharochiton pelliserpentis occurs in New Zealand, New South Wales, and Tasmania (Fig. 50). It has been reported from the Pliocene of New Zealand by Hutton (1886) and Suter (1921). *Sypharochiton* may be extremely abundant, reaching a density of $228/m^2$; it occurs in a variety of habitats and survives, at least temporarily, in salinities as low as 13.3 ppt and as high as 45.8 ppt (Boyle 1970).

Material examined.—New Zealand: North Island: North Cape (ZMK); Bay of Islands (BMNH); Takapuna (ANSP, BMNH); Auckland (ANSP, IRSN, MCZ, USNM, ZMHU); Ponui Is. (NRS, ZMK); Slipper Is. (ZMK); Tauranga (RNHL); Beacon Reef, Tauranga (DMNH); Mt. Maunganui (ANSP, DMNH); Mahia Peninsula (NRS, ZMK); Wellington (ANSP, BMNH, MCZ, MNHNP); Island Bay, Wellington (MCZ); Karaka Bay, Wellington Harbour (BMNH); under boulders, Opunake (MCZ); New Plymouth (ZMK); Manukau Harbour (MCZ). South Island: Lyttleton (IRSN, NRS, MNHNP); Akaroa (IRSN, NRS, ZMK); Timaru (ANSP); Otago Harbour (MNHNP); Near marine lab., Portobello, Otago Harbour (MCZ, RCB); Foveaux Strait (RNHL); Stewart Is. (ANSP, IRSN); Paterson Inlet, Stewart Is. (NRS, ZMK); Port Pegasus, Stewart Is. (NRS, ZMK); Sumner (RNHL, ZMA, ZMHU). Australia: New South Wales: Sydney (IRSN, USNM): Port Jackson, Sydney (ANSP, BMNH, MCZ, MNHNP, ZMHU); Green Point, Watson's Bay, Port Jackson (ANSP); Bottle and Glass Rocks, Port Jackson (MCZ); Long Reef, Sydney (MCZ, ZMHU); The Spit, Port Jackson (ANSP); Tamarama, Sydney (MCZ, RCB); Shelly Beach, Manly, Sydney (MCZ, RCB); Marouba (BMNH, RNHL, ZMHU); Botany Bay (ZMHU); Shell Harbour (ANSP); Huskisson, Jervis Bay (BMNH); Cave Bay, Camping ground, Jervis Bay (MCZ); Twofold Bay, Eden (MCZ, RCB). Tasmania: (ANSP); Bridgport (MCZ); Port Arthur (ANSP, MCZ); Frederick Henry Bay (ANSP, ZMHU); Bellerive (BMNH); Hobart (MCZ); Brown's River, mouth of Derwent River (ANSP, NRS); Adventure Bay, South Bruny (MCZ); Robbins Is. (MNHNP, USNM); Stanley (MCZ, RCB).

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DIPLOCARDIA HULBERTI AND *D. RUGOSA,* NEW EARTHWORMS (ANNELIDA: OLIGOCHAETA: MEGASCOLECIDAE) FROM KANSAS

Samuel W. James

Abstract.—Two species of the megascolecid earthworm genus *Diplocardia* (subfamily Acanthodrilinae) are described from collections made in tallgrass prairie in north-central Kansas. *Diplocardia hulberti* has similarities to *D. meansi* and some undescribed material in Gates (1977), while *D. rugosa* appears to be closely related to *D. smithii.*

Studies of earthworms in tallgrass prairie of the Flint Hills region of Kansas resulted in the collection of two species of *Diplocardia* that appear to be unlike any previously described members of the genus. Both species were found on the Konza Prairie Research Natural Area (KPRNA) in Geary and Riley counties, a large tract of tallgrass prairie maintained by The Nature Conservancy and Kansas State University for research. Apart from riparian forests, vegetation is dominated by the grasses *Andropogon gerardii* Vitmana, *A. scoparius* Michx., *Panicum virgatum* L., and *Sorghastrum nutans* L. Soils are silty clay loams and silty clays of the Florence-Benfield series. Mean annual precipitation is 82 cm, but the region is prone to drought and temperature extremes. Consequently earthworm activity is greatest in the spring and fall, though the *Diplocardias* may remain active all summer if rainfall is sufficient.

The species described below were determined to be new on the basis of Gates (1977). I did not check any museum collections for previously undetected individuals of these species. The following descriptions are based on observations of five clitellate individuals per species. Dissected holotypes and undissected paratypes have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Jamieson (1978) has summarized the controversy over the assignment of family rank to the Acanthodrilinae. I have chosen to follow the classification of Jamieson (1978) and Brinkhurst & Jamieson (1971), pending further developments in this area.

Diplocardia hulberti, new species
Figs. 1A, 2A, B

Description.—External characteristics: 32–50 by 1.3–2.1 mm, width at segment xxx, body cylindrical in cross section throughout, widest point at segments vii–viii, narrowing slightly before the clitellum; segments 91, 98, 99, 100, 106. Setae closely paired throughout, conspicuous as black dots in fixed specimens; setal formula *AA:AB:BC:CD* = 5:1.7:4:2. Prostomium tanylobous to nearly tanylobous, segments biannulate in viii–xii, triannulate after clitellum. Epidermis and body wall unpigmented but may appear grayish due to presence of dark pigment on peritoneum and septa in segments ix–xii. When alive and when preserved, worm has curdled appearance in head and tail regions, due to small white inclusions in body wall. Alive, annular clitellum bright yellow; preserved, orange-brown. Nephridiopores not found. First dorsal pore at 6/7 or 7/8, to within a few segments of end.

Spermathecal pores on small protrusions

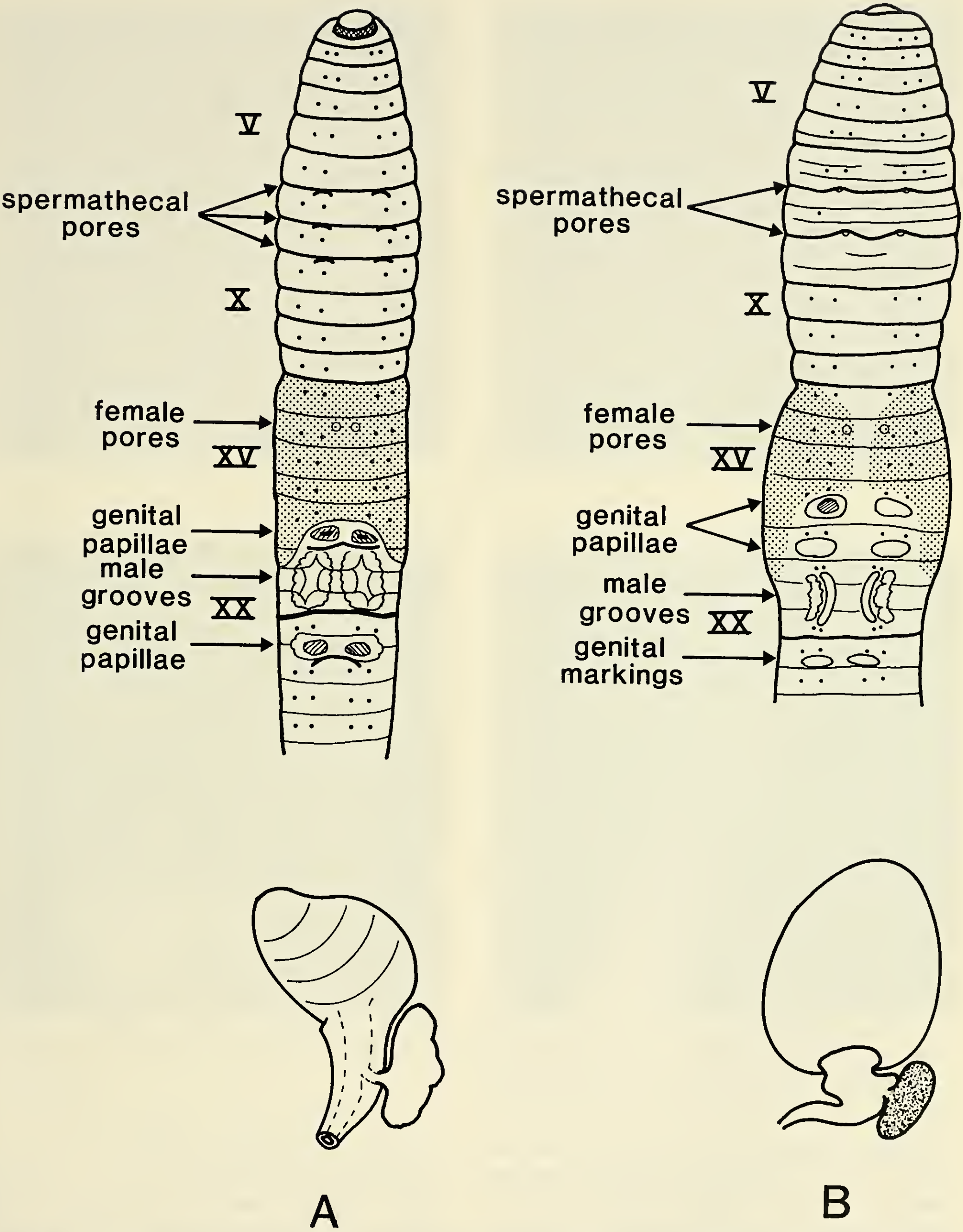

Fig. 1. A, *Diplocardia hulberti,* ventral view and spermatheca; B, *Diplocardia rugosa,* ventral view and spermatheca.

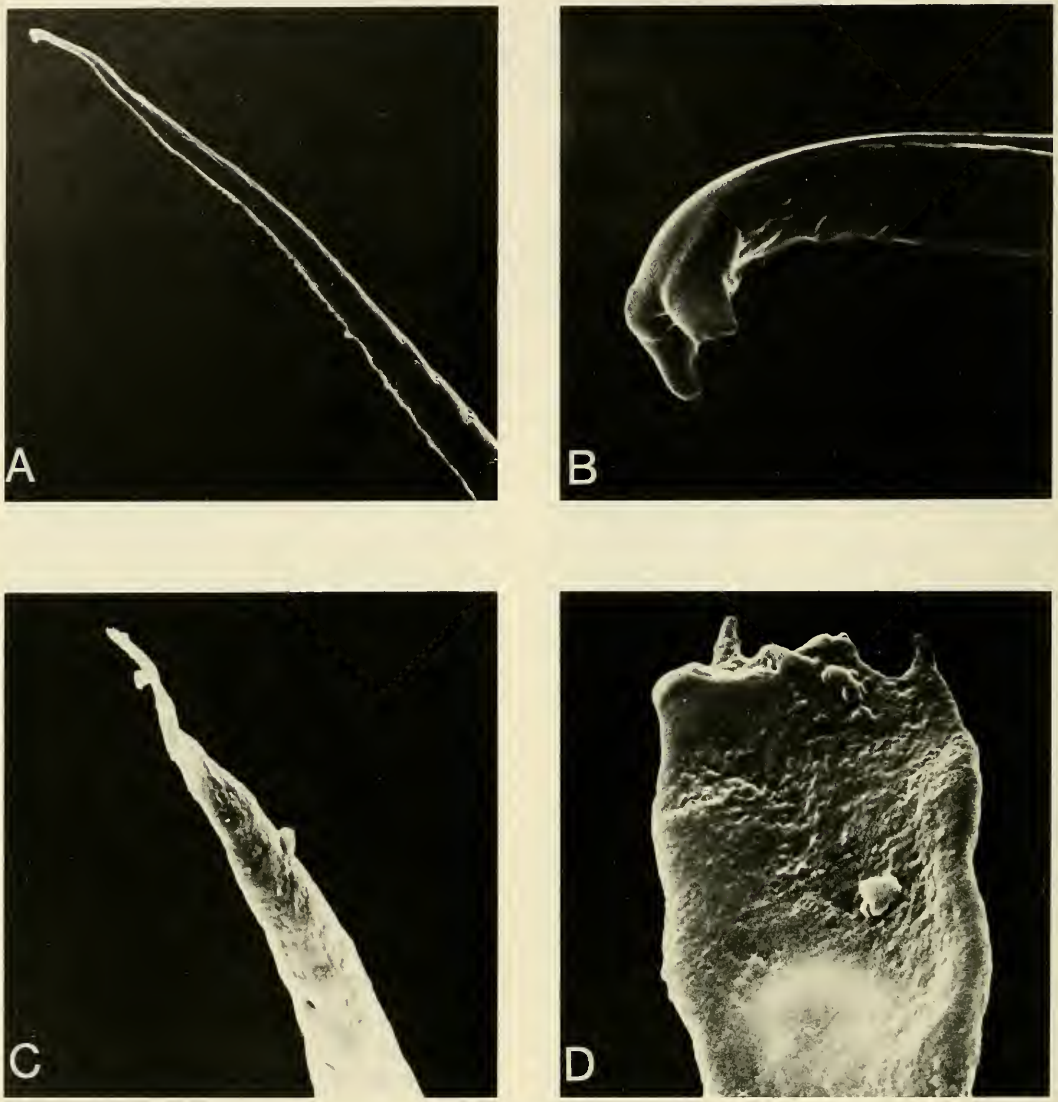

Fig. 2. *Diplocardia hulberti,* penial setae from segment xx: A, Shaft (1500×); B, Tip (16,000×). *Diplocardia rugosa,* penial seta from segment xx: C, Shaft (2500×); D, Tip (16,000×). Irregular lumps in C and D are debris.

at leading edges of segments vii–ix, just lateral to setae *a*. Ovipores in xiii, presetal and median to setae *a* in small oval area faintly lighter than surrounding clitellar development. Genital markings paired, postsetal in xvii, centered on line of setae *A,* and paired on furrow 21/22, on or slightly median to line *A*. Male grooves from xviii–xx, straight to slightly curved, concavity facing laterally, grooves within thickened raised area. Furrows 17/18 and 20/21 typically very deep on ventral side (see Fig. 1).

Setae in spermathecal and adjacent segments not modified; ambulatory setae sigmoid and unornamented. Penial setae (Fig. 2A, B) 800 × 10 microns, sigmoid, distal quarter slightly ornamented except on narrow distal portion. Tips bifurcate and forming small hooks.

Internal characteristics: Septa 6/7–10/11 heavily muscled, in 11/12–13/14 musculature decreases to typical scant amount. Transeptal muscles in vii to xii, post-septal in vii to body wall in viii, etc.; these muscles at middorsal and laterally. Black pigment granules on septa 9/10–12/13, sometimes on peritoneum and blood vessels in intervening segments.

Alimentary canal containing 2 gizzards (v and vi) distinctly divided at septum 5/6. Esophagous smooth externally, without pouches or extramural calciferous glands, internal texture consisting of low knobs in anterior part, changing to low longitudinal folds, best developed at intersegmental boundaries, in segments xiv–xvi. Calciferous lamellae lacking. Glandular mass on dorsal side of esophagous in xiv; small iridescent glands at middorsal on esophagous in vii–ix, paired lateral glands of similar appearance in vii and viii. Intestinal origin in xvii. Intestinal constriction present at 20/21; villous internal texture persisting to end of typhlosole. Blood sinuses present in segments xvii–xxv; at most septal constrictions a blood vessel visible in longitudinal section. Simple lamelliform typhlosole less than one-third of lumen diameter arising in xix or xx, becoming rudimentary and vanishing by xl–xlv.

Nephridia 2 per segment, without bladder, extending from setal follicles of *A* to near *D,* duct to external nephridiopore at level of and slightly anterior to *D.* Anterior to intestine, tubule coiling resulting in complicated globular form; from xvii posteriorly tubule forms 2 or 3 loops flattened against body wall.

Vascular system consisting of subintestinal trunk with connections to septa, nephridia, and body wall, these collecting to large, chloragogen covered lateral vessels connecting to similarly covered and single dorsal vessel. Small vessels arising from subintestinal going to intestinal wall; dorsally, small vessels connecting intestinal circulation to dorsal vessel. Dorsal vessel continuing forwards onto pharynx, where it divides in iii and descends to ventral vessel. Supra-esophageal vessel ix–xii, where it dives into esophageal wall. Extra-esophageal vessels v to xii; in xiii, diverging to body wall and branching repeatedly as they supply clitellar region. These fine vessels appearing to extend no farther than xvii. Commissures vi–xii, in vi oriented ventrally-anteriorly, connecting to extra-esophageal vessel and ventral vessel; commissures of vii and viii lateral, those of ix–xii having single valve each and lateral-esophageal.

First 2 segmental nerves of a side emerging separately from ventral nerve cord and partly fusing together. Ventral nerve cord bifurcating in iii to join above pharynx.

Body wall longitudinal musculature interrupted by setal follicles, latter lens-shaped and conspicuous.

Male sexual system reduced; no coagulum (developing sperm) and no testes found in x, xi; funnels in x, xi, not iridescent. Seminal vesicles preseptal in ix, postseptal in xii, divided into many lobes, gray to darkly pigmented, often reaching only to mid-lateral, that of ix larger than vesicle of xii. Prostates 0.6 × 0.8 mm, confined to xviii and xx, or reaching into next segment anterior, nearly completely covered by intestine. Prostatic ducts half length of gland or shorter, without muscular sheen, with one or two short kinks or coils, meeting body wall at *B,* behind septa 17/18, 19/20. Penisetal muscle bundles meeting body wall near duct. Numerous transverse muscle bands in prostatic region. Vasa deferentia meeting just posterior to 11/12, running side-by-side under peritoneum to xviii, where they dive into body wall near prostatic ducts.

Ovaries in xiii, consisting of tight clusters of short strings bearing few eggs each, whole appearing like cluster of grapes, sometimes with black pigmentation. Ovarian funnels at anterior face of 13/14, open end gently folded, with flap curved down over opening. Spermathecae (Fig. 1) in vii–ix, duct shorter than ampulla, diverticulum on lateral face of duct, attached at its middle by short stalk, or sessile in appearance but only attached at middle, diverticulum ovate, undivided.

Spermathecae erect in segments, generally with ampullae tucked under esophagous and diverticula adjacent to body wall.

Holotype: 250 m west of stone house, Irwin silty clay, Konza Prairie Research Natural Area, Riley Co. Kansas; 22 May 1981, Samuel W. James, USNM 101808.

Paratypes (4): 250 m west of stone house, Irwin silty clay, Konza Prairie Research Natural Area, Riley Co. Kansas; 22 May 1981, Samuel W. James, USNM 101809.

Ingesta, parasites: Mineral soil, fine root fragments and what is apparently grass leaf litter made up the bulk of ingesta. One 3 mm long nematode was found in the gut of one specimen.

Remarks.—The above description is based on specimens taken from the type locality. Other specimens have been found in the same soil type (Irwin silty clay loam), but not in other soils, on other sites in KPRNA, some of which are in Geary County. A single specimen with strong affinities to the KPRNA worms was found in the author's lawn at 1726 Colorado St. Manhattan, Kansas, also Riley County. However, until more specimens can be obtained, it seemed best to omit it from the present description. The reasons are as follows: it had genital markings at 15/16 and 16/17, segments x and xi were filled with coagulum, the spermathecal duct was more sharply differentiated from the ampulla, its first dorsal pore was at 9/10, and the arrangement of segmental nerves arising from the ventral nerve cord was markedly different, the anteriormost nerve single, and a pair arising posteriorly and remaining separate. The collection site is separated from KPRNA by 12 kilometers and a large river; hence the possibility of subspecific variation needs attention.

Diplocardia hulberti is apparently male-sterile and presumably parthenogenetic. No iridescence was detected on any diverticulum or sperm funnel examined, and all specimens were fully clitellate.

Behaviorally this species is distinct from most members of the genus found on KPRNA in that it actively flees when in hand. The others become semi-rigid and may excrete a little coelomic fluid, except *D. prosenteris,* which flees and oozes. The active nature of *D. hulberti* and presence of leaf litter in the gut suggest that it is active at or near the soil surface. *Diplocardia hulberti* is named in honor of the late Lloyd C. Hulbert, whose enthusiasm led to the establishment of KPRNA and consequently to the author's choice of research site. He is therefore partly responsible for the discovery of this worm.

Affinities.—In Gates' (1977) key, the characters of *D. hulberti* lead to the couplet containing *D. meansi* Gates and an undescribed species, *D.* sp. II. It can be distinguished from both these by size and number of segments (smaller in each case), and from *D.* sp. II by its smaller, ovate prostates, the dark internal pigmentation, hooked tips of the penial setae, and the clear locations of the spermathecal pores. *Diplocardia hulberti* is the smallest sexthecal *Diplocardia* known. The following combination of characters will distinguish *D. hulberti* from all other known members of the genus: three pairs of spermathecae, dorsal blood vessel single throughout, last hearts in xii, prostomium tanylobous, abundant pigment granules on septa and vascular system in preclitellar segments, annular clitellum, spermathecal diverticulum sessile or with very short slender stalk, spermathecal duct without a crypt, tips of penial setae hooked.

Diplocardia rugosa, new species

Figs. 1B, 2C, D

Description.—External characteristics: 30–45 × 2 mm, width at segment xxx, body cylindrical throughout, widest at clitellum and nearly as wide in spermathecal segments. Segments 112, 113, 113, 122, 130, biannulate in vi, triannulate vii-end. Prostomium tanylobous and smooth; periproct smooth, anus a vertically oriented lenticular opening. Setae closely paired throughout, *AA:AB:BC:CD* = 16:3:14:4, *DD* < ½ circumference. Setae frequently missing or displaced in segments vii–x, xix, xx. Body unpigmented, color when live pink to gray, pale gray with brown clitellum when preserved. Nephridiopores at *D*, only found anterior to clitellum. First dorsal pore at 8/9 or 9/10, dorsal pores extending to tail.

Spermathecal pores at *A* on tips of prominent, forward leaning protuberances, high points of ridges which make up leading edges of segments viii and ix. Posterior ⅔ of ix and anterior ⅔ of x broad and smooth. Ovipores presetal and median to *a* in xiv, enclosed in faint oval area. Clitellar development lacking along narrow strip at midventral, roughly equal in width to spacing between setae *A* and *B*. Genital markings paired and postsetal, centered on *AB* in xvi, xvii, and xxi. Extra unpaired genital markings have been seen in xv. Epidermis thickened in area bounded by genital markings and male field, with deep furrows adjacent to genital markings. Male grooves having thickened ridges lateral to them; grooves curved with concave side facing laterally (Fig. 1); grooves extending from equator of xviii to first third of xx. Penial setae visible in close pairs at ends of grooves, just inside line of setae *A*.

Setae in spermathecal and adjacent segments unmodified, may be missing. Ambulatory setae 160 × 13 microns, sigmoid, unornamented. Penial setae 350 × 10 microns, tip flattened, shaft slightly sculpted (Fig. 2C, D).

Internal characteristics: Septum 6/7 having light musculature, 7/8, 8/9 heavy, musculature decreasing to few radial strands in 12/13, 13/14. Trans-septal muscles 4 per segment in vii–xiii, those in vii attached to posterior face of 6/7 near gut and to body wall in viii, rest following this pattern.

Gizzards in v, vi, with distinct division but no constriction between them. Esophagous lacking calciferous lamellae and extramural calciferous glands, internal texture pebble-grained, low longitudinal folds found only at segmental boundaries. Coagulated glandular(?) material on dorsal face of esophagous in xiv, xv, pairs of small iridescent glands on dorsal face in vii, viii, and sometimes ix. Intestinal origin in xvii; its internal texture villous with numerous lateral folds in segments xvii–xxi, after which villousness and lateral folding decreasing. Blood sinuses present to xxv. A simple lamelliform typhlosole begins in xix and ends in 1.

Nephridia 2 per segment, without bladder, attached to septa near setae *B*, extending to *D*, where tubules join body wall. In segments anterior to intestine, nephridia complexly looped and coiled into globular shapes, while in intestinal segments, tubule makes single descending loop and turns upwards into a coil. These latter nephridia flattened against body wall.

Dorsal vessel single throughout, breaking into small descending vessels in iii. In intestinal segments, having chloragogen on its lateral edges. Subintestinal trunk supplying blood to intestine via short vessels, and to body wall and nephridia via single pair of segmental vessels per segment. Lateral vessel takes blood from these parts to dorsal vessel. Intestinal circulation completed by 2 connections per segment to dorsal vessel. Segmental vessels in clitellar region larger than elsewhere. Supra-esophageal vessel from ix to xiii, where it dives into esophageal wall; extra-esophageals from v to xiii, where they diverge to body wall and branch out through clitellar segments. In v and vi, extra-esophageals send two vessels per segment to ventral vessel. Hearts in ix–xii, lateral-esophageal. Commissures in v–viii, connecting dorsal vessel to ventral.

Anterior segmental nerve on a side of ventral nerve cord separated by some distance from second and third nerves, which emerge adjacent to each other and run separately to body wall.

Testes and funnels free in x, xi, with coelomic cavities of these segments filled with coagulum. Funnels highly iridescent and ovate with wavy edges. Seminal vesicles of xii larger than those of ix, all divided into numerous irregular lobes. Vasa deferentia originating at base of each funnel and running side-by-side from xii under peritoneum to insertion of prostatic duct of xviii. Flattened tubular prostates 0.4 × 3 mm, completely surrounding intestine in segments xix–xxii, may extend into xvii, xxiii. Prostatic ducts short (0.6 mm), straight, lacking muscular sheen; meeting body wall postseptally in xviii, xx next to penisetal follicles. Penisetal follicles short finger-like projections with long strand of muscle extending from proximal tip diagonally back to body wall. Numerous transverse muscle bands in prostatic segments.

Ovaries in xiii, consisting of several strings emanating from ventral insertion of 12/13. Each of these strings dividing to form subcluster with many short strings of ova. Ovarian funnels in xiii, trumpet-shaped in cross section. Tubular part of funnel extending through 13/14 to body wall. Spermathecae (Fig. 1) consisting of broad ampulla attached to thick, sigmoid duct. On lateral face of duct, ovate diverticulum attached at its middle by short stalk. Some diverticula iridescent, no apparent internal divisions. Spermathecal orientation variable, sometimes erect and wrapped around esophagous, and others aimed posteriorly under esophagous.

Holotype.—Approximately 1 km east of west boundary of KPRNA, just south of Riley Co. line, in Geary Co., Kansas; thin, rocky soils of ridgetops under tallgrass prairie; 29 May 1981, Samuel W. James, USNM 101810.

Paratypes (4).—Approximately 1 km east of west boundary of KPRNA, just south of Riley Co. line, in Geary Co., Kansas; thin, rocky soils of ridgetops under tallgrass prairie; 29 May 1981, Samuel W. James, USNM 101811.

Remarks.—Specimens were taken from shallow, rocky soils (Florence silt loam) on ridgetops in the portion of KPRNA in Geary county. To date, *D. rugosa* is known to occur only in the higher ground. It and *D. smithii* McNab & McKey-Fender make up the bulk of native earthworm biomass in upland sites of KPRNA, where both are abundant. Specimens have also been found in upland prairie 8 kilometers south of Manhattan, Kansas, just east of Kansas highway 177 on KPRNA, in Riley County.

The epithet reflects the appearance given the worm by the ridges and protuberances associated with the spermathecal pores.

Affinities.—Regarding the clitellum as saddle-shaped, *D. rugosa* arrives at couplet 12 in Gates (1977), where it is seemingly his "sp. I." Gates' sp. I does not greatly resemble *D. rugosa* in the few characters given in Gates (1977), and it was collected in the Ouachita National Forest of Arkansas. Therefore I do not consider the two to be one species. Gates considers his sp. I to be very similar to *D. smithii.* Differences between *D. rugosa* and *D. smithii* include the larger size of the latter, characters of the penial setae, the prostomium, location of first dorsal pore, structure of the spermathecae, and openings of the spermathecal pores.

If the clitellum be considered annular, *D. rugosa* keys to *D. invecta* Gates, previously described from unknown locations in Texas and Mexico (Gates 1955, 1977). However, differences in penial setae, prostatic ducts, genital markings, and spermathecae prevent union of the two groups.

The following combination of characters is unique to *D. rugosa* among known members of the genus: last hearts in xii, no calciferous lamellae, quadrithecal with non-cryptate spermathecal ducts, spermathecal diverticulum attached by a short stalk, saddle-shaped clitellum, tanylobous prostomium, and intestinal origin in xvii.

Acknowledgments

The author thanks Edward Easton of the British Museum (Natural History) for invaluable assistance in the early stages of his study of the anatomy of *Diplocardias,* and William Fender for helpful suggestions on technique. Ted Barkley and Henry D. Blocker reviewed an early version of the manuscript.

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PROC. BIOL. SOC. WASH.
101(2), 1988, p. 308

THE CORRECT NAME OF *CERATODRILUS ORPHIORHYSIS* HOLT, 1960 (ANNELIDA: BRANCHIOBDELLIDA)

Perry C. Holt

Recently in the preparation of another paper on branchiobdellidans, my attention was again called to the misspellings in my paper on the genus *Ceratodrilus* Hall, 1914. In the title itself the word "Oligochaeta" (no longer applicable to the branchiobdellidans) is misspelled "Obligochaeta." The spelling "*orphiorhysis*" (Holt 1960:60) as the name of a species described therein and assigned to *Ceratodrilus* is an inadvertent error attributable to the failure of the editor to submit page proof of the paper in which it occurs to me after its setting in type; elsewhere in the paper (Holt 1960:60 et seq.) the name is spelled "*ophiorhysis*" as I intended. The name "*ophiorhysis*" is from the Greek and is intended to mean "Snake River."

Since it is unlikely that I will write again on the genus or its included species, it seems appropriate to take this means of correcting these errors. Acting as the first revisor (ICZN Article 32(b)(i)), I select *ophiorhysis* as the correct original spelling. The name *orphiorhysis* then becomes an incorrect original spelling (ICZN Article 32(c)(iv)).

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PARASTEPHOS ESTERLYI, A NEW SPECIES OF COPEPOD (STEPHIDAE: CALANOIDA: CRUSTACEA) FROM SAN DIEGO BAY, CALIFORNIA

Abraham Fleminger

Abstract.—*Parastephos esterlyi,* the third species of the genus, is described from San Diego Bay, California. It resembles *P. occatum* Damkaer but differs in its longer body, in the symmetrical and shorter genital segment having different armament including a pair of spines flanking the genital antrum, and in the details of the fifth legs in both males and females.

Copepods of the family Stephidae do not in general occur in routine zooplankton samples. Based on capture records and comments in the literature Damkaer (1971) suggests that they are hyperbenthic in habitat, living just above the sea floor in or near the neritic zone and on occasion swimming up into the water column. Three genera are known. *Stephos,* with about 19 described species and a distribution encompassing the northern and southern hemisphere, is the most diverse and widespread. The remaining two genera are based on isolated records of a few species from the northern hemisphere. *Parastephos* consists of *P. pallidus* Sars, reported from the Norwegian and Scottish coasts (Sars 1903; Scott 1903) and *P. occatum* Damkaer, from Dabob Bay and Puget Sound, Washington (Damkaer 1971). The genus *Miostephos* is also represented by two known species, one from Cuba, *M. cubrobex* Bowman (1976) and one from Bermuda, *M. leamingtonensis* Yeatman (1980). I now report a new species of *Parastephos* collected in routine plankton tows taken with an open conical net in shallow water (depth ~ 2 m) at the southern end of San Diego Bay, Chula Vista, California.

Parastephos esterlyi, new species
Figs. 1–19

Material examined.—A. 1 male, 1 female, San Diego Bay, 21 Mar 1979, 0120 hrs., 32°36.6′N, 117°06.3′W (net tow taken within intake channel of South Bay Electrical Generating Plant, Chula Vista, California). B. 1 male, San Diego Bay, 21 Oct 1979, 2246 hrs., 32°37′N, 117°07′W (net tow taken about 1.6 km west of South Bay Electrical Generating Plant, Chula Vista, California). C. 5 males, 9 females, 3 st. V copepodids, San Diego Bay, 23 Jan 1980, 2302 hrs., 32°37′N, 117°07′W (same locality as B above). Specimens deposited in the National Museum of Natural History (USNM), Washington, D.C.

Types.—Female holotype USNM 234190 selected from C above; paratypes, all remaining adult specimens, USNM 234191–234192.

Measurements.—See Table 1.

Description.—The new species is most similar morphologically to *P. occatum* though slightly larger in length and differing in details of the genital segment, in the length

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Abraham Fleminger died on 13 January 1988, before this paper was set for publication. His life's work was the systematics, biogeography, and evolution of marine copepods, and the curatorship of the Scripps Institution of Oceanography collection of zooplankton. The present contribution exemplifies the building blocks from which he synthesized larger structures.

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Table 1.—Measurements following procedures of Fleminger (1967).

	Total length, mm				Prosome-Urosome length ratio	
Adult	$\bar{x}$	Range	s	No.	Med.	Range
Female	1.267 ± 0.043 (95% CL)	1.14–1.33	0.0561	9	2.12:1	1.9–2.25:1
Male	1.225 ± 0.016	1.21–1.26	0.0177	7	2.33:1	2.19–2.55:1

of the first antenna relative to the urosome, and in the fifth pair of legs relative to the length of the urosome. All references to morphology of *P. occatum* and *P. pallidus* are based on published descriptions of the two species.

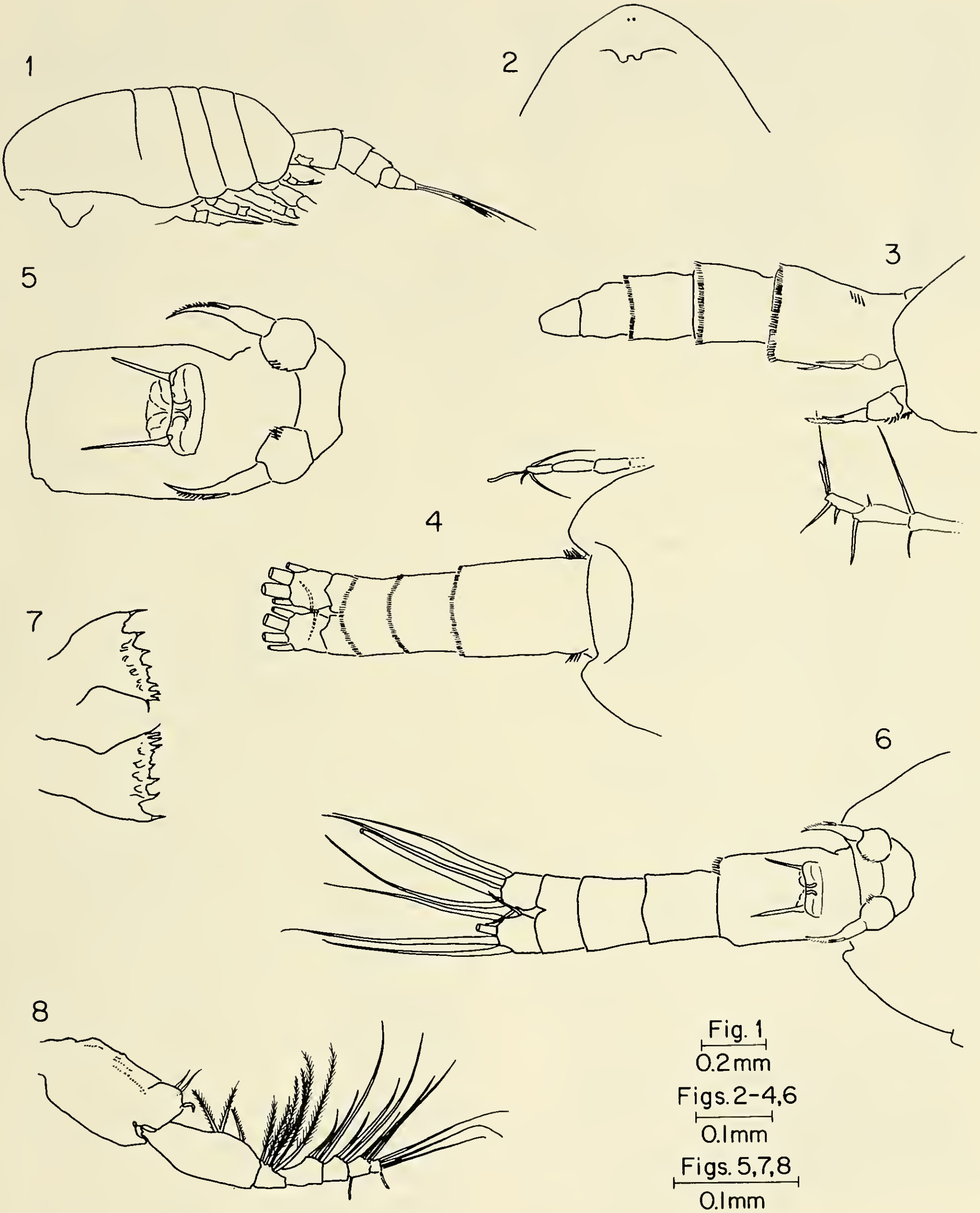
Female.—Cephalosome vaulted in lateral view (Fig. 1); rostrum without elongate filaments but indicated by pair of small knobs seen in ventral view (Fig. 2). Posteriormost pediger bearing leg pairs 4 and 5 with distal ends symmetrial and rounded in lateral view (Fig. 3). Urosome about half length of prosome, with 4 segments and caudal furca (Figs. 1, 3, 4); genital segment longest, being slightly shorter than combined lengths of urosome segments 2 and 3 (Figs. 1, 3, 4); in *P. occatum,* genital segment longer than combined lengths of urosome segments 2, 3 and 4. In dorsal view gential segment in new species virtually symmetrical, several fine hairs occur in anteroposterior row on either side of proximal end (Fig. 4); in dorsal view of *P. occatum* genital segment asymmetrical and with anterolateral semi-encircling ridge on both sides, bordered by row of fine spinules. In lateral view genital segment of new species not protuberant ventrally (Fig. 3) as in *P. occatum.* In ventral view genital antrum (genital opening) with pair of elongate spines of unequal length extending posteriorly from left and right posterior border of antrum beneath antrum's cover plate (Figs. 5, 6); these spines not reported in descriptions of *P. occatum* and *P. pallidus.* Setation of furcal rami as in *P. occatum,* 4 posteriorly directed setae, middle 2 being more robust, and a fifth short seta extending ventrally from medial border (Fig. 6).

First antenna with 24 segments; setation and aesthetasc number as in *P. occatum* but overall length shorter, reaching posteriad to midlength of genital segment (Figs. 3, 4) as in *P. pallidus;* first antenna in *P. occatum* reaches posteriad to anal segment.

Setation and morphology of other cephalic appendages similar to those of *P. occatum.* Small differences in appearance of gnathobase of mandible (Fig. 7) and maxilliped (Fig. 8) relative to those in *P. occatum* (Damkaer, 1971:fig. 2e) appear to reflect angle of view when figure of mandible was drafted and sexual differences in maxilliped, respectively.

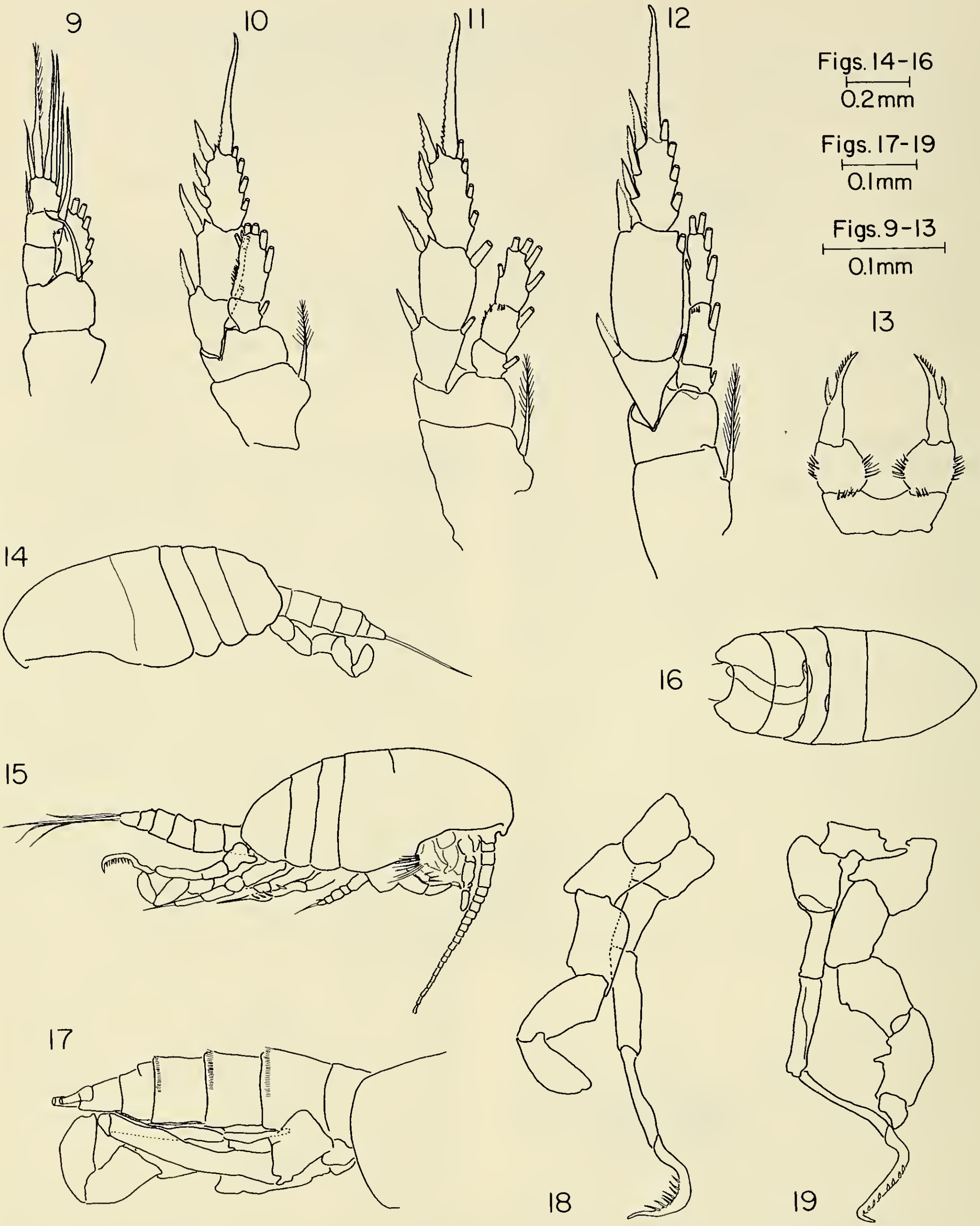
Meristics of swimming legs (Figs. 9–12) similar to those of *P. occatum;* small differences between the new species and *P. occatum* in spinules on rami (Figs. 10–12) compared to those shown by Damkaer (1971:fig. 3c–f) may be due to sexual as well as species differences. Fourth pair of legs symmetrical in all specimens, large second exopodal segment and relatively short third exopodal segment typical of all available specimens (Fig. 12).

Fifth pair of legs symmetrical (Fig. 13) resembling those in *P. occatum* but proportionally shorter, when extended posteriad reaching barely past midlength of genital segment (Fig. 3); in *P. occatum* fifth legs extend posteriad to reach distal end of urosome segment 2. In *P. pallidus,* fifth legs asymmetrical, longer left leg reaching beyond midlength of urosome segment 2. Segment 3 of fifth legs with lateral spine. Origin of lateral spine relative to length of segment 3 distinctive; in *P. esterlyi* slightly more than half the length of segment 3 lies distal to insertion of lateral spine (Fig. 13); in *P. occatum* more than two thirds of length of segment 3 lies distal to insertion of lateral



Figs. 1–8. *Parastephos esterlyi,* adult female: 1, Left, lateral; 2, Forehead, ventral; 3, Pediger 4–5, urosome, fifth legs, distal ends of first antennae, right lateral; 4, Pediger 4–5, urosome, distal ends of first antennae, dorsal; 5, Genital segment, fifth legs, ventral; 6, Pediger 4–5, urosome, fifth legs, ventral; 7, Gnathobase of mandible, posterior; 8, Right maxilliped, lateral.

spine; in shorter right leg of *P. pallidus* more than four fifths of length of segment 3 lies distal to insertion of lateral spine. Distal end of segment 3 with larger spinules along lateral margin, fewer smaller spinules along medial margin; lateral spine on segment 3 with spinules along medial and lateral margins.



Figs. 9–13. *Parastephos esterlyi,* adult female: 9, First swimming leg, posterior; 10, Second swimming leg, posterior; 11, Third swimming leg, posterior; 12, fourth swimming leg, posterior; 13, Fifth legs.

Figs. 14–19. *Parastephos esterlyi,* adult male: 14, Left, lateral; 15, Right, lateral; 16, Prosome, dorsal; 17, Pediger 4–5, urosome, fifth legs, right lateral; 18, Fifth legs, posterior; 19, Fifth legs, anterior.

Male.—Males and females overlap in prosome-urosome length ratios and in overall length. Adult male distinguished by short genital segment, 5-segmented urosome, and robust, elongate pair of fifth legs usually held in folded position parallel to ventral side of urosome and about as long as urosome (Figs. 14, 15, 17).

Relative length of first antenna slightly shorter than in female, reaching posteriad to pediger 4~5 (Fig. 15); in *P. occatum* male first antenna reaches to caudal furca; setation and aesthetasc number as in *P. occatum.*

Fifth pair of legs morophologically similar to that of *P. occatum* (Figs. 18, 19), differing primarily in being shorter in length of rami relative to length of urosome. Left leg in typical position (Fig. 17) with terminal segment 5 extended dorsad under distal end of caudal furca. Right leg usually folded, i.e., with distalmost segments 4 and 5 extended anteriad adjacent to posteriorly directed segments 1 to 3 (Fig. 17); right leg in folded position with distal end of segment 3 reaching anal segment; when fully extended distal half of segment 5 reaches beyond caudal furca (Fig. 15). In *P. occatum* left leg with segments 4 and 5 extending beyond caudal furca; folded right leg with distal end of segment 3 reaching distal end of caudal furca, when right leg extended posteriorly both segments 4 and 5 reach beyond caudal furca. Fifth legs in *P. pallidus* relatively short as in *P. esterlyi* but apex of terminal segment 5 of left leg pointed, and segment 3 of left leg bearing a lateral lobe in addition to more medial segment 4. In the new species apex of terminal segment of left leg rounded and segment 3 lacks lateral lobe (Fig. 18).

Etymology.—This species is named to honor C. O. Esterly and his pioneering studies on the copepods of the California Current. During the course of the first three decades of the 20th century Dr. Esterly was the first copepod specialist associated with the Southern California Marine Laboratory (Ritter 1912) that ultimately became the Scripps Institution of Oceanography.

Acknowledgments

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RECORDS OF CYCLOPOID AND HARPACTICOID COPEPODS (CRUSTACEA) FROM A SPRING IN WASHINGTON, D.C.

Janet W. Reid

Abstract.—The copepods *Acanthocyclops vernalis* (Fischer) and *Eucyclops agilis* (Koch) (Cyclopoida) and *Attheyella* (*Mrazekiella*) *illinoisensis* (S. A. Forbes) and *Attheyella* (*M.*) *spinipes* Reid (Harpacticoidea) were collected from a spring in Fort Mahan Park, Washington, D.C. Individuals of the Fort Mahan Park population of *A. spinipes* varied morphologically in some respects from the type population, described from a spring in Rock Creek Stream Valley Park, Maryland.

Messrs. Stephen W. Syphax and Bernard Raftery of the National Park Service brought a sample of leaves and detritus collected from a spring seepage at Fort Mahan, Washington, D.C., to Dr. Thomas E. Bowman, Department of Invertebrate Zoology, National Museum of Natural History (USNM), for determination of aquatic invertebrates present. In the sample was an amphipod, *Stygobromus tenuis* (Smith) (det. Dr. John R. Holsinger) and four species of copepods (Crustacea). Individuals of *Acanthocyclops vernalis* (Fischer) and *Attheyella* (*Mrazekiella*) *spinipes* Reid were abundant, and several individuals of *Eucyclops agilis* (Koch) and *Attheyella* (*M.*) *illinoisensis* were also present. The distribution of urosomal papillae and the spination formula in the specimens of *A. illinoisensis* agree with those of a male from a spring in Rock Creek Park, Maryland (Reid 1987). Some morphological variations of the Fort Mahan population of *A. spinipes* from the type population are described below.

Attheyella (*Mrazekiella*) *spinipes* Reid
Figs. 1–3

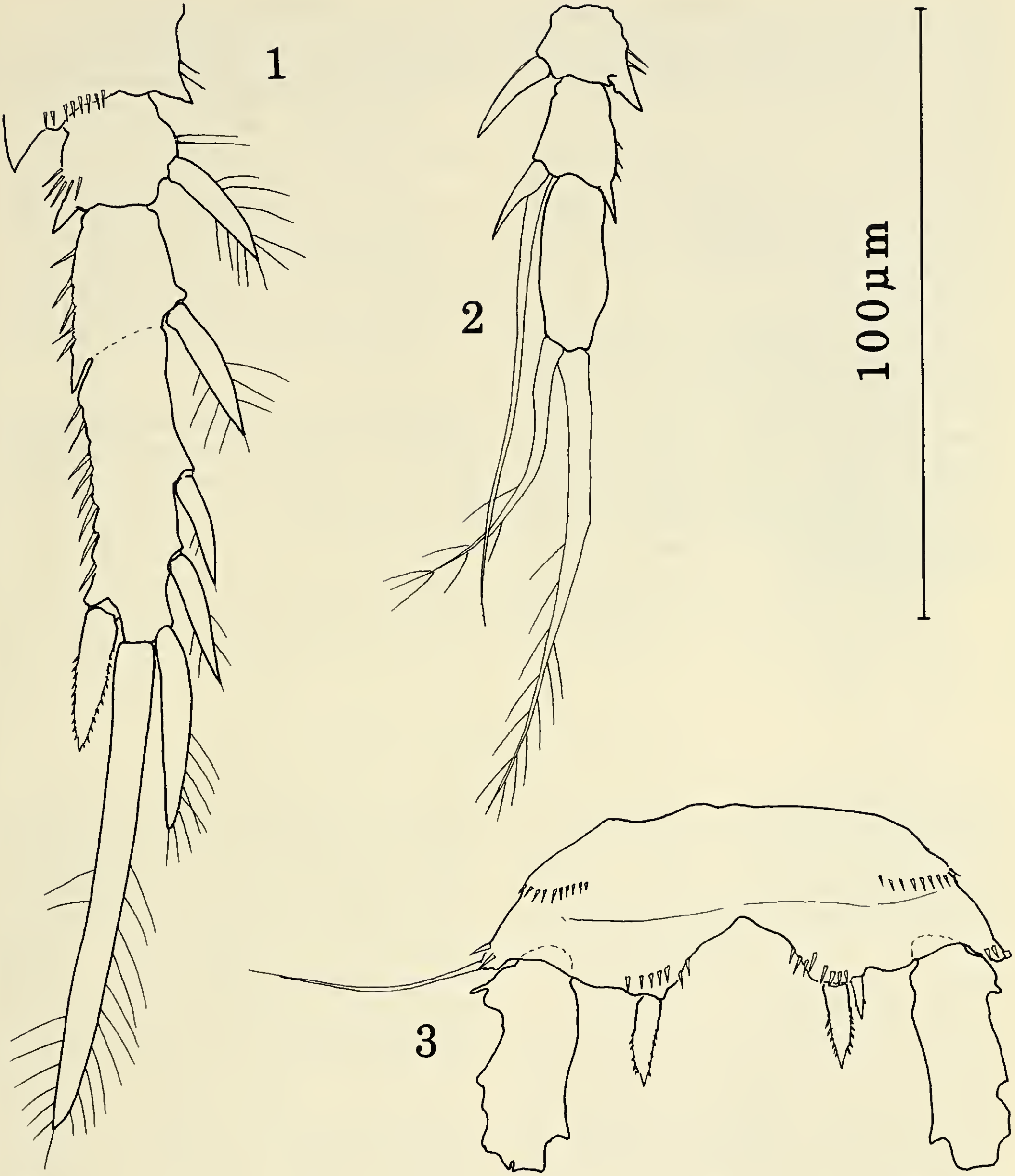
Material.—2 ♀ and 11 ♂, dissected, and 90+ ♀ and ♂, alcohol-preserved, USNM 234102. All collected 26 Jun 1987 by S. W. Syphax and B. Raftery from sediment and leaves in spring seepage at Fort Mahan Park, 42d and Clay Streets, S. E., Washington, D.C., 38°53′44″N, 76°56′34″W, in drainage basin of Watts Branch, an affluent of the Anacostia River.

Description.—Endopods of legs 2 and 3 of females and leg 2 of males appeared to consist of 2 articles only, since the joint (represented as a dotted line in Fig. 1) between articles 2 and 3 was visible indistinctly and only on the anterior surface. The acute distolateral process of article 2 was present in all specimens. If these endopods are taken to consist of 2 articles, the setation formula for major armament becomes, in the female:

Leg 2	enp 1–0; 3,1,1
Leg 3	enp 1–1; 3,2,1

In the population from the type locality, a spring in Rock Creek Park, Maryland (Reid 1987), these joints are distinct and the endopods clearly consist of 3 articles. No variability in major setation was observed in either population.

In all males from the Fort Mahan spring, endopods of leg 3 consist of 3 distinct ar-



Figs. 1–3. *Attheyella* (*Mrazekiella*) *spinipes* Reid, specimens from Fort Mahan spring: 1, Female: Leg 3, endopod, anterior; 2–3, Male: 2, Leg 3, endopod, posterior; 3, Leg 5, fused basipods, anterior.

ticles (Fig. 2). Article 2 bears a spine inserted posteriorly to the long slender apophysis. The apophysis bears 2 minute barbs near its tip; such barbs could not be distinguished in males from the type population. In most males from Fort Mahan, both terminal setae of leg 3 are bent medially.

A male from the type population bears 2 spines on the medial expansion of one basipod of leg 5, but only the larger medial spine on the other basipod. Of 11 dissected males from the Fort Mahan population, only 2 bear 2 spines on each basipod; 2 bear 1 spine on one basipod and 2 on the other; and 7 possess only 1 spine on each basipod. In each case, the stouter medial spine is retained. The fused basipods appear somewhat broader than previously interpreted, and bear rows of spinules on the ventral surface (Fig. 3).

Variability in major and minor armament and even articulation of swimming legs is common within species of harpacticoid copepods and more specifically in the genus *Attheyella* (Coker 1934; Wilson & Yeatman 1958). Workers should be aware of the possibility of such variability when making species determinations and when constructing keys.

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PHYLOGENETIC ANALYSIS OF THE EUDACTYLINIDAE (CRUSTACEA: COPEPODA: SIPHONOSTOMATOIDA), WITH DESCRIPTIONS OF TWO NEW GENERA

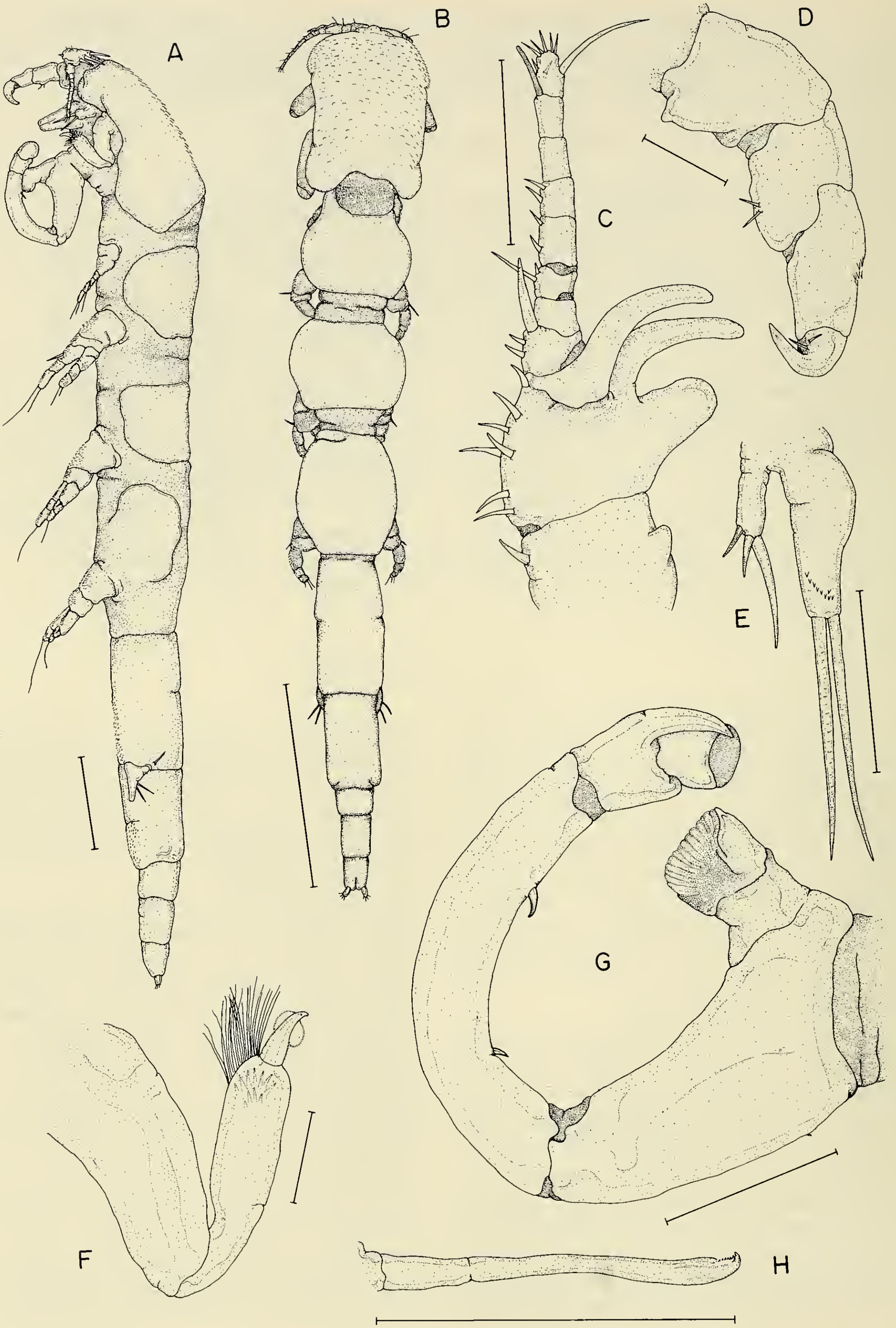
Gregory B. Deets and Ju-shey Ho

Abstract.—Specimens of representative species of eudactylinid genera were reexamined and some (*Eudactylinodes niger, Eudactylinella alba*) redescribed. *Eudactylinodes uncinata* (Wilson, 1908) is relegated to a junior synonym of *E. niger.* Two new genera (*Carnifossorius* and *Heterocladius*) are described based on newly collected material. Analysis of 90 morphological characters revealed that the eudactylinids, a family of siphonostomatoid copepods parasitic on elasmobranchs, have colonized telosts twice since their association with elasmobranch hosts. *Jusheyus* represents the invasion of Perciformes, and *Heterocladius* of Salmoniformes. The same phylogenetic analysis suggests that *Protodactylina* is a valid genus; it represents the most primitive eudactylinid occurring on one of the most primitive families of extant elasmobranch. *Bariaka* and *Nemesis* are sister taxa on a clade that occurs predominantly on Lamniformes and Carcharhiniformes. *Eudactylina* and *Eudactylinodes* are sister taxa on a clade infecting a systematically broader range of hosts. *Eudactylinella, Eudactylinopsis,* and *Carnifossorius* belong to a clade specific to Rajiformes.

In 1979, Kabata redefined the family Eudactylinidae and removed from it *Kroyeria* van Beneden, 1853 and *Kroeyerina* Wilson, 1932,to form a new family called Kroyeriidae. The revised Eudactylinidae then consisted of seven genera, namely, *Bariaka* Cressey, 1966; *Eudactylina* van Beneden, 1853; *Eudactylinella* Wilson, 1932; *Eudactylinodes* Wilson, 1932; *Eudactylinopsis* Pillai, 1966; *Nemesis* Risso, 1826; and *Protodactylina* Laubier, 1966.

These two families of siphonostomatoid copepods, consisting of nearly 60 species, have been considered parasites of elasmobranchs. They live amongst the gill or nasal lamellae of their hosts. However, in the early 1980's, one of us (JSH) discovered a new eudactylinid amongst several lots of parasitic copepods that had been recovered from deep-sea teleosts (Ho 1985), and recently, Deets & Benz (1987) reported another eudactylinid from a species of Australian sea bass. Therefore, we attempt in this report to elucidate the phylogenetic relationships between these teleost-parasitizing and elasmobranch-parasitizing eudactylinids through a phylogenetic analysis employing the cladistic approach.

When Wilson (1932) proposed the family Eudactylinidae, he included in it two new genera, *Eudactylinella* and *Eudactylinodes.* Since the type species of these two genera have never been adequately characterized, we reexamined the type specimens of *Eudactylinella alba* Wilson, 1932 and *Eudactylinodes niger* (Wilson, 1922) which are deposited in the U.S. National Museum of Natural History. Redescriptions of these two species are included in this report, because they are part of the necessary source for extracting information to conduct the proposed phylogenetic analysis. While working on this project, another new form of eudactylinid was discovered from a Siamese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rhinobatid in the collection of the California Academy of Science in San Francisco. The description of this new genus together with the one from a deep-sea teleost will be given in the following before discussing the phylogenetic analysis of the eudactylinid genera.

Eudactylinodes niger (Wilson, 1905)
Figs. 1–2

Material examined.—USNM 54071, containing 19 paratypes from gills of sand shark, *Eugomophodes littoralis,* collected at Woods Hole, Massachusetts, July, 1902.

Female.—Body (Figs. 1A, B) bearing denticles on dorsal surface of cephalothorax, anterior surface of legs 1–4, and ventral surface of 5th pediger. Cephalothorax distinctly longer than wide; carapace with emarginate posterior margin and lateral sides. First 3 free somites about as wide as cephalothorax, 5th pediger distinctly narrower and notched laterally. Genital complex longer than wide, with posterodorsally located oviducal openings. Abdomen 3-segmented, middle segment largest. Caudal ramus (Fig. 2B) small, bearing 5 elements: 1 setiform (inner subterminal) and 4 spiniform.

First antenna (Fig. 1C) 10-segmented, divisible into robust base (2 segments) and slender shaft (8 segments). First segment with 1 small seta on anterior margin and 1 thumb-like process on posterior surface. Second segment produced posteriorly into a large blunt process bearing 2 large, curved hooks on terminal surface and 7 small setae on anterior margin. Armature of 8-segmented shaft part: 2+1 spine, 0,2,2,2,0,1 aesthete, and 8. Second antenna (Fig. 1D) 3-segmented; first segment unarmed, second segment with 2 inner setae, third segment armed distally with large hook bearing 2 basal setae. Patch of denticles on mid-outer surface of third segment. Mandible (Fig. 1H) indistinctly 2-segmented, cutting blade armed with very fine teeth. First maxilla (Fig. 1E) biramous, with large endopod carrying 2 long setae and small exopod tipped by 1 long and 2 short setae. Second maxilla (Fig. 1F) 2-segmented; basal segment (lacertus) unarmed, but distal segment (branchium) armed terminally with subterminal cluster of long, thin bristles and another cluster of denticles; calamus a hook with lateral hyaline membranes. Maxilliped (Fig. 1G) 3-segmented, chelate, powerful (Fig. 1A). Basal segment small. Middle segment (corpus) with its myxa enlarged to form mitt-like receptacle. Terminal segment (subchela) long and arched, shaft bearing subterminal inner seta and claw with enlarged base carrying below hook a hollowed terminal piece.

Legs 1–4 biramous, with 3-segmented rami, their spines (Roman numerals) and setae (Arabic numerals) as follows:

Leg 1	Prp	0-0; 1-0	Exp	1-0; 1-0; 4
			Enp	0-I; 0-2; 5
Leg 2	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-I; 0-0; 4
Leg 3	Prp	0-0; 1-0	Exp	I-0; I-0; II,1
			Enp	0-1; 0-0; I,2
Leg 4	Prp	0-0; 1-0	Exp	I-0; I-0; II,1
			Enp	0-I; 0-0; I,2

Leg 1 exopod (Fig. 2A) smaller than endopod. Outer surface of leg 1 endopod bearing irregular protrusion near base. Outer distal corners of first 2 segments in leg 1 endopod produced into spiniform process. Similar spiniform process also developed in first segment of leg 2 endopod (Fig. 2C) and leg 3 endopod (Fig. 2D). Leg 4 similar to

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←

Fig. 1. *Eudactylinodes niger* Wilson, female: A, Habitus lateral; B, Habitus dorsal; C, First antenna; D, Second antenna; E, First maxilla; F, Second maxilla; G, Maxilliped; H, Mandible. Scales: 0.3 mm in A; 0 mm in B; 0.1 mm in C, G, H; 0.5 mm in D, E, F.

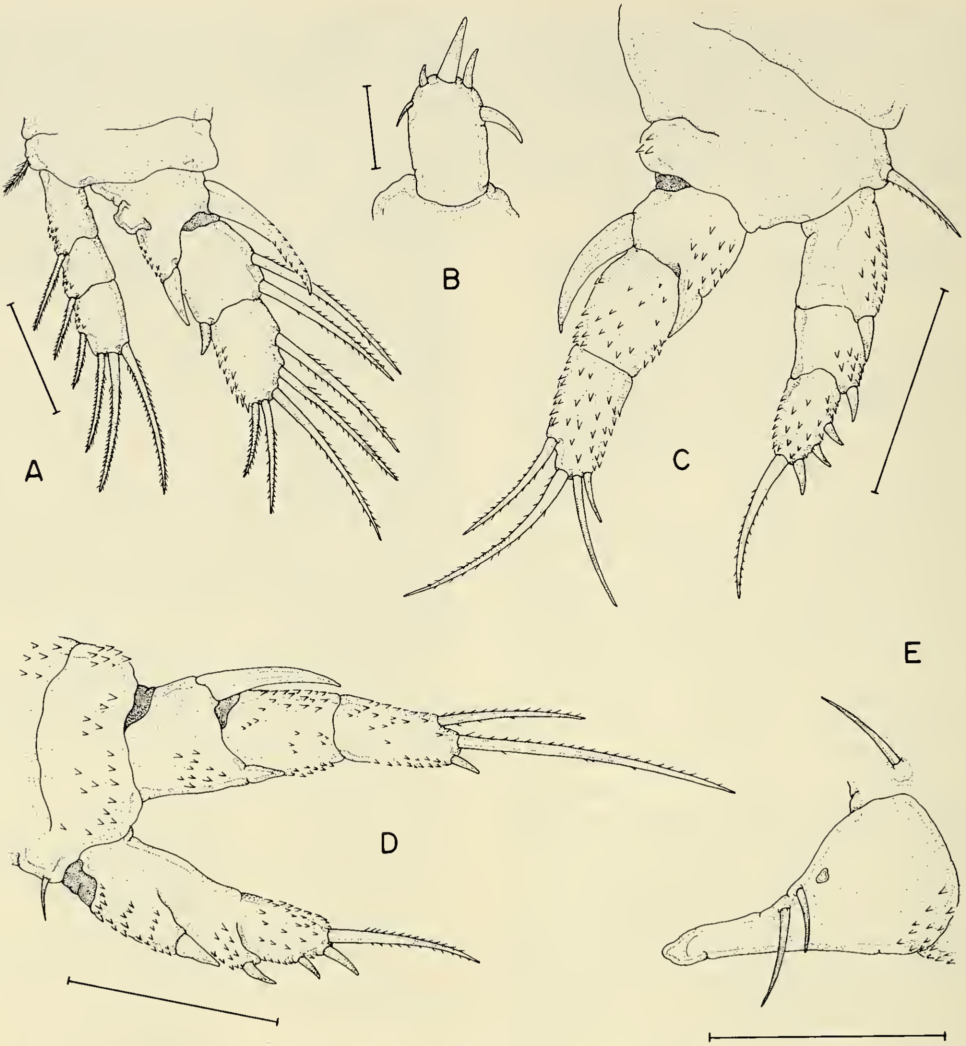

Fig. 2. *Eudactylinodes niger* Wilson, female: A, Leg 1; B, Caudal ramus; C, Leg 2; D, Leg 3; E, Leg 5. Scales: 0.05 mm in A; 0.02 mm in B; 0.1 mm in C, D, E.

leg 3, both with partly fused proximal segments in exopod (Fig. 2D). Free segments of leg 5 (Fig. 2E) carrying on dorsal surface 1 small spiniform process and 2 setae.

Male.—Not represented in USNM collection.

Remarks.—Since the gender of *Eudactylinodes* is masculine and *nigra* is feminine, it is mandatory to change the species name to the masculine, *niger.*

This species was first described by Wilson (1905) without illustrations. However, when it was redescribed with a set of illustrations (Wilson 1922), a pair of strange spines were shown coming off the posterior corners of the carapace. Curiously, this pair of spines were not mentioned in the text, neither in the original nor in the subsequent redescription. Nevertheless, in 1932, Wilson used this curious pair of spines as a major species distinction to separate the two species of his newly proposed genus, *Eudactylinodes.*

Through the assistance of Dr. Masahiro Dojiri we learned that the remaining specimens of *E. niger* deposited in the National Museum of Natural History (USNM 54070 and 54072) do not carry such spines either. Furthermore, reexamination of specimens in the type-lot of *E. uncinata* (Wilson, 1908) (USNM 38558: "from the gills of the soupfin shark, *Galeorhinus zyopterus* at La Jolla, California") revealed no significant morphological distinctions between it and *E. niger.* Therefore, we propose to relegate *E. uncinata* to a junior synonym of *E. niger.* Recently, Deets and Benz (1986a) described a new species of *Eudactylinodes, E. keratophagus,* from two species of horn sharks from off southern California and Baja California.

Eudactylinella alba Wilson, 1932
Figs. 3–6

Material examined.—USNM 5667, containing 3 females and one male taken from gills and nostrils of a sting ray, *Dasybatus marinus,* collected on Marthas Vineyard, Massachusetts, July, 1926.

Female.—Body (Fig. 3A) with distinct tagmosis. First pediger forming intersegmental area between cephalosome and second pediger, latter largest somite of body. Fifth pediger distinctly wider than long. Genital complex distinctly longer than wide, covered with spinules on ventral surface; genital opening on dorsolateral surface near anterior margin. Abdomen 2-segmented, both somites bearing spinules on ventral surface. Caudal ramus about 1.5 times longer than wide, bearing 6 elements as shown in Fig. 4E.

First antenna (Fig. 3C) 11-segmented, first and second segments partly fused. Armament of these segments: 1, 2, 2, 2, 1, 3, 1, 4, 1, 1+1 aesthete, and 10. Second antenna (Fig. 3B) 3-segmented; first segment unarmed second segment with 1 seta and anterodistal patch of denticles, third segment with anterobasal patch of denticles. Terminal claw with 2 basal setae. Mandible (Fig. 3G) bearing 8 teeth on cutting blade. First maxilla (Fig. 3F) biramous; endopod with denticles, tipped with 2 setae bearing spinules; exopod a long, bluntly pointed process carrying 2 short setae at about midlength. Second maxilla (Fig. 3D) 2-segmented; lacertus bearing small, proximal process and brachium, patch of denticles, tufts of bristles and terminal claw with two rows of fine denticles. Maxilliped 3-segmented (Fig. 3A), with huge basal segment. Corpus maxillipedis not swollen, its myxa bearing small spiniform process. Subchela an uncinate, single claw.

Legs 1–4 biramous, with 3-segmented rami, their spines (Roman numerals) and setae (Arabic numerals) as follows:

Leg 1	Prp	0-0; 1-I	Exp	I-0; I-0; IV
			Enp	0-0; 0-0; I
Leg 2	Prp	0-0; 0-0	Exp	I-0; I-0; III,I
			Enp	0-0; 0-0; 0
Leg 3	Prp	0-0; 0-0	Exp	I-0; I-0; III,I
			Enp	0-0; 0-0; I
Leg 4	Prp	0-0; 0-0	Exp	I-0; I-0; III,I
			Enp	0-0; 0-0; I

Outer-distal corners of endopodal segments in Leg 1 (Fig. 4A) protruded into small spiniform process. Third endopodal segment of leg 2 (Fig. 4B) a stout spiniform process with serrate outer edge; second segment of same ramus protruded distolaterally into large, bifid process. Leg 3 (Fig. 4C) and leg 4 (Fig. 4D) rather alike in segmentation and armature, both with first endopodal segment greatly protruded. Leg 5 (Fig. 4F) broad, sparsely covered with denticles and armed with 2 terminal setae and 1 subterminal seta.

Male.—Body (Fig. 5A) more slender than female; with much reduced fifth pediger. Genital somite wider anteriorly, with several rows of spinules on posterior part of ventral surface. Abdomen 4-segmented, each somite bearing spinules on ventral surface. Caudal ramus (Fig. 6G) about 2.4 times

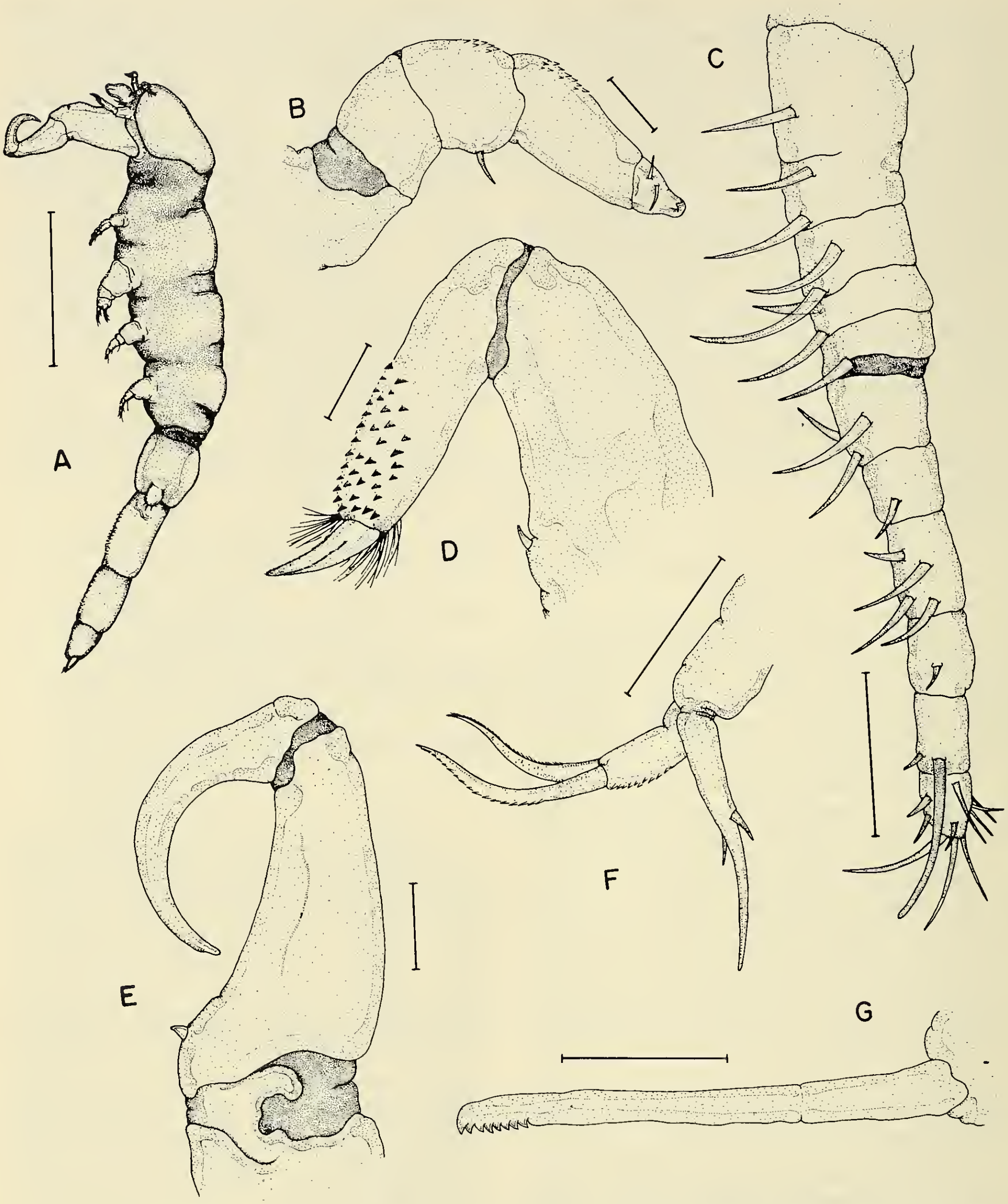

Fig. 3. *Eudactylinella alba* Wilson, female: A, Habitus lateral; B, Second antenna; C, First antenna; D, Second maxilla; E, Maxilliped; F, First maxilla; G, Mandible. Scales: 1 mm in A; 0.1 mm in E; 0.5 mm in B, C, D, F, G.

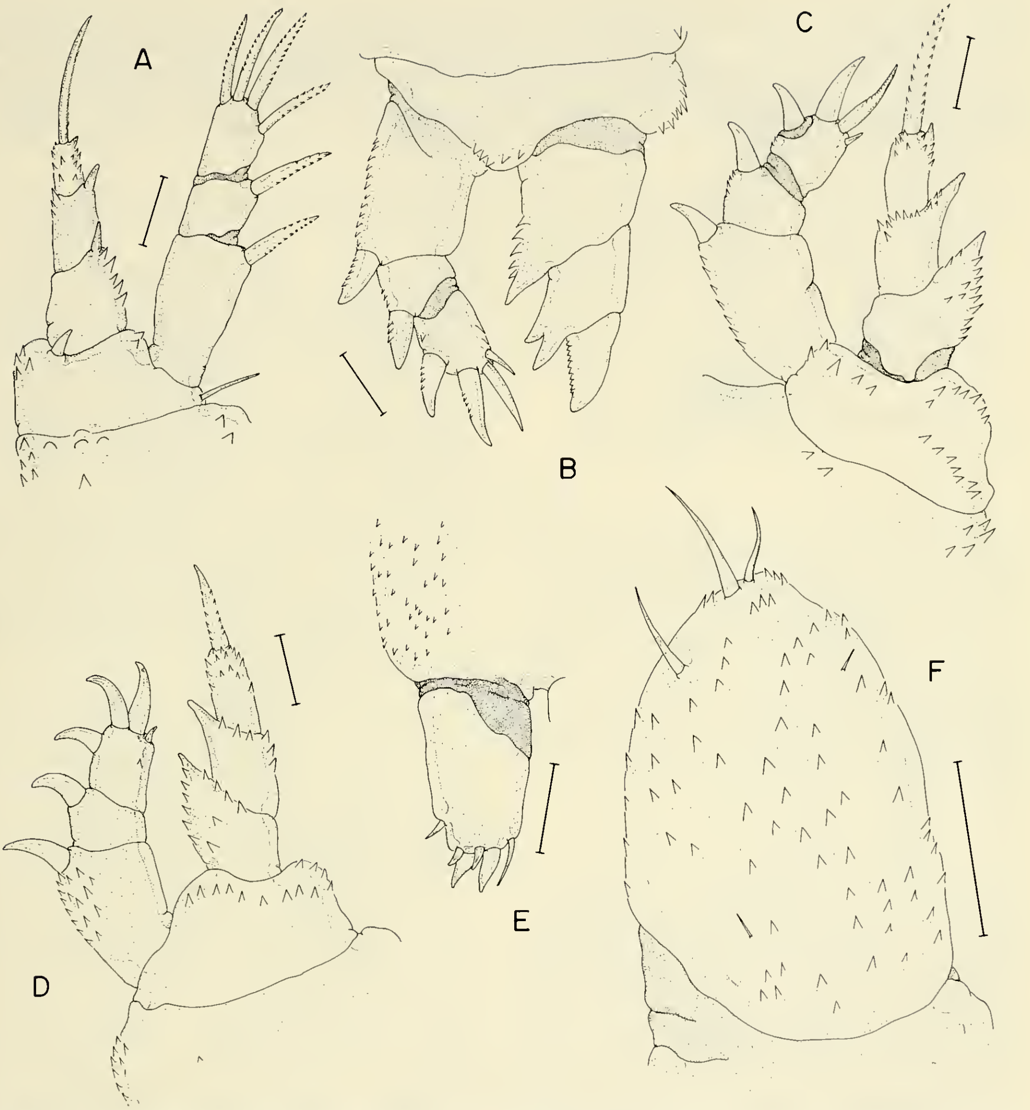

Fig. 4. *Eudactylinella alba* Wilson, female: A, Leg 1; B, Leg 2; C, Leg 3; D, Leg 4; E, Caudal ramus; F, Leg 5. Scales: 0.05 mm in A–F.

longer than wide, carrying 3 small, simple setae and 3 long plumose, terminal setae.

First antenna (Fig. 5B) geniculate, 15-segmented. Armature of these segments: 1, 2, 2, 5, 2, 1, 8, 1, 2, 2, 3, 3, 3, 1+1 aesthete, and 8. Second antenna (Fig. 5C) slender, 3-segmented; first and third segments unarmed but second segment bearing 2 setae on swollen inner surface; terminal claw with 2 basal setae. Mandible (Fig. 5G) as in female. First maxilla (Fig. 5E) resembling that in female, except for fine ornamentation on endopod. Second maxilla (Fig. 5D) different from female in lacking basal element on lacertus. Maxilliped (Fig. 5F) showing sexual dimorphism in ornamentation on corpus and 2 small spiniform processes on subchela.

Formulae of spines (Roman numerals) and setae (Arabic numerals) on legs 1–4 (Figs. 6A–D) as follows:

Leg 1	Prp	0-0; 1-1	Exp	I-1; I-1; I,5
			Enp	0-1; 0-1; 5
Leg 2	Prp	0-0; 1-0	Exp	I-1; I-1; II,1,4
			Enp	0-1; 0-1; 6
Leg 3	Prp	0-0; 1-0	Exp	I-1; I-1; I,5
			Enp	0-1; 0-2; I,3
Leg 4	Prp	0-0; 1-0	Exp	I-1; I-1; II,4
			Enp	0-1; 0-2; I,2

Leg 5 (Fig. 5F) reduced; free segment tipped with 3 simple setae. Leg 6 (Fig. 5E) represented by 3 small setae at posterolateral corner of genital complex (see Fig. 5A).

Remarks.—Since its original report, *E. alba* has been recorded from sting rays in Gulf of Mexico (Bere 1936), off Beaufort, North Carolina (Pearse 1948), and in the Mediterranean (Essafi and Raibaut 1977).

Heterocladius, new genus

Female.—Cephalothorax including first pediger, covered by a dorsal shield, remaining part of prosome consisting of second, third, and fourth pedigers, each with well developed tergum. Urosome consisting of fifth pediger, genital complex, and 2-segmented abdomen. Caudal rami absent. First antenna straight, 10-segmented. Second antenna 3-segmented, with uncinate terminal claw. Oral appendages generally as in *Eudactylina.* First 4 pairs of legs biramous, exopods distinctly shorter than endopods; rami 2- to 3-segmented. Fifth leg with one free segment.

Parasitic on gill of teleosts.

Male.—Unknown.

Type species.—*Heterocladius abyssetes,* n. sp.

Etymology.—The generic name is a combination of the Greek *heter* (=other, different) and *clad* (=a branch, sprout), alluding to the occurrence of this parasite on teleosts and not on elasmobranchs as in most other members of the Eudactylinidae. Gender masculine.

Heterocladius abyssetes, new species
Figs. 7–8

Material examined.—1 female (Holotype, USNM 204952) on gill of an *Alepocephalus agassizi* collected at 39°13′N, 71°53′W (1919–1974 m) on 18 Nov 1973. Appendages of holotype removed and mounted on slide, also deposited in USNM.

Female.—Body (Fig. 7A, B) with slightly swollen metasome. Cephalothorax covered by large dorsal shield with prominent lateral notches. Two abdominal somites narrower than genital complex (Fig. 8F). Egg sac (Fig. 8G) uniseriate, nearly as long as body. Total length of body 2.33 mm.

First antenna (Fig. 7C) 10-segmented, armature of these segments: 0, 3, 0, 3, 0, 1, 4, 0, 1, and 9. Second antenna (Fig. 7E) 3-segmented: basal segment small and unarmed; middle segment enlarged and carrying subterminally on medial surface an articulated process tipped with seta; distal segment unarmed. Terminal claw bearing stout seta at base. Mandible (Fig. 7D) 2-segmented, cutting blade armed with 8 teeth. First maxilla (Fig. 7F) biramous: endopod large, tipped with 2 long setae; exopod a pointed process bearing barb at about midpoint. Second maxilla (Fig. 7G) 2-segmented: lacertus large, but unarmed; brachium beaing subterminally a tuft of bristles. Terminal claw (Fig. 7H) armed with several rows of teeth. Maxilliped (Fig. 7I) subchelate and 3-segmented; basal segment large; corpus robust, myxa protruded into large stout spine, and bearing small, medial spiniform process; subchela armed with 3 spiniform processes on medial surface.

Legs 1–4 (Figs. 8A–D) biramous, their spines (Roman numerals) and setae (Arabic numerals) as follows:

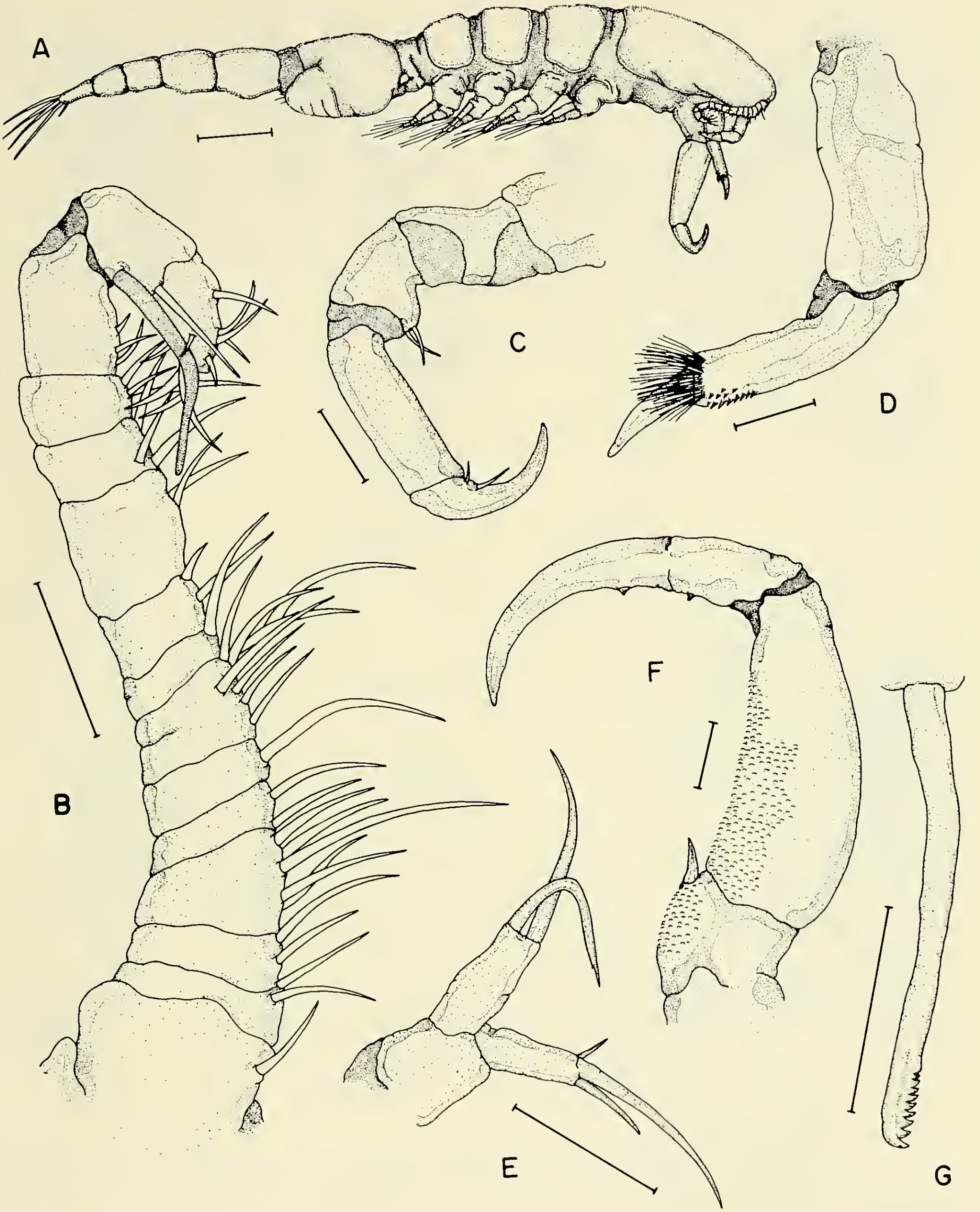

Fig. 5. *Eudactylinella alba* Wilson, male: A, Habitus lateral; B, First antenna; C, Second antenna; D, Second maxilla; E, First maxilla; F, Maxilliped; G, Mandible. Scales: 0.2 mm in A; 0.05 mm in B–G.

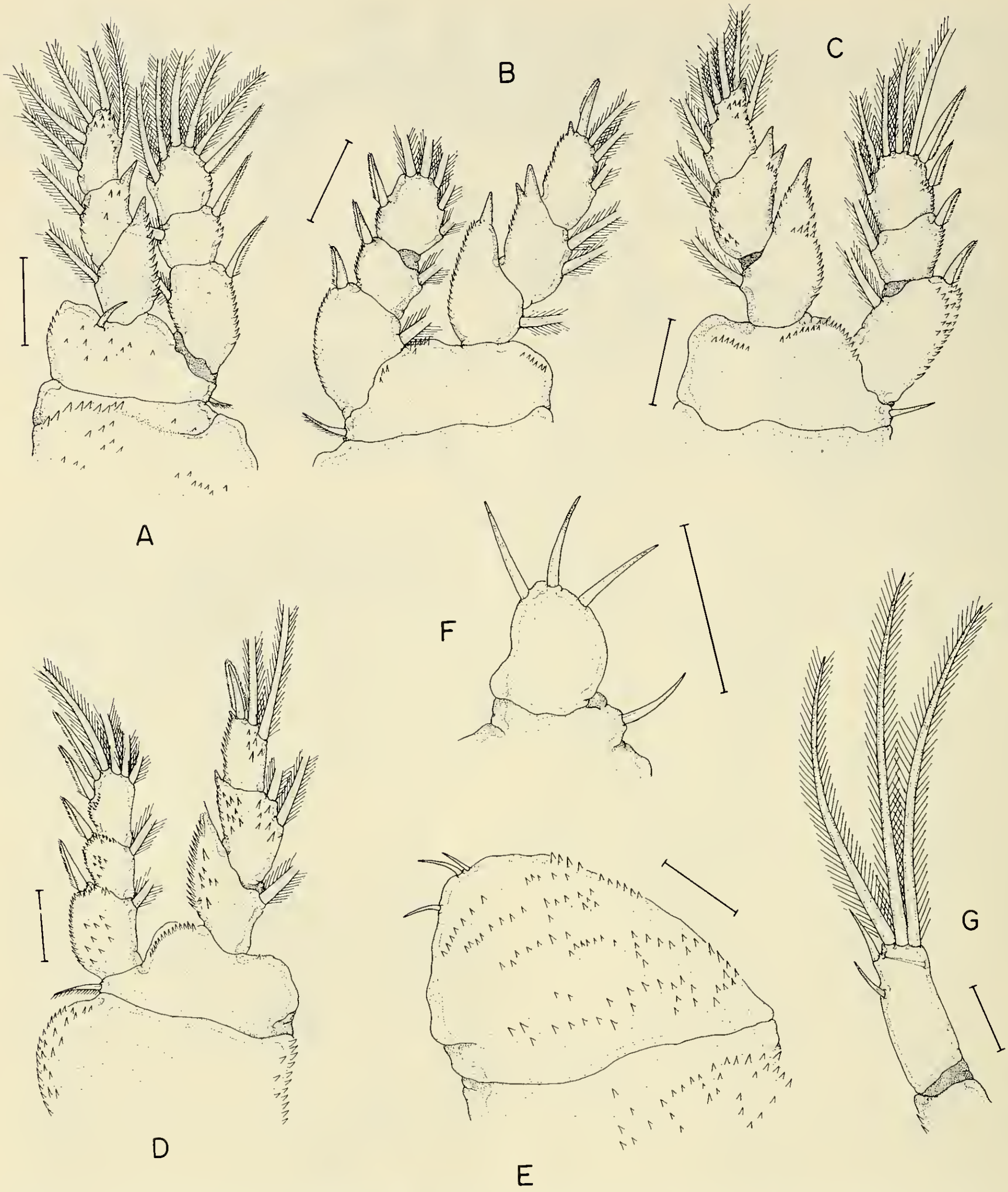

Fig. 6. *Eudactylinella alba* Wilson, male: A, Leg 1; B, Leg 3; C, Leg 2; D, Leg 4; E, Leg 6; F, Leg 5; G, Caudal ramus. Scales: 0.05 mm in A–G.

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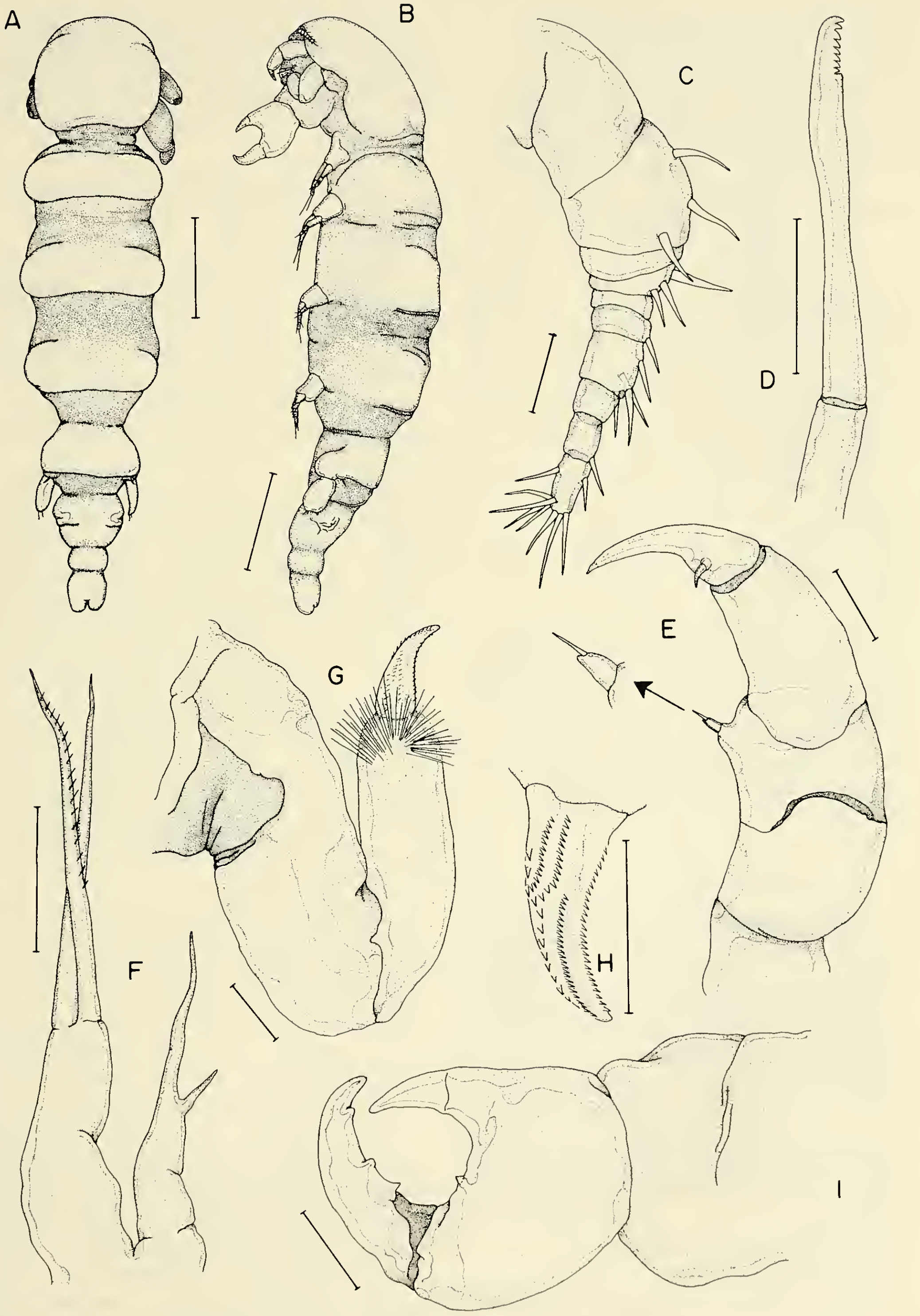
Fig. 7. *Heterocladius abyssetes,* n. gen., n. sp., female: A, Habitus dorsal; B, Habitus lateral; C, First antenna; D, Mandible; E, Second antenna; F, First maxilla; G, Second maxilla; H, Tip of second maxilla; I, Maxilliped. Scales: 0.5 mm in A, B; 0.1 mm in C, I; 0.05 mm in D–H.


A
B
C
D
E
F
G
H
I

Leg 1	Prp	0-0; 1-0	Exp	I-0; I-0; I,5
			Enp	0-I; 0-1; I,5
Leg 2	Prp	0-0; 1-0	Exp	I-0; I-0; II,4
			Enp	0-I; 0-I; I,5
Leg 3	Prp	0-0; 1-0	Exp	I-0; I-0; II,4
			Enp	0-I; 0-1; I,3
Leg 4	Prp	0-0; 1-0	Exp	I-0; II,3
			Enp	0-I; 0-1; I,2

Exopod smaller than endopod in all legs and inner element on first endopodal segments always a large spine. Proximal 2 segments of first exopod incompletely fused (see Fig. 8A) but fourth exopod distinctly 2-segmented. Fifth leg (Fig. 8E) bearing 3 small terminal setae on free segment.

Etymology.—The specific name is a combination of the Greek *abyss* (=deep, bottomless) and *etes* (=a suffix meaning "to dwell"), alluding to its occurrence on a deep-sea host.

Remarks.—This new form of eudactylinid is characterized by the following features: (1) 10-segmented first antenna, (2) basal segments of first exopod partly fused, (3) terminal segment of third endopod armed with 1 spine and 3 setae, and (4) leg 4 with 2-segmented exopod and 3-segmented endopod.

Carnifossorius, new genus

Female.—Body greatly elongated and cylindrical, with leg 1 located far behind maxillipeds. Fifth pediger fused with genital complex and greatly elongated. Abdominal segments fused into long cylinder. Caudal ramus carrying 6 reduced elements. First antenna indistinctly 10-segmented. Second antenna 3-segmented, slender, and weak. Oral appendages generally as in *Eudactylina.* First four pairs of legs biramous, with 3-segmented rami. Fifth leg reduced to tuft of 4 setae.

Mesoparasite of guitarfish.

Male.—Unknown.

Type-species.—*Carnifossorius siamensis,* n. sp.

Etymology.—The generic name is a combination of the Latin *Carn* (=flesh) and *fossor* (=a digger), aluding to its unusual manner of borirng into the host's tissue. Gender masculine.

Carnifossorius siamensis, new species

Figs. 9–10

Material examined.—Several females embedded in branchial septa and walls of buccal cavity of 2 female *Rhina ancylostoma* collected during NAGA Expedition in May, 1961 to Gulf of Siam, Thailand. Holotype (CASIZ 057395) deposited in California Academy of Science, where the hosts were kept.

Female.—Body (Fig. 9A) greatly elongated and divisible into 3 regions: anterior region consisting of prosome with much elongated first pediger; middle region consisting of prolonged fifth pediger and gential complex; posterior region consisting of elongate, fused abdominal somites. Cephalosome bulbous, wider than long. Distinct construction in anterior region between third and fourth pedigers. Egg sac attachment area located lateroventrally near posterior end of middle region. Abdomen unsegmented. Caudal ramus (Fig. 10G) small, tipped with 6 elements. Total length of body 6.84 mm (6.58–6.95 mm).

Rostrum prominent, with ventrolateral protrusion serving as base for first antenna (Figs. 9D, E). First antenna (Fig. 9E) indistinctly 10-segmented, armament of these segments: 1, 2, 1, 2, 2, 1, 3, 2, 2+1 aesthete, and 13. Base of first antenna bearing thumb-like protuberance (see Fig. 9E). Second antenna (Fig. 9F) relatively small, feeble, and 3-segmented; both basal and terminal segments unarmed, but middle segment carrying seta; terminal claw with 2 setae at base. Mandible (Fig. 9H) short, with 9 teeth on cutting blade. First maxilla (Fig. 10A) biramous: endopod robust, tipped with 2 setae; exopod a pointed process bearing 2 small setae at about midlength. Second maxilla

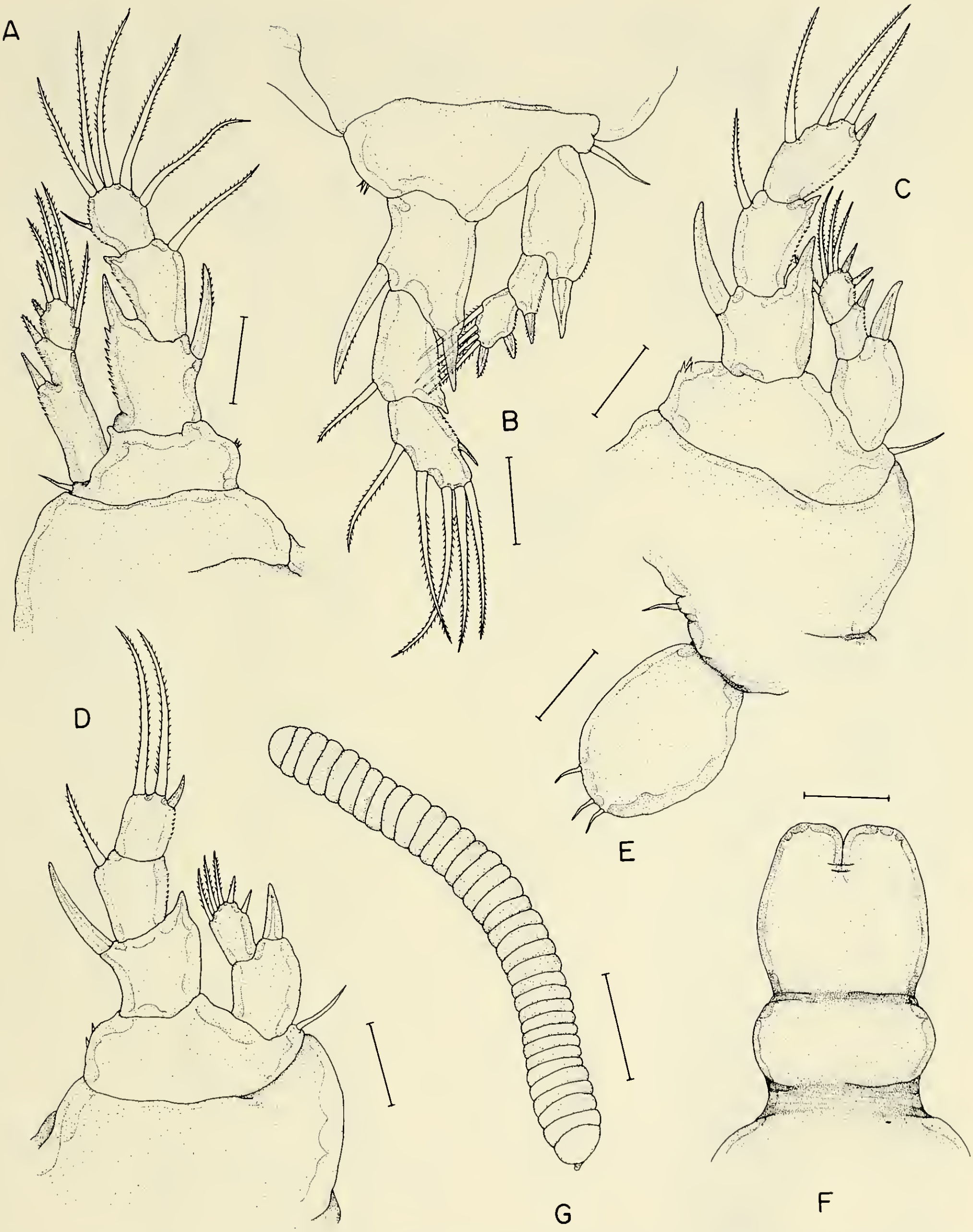


Fig. 8. *Heterocladius abyssetes,* n. gen., n. sp., female: A, Leg 1; B, Leg 2; C, Leg 3; D, Leg 4; E, Leg 5; F, Abdomen; G, Egg sac. Scales: 0.05 mm in A–D; 0.1 mm in E, F; 0.5 mm in G.

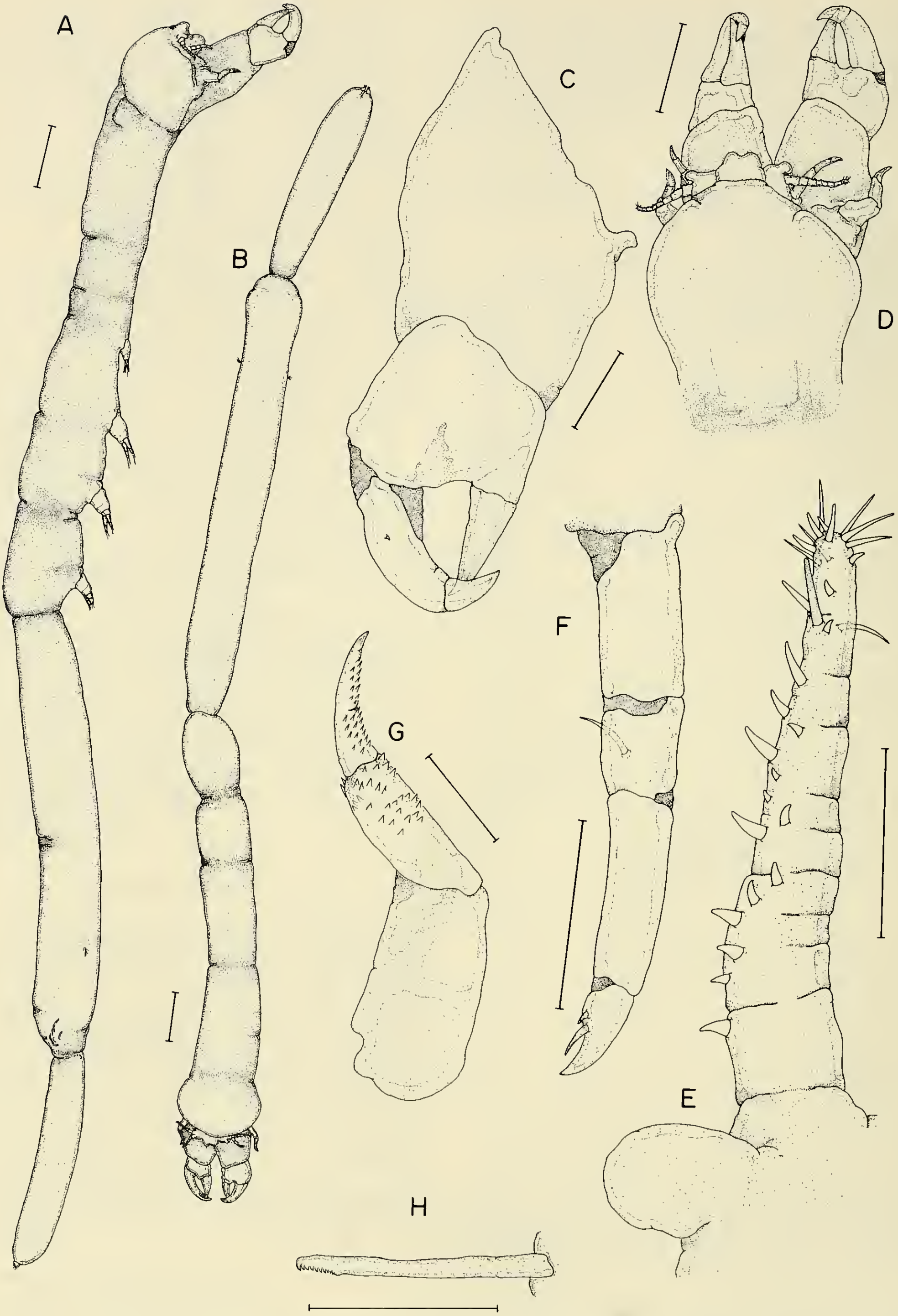


Fig. 9. *Carnifossorius siamensis,* n. gen., n. sp., female: A, Habitus lateral; B, Habitus dorsal; C, Maxilliped; D, Cephalothorax dorsal; E, First antenna; F, Second antenna; G, Second maxilla; H, Mandible. Scale: 0.1 mm in A–C; 0.2 mm in D; 0.05 mm in E–H.

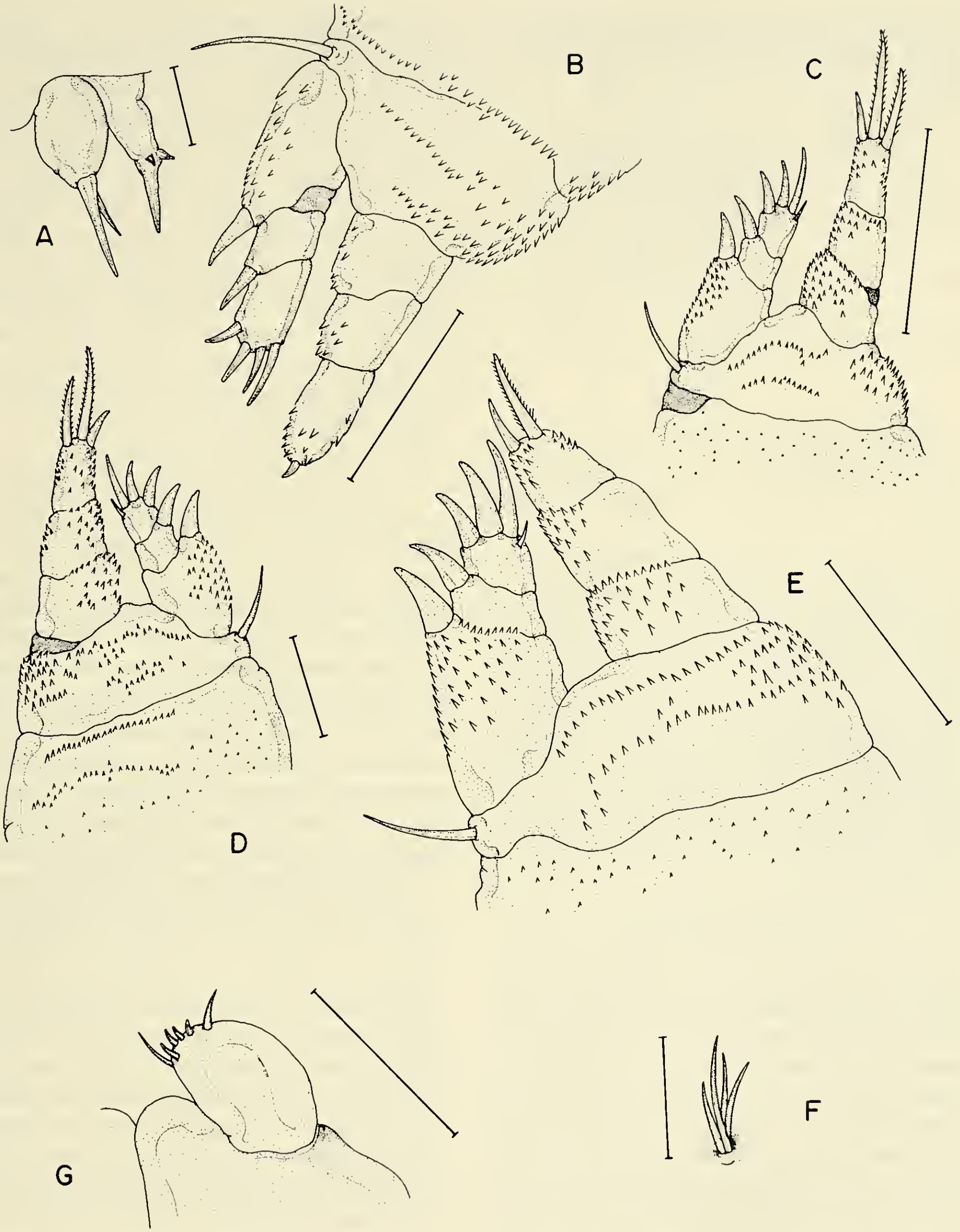


Fig. 10. *Carnifossorius siamensis*, n. gen., n. sp., female: A, First maxilla; B, Leg 1; C, Leg 2; D, Leg 3; E, Leg 4; F, Leg 5; G, Caudal ramus. Scales: 0.02 mm in A; 0.1 mm in C; 0.03 mm in F; 0.05 mm in B, D, E, G.

(Fig. 9G) 2-segmented: lacertus largest but unarmed, and brachium carrying denticles; terminal claw armed with scattered denticles. Maxilliped (Fig. 9C) subchelate and 3-segmented: basal segment large; corpus short and broad, with myxa protruded into large spine; subchela short and unarmed, terminal claw with pocket for receiving tip of myxa.

Legs 1–4 (Figs. 10B–E) biramous with

3-segmented rami, their spines (Roman numerals) and setae (Arabic numerals) as follows:

Leg 1	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; 1
Leg 2	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; I,2
Leg 3	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; I,2
Leg 4	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; I,1

Leg 5 (Fig. 10F) extremely reduced, being represented by tuft of 4 setae in posterior quarter of middle region of body (see Figs. 9A, B).

Etymology.—The species is named after the location of its host—Gulf of Siam.

Remarks.—This is the most modified eudactylinid ever reported. Its unusually elongate body is undoubtedly the result of a mesoparasitic mode of life. About one-fifth of its greatly elongated body (up to the part bearing the first pair of legs) was buried in the host tissue. The absence of a free segment in leg 5 is another unusual feature of this new form.

Phylogenetic Analysis

We have endeavored to examine specimens of representative species of all eudactylinid genera. However, we were unable to obtain specimens of the monotypic genus, *Eudactylinopsis,* which is so far known only from *Pristis* sp. in Trivandrum, India. Therefore, in the following analysis, anatomical information for *Eudactylinopsis* was taken from the original description of *E. curvatus* given by Pillai (1968). Inasmuch as three eudactylinid genera are known only from females, the analysis below is based solely on the female characters.

Several families of siphonostomatoids are remarkable in bearing certain primitive traits, like having an exopod in the second antenna, or a palp in the mandible. We consider the siphonostomatoids that possess unmodified bodies and these two primitive traits as outgroups for the Eudactylinidae. There are three such families: Brychiopontiidae Humes, 1974; Dinopontiidae Murnane, 1967; and Dirivultidae Humes & Dojiri, 1980; all are associates of marine invertebrates. Ninety characters (see Appendix 1) were identified and employed in reconstructing the phylogeny of the Eudactylinidae; the states in each of these characters were polarized by referring to the composite out group consisting of these three families (see Maddison et al. 1984).

Both ordered and unordered cladograms were generated using the Branch and Bound algorithm from the phylogenetic computer package PAUP version 2.4 (written by David L. Swofford). The ordered analysis yielded six trees of tree length 174 steps, with a consistency index of 0.79. The tree with the lowest F-ratio, 5.650, was chosen and reproduced in Fig. 11 (Brooks et al. 1986). For the unordered analysis the 24 transformation series with multistates were unordered, allowing the cladogram to be generated based on the remaining 66 (73%) binary state characters (see PAUP documentation). This analysis generated a single tree (Fig. 13) with a tree length of 159 steps, a consistency index of 0.86, and an F-ratio of 1.98.

Both ordered and unordered analyses rejected Cressey's (1977) treatment of relegating *Protodactylina* to a junior synonym of *Bariaka,* therefore, we resurrect *Protodactylina.* It is noteworthy that this most primitive genus of eudactylinids is also a parasite of one of the most primitive families of extant elasmobranchs—Hexanchidae. Only one species is known in *Protodactylina* but it has a fairly wide distribution, occurring in the Mediterranean (Laubier et al. 1966; Schirl 1978) and off northern California (Cressey 1977).

The sister group between *Bariaka* and *Nemesis* is strongly suggested in our phylogenetic analysis. Many species of sharks

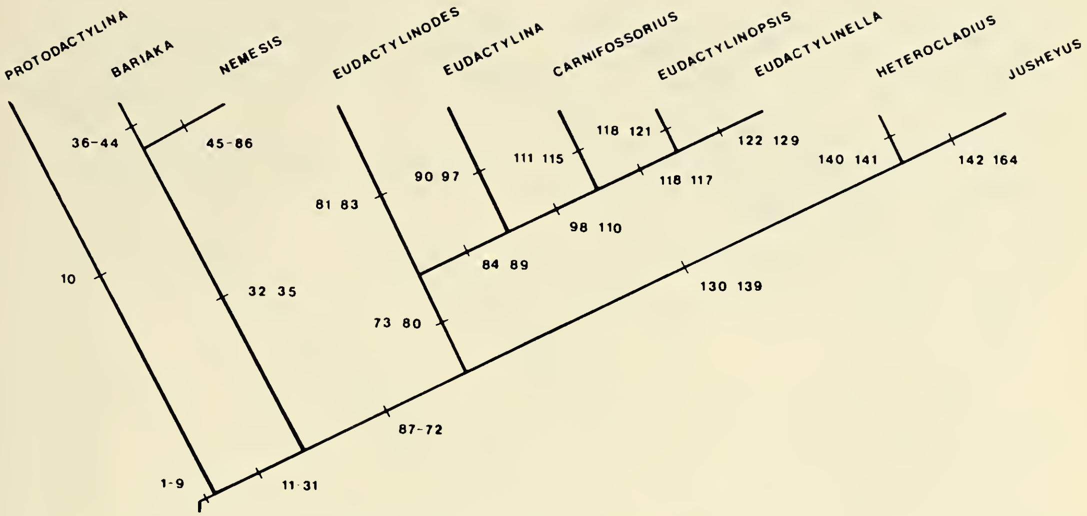


Fig. 11. Cladogram of eudactylinid genera based on ordered analysis.

have been reported to host *Nemesis,* but so far they are confined to the Carcharhiniformes and Laminiformes, particularly those occurring in the North Atlantic, for six of the seven valid species are known from that part of the ocean. *Bariaka* contains only one species; it is known from the bigeye thresher off Madagascar (Cressey 1966), New England (Benz 1986), and southern California (Deets, unpublished). Therefore, this second clade of eudactylinids seems to prefer laminiform sharks.

The major difference between the two cladograms lies in the 6-genera clade which is the sister group of *Jusheyus* (see Fig. 13). The two teleost-parasitizing eudactylinid genera were depicted as sister taxa in the ordered analysis (Fig. 11), but in the unordered analysis they are not (see Fig. 13). This difference is more apparent upon inspecting the host summary cladogram (Fig. 12).

The cladogram in Fig. 12 represents the phylogenetic relationships of the eudactylinids' hosts based on the phylogeny of the parasites obtained from the ordered analysis. It was produced by replacing the parasite genera in Fig. 11 with their respective host families or orders. To place information on this host summary cladogram, we used only the *multiple* and *well* documented records. For instance, Kabata's (1970) report of two male *Nemesis* sp. on *Dasyatis kuhli* from Australia was not taken into consideration, due to its single documentation from a doubtful host. The host summary cladogram shown in Fig. 12 suggests a single colonization of teleosts, but the more parsimonious unordered cladogram (Fig. 13) indicates two independent colonizations, once on Perciformes (Percichthyidae) and another on Salmoniformes (Alepocephalidae). A single invasion hypothesis is more parsimonious, but, ironically, the cladogram (Fig. 11) suggesting such occurrence has a lower consistency index and a longer tree length. Is this a genuine contradiction? We think not. To postulate a single invasion one must invoke assumptions that eudactylinids had become associated with the ancestor of Euteleostei and subsequently dissociated (secondarily lost) from Ostariophysi, Stenopterygii, Scopleomorpha, and Paracanthopterygii; whereas to accept two independent invasions, no multiple assumptions of subsequent dissociation are necessary. Therefore, the host-parasite associations do not contradict the phyloge-

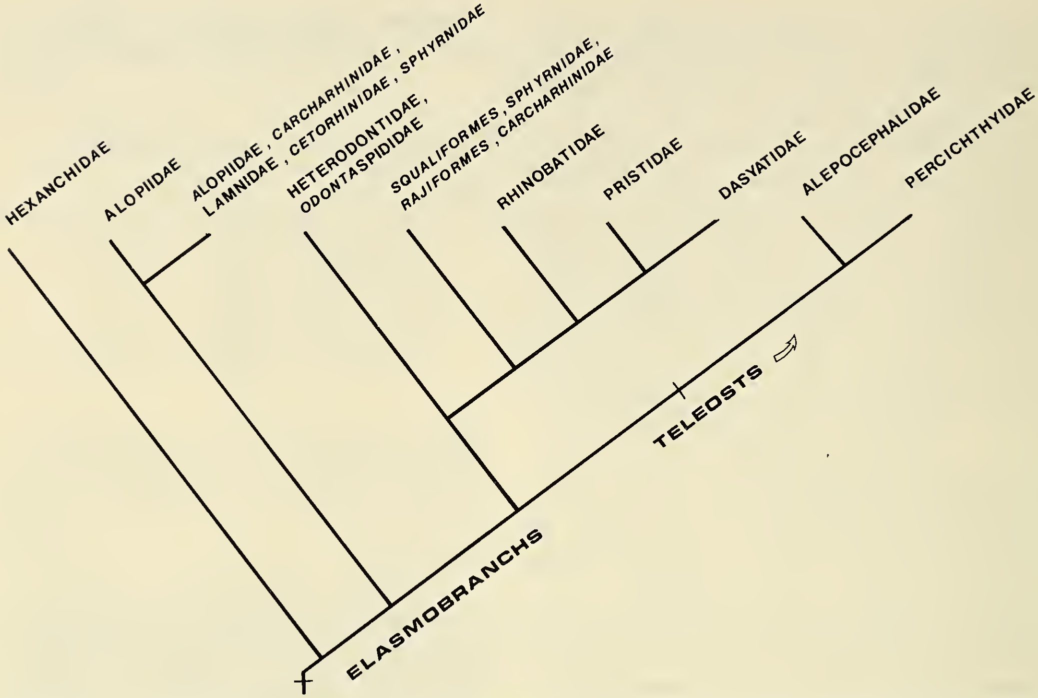


Fig. 12. Host summary cladogram. A parasite cladogram from ordered analysis with host Family or Order superimposed. Showing one host shift from elasmobranchs to teleosts.

netic hypothesis resulting from the unordered analysis.

Eudactylina is by far the largest genus of the eudactylinids, consisting of 26 species. The genus has a systematically broader host association; it is found on Carcharhiniformes, Squaliformes, and Rajiformes. It is interesting to note that 73% (19 species) of *Eudactylina* occur in the North Atlantic (including the Mediterranean) and only five species (19%) are reported from the entire Pacific Ocean (Ho & McKinney 1981). Does this mean the North Atlantic was the cradle of *Eudactylina*? A phylogenetic analysis of the genus is necessary to provide an answer. The sister group of this genus, *Eudactylinodes,* is a much smaller genus, with only two species occurring in North American waters off both east and west coasts.

The remaining three genera, *Eudactylinella, Eudactylinopsis,* and *Carnifossorius,* are monophyletic in both ordered and unordered cladograms. This monophyletic hypothesis is also supported by their host-parasite association, for they are so far known only from the rajiform elasmobranchs. Also, from the standpoint of historical biogeography, the unordered cladogram (Fig. 13) is to be selected, because it indicates that cladogenesis in this part of the eudactylinid phylogeny was caused by a vicariant event—the collision of the Africa-Arabia land mass with Eurasia.

We speculate that the ancestor of these rajiform-parasitizing eudactylinids lived in the Tethys Sea between Laurasia and Gondwana before the time of the Oligocene–Miocene transition, when (about 35 million years ago) the African continent came into contact with Eurasia. After the Tethys Sea was cut into two parts, the eudactylinids in the eastern Tethys (Indian Ocean) gave rise to

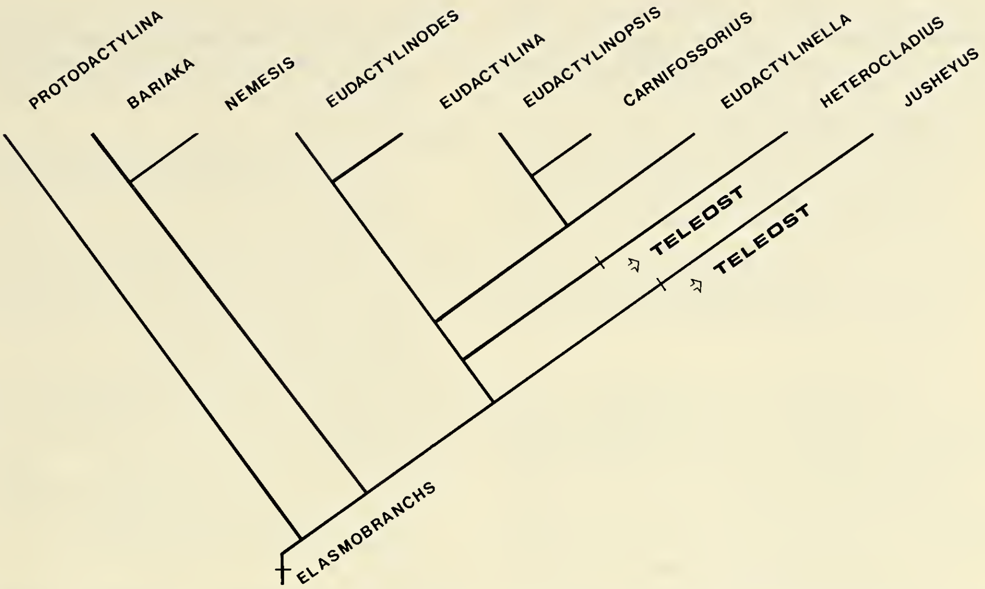


Fig. 13. Cladogram of eudactylinid genera based on unordered analysis. Host-parasite associations same as in Fig. 12. Showing two independent colonizations of teleosts.

Eudactylinopsis and *Carnifossorius* and those in the western Tethys (Atlantic Ocean, including the Mediterranean) evolved into *Eudactylinella.* Current distribution of these three genera supports this hypothesis: *Eudactylinopsis* is found in the Arabian Sea (Pillai 1968), *Carnifossorius,* in the Gulf of Siam (present report), and *Eudactylinella,* in the western North Atlantic (Wilson 1932; Pearse 1948), Gulf of Mexico (Bere 1936), and the Mediterranean Sea (Essafi & Raibaut 1977).

In conclusion, based on the 90 selected morphological characters, the cladogram reproduced in Fig. 13 is the best representation of the eudactylinid phylogeny.

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Appendix 1.—Characters and their states used in the cladistic analysis. Plesiomorphic (code 0) or linkage state given first followed by character state 1 and 2, 3, 4, 5, and 6 if necessary. Numbers in parentheses identify corresponding character states on the cladogram in Fig. 11. Roman numerals denote spines, Arabic numerals represent setae regarding leg formula characters.

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1. Coxopodal seta: present/absent (11)
2. Genital complex: short/elongate (111)
3. Dorsal thoracic stylets: absent/present (142)
4. Egg sacs: multiseriate (143)/uniseriate (1)
5. Number of abdominal segments: four (144)/three (12)/two (140) (122) (84)/one (98)
6. Number of free thoracic somites: five (145)/four (2)
7. Number of first antenna segments: 17–18/13–14 (13)/10–11 (67)/8 (118)/5 (90)
8. First antenna basal protuberance: absent/present (112)
9. First antenna flexion: absent (99)/present (73)
10. First antenna second segment armature: typical setae/one large claw (91)
11. First antenna second segment armature: typical setae/three large claws (81)
12. Exopod of first maxilla: three terminal elements/two terminal elements (130)
13. Claw of second maxilla: pinnate seta/rugose (3)/with short setules (82)/with paired denticles (68)/with scattered denticles (113)
14. Claw of second maxilla: with paired denticles/with serrated membranous expansions (146)
15. Claw of maxilliped: simple, armed with spines/simple, naked (123)
16. Claw of maxilliped: simple, armed with spines (100)/complex cuticular concavity (74 (119)
17. Claw of maxilliped: simple, armed with spines/with pocket (114)
18. Myxa of maxilliped: absent/slight, with spine (4) (124) (147)/large, forming chela (69) (101)/membrane (75)
19. Myxa of maxilliped: absent/with dual tines (36) (10)
20. First exopod segment number: three/three, partially fused (131)/two (148)
21. First exopod segment number: three/two, modified (45)
22. First exopod distal segment formula: III,5/II,5 (5)/II,4 (14)/V (120)/IV (85)/III (92)
23. First exopod distal segment formula: II,4/VI (32)/IV (46)
24. First exopod distal segment formula: II,4/4 (83)
25. First exopod second segment formula: I,1/I,0 (70)
26. First exopod proximal segment formula: I,1 (47)/I,0 (15)
27. First exopod proximal segment formula: I,1/modified (48)
28. First endopod segment number: three/two (149)
29. First endopod segment number: three/two, modified (49)
30. First endopod distal segment formula: 6 (132)/(16) (125)/III (102)/I (115)
31. First endopod distal segment formula: 6/I,5 (133)/I,4 (150)
32. First endopod distal segment formula: 5/2 (93)/1 (126)
33. First endopod distal segment formula: 5/modified III (50)
34. First endopod distal segment formula: 5/modified II (37)
35. First endopod proximal segment formula: 0,1/modified (51)
36. First endopod proximal segment formula: 0,1/0,0 (38) (76)
37. Second exopod segment number: three/two (151)
38. Second exopod segment number: three/modified two (52)
39. Second exopod distal segment formula: 9/III,6 (6)/III,1 (77)/IV (103)
40. Second exopod distal segment formula: III,6/VIII (33)
41. Second exopod distal segment formula: III,6/II,4 (134)/II,3 (152)
42. Second exopod distal segment formula: III,1/III (94)
43. Second exopod middle segment formula: I,1/I,0 (17)
44. Second exopod proximal segment formula: I,1 (53)/I,0 (18)
45. Second exopod proximal segment formula: I,1/modified I,1 (54)
46. Second endopod segment number: three/two (153)
47. Second endopod segment number: three/modified two (55)
48. Second endopod distal segment formula: 6/I,5 (19)/II,2 (78)/IV (121)/III (104)/modified 0 (127)
49. Second endopod distal segment formula: I,5/I,3 (154)
50. Second endopod distal segment formula: I,5/VI (56)

Appendix 1.—Continued.

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51. Second endopod distal segment formula: I,5/modified II (39)
52. Second endopod distal segment formula: II,2/2 (95)
53. Second endopod middle segment formula: 0,2/0,1 (135)/0,0 (20)
54. Second endopod proximal segment formula: 0,1 (86) (155)/0, I (21)
55. Second endopod proximal segment formula: 0,1/0,0 (87)
56. Third exopod segment number: three/two (156)
57. Third exopod segment number: three/modified two (57)
58. Third exopod distal segment formula: 9/II,6 (7)/II,4 (22) (105)/II,1 (79)
59. Third exopod distal segment formula: II,6/VII (34)/VI (40)
60. Third exopod distal segment formula: II,4/II,3 (157)
61. Third exopod distal segment formula: II,4/IV (106)
62. Third exopod middle segment formula: I,1/I,0 (23)
63. Third exopod proximal segment formula: I,1 (58)/I,0 (24)/0,0 (158)
64. Third exopod proximal segment formula: I,1/modified I,I (59)
65. Third endopod segment number: three/two (159)
66. Third endopod segment number: three/modified two (60)
67. Third endopod distal segment formula: 5/I,4 (25)/I,3 (141)/I,2 (71)/III (107)/I (116)/I, toothed (128)
68. Third endopod distal segment formula: I,4/I (41)
69. Third endopod distal segment formula: I,4/V (61)
70. Third endopod distal segment formula: I,2/2 (96)
71. Third endopod middle segment formula: 0,2/0.1 (136)/0,0 (26)
72. Third endopod proximal segment formula: 0,1/0,I (88) (42)
73. Fourth exopod segment number: three/two (160)
74. Fourth exopod segment number: three/modified two (62)
75. Fourth exopod distal segment formula: 9/II,6 (8)/II,3 (72)/IV (108)
76. Fourth exopod distal segment formula: II,3/I,4 (161)
77. Fourth exopod distal segment formula: II,6/IV (35)
78. Fourth exopod distal segment formula: II,3/II,1 (80)
79. Fourth exopod middle segment formula: I,1/I,0 (27)/0,0 (137)
80. Fourth exopod proximal segment formula: I,1/I,0 (28)/0,0 (162)
81. Fourth endopod segment number: three/two (163)
82. Fourth endopod segment number: three/modified two (63)
83. Fourth endopod distal segment formula: 5 (64)/I,2 (9)/I,1 (110)/I (117)/I, toothed (129)
84. Fourth endopod distal segment formula: I,2/modified I (43)
85. Fourth endopod distal segment formula: I,2/2 (97)
86. Fourth endopod distal segment formula: 5/V (65)
87. Fourth endopod middle segment formula: 0,2/0,1 (138)/0,0 (29)
88. Fourth endopod proximal segment formula: 0,1/0,I (30)/0,0 (44) (89)
89. Fourth endopod proximal segment formula: 0,I/I,I (66)
90. Caudal ramus elements: pinnate (139)/naked (31)

Appendix 2.—Character data matrix for the Eudactylinidae. Codes 0 through 6 identify particular characters (note that code 0 does not necessarily indicate an absence). Determination of the plesiomorphic state of the 90 transformtion series was obtained by reference to the composite outgroup referred to in text. Code 9 refers to missing data.

000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000	Outgroup
000101000000100001100100000000000000000010000000000000000000000000010000000010000000100000001000000010000000	*Protodactylina*
100111100000100001100210010001000101001100110001001021000120011000110021001010110011002201	*Bariaka*
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10012120000030100100040011000102000100300011000500002010020011100060021003000110040002201	*Eudactylinella*
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101(2), 1988, pp. 340–345

PSEUDOPANDARUS AUSTRALIS, A NEW SPECIES OF PANDARID COPEPOD FROM AUSTRALIAN SHARKS

Roger Cressey and Colin Simpfendorfer

Abstract.—Pseudopandarus australis is described from 5 species of sharks from the east coast of Australia. It differs from other known species of *Pseudopandarus* by the presence of only 1 small spine on the endopod of the first leg.

In 1950 Kirtisinghe described a new genus and species of pandarid copepod, *Pseudopandarus gracilis.* Gnanamuthu (1951) described a second species, *P. longus,* and Rangnekar and Rangnekar described *P. bombayensis* and *P. shiinoi* from Bombay in 1972. Until now all species were known only from the Indian Ocean and Japan. The second author recently collected a fifth species from 2 species of *Rhizoprionodon* from waters off Townsville, North Queensland, Australia. This new species is the first *Pseudopandarus* reported from the South Pacific.

Pseudopandarus australis, new species
Figs. 1–21

Material examined.—12 females (3 immature) and 3 males from *Rhizoprionodon acutus,* and 3 females from *R. taylori* out of Cleveland Bay and Townsville Harbour, Queensland, Australia. Other material was collected by C.S. from other hosts (see remarks) but not examined for this description. Holotype from *R. taylori* and paratypes from *R. acutus* are deposited in the Australian Museum except for 2 paratypes from *R. acutus* deposited in the National Museum of Natural History (USNM) Smithsonian Institution, Washington, D.C. (USNM 234429).

Female.—Body form as in Fig. 1. Total length 4.43 mm. Greatest width at genital segment 1.32 mm. Cephalon somewhat longer than wide (1.2 × 0.9 mm). Genital segment longer than wide (1.98 × 1.32 mm). Two dorsal thoracic plates between cephalon and genital segment. Abdomen (Fig. 2) small, somewhat wider than long (329 × 272 μm). Caudal rami (see Fig. 2) somewhat triangular, widest posteriorly, somewhat longer than wide (103 and 85 μm) and bearing an outer short seta and 5 terminal spines.

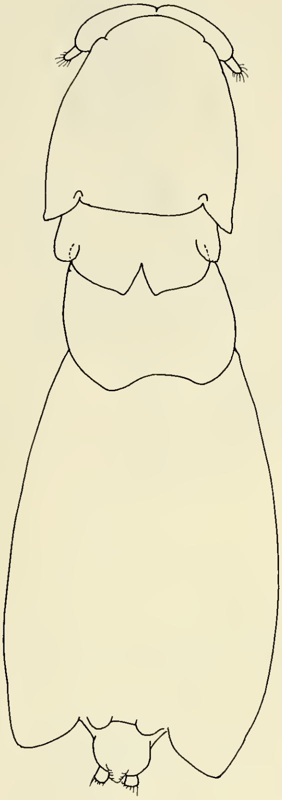
First antenna (Fig. 3) 2-segmented, bearing 13 plumose and 11 naked setae on first segment and 3 lateral and 9 terminal setae on second segment. Second antenna (Fig. 4) 3-segmented, terminal segment bearing 1 stout recurved spine and 2 shorter terminal spines. Mouth tube (Fig. 5) triangular, much longer than wide. First maxillae at base of

→

Figs. 1–8. *Pseudopandarus australis,* female: 1, Dorsal; 2, Abdomen and caudal rami, ventral; 3, First antenna; 4, Second antenna; 5, First maxillae and mouth tube; 6, Second maxilla; 7, Maxilliped; 8, First leg.

Figs. 9–14. *Pseudopandarus australis,* 9–12 female: 9, Second leg; 10, Third leg; 11, Fourth leg; 12, Fifth leg. 13–14 Male: 13, Dorsal; 14, Genital segment, abdomen, and caudal rami, ventral.

Figs. 15–21. *Pseudopandarus australis,* male: 15, Abdomen and caudal rami, ventral; 16, Second maxilla; 17, Maxilliped; 18, First leg; 19, Second leg; 20, Third leg; 21, Fourth leg.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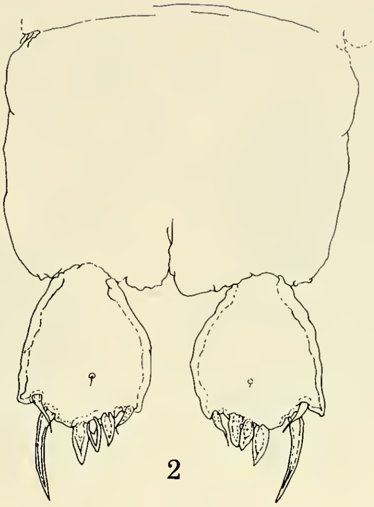
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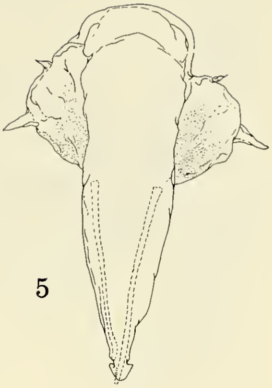
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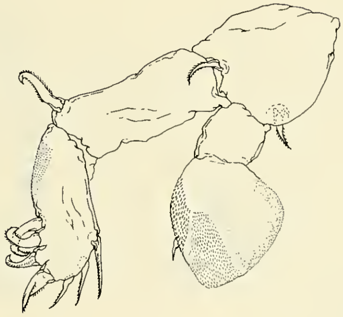
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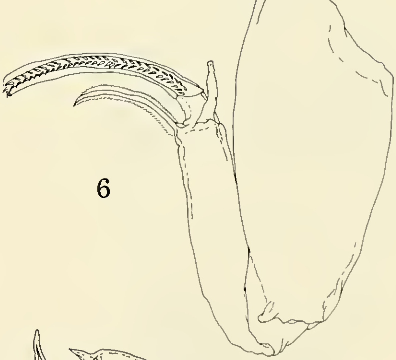
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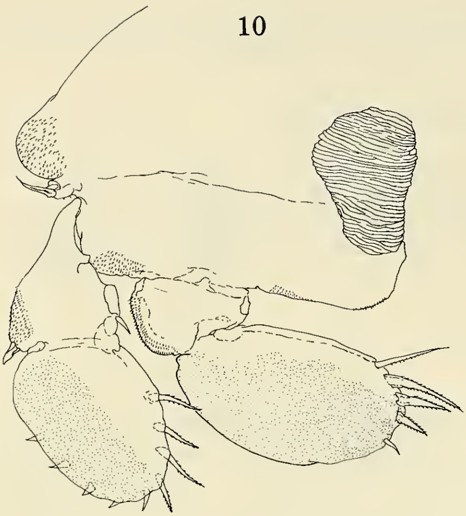

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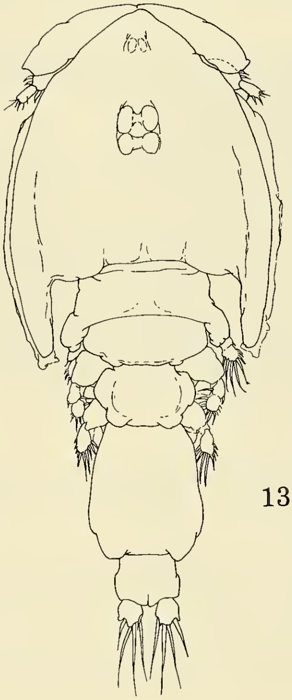

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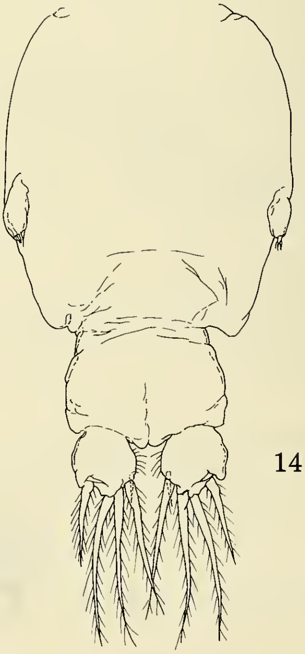

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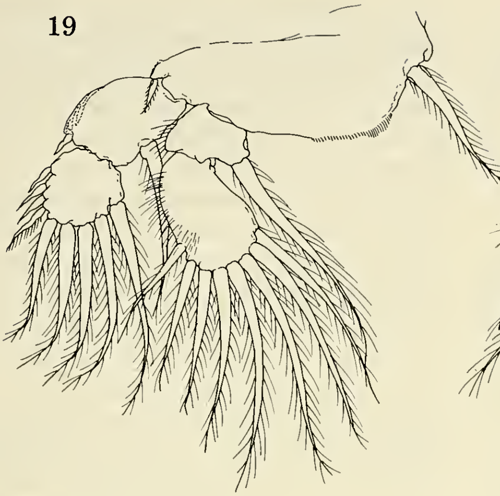
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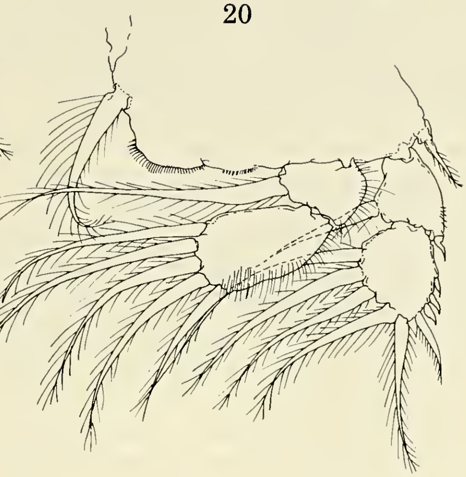
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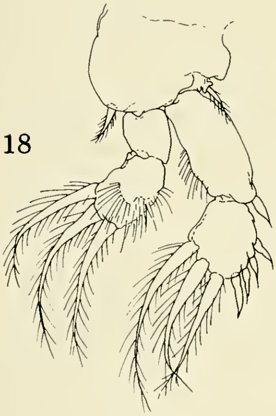
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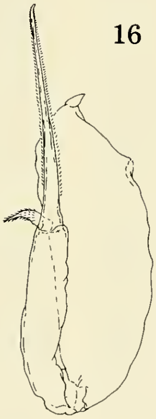
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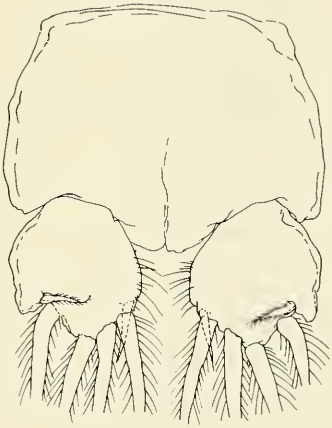
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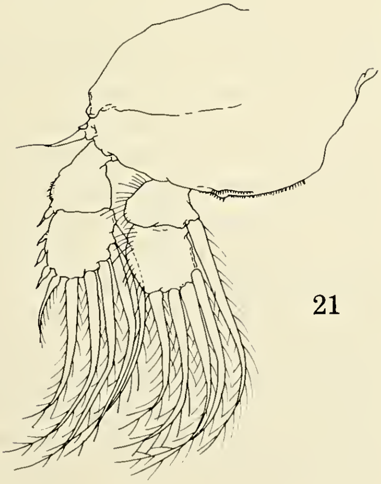
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mouth tube (Fig. 5), each composed of a lateral projection bearing 2 short spines. Second maxilla (Fig. 6) with robust basal segment, and slender second segment bearing 1 toothed terminal spine, 1 subterminal shorter fringed spine, and 1 subterminal membranous process. Maxilliped (Fig. 7) robust and armed as in the figure.

Leg 1 (Fig. 8) with 2 short setae on basipod; exopod 2-segmented, first segment about twice as long as wide and bearing a short seta at outer distal corner, second segment with 7 outer to inner setae around distal third, setae armed with short spinules as in the figure; endopod 2-segmented, first segment short, unarmed, second segment about twice as long and wide as first and with 1 very small seta on mid-outer edge and 2 patches of spinules (outermost heavier than midpatch, inner patch finest). Leg 2 (Fig. 9) rami 2-segmented, exopod first segment with outer distal spine, last segment with 9 spines, 2 terminalmost very short; endopod first segment without setae, last segment with 7 setae, lateralmost 3 very short; both rami armed with patches of spinules as in the figure. Leg 3 (Fig. 10) similar to leg 2 except endopod last segment with only 5 setae. Leg 4 (Fig. 11) rami 1-segmented, exopod about twice as long as wide, bearing 10 setae from outer to inner margins; endopod with 3 terminal setae; leg armed with patches of spinules as in the figure. Leg 5 (Fig. 12) a small, palplike process bearing 4 setae, attached to ventral surface of genital segment lateral to origin of abdomen.

Male.—Body form as in Fig. 13. Total length 1.91 mm. Cephalon longer than wide (1.17 × 0.93 mm). Genital segment (Fig. 14) somewhat longer than wide (0.40 × 0.37 mm). Abdomen (Fig. 15) wider than long (0.21 × 0.19 mm). Caudal rami (see Fig. 15) slightly longer than wide (0.1 × 0.08 mm), longest seta 0.23 mm.

Cephalic appendages as in female except second maxilla (Fig. 16) with only 2 terminal processes, longest process with lateral fringes rather than spinules as in female, third membranous process (in female) absent. Maxilliped (Fig. 17) robust as in the female but without rugose areas present in female, a membranous spine on terminal claw not seen in female.

Leg 1 (Fig. 18) exopod 2-segmented; first segment bearing a naked spine at outer distal corner; last segment bearing 4 outer, naked spines and 3 terminal plumose setae; endopod 2-segmented; first segment unarmed, last segment with 3 plumose setae. Leg 2 (Fig. 19) exopod 2-segmented; first segment with an outer distal spine and an inner seta, last segment with 3 short, naked outer setae, a longer spinule plumose on inner margin and 5 terminal to inner plumose setae; endopod first segment with a long, plumose inner seta, last segment with 8 terminal plumose setae. Leg 3 (Fig. 20) exopod as in leg 2 except rugose area on outer margin of first segment lacking; endopod as in leg 2 except last segment with 5 plumose setae (8 in leg 2). Leg 4 (Fig. 21) as in leg 3 except endopod last segment with only 4 plumose setae.

Remarks.—Females of the new species can be separated from the 4 known species by the presence of only 1 small spine on the endopod of the first leg (*gracilis*-3), (*longus*-3), (*bombayensis*-3), (*shiinoi*-2), and by the presence of 3 setae on the endopod of the fourth leg (*gracilis*-2), (*longus*-5), (*bombayensis*-4), (*shiinoi*-5). In general, the new species appears to be most closely related to *P. longus* which is known, so far, only from South Africa and Ceylon. *Pseudopandarus longus* has been reported from *Rhizoprionodon,* the same genus of sharks from which this new species is reported from the east coast of Australia. *Pseudopandarus australis* has been taken from 5 species of sharks, *Rhizoprionodon acutus, R. taylori, Carcharhinus dussumieri, Hemigaleus microstoma,* and *Sphyrna lewini.* Rates of infestation by the female parasites are high for both species of *Rhizoprionodon* (*R. acutus* 57.2% and *R. taylori* 47.4%), but is only minor for the other species (less than 5%). Males occur only rarely (about 5%) on *Rhizoprionodon* spp. and *H. microstoma,* and have not been recorded from the other species. Attachment of the females to the host is commonly in the pectoral, pelvic, and caudal regions, while males have been found attached on the flanks and nape.

Etymology.—australis alludes to the discovery of this new species from the east coast of Australia.

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HADROMASTAX MERGA, A NEW GENUS AND SPECIES OF MARINE ISOPOD CRUSTACEAN (LIMNORIIDAE) FROM SOUTHEASTERN AUSTRALIA, WITH DISCUSSION ON THE STATUS OF THE FAMILIES KEUPHYLIIDAE AND LYNSEIIDAE

Neil L. Bruce

Abstract.—*Hadromastax merga* is described and placed in the Limnoriidae. The genus has a morphology atypical for the Limnoriidae as the family has previously been defined, with only two pleonites visible dorsally (these forming a pair of backwardly-directed processes), massive mandible with a conical incisor, anterolateral uropods forming a tail fan and a posteriorly truncate pleotelson. Discussion is given on characters used to define Limnoriidae and the related families Keuphyliidae and Lynseiidae.

Hadromastax was collected from a depth of 155 meters off Newcastle, New South Wales, Australia.

The Flabellifera now comprises 14 recognized families. The list given by Bowman and Abele (1982) is now dated, and the currently accepted number of families is one less than was listed. The families Alcironidae, Argathonidae, and Excorallanidae are all synonyms of Corallanidae (see Bruce et al. 1982); Bathynomidae and Eurydicidae are synonyms of Cirolanidae (see Bruce 1986); Anciniidae is a synonym of Sphaeromatidae (see Iverson 1982). Table 1 includes all the families of the Flabellifera with an approximate assessment of their size. Half of these families are "small," with less than 10 species, and of these only one, the Bathynataliidae (see Bruce 1985) contains more than a single genus. Four of the "small" families are monotypic (see Table 1).

Two recently established monotypic families (Keuphyliidae Bruce, 1980, and Lynseiidae Poore, 1987) show close affinities to the Limnoriidae. The new genus described here could, on some grounds, also be established as a new family. The traditional characters used to define the Limnoriidae are absent, and it is abundantly distinct from all other flabelliferan families. As indicated in the discussion, the new genus seems better retained within the Limnoriidae.

Family Limnoriidae Dana, 1853
Hadromastax, new genus

Diagnosis.—Cephalon freely articulating, not immersed in pereonite 1. Coxae present on pereonite 1; posterior margins of coxae of pereonites 1 and 2 concealed by anterior margin of next coxae. Pleon with 2 pleonites visible in dorsal view, 4 pleonites visible in ventral view; 2 dorsally visible pleonites forming 2 united posteriorly directed processes. Pleotelson with posterior margin truncate.

Frontal lamina and clypeus absent, labrum present. Mandible massive, incisor conical, heavily sclerotized; palp 3-articled, small, about 0.2 length of mandible; lacinia mobilis represented by single seta. Maxillule, medial lobe with 3 elongate blade-like spines projecting medially and one short stout spine projecting anteriorly. Maxilliped, endite without coupling hooks. Antennular and antennal bases not contiguous. Uropod peduncle posteromedial margin

Table 1.—Families of the Flabellifera, with an indication of their approximate size.

Aegidae Leach, 1815	5 genera, 100+ species
Anuropidae Stebbing, 1893*	1 genus, 7 species
Bathynataliidae Kensley, 1978	3 genera, 3 species
Cirolanidae Dana, 1853	45+ genera, 400+ species
Corallanidae Hansen, 1890	6 genera, 60+ species
Cymothoidae Leach, 1818	40+ genera, uncertain number of species
Keuphyliidae Bruce, 1980	1 genus, 1 species
Limnoriidae Dana, 1853	3 genera, 60+ species
Lynseiidae Poore, 1987	1 genus, 1 species
Phoratopodidae Hale, 1925	1 genus, 1 species
Plakarthriidae Richardson, 1904	1 genus, 1 species
Serolidae Dana, 1852	3 genera, 80+ species
Sphaeromatidae Edwards, 1840	80+ genera, 500+ species
Tridentellidae Bruce, 1984	1 genus, 11 species

* The correct spelling, see Bacescu and Holthuis (1983) and Anonymous (1985).

produced, endopod articulating separately and posterior to exopod.

Type species.—*Hadromastax merga,* new species, by monotypy, and original designation.

Remarks.—This isopod is readily separated from all other Flabellifera by the unique pleonal structure, the two dorsal processes being formed by two interlocked pleonites, and by the separate articulation of the uropodal rami.

The morphology of the pleon, with the two posteriorly projecting pleonites, prevents observation of how the dorsal pleonites are arranged, but in lateral and ventral view it can be seen that the pleotelson is not fused to the pleon.

The presence of free coxal plates on pereonite 1 is sufficiently unusual within the Isopoda to preclude assessment of its significance. Wilson (1980) has shown that it may be present in certain Asellota in ovigerous females, and indicated the dangers of overinterpreting this character.

Etymology.—The name is derived from two Greek words *hadros* (well developed, strong) and *mastax* (jaws). Gender feminine.

Hadromastax merga, new species
Figs. 1–3

Material.—Holotype, female (non-ovig. 2.5 mm), off Newcastle, NSW, 33°06.2′S, 156°09.3′E, 7 Oct 1982, 154–165 m, coll. W. Ponder and R. T. Springthorpe on RV *Tangaroa* (AM P371144).

Description.—Female: Body about 2.2 times as long as wide, eyes lateral. Dorsal surfaces of pereonites 2–7 covered with small tubercles and scattered plumose setae; pereonites 2–5 each with medial transverse depression, posterior margins of pereonites 3–7 with acute denticles; anterior margin of coxae 2 and 4, posterior margin of coxae 3, 5–7 with small acute denticles. Pleon and pleotelson dorsal surfaces with small tubercles and scattered plumose setae; pleotelson anteriorly domed, posteriorly flat, with numerous plumose setae.

Antennule peduncle article 4 minute, with articulating brush-tipped seta; flagellum 2-articled, article 2 with single aesthetasc. Antenna slightly shorter than antennule, flagellum article 1 elongate, articles 2–4 short; distal margin of each flagellar article with 3 or 4 setae. Mandible massive, incisor pro-

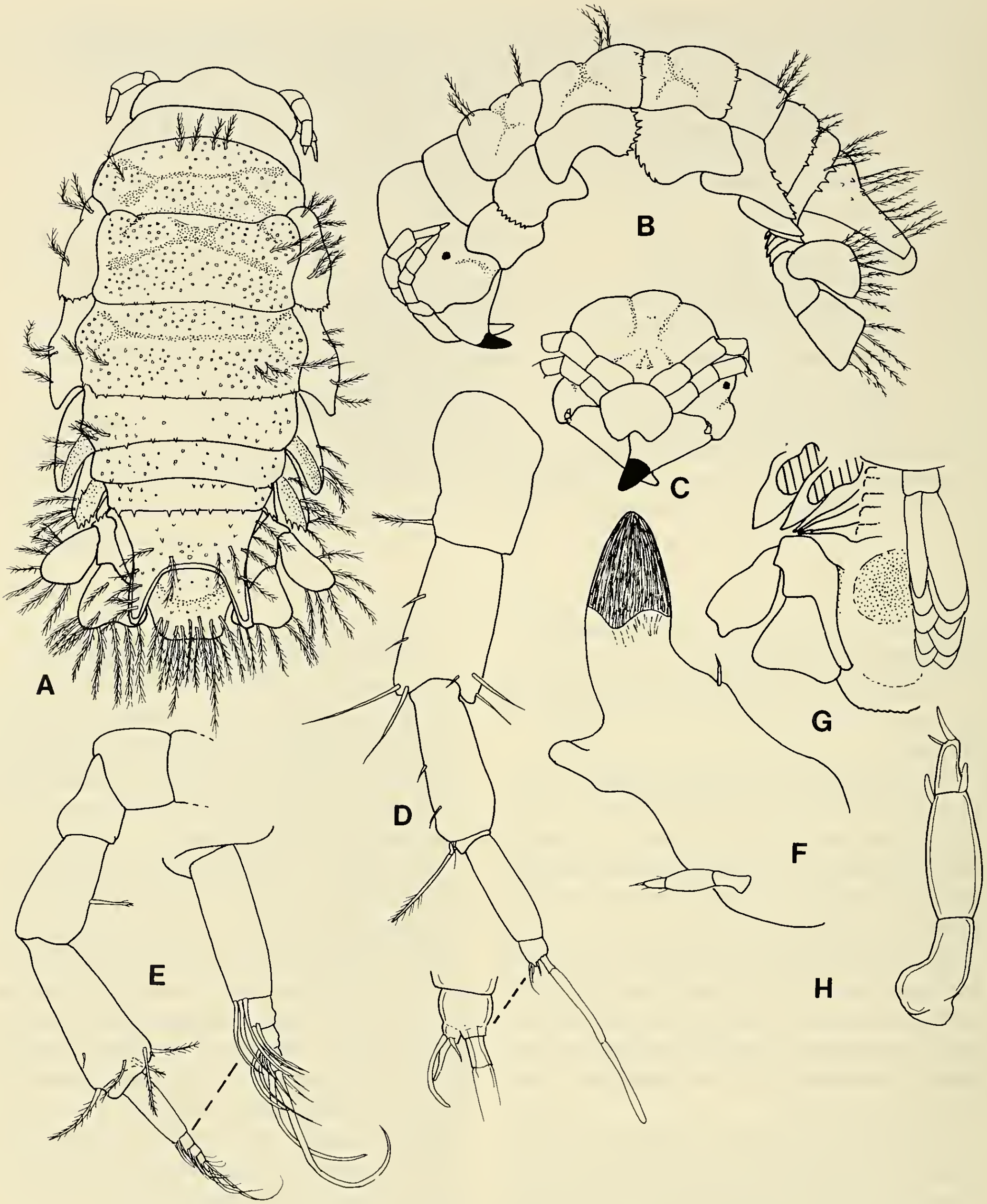

Fig. 1. *Hadromastax merga,* holotype: A, Dorsal view; B, Lateral view; C, Frontal view of cephalon; D, Antennule and detail; E, Antenna and detail; F, Right mandible; G, Pleon and pleotelson in ventral view, after dissection; H, Mandibular palp.

jecting well beyond labrum. Maxilliped palp article 2 with large plumose seta at mediodistal angle of article 2; article 3 with 3 plumose setae at mediodistal angle and 1 seta on lateral margin; article 4 with 3 plumose setae, and article 5 with 5 setae, one being plumose.

Pereopods 1–6 similar, pereopod 7 smaller

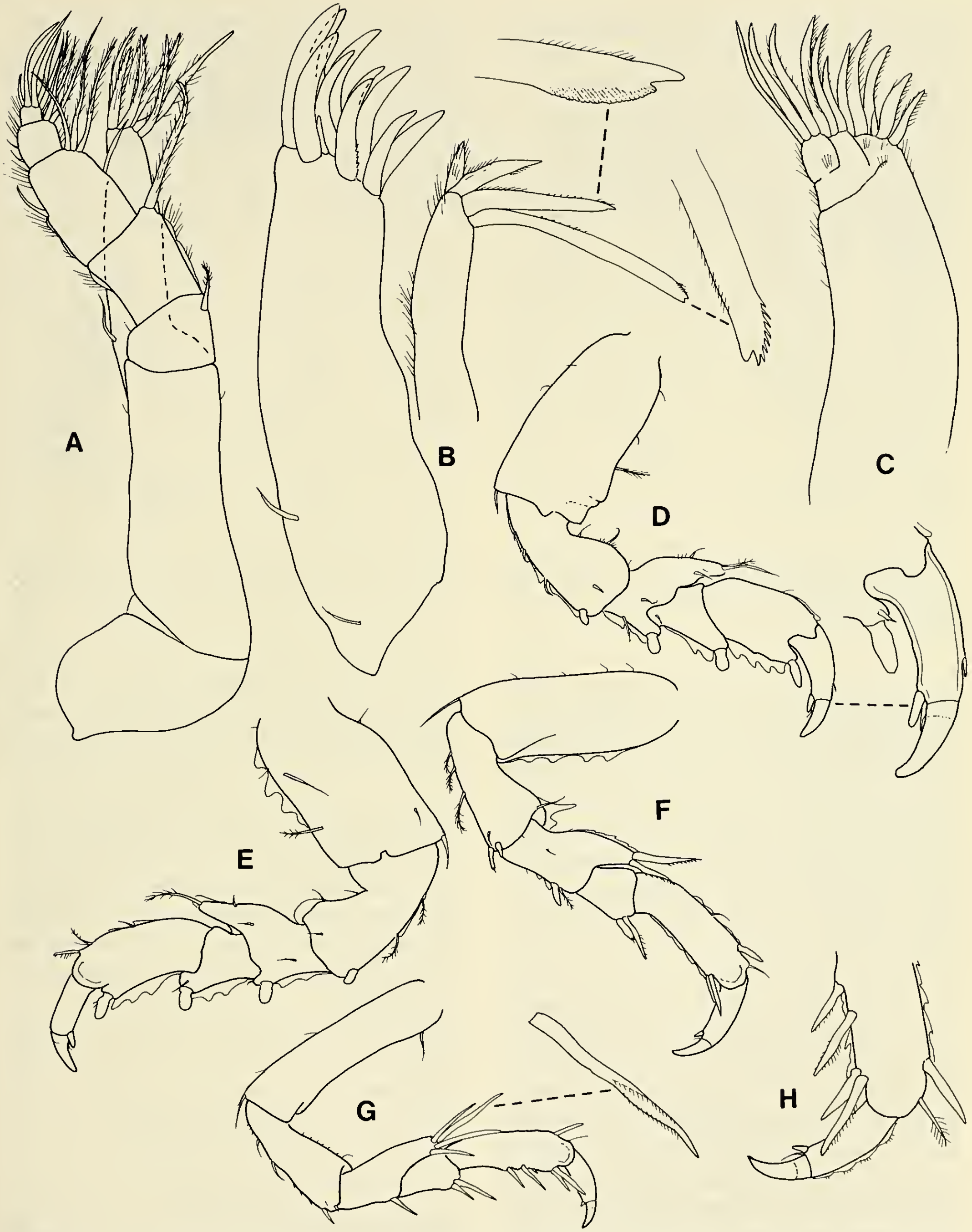

Fig. 2. *Hadromastax merga,* holotype: A, Maxilliped; B, Maxillule; C, Maxilla; D, Pereopod 1; E, Pereopod 2; F, Pereopod 6; G, Pereopod 7; H, Pereopod 7, dactylus.

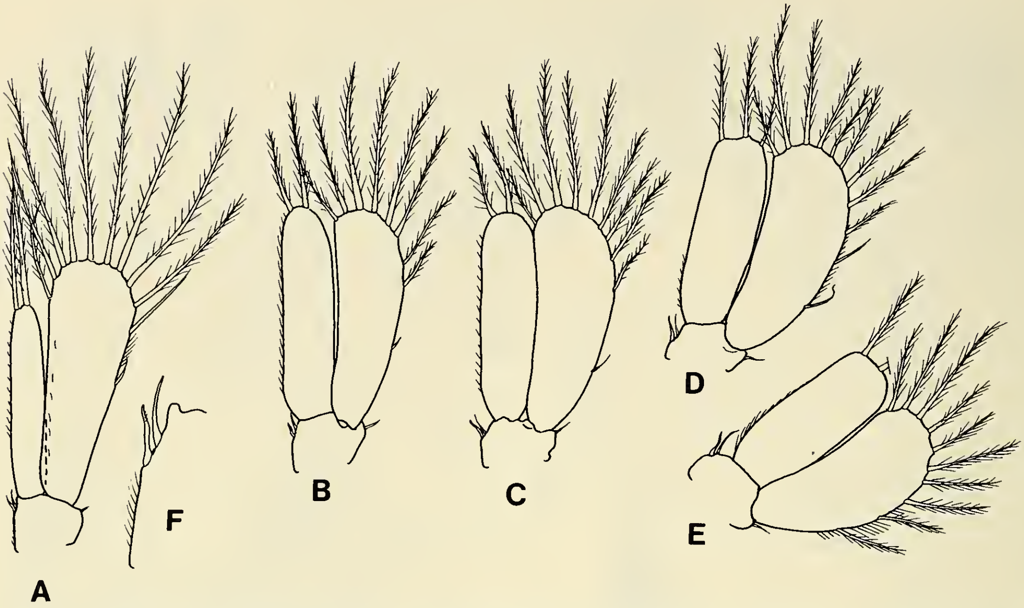

Fig. 3. *Hadromastax merga,* holotype: A–E, Pleopods 1–5, respectively; F, Pleopod 1, peduncle medial margin.

and more slender than 6. Pereopod 1 with large tubercular spine at posterodistal angles of ischium, merus, carpus, and propodus; anterodistal margin of merus produced, with 2 setae; posterior margins of all articles except basis with cuticular serrations. Pereopods 2–6 similar to pereopod 1, but becoming increasingly slender towards posterior; basis anterior margin with cuticular serrations.

Pleopod rami elongate, becoming wider from 1 to 5; all rami with marginal plumose setae; all endopods with 2 terminal setae except for pleopod 4 which has 3. Lateral and medial margins of rami of pleopod 1 straight; lateral margins of exopods of pleopods 2 to 5 becoming increasingly convex. Uropod rami with long plumose marginal setae; exopod subovate, inserted anterolaterally; endopod inserted mediolaterally and not overlapped by exopod, widening distally, posterior margin indented.

Male.—Not known.

Color in alcohol.—White, no chromatophores apparent.

Remarks.—The precise habitat of this species is unknown. Wolff (1979) discussed use of wood as food, refuge, or substrate for deep sea isopods (>1500 meters), and found it to be common in both the shallow and the deep sea. The massive mandible and lack of molar process, spine row, and vestigial lacinia mobilis is indicative of hard biting (see Dahl & Hessler 1982). *Hadromastax* may also feed on wood. Long setae and expanded uropods suggest that it is not a wood borer.

The species is known only from the type locality.

Etymology.—*merga* is a Latin word meaning a two-pronged pitchfork.

Discussion

Poore (1987), in establishing the family Lynseiidae listed the apomorphies that define the Limnoriidae. These were: "spherical mobile head; broad operculate pleotelson; four digestive caeca, and unilobed testis (Menzies 1957); and at least one claw-shaped uropodal ramus." The state of the digestive caeca and testis is not known for most families, and comparisons are not possible. Of the remaining characters one claw-shaped uropod ramus is shared with the family Keuphyliidae; the broad operculate pleotelson (i.e., covering uropods) occurs in other families of Flabellifera, and a degree of cephalic mobility is seen in some cirolanids (e.g., *Eurydice*). This then leaves no unique apomorphies that define the Limnoriidae.

The synapomorphies given for Limnoriidae and Lynseiidae by Poore (1987) are cylindrical bodies (semicircular in cross-section is more precise) with freely articulating cephalon; and a strong secondary unguis on all pereopods. The latter character is strongly expressed in Lynseiidae, but in the Limnoriidae it is less well developed and differs little from that shown by the Keuphyliidae and many genera of Cirolanidae (e.g., *Excirolana, Cirolana, Hansenolana,* see Bruce 1986) or Sphaeromatidae (e.g., all genera figured by Harrison & Holdich 1982, 1984). The synapomorphies are reduced to a single character: the freely articulating cephalon.

Body shape (flattened versus semicircular) is not acceptable as a family character, there being several currently accepted families in which both forms occur (e.g., commonly in the Cirolanidae and Sphaeromatidae). The variation in morphology of uropod rami displayed between Limnoriidae, Keuphyliidae, and Lynseiidae is entirely similar to that shown within the Bathynataliidae, and including *Hadromastax,* is similar to that shown by the Cirolanidae or Sphaeromatidae.

Comparing appendages between Limnoriidae, Keuphyliidae, Lynseiidae, and *Hadromastax* the following characters are essentially the same throughout: the antennule peduncle is short, with three articles, and a fourth fused article; the flagellum very short. The antennal peduncle has five articles, and a short flagellum. The mandible palp is present or absent in the Limnoriidae, absent in Keuphyliidae and Lynseiidae, and present in *Hadromastax.* The mandibular incisor, lacinia mobilis, and spine row of Keuphyliidae and Lynseiidae fit within the range of morphology shown by the Limnoriidae. The maxillule has 8–10 stout spines on the lateral lobe, and 3–4 plumose spines on the medial lobe (except in *Hadromastax* where these are blade-like). The maxilla is similar throughout. The pereopods are all essentially similar, all having a prominent secondary unguis on the dactylus, pectinate spines and cuticular nodules or serrations (except that nodules and serrations are absent in the Keuphyliidae). The pleopods of limnoriids, Lynseiidae, and *Hadromastax* are all similar, and of the typical flabelliferan form. The pleopods of *Keuphylia* differ in having the medial margin of the peduncle produced. The uropods are similar throughout except for those of *Hadromastax* which show the plesiomorphic flabelliferan condition.

The morphological characters that unite *Hadromastax* with the Limnoriidae are: cephalon shape and articulation; antennule; antenna; mouthparts (except for the maxillule inner lobe spines, which are blade-like); pereopod morphology, and pleopod morphology. The characters which immediately separate *Hadromastax* from the other limnoriid genera are the large flat uropodal rami, narrow truncate pleotelson, and the reduced pleon with two large dorsal processes.

Among related isopods the group of families forming the Cirolanidae-Cymothoidae lineage are all defined by mouthpart characters. Other flabelliferan families utilize somatic characters (Sphaeromatidae, Serolidae), although recent work indicates that the mouthparts of these families could also be diagnostic (e.g., Harrison & Holdich 1984, and their works cited therein; Harrison & Poore 1984). In general, flabelliferan mouthparts are conservative and provide the most useful features for differentiating families. If a revision of the family

Limnoriidae is undertaken mouthpart morphology will probably yield the most informative characters for defining the family.

A similar situation existed with the family Corallanidae Hansen: the family Corallanidae contained four genera, and there were three other very closely related families. Bruce et al. (1982) attempted to introduce a diagnosis that was consistent with those for the larger flabelliferan families within the Cirolanidae-Cymothoidae lineage. These families, now synonymized, were all easily recognizable, but were based on characters that were clearly of generic significance.

Phycolimnoria clarkae Kensley & Schotte, 1987, has uropoda which are essentially identical to those of *Lyseia.* The presence of simple uropoda in a species that is inarguably a limnoriid further weakens the utility of that appendage in diagnosing the family Limnoriidae.

What is apparent is that the characters currently being used to define the Limnoriidae are not necessarily those of most phylogenetic value. The differences in pleopod, pleotelson, and uropod morphology of the families under discussion, in view of the variation shown in these structures in other flabelliferan families, are best regarded as being of generic value. The family Limnoriidae was revised by Menzies (1957), but this work is not comparable in descriptive detail to contemporary isopod taxonomy, and it is not possible to assess morphological variation within the family. Equally, it is not possible to provide a new family diagnosis without the detailed redescription of at least some representatives of the limnoriid genera. At this point I do not propose to unite the families Keuphyliidae and Lynseiidae with the Limnoriidae, but place this new genus within the Limnoriidae. The resolution of the status of Keuphyliidae, Lynseiidae and *Hadromastax* will only come about when the family Limnoriidae is revised.

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TONOCOTE INTROFLEXIDUS, A NEW SPECIES OF MARINE AMPHIPOD FROM ARGENTINA (CRUSTACEA: GAMMARIDEA: AMPHIPODA)

Janice Clark and J. L. Barnard

Abstract.—A new species of marine zobrachoid amphipod, *Tonocote introflexidus,* is described from the Magellan Strait. It differs from the type-species, *T. magellani,* in the presence of a long, inwardly pointing hook on epimeron 3, 11 (versus 8) spines on the outer plate of maxilla 1, and is otherwise much better armed on pereopods 3–7 and uropods 1–2. The new species slightly intermediates *Tonocote* with the Australian *Prantinus* but *Tonocote* continues to demonstrate valid generic characters.

References used in the identification process are: Clark & Barnard (1986) and Barnard & Drummond (1978, 1982). Methods of morphological description follow those of Barnard & Drummond (1978).

Zobrachoidae Barnard & Drummond, 1982

Diagnosis.—Rostrum well developed (for haustorioids), cheek poorly developed. Antenna 1 variable, article 1 short (typical) or elongate (apomorphic), articles 2–3 progressively shorter (typical) or elongate (apomorphic), flagella elongate (typical) or not (apomorphic), articles of peduncle weakly (typical) to strongly geniculate. Antenna 2 of haustorius form, article 4 expanded (plesiomorphic) or weakly so (apomorphic), article 5 shorter and narrower than article 4, at least article 4 furnished with 1 or more longitudinal rows of facial armaments, ventral margin of article 4 with at least 3 kinds of setae: (1) elongate plumes, (2) shorter and stiffer glassy spines (often set in clusters) and, (3) bulbous-based penicillate setules; flagellum longer than article 4 of peduncle. Prebuccal complex massive, upper lip usually dominant. Mandibles bearing elongate strongly toothed incisors, rakers almost simple and numerous (4 or more), molar large, strongly extended, not triturative but with several strong cusps, usually 1 of these forming accessory chopper; palp 3-articulate, article 3 with numerous outer setae, setae awned (apomorphic) or not (typical and plesiomorphic). Lower lip with fleshy, fused inner lobes, mandibular extensions of outer lobes well developed. Maxilla 1 with uniarticulate palp, inner plate with more than 3 setae. Maxilla 2 ordinary, inner plate with poorly developed oblique facial row of setae. Maxillipeds with unexpanded bases, normally enlarged plates, outer medially spinose; palp 4-articulate, article 2 expanded, article 4 almost unguiform, at least 2+ setae apically. No baler lobes on maxillae or maxillipeds.

Coxa 2 small to medium, larger than coxa 1 and forming stepped intergrade between coxa 1 and coxa 3, coxa 4 dominant, coxa 3 lacking deep posteroventral lobe. Coxal gills on segments 2–6 or 2–5. Brood plates slender.

Gnathopods feeble, subchelate, grossly alike in proportions, carpi elongate, article 3 short. Article 5 of pereopods 3–4 broad, slightly expanded, not deeply lobate; dactyls of pereopods 3–5 well developed, those of pereopods 6–7 variable; pereopod 5 of haustorius form, articles 2, 4, 5 and 6 expanded, articles 5–6 with extensive facial rows of spines, pereopods 6–7 alike, article 4 broader than 6, articles 4–5 weakly expanded; no pereopod with underslung articulation.

Pleopod 2 usually inferior in size, number of articles, or setation; peduncles of pleopod not longer than wide, inner rami inferior, coupling hooks paired on each pleopod, usually inner rami bearing one basal clothespin spine. Epimeron 1 moderately to strongly developed; epimeron 2 dominant in setation, often dominant in size.

Urosomites ordinary, though often furnished with lateral teeth. Rami of uropods 1–2 linguiform, setose (not spinose); uropod 3 of ordinary gammarid-phoxocephalid kind, outer ramus dominant, 2-articulate, peduncle short, flat, expanded; rami poorly setose apically.

Telson variable in length, deeply cleft. Sexual dimorphism weak.

Variables.—Right and left laciniae mobiles not alike, right, if present, not distinct from raker row (*Zobracho* and *Tonocote*), outer setae of palp article 3 awned (apomorphic) or not (typical and plesiomorphic). Maxillipedal palp article 4 multisetose or with main nail and 2 setules (*Prantinus*). Article 5 of pereopods 3–4 with thick posterior spines or only distal spines present.

Type genus.—*Zobracho* Barnard, 1961.

Composition.—*Bumeralius, Prantinus, Tonocote.*

Relationship.—Differing from the Urohaustoriidae in the well developed side plate (epimeron) of pleonite 1.

Key to the Genera of Zobrachoidae (Males)

1\. Antenna 1 of urothoe form 2
– Antenna 1 of haustorius form 3
2\. Antenna 2 article 4 broad, epimeron 2 much smaller than 3 .... *Tonocote* Clark & Barnard, 1986
– Antenna 2 article 4 slender, epimeron 2 as large as 3 .... *Prantinus* Barnard & Drummond, 1982
3\. Telson elongate, rami of uropods 1–2 with many medial setae, no basoventral setae .... *Zobracho* Barnard, 1961
– Telson short, rami of uropods 1–2 lacking medial setae, bearing basoventral setae .... *Bumeralius* Barnard & Drummond, 1982

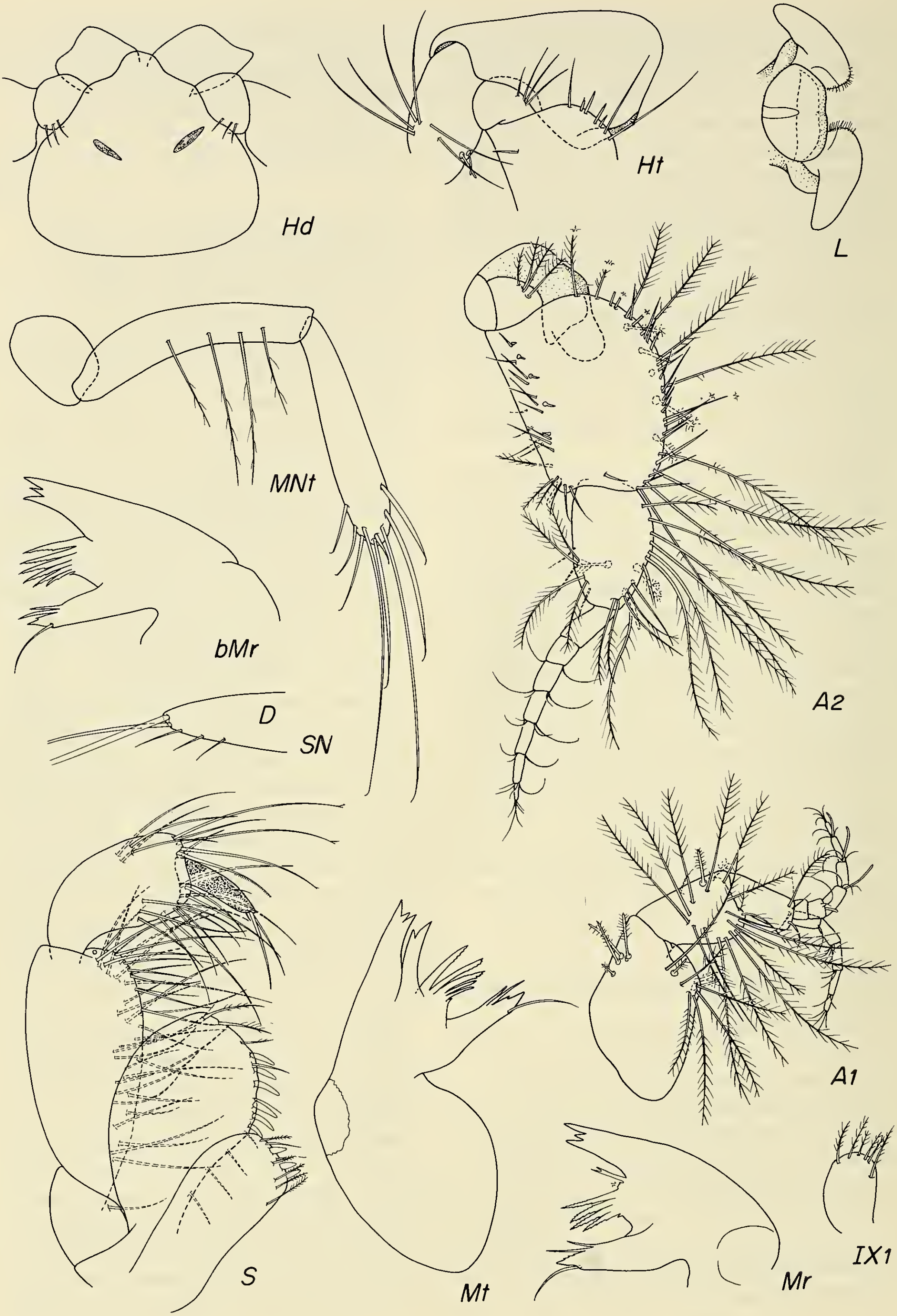
Tonocote Clark & Barnard, 1986

Tonocote Clark & Barnard, 1986:227–228.

Diagnosis (emendations in italics).—Rostrum short and broad but head extended strongly anteriad from antennal notch. Peduncle of antenna 1 somewhat elongate, stout, articles 2 and 3 of peduncle progressively shortened, geniculate between articles 1 and 2, both flagella moderately long. Aesthetascs simple. Antenna 2 of full haustorius form, article 4 expanded, article 5 small, articles 4–5 with facial armaments (5 weakly), article 4 with long ventral setae, subventral clusters of simple setae and facial armament row. Mandibular incisors slightly extended, of ordinary thickness, toothed; rakers 5 or more, serrate; molar small, thin, extended, with 1 main and 3–5 subapical cusps plus 3 marginal setae; setae of palp article 3 not awned, apically hooked. Inner plate of maxilla 1 of medium size, sparsely setose, *outer plate with 8–11 spines,* palp short. Inner plate of maxilla 2 with weakly submarginal row of sparse setae. Article 3 of maxilliped not extraordinarily elongate, slightly expanded apically, dactyl unguiform, elongate, bearing apical nail and subsidiary setae.

Coxae 1–4 progressively larger, each slightly produced posteroventrally, coxae 1–2 small, subequal in size; coxae 2–6 with simple gills; oostegites unknown.

Gnathopods small, grossly alike, carpi elongate, propodi somewhat smaller, mitteliform, subchelate, but palm more transverse on gnathopod 2 than on gnathopod 1. Dactyls of pereopods 3–7 distinguishable but on pereopods 6–7 often hidden among similar spines, those of pereopods 3–5 large,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those of pereopods 6–7 very small; dactyl of pereopod 5 blade-like, lacking spines. Article 2 of pereopods 5–7 expanded but less strongly on pereopod 6 than on 5 and 7; distal articles of pereopod 6 moderately widened, 7 more expanded; pereopods 6–7 otherwise similar, dominating pereopod 5.

Pleopod 2 slightly inferior, inner rami shorter than outer. Epimeron 2 dominantly setose, epimeron 3 dominant in size. Urosomites weakly produced and weakly setose ventrally. Rami of uropods 1–3 evenly sublinguiform, *each outer ramus bearing 2–3 apical plumose setae, each inner ramus bearing 1–2 apical plumose setae*; peduncles weakly setose. Uropod 3 inner ramus with one basomedial seta. Telson short, broader than long.

Description (emendations in italics).—Eyes weak, ocular ganglia visible. Dorsolateral surface of article 1 on antenna 1 furnished with small, poorly organized group of setae; article 2 moderately setose dorsolaterally; article 3 poorly setose. Article 3 of antenna 2 short, sparsely setose, flagellum much longer than article 4 of peduncle. No calceoli observed.

Right lacinia mobilis, if present, slender, small, bifid or not, left slender, bifid. Lower lip lacking cones. Inner plate of maxilla 1 with sparse apical and medial setae; several spines on outer plate bifid. Inner plate of maxilliped with 3 stout apical spines.

Coxa 1 poorly to very setose, coxae 2–3 poorly setose, coxae 4 moderately setose. Gills forming stepped intergrades with gill 2 dominant. Gnathopod 2 lacking surficial buttons.

Pereopods 3–4 lacking extensive posteroproximal spines on article 5.

Uropods with sparse dorsal setae, medial margins of peduncles sparsely setose.

Type species.—Tonocote magellani Clark & Barnard, 1986.

Composition.—Tonocote introflexidus, new species.

Relationship.—Despite a few convergences towards *Prantinus* Barnard & Drummond (1982) as represented in our new species, *Tonocote* continues to differ from *Prantinus* in: (1) the small and weakly setose epimeron 2; (2) the sharp posteroventral corner of epimeron 3; (3) the poor medial setation of the inner plate on maxilla 2 in adults; (4) the much stouter antennae 1–2; and (5) the narrow and mitelliform propodi of gnathopods 1–2. A principal character no longer differentiating the two genera is the extensive posteroproximal spination on article 5 of pereopods 3–4 formerly limited to *Prantinus*; our new species and especially one aberrant female, has this spination well or better developed than heretofore observed in the type-species of *Tonocote.*

Tonocote introflexidus, new species
Figs. 1–5

Diagnosis.—Epimeron 3 with large posteroventral hook curled inward; outer plate of maxilla 1 with 11 spines; armaments on pereopods 3–7 much denser than in type-species.

Description of male.—Holotype male "d," 4.74 mm; head about 90 percent as long as

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Fig. 1. *Tonocote introflexidus,* unattributed figures = holotype, male "d" 4.74 mm (USNM 195180); b = female "b" 6.43 mm (USNM 235030). Upper case letters refer to parts; lower case letters to left of uppercase letters refer to specimens noted in legends; lower case letters to right of uppercase refer to adjectival modifications in list: A, Antenna; C, Coxa; D, Dactyl; E, Epimeron(a); G, Gnathopod; H, Head; I, Inner plate or ramus; J, Pleopodal coupling hooks; L, Labium; M, Mandible; N, Palp; O, Outer plate or ramus; P, Pereopod; R, Uropod; S, Maxilliped; T, Telson; U, Labrum; W, Pleon; X, Maxilla; Y, Pleopod; Z, Gill; a, Anterior; d, Dorsal; p, Posterior; r, Right; s, Setae removed; t, Left.

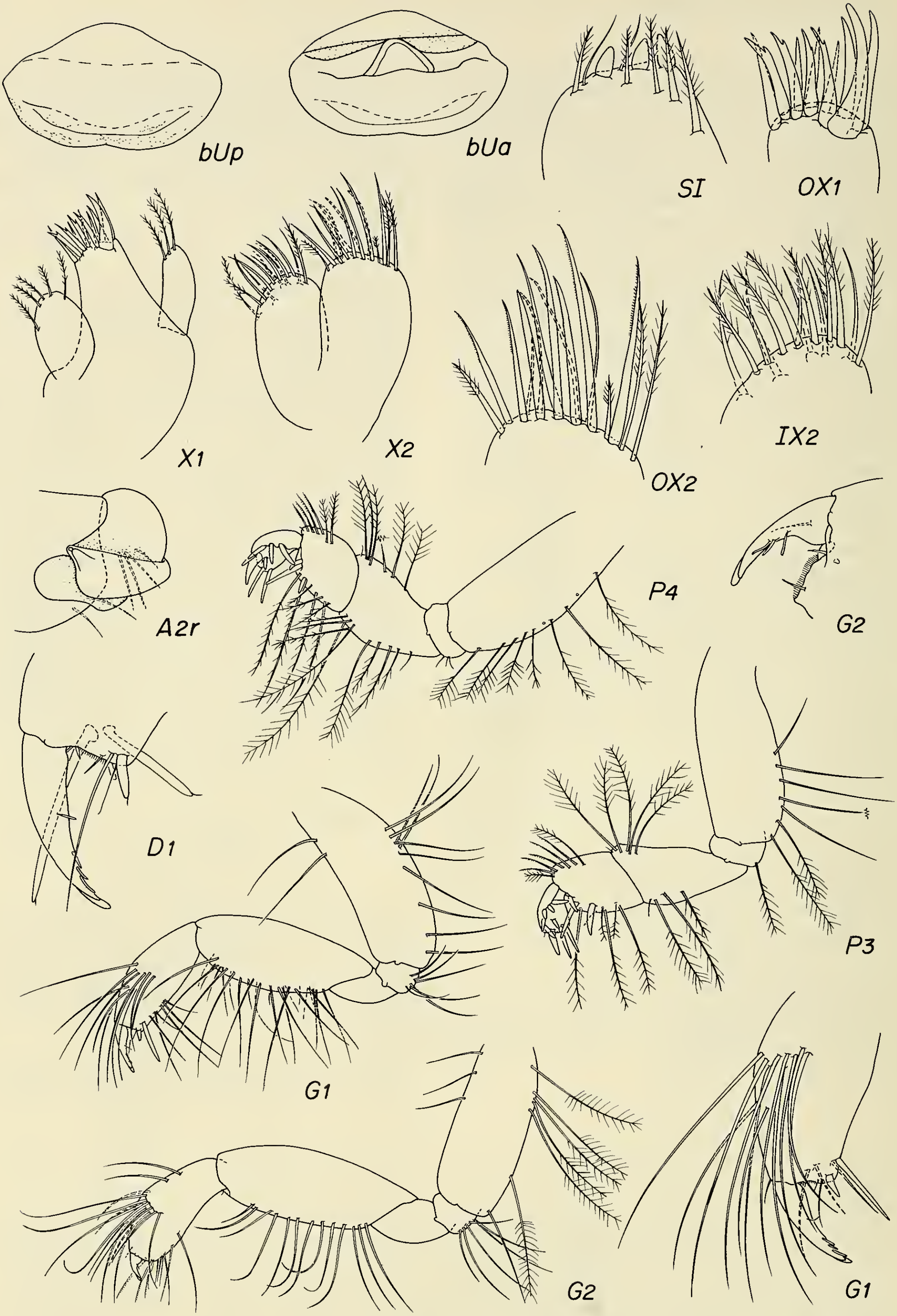

Fig. 2. *Tonocote introflexidus,* unattributed figures = holotype, male "d" 4.74 mm; b = female "b" 6.43 mm. Letter codes, refer to Fig. 1.

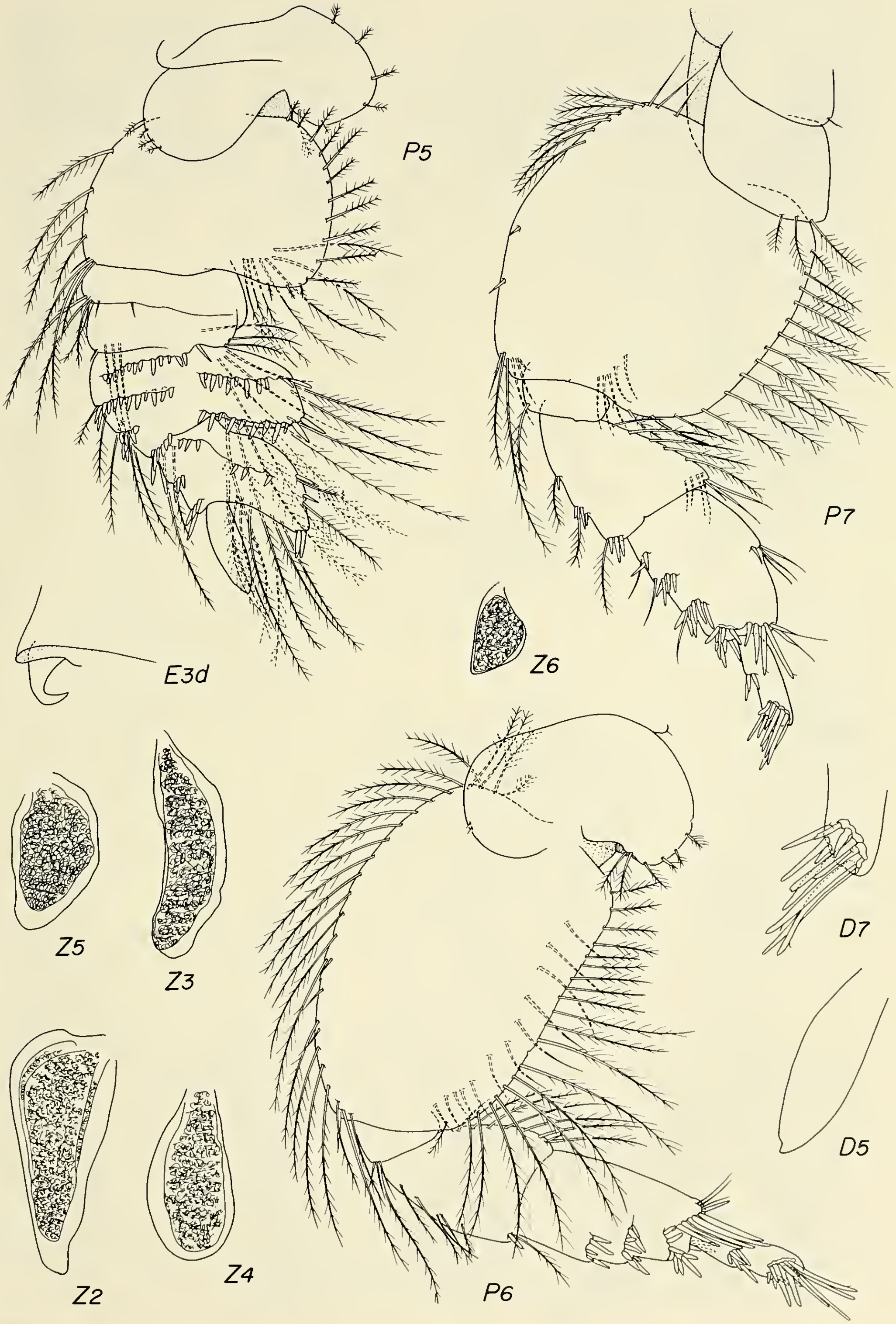

Fig. 3. *Tonocote introflexidus*, holotype. Letter codes, refer to Fig. 1.

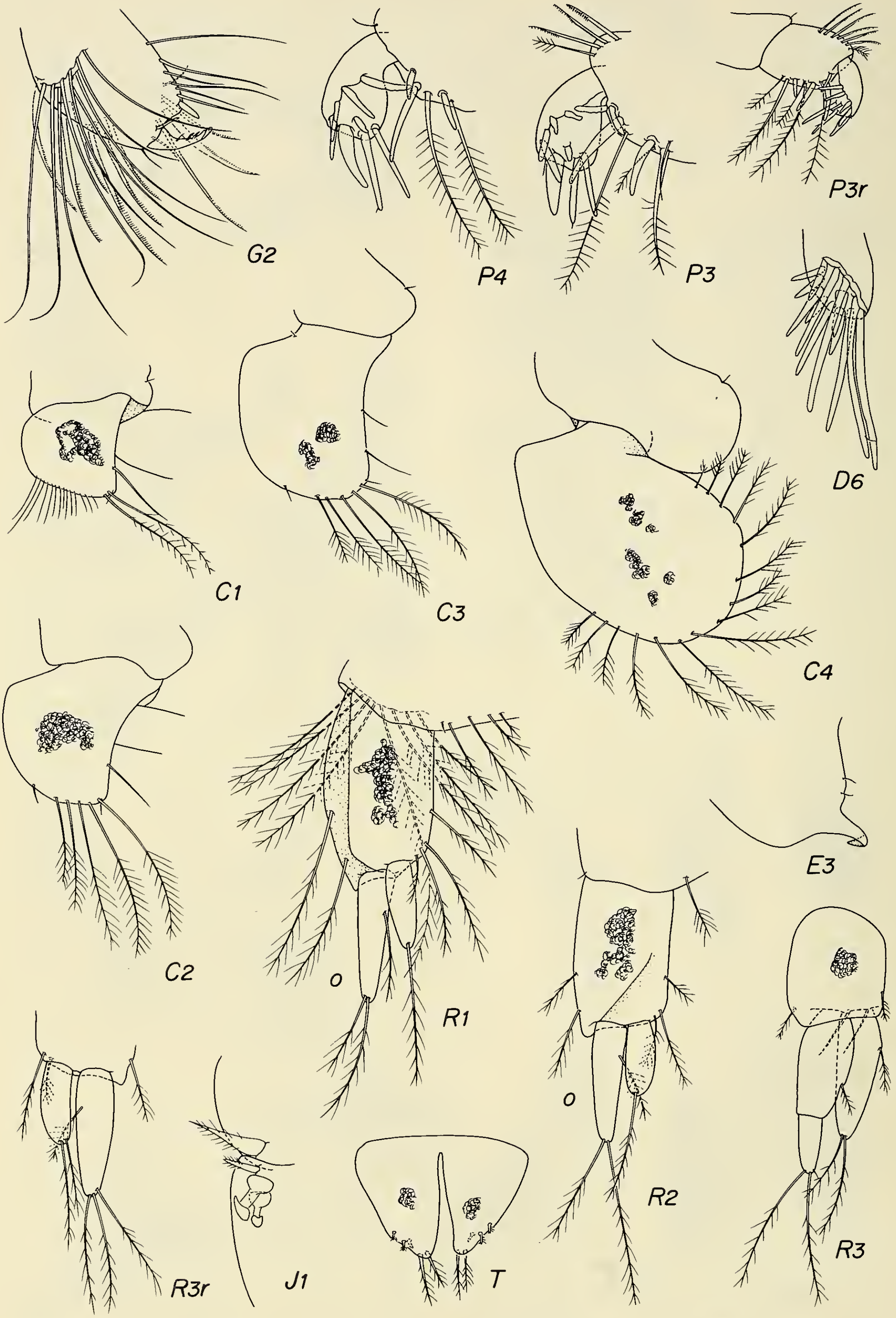

Fig. 4. *Tonocote introflexidus,* holotype. Letter codes, refer to Fig. 1.

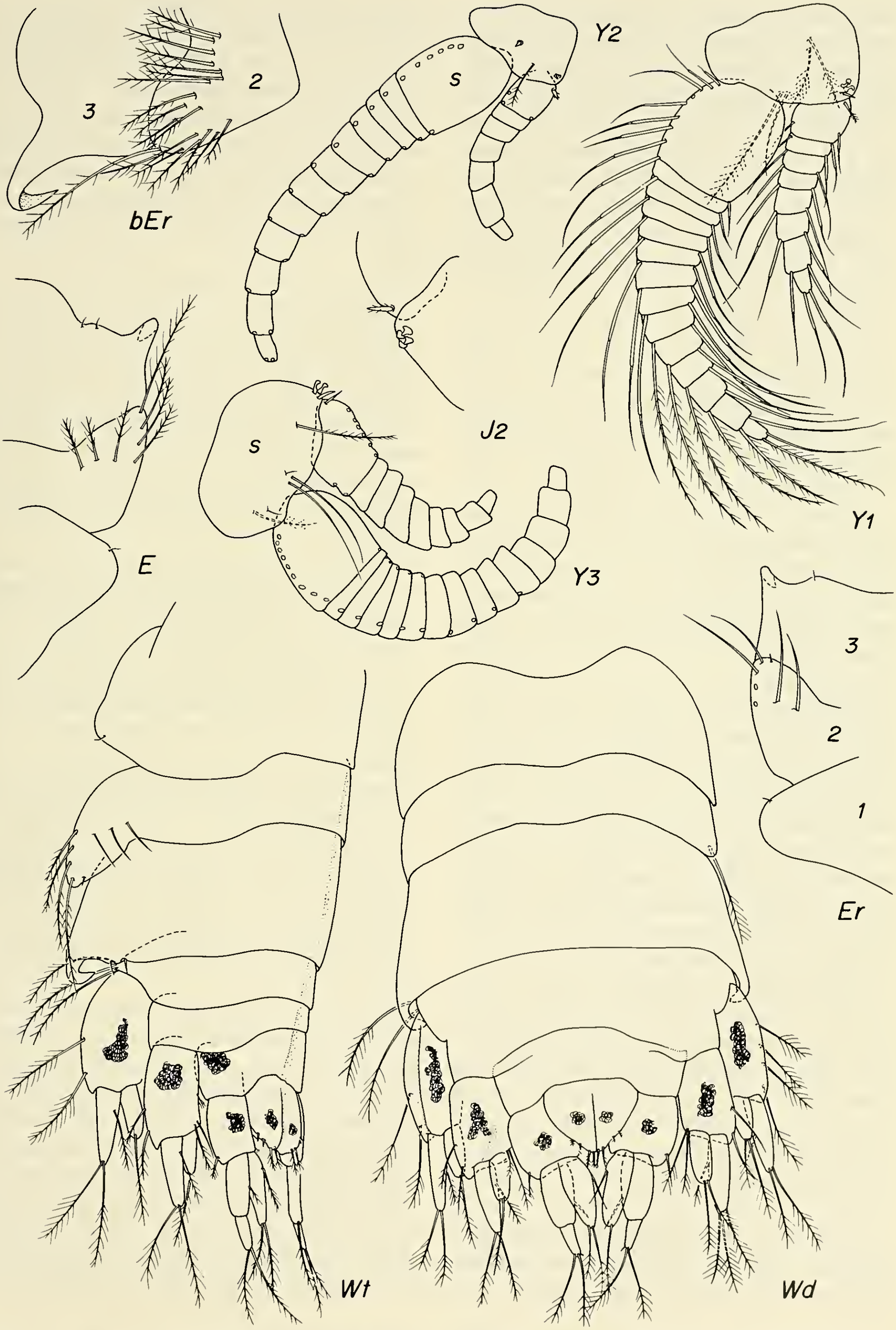

Fig. 5. *Tonocote introflexidus,* unattributed figures = holotype; b = USNM 235030. Letter codes, refer to Fig. 1.

wide, rostrum about 25 percent as long as remainder of head, eyes represented by their attendant ganglia, actual ommatidia or pigment not discerned. Facial formula of setae on article 1 of antenna 1, ventral = 5 penicillate, dorsal = 6 setae + 3 medium penicillate (noting that dorsal–ventral aspects reversed from normal, non-urothoid kind of antenna 1); article 2 with 7 dorsomarginal setae, 1 apicodistal seta and facial circle of 9 long plumose setae; primary flagellum with 6 articles, aesthetasc formula = 0-1-1-1-1-1, accessory flagellum of 5 articles. Article 3 of antenna 2 with 4 medium setae; facial formula of spines on article 4 = 1-1-2-3-3 (each set also having one small penicillate spine); article 5 = 4 seta dorsally, 5 facial ventrally; flagellum of 6.5 articles.

Upper lip with granulations. Right and left mandibular incisors with 2+ teeth each; right lacinia mobilis probably absent or represented by first element in bundle of rakers, left lacinia mobilis large and bifid; 7 right rakers, 6 left; each molar with large main cusp bearing 2 long thin basal accessory cusps and apposing minor cusps on each side more apical, plus longer thin seta from base opposite to most basal accessory cusp; article 3 of palp as long as article 2, latter with 4 (right = 5) facial setae, spine formula on left and right article 3 = 4-1-3-1 and 4-1-2-1. Inner plate of maxilla 1 bearing 3 apical, one mediofacial, and 1 (R = 2) laterofacial seta; outer plate with 11 spines; palp with 3 apical setae.

Inner plate of maxilliped with 3 stout spines, 6–7 submarginal setae and 2 apical setae; medial margin of outer plate with ragged mixture of spines and scattered small setae, apex with 2 setae; article 2 of palp with row of 3 mediofacial setae; article 3 with 3 medial facial setae, 2 lateral facial setae, and large serrate spine at base of dactyl.

Coxa 1 subrectangular, convex anteriorly, bearing 13 (right = 14) setae on ventral margin, 1 seta on posterior margin and 2 long plumes and 1 setule posteroventrally; coxa 2 similar in shape to coxa 1 but anterior convexity greater, with 1 short seta and 5 long posteroventral plumes and 1 setule and 1 medium seta on posterior margin; coxa 3 similar to coxa 2 but more elongate and with 2 medium setae on posterior margin, coxa 4 adze-shaped with 15 long plumose setae along anterior, ventral and posterior margins.

Setal and spine formulas on pereopod 3 = 5, 7, 2-1 (R = 2-1-1), 5+2+1; on pereopod 4 = 6, 2-1, 4+2+1; article 5 anterior armament combining plumose setae (range 0–2) and serrate spines (5 on pereopod 3, 6 on pereopod 4); margins of articles 5–6 not serrate. Article 2 of pereopods 5–7 well armed, with long setae posteriorly; dactyl of pereopod 5 with small apical tooth pointing anteriorly.

Peduncular spine formulas of pleopods 1–3 = 2 and 1, 2 and 0, 2 and 1; segmental formulas = 14-8, 12-7, 15-9 (right = 15-10); basal setal formulas = 9 (right = 10)-1-2-2, 6 (right = 7)-1-2-1, 9 (right = 8)-1-2-6 (right = 4), two midapical peduncular setae each on pleopods 1 and 3 and one on pleopod 2.

Epimeron 1 rounded quadrate, with 1 tiny setule posteroventrally; epimeron 2 extended posteroventrally, posterior margin notched 3 (R = 2) facial, 4 posteroventral setae and 1 tiny posterior seta; epimeron 3 sharply produced and bent inward posteroventrally, with 1–2 setules on posterior margin.

Lateral margin of peduncle on uropod 1 with 2 (R = 4) setae, of uropod 2 with 2 setae, of uropod 3 with 1 seta. Uropod 3 with 2 ventral setae at base of rami. Apicomedial corner of peduncle on uropod 1 with 3 setae, of uropod 2 with 2 setae; medial margins each with 1 seta; inner rami of uropods 1–2 extending 50 percent along outer; uropods 1–3 with 1 seta on medial margin of each outer ramus; uropod 3 inner ramus with 1 medial seta. Apical setae of outer and inner rami on uropods 1–3 = 2 and 1 (R = 2 and 2), 2 and 1 (R = 2 and 3), 2 and 2 (R = 2 and 1).

Telson about 1.5 times as wide as long, weakly alate laterally, cleft about 85 percent of its length, each apex with 2 long plumes, each side with 2 small penicillate setules on dorsal surface and 1 on ventral surface.

Glands discernible in coxae 1–4, peduncles of uropods 1–3, and telson.

Male "a," 3.73 mm.—Differences from male "d": Antenna 1 with 2 apicodistal setae; primary flagellum with 6 articles; aesthetasc formula = 1-1-1-1-1. Antenna 2 article 3 with 3 medium setae. Left and right mandibles with 5 rakers (no lacinia mobilis on right); article 3 of mandibular palp spine formula = 4-1-4-1 (R = 3-1-3). Maxilla 2 inner plate less setose. Maxilliped inner plate (left side) with 7 submarginal setae; outer plate (right side) with 3 apical setae; palp article 3 with 2 mediofacial setae; right side lacking serrate spine at base of dactyl. Coxa 1 with 16 ventral setae (right side missing). Gnathopod 2 article 5 with 16 posterior setae; pereopod 3 (left) article 6 formula = 4 + 1 + 2; pereopod 4 article 4 with 7 anterior setae, article 5 anterior group of setae with no plumose setae; setal and spine formula on right side = 6, 5, 2-0, 5+2+1; pereopod 6 article 5 with one additional group of spines. Peduncular spine formula of pleopod 1 (left) = 9-1-3-2; 5 peduncular setae; peduncular spine formula on pleopod 2 = 7-1-2-2 (left), 6-1-2-2 (right), segmental formula on right = 13-7; pleopod 3 segmental formulas = 15-10 (left), 15-11 (right); spine formulas = 7-1-2-4 (left), 9-2-2-3 (right); peduncle left side with an extra seta. Epimera 2 with 2 facial (R = 3) setae. Uropod 1 peduncle with 1 more apicomedial seta, lateral margin of right with 3 setae; uropod 2 lacking mid-medial seta on peduncle; uropod 3 peduncle with 3 ventral setae at base of rami.

Female "b," 6.43 mm.—Differences from male "d": In general more setose and spinose than male "d." Accessory flagellum with 6 articles; article 2 with 10 dorsomarginal setae, 9 setae in facial circle plus 7 other facial setae scattered in ventrodistal area. Antenna 2 article 3 with 5 (R = 6) medium setae; flagellum (left) with 7 articles (right = broken). Right and left mandibles with 6 rakers, right with simple "lacinia mobilis"; palp article 2 with 10 facial setae, article 3 spine formula (left and right) = 6-1-4-1 (R = 5-1-4-1). Inner plate (right) of maxilla 1 bearing 2 apical, 1 mediofacial and 4 lateral facial setae. Maxilliped inner plate with 7 submarginal setae; apex of outer plate with 4 setae; article 2 of palp with row of 4 mediofacial setae; article 3 with 6 mediofacial setae and 6 lateral facial setae; palp with 2 (R = 3) inner setae. Coxa 1 with 29 ventral setae and 3 long posterior apical setae; coxa 2 with 8 ventral setae; coxa 3 with 7 long ventral and 4 posterior setae (right = 8 ventral and 3 posterior); coxa 4 with 23 total setae. Setal and spine formulas on pereopod 3 = 7, 9, 2-1-1-1-1, 6+3+1 (right = 8, 9, 2-1-1-1-1, 7+3+1); on pereopod 4 = 8, 9, 2-1-1, 7+3+1; pereopod 5 article 6 with extra row of anterior spines; pereopod 6 article 5 with 2 extra rows of spines, article 6 with 1 extra row of spines; pereopod 7 article 4 (right side only) with extra group of spines; articles 5 and 6 with an extra row of anterior spines each. Segmental formulas of right sided pleopods 1–3 = 18-11, 16-10, 20-14; basal setal formulas = 10-3-3-3, 6-2-2-1, 9-2-3-5; peduncular setae = 9 on pleopod 1, 6 on pleopod 2, 14 on pleopod 3 (scattered in 5 separate groups). Epimeron 2 with 14 facial and 5 ventral setae; epimeron 3 with a more pronounced, larger tooth. Uropods 1–3 with more produced apicolateral corners; lateral margin of peduncle on uropod 1 with 6 setae, of uropod 2 with 4 setae, of uropod 3 with 3 setae; uropod 1 with 1 apicolateral seta; apicomedial corner of peduncle on uropods 2–3 with 3 setae each; medial margin of uropod 1 with 5 setae, or uropod 2 with 3 setae, of

Table 1.—Variability in setation of uropods 1, 2, 3.

	U1	U2	U3
	Apical setae: outer ramus/inner ramus		
Male D	2/1 (R = 2/2)	2/1 (R = 3/2)	2/2 (R = 2/1)
Male A	2/1	2/1	2/1
Male C	2/2 (R = 2/1)	2/1	2/1 (R = 2/2)
Female B	2/2	2/2	2/1
Juvenile E	2/1	2/1	2/1
	Medial setae: outer ramus/inner ramus		
Male D	1/0	1/0	1/1
Male A	1/0	1/0	1/2
Male C	1/0	1/0	1/2
Female B	2/1	2/1	1/3
Juvenile E	0/0	0/0	0/1

uropod 3 with 4 setae; inner rami of uropods 1–2 extending 75 percent along outer; uropods 1–2 outer rami with 2 medial setae each; uropod 3 outer ramus with 1 medial seta; inner ramus of uropods 1–2 with 1 seta each, uropod 3 with 3; apical setae of outer and inner rami on uropods 1–3 = 2 and 2, 2 and 2, 2 and 1. Telson with 4 apical setae.

Discussion.—Our new species always has all of the right raker spines clumped together; in the holotype the first raker is bifid but in the other specimens it is not. We do not know if the first raker is a lacinia mobilis or not. In *T. magellani* the first spine was figured as similar to the other rakers.

The apicoanterior setae of article 5 on pereopods 3–4 are diverse, some being plumose and others serrate. In the past, Barnard & Drummond (1978, 1982) and Clark & Barnard (1986) have not discriminated between kinds of armaments in a cluster in the formula originally proposed by Barnard & Drummond (1978). These setal forms are quite variable in the 5 specimens of our new species because some specimens lack the plumose members in the clusters.

Female "b" is exceptional in our 5 specimens in having full posteroproximal spination on article 5 of pereopods 3–4 like *Prantinus.* This destroys a former generic distinction between *Tonocote* and *Prantinus.*

Relationship.—This species differs from *T. magellani* in the presence of 11 spines (versus 8) on the outer plate of maxilla 1 as in *Prantinus*; the large hook on epimeron 3; the denser facial spines on articles 5–6 of pereopod 5 (on article 5 there are 32 spines versus 12 on the type, on article 6 there are 9 spines versus 4); the denser marginal armaments on pereopods 6–7; an added 1–2 posterior spines on articles 5–6 of pereopods 3–4, but, except in female "b" (see above), not as extensively spinose as in *Prantinus*; inner ramus of uropods 1–2 with either 1 or 2 apical setae (versus 1 in *T. magellani* and *Prantinus*); outer ramus of uropod 2 with up to 3 setae (versus 1 in the other taxa).

Illustrations.—Complete setosity not shown on pleopods.

Holotype.—Deposited in the National Museum of Natural History (USNM), Washington, D.C., USNM 195180, male "d," 4.74 mm (illustrated).

Type locality.—Eastern Straits of Magellan, 52°33.5'S, 68°57.5'W, 11 m, 9 Apr 1976, coll. Dr. Victor A. Gallardo.

Paratypes.—From the type locality: male "a," 3.73 mm (USNM 235032); female "b," 6.43 mm (USNM 235030); male "c," 4.74 mm (USNM 235031); juvenile "e," 2,32 mm (USNM 235033).

Etymology.—introflexidus, Latin, prefix "intro," within, inward; "flectere, flexum" to bend, to turn; suffix "idus," in a state or condition, referring to the inward turning epimeron 3.

Distribution.—Straits of Magellan, 11–16 m.

Acknowledgments

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101(2), 1988, pp. 366–374

VADOSIAPUS COPACABANUS, A NEW GENUS AND SPECIES OF EXOEDICEROTIDAE FROM BRAZIL (CRUSTACEA, AMPHIPODA)

J. L. Barnard and James Darwin Thomas

Abstract.—*Vadosiapus copacabanus,* n. gen. is described from the surf zone on the beach at Copacabana, Rio de Janeiro, Brazil. The genus and unique species is related to the three known species of *Bathyporeiapus,* which range southward from Brazil through the Magellan region of South America. *Vadosiapus* is distinguished from *Bathyporeiapus* in the odd phoxocephalid-like article 3 of the mandibular palp, the nonsinuate epimeron 2, the broadened telson bearing only midsagittal armaments and the enlarged dactyl of gnathopod 2.

Bathyporeiapus is a temperate South American genus of 3 species (see below), ranging from Santos, Brazil into the Magellanic region. These species generally live on coarse sand in heavy surf zones. *Bathyporeiapus* belongs to the Exoedicerotidae (Barnard & Drummond 1982), a family considered to be more primitive than, but not necessarily directly ancestral to, the Oedicerotidae. The Exoedicerotidae now have 11 genera with 19 species and probably all are very shallow surf-zone species. The Oedicerotidae, with 188 species in 30 genera, have only a few surf-zone species (especially in *Synchelidium* and *Monoculodes*), but has generally radiated widely into deeper and calmer waters and into the abyss.

The Exoedicerotidae are primarily confined to "Gondwanan" seas except for 3 species which have penetrated into the tropics. Oedicerotidae are richly represented in all seas and bear the apomorphic distinctions of fused eyes or loss of eyes and the loss of apical armaments on uropods 1–2.

We present (1) two updated keys to the genera of Exoedicerotidae, the second key of which emphasizes adult male characters of spine fields on the gnathopods; (2) an updated key to the species of and a revised diagnosis of *Bathyporeiapus* in the style to be presented soon in Barnard and Karaman's "The Families and Genera of Marine Gammaridea." Biogeographic code numbers in brackets and Professor Stock's classification of setae on the mandibular palp are described in Barnard & Barnard (1983).

Key 1 to the Genera of Exoedicerotidae

1. Uropod 3 composed of peduncle only .... *Metoediceros*
– Uropod 3 with 1–2 rami 2
2. Uropod 3 with 1 ramus *Notoediceros*
– Uropod 3 with 2 rami 3
3. Gnathopods well developed 4
– Gnathopods mittenform or inferior 7
4. Epimera 1–3 with many marginal setae .... *Patuki*
– All setae, if present, on epimera 1–3 facial, not marginal 5
5. Pereopods 3–4 with large dactyl, setae sparse ... *Metoediceropsis* male
– Pereopods 3–4 with dactyl vestigial, setae dense 6
6. Gill of coxa 5 small or vestigial, primary flagellum of antenna 1 with diverse armament, male and female gnathopods diverse .... *Exoediceros*
– Gill 5 ordinary, armament of pri-

mary flagellum on antenna 1 homogeneous, gnathopods of both sexes alike .... *Exoediceroides*

7. Molar feeble, simple, conical, not triturative, with apical spine .... *Exoediceropsis*
– Molar strong, triturative 8
8. Inner plate of maxilla 2 widely setose, maxilla 2 with submarginal facial inner setal row, dactyls of pereopods 3–6 ordinary 9
– Inner plate of maxilla 1 naked, maxilla 2 lacking facial or submarginal inner row of setae, dactyls of pereopods 3–6 vestigial .. 10
9. Uropod 3 dominant, much larger than uropod 1, strongly spinose . ... *Parhalimedon*
– Uropod 3 ordinary, lacking major spines .... *Kanaloa*
10. Epimeron 2 with posteroventral tooth, article 3 of mandibular palp not beveled, with A–B or D setae besides E-setae ...... *Bathyporeiapus*
– Epimeron 2 lacking tooth, article 3 of mandibular palp beveled, lacking A–B setae, all setae (E) on bevel .... *Vadosiapus*

Key 2 to the Genera of Exoedicerotidae (Especially Adult Males)

1. Male gnathopods with spine fields on propodi near apices of dactyls 2
– Male gnathopods lacking propodal spine fields 3
2a. Uropod 3 with 2 rami .. *Exoediceros*
b. Uropod 3 with 1 ramus .... *Notoediceros*
c. Uropod 3 lacking rami .... *Metoediceros*
3. Gnathopods ordinary, large 4
– Gnathopods mittenform or gnathopod 2 almost simple ....couplet 7 of Key 1
4. Epimera 1–3 with many marginal setae .... *Patuki*
– All setae of epimera 1–3, if present, facial .... *Exoediceroides*

Bathyporeiapus Schellenberg

Bathyporeiapus Schellenberg, 1931:154 (*Bathyporeiapus magellanicus* Schellenberg, 1931, monotypy).

Description.—Rostrum of moderate length, acute or downturned. Eyes bilateral, small. Article 3 of antenna 1 elongate, flagellar articles and armaments not diverse in type, weakly so in one species. Accessory flagellum "absent."

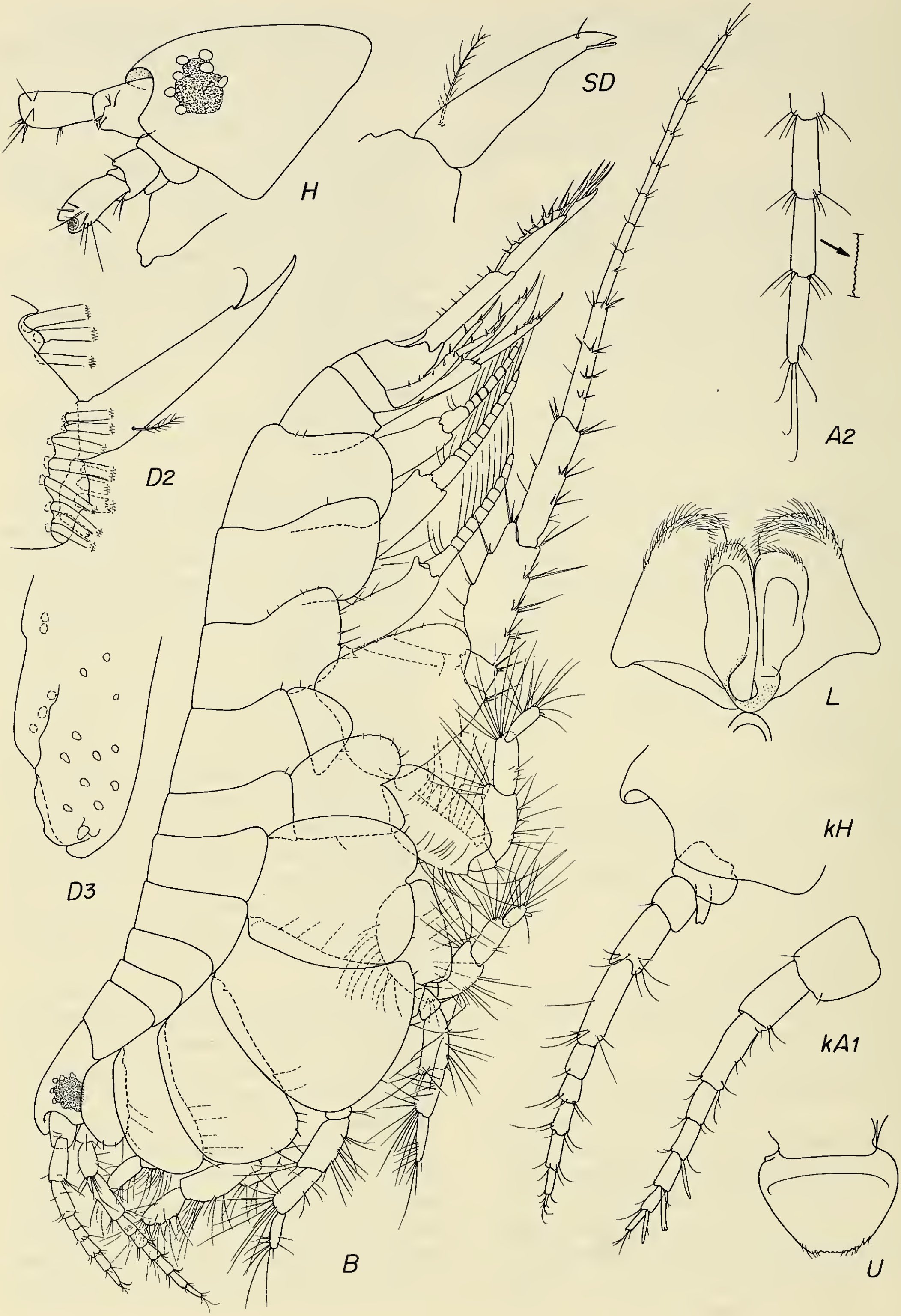
Cutting edge of mandible projecting and weakly toothed; molar large, weakly ridged; palp article 3 short, clavate or sublinear, without beveled apex, with A–B and D setae on sides of article 3. Inner plate of maxilla 1 lacking setae, outer plate with 7–9 spines. Plates of maxilla 2 strongly distinct in size, inner plate setose medially but without facial row of setae. Dactyl of maxilliped unguiform and long.

Coxae 1–4 large, coxa 5 scarcely shorter than coxa 4.

Gnathopods diverse, ?not sexually dimorphic, feeble, gnathopod 1 barely subchelate, carpus not lobate, much longer than propodus, latter expanded, palm oblique, gnathopod 2 much longer than gnathopod 1, simple, slender, carpus not lobate, very elongate, propodus also elongate; dactyl of gnathopod 2 vestigial; palms without spine fields.

Dactyls of pereopods 3–4 vestigial or absent. Dactyls of pereopods 5–6 vestigial, of pereopod 7 multiarticulate; article 2 of pereopod 7 broad but scarcely lobate posteroventrally. Gill of pereopod 5 [?ordinary].

Epimera 1–2 with setae on margins, epimeron 2 with tooth, epimeron 3 naked. Extension of uropods 1–3 diverse; uropod 2 shortest; uropod 2 not exceeding end of peduncle on uropod 3. Uropod 3 well developed but not huge, with 2 well developed rami, peduncle longer than rami of uropod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2. Telson not broader than long, apical armaments bilateral.

Relationship.—Differing from *Exoediceros* and *Exoediceroides* in the feeble, diverse gnathopods, with vestigial to moderate dactyl on gnathopod 2, lack of setae on the inner plate of maxilla 1, lack of facial setal row on the inner plate of maxilla 2, and the elongate article 3 of antenna 1.

Species.—*bisetosus* Escofet, 1970, 1971 [753]; *magellanicus* Schellenberg, 1931 [864]; *ruffoi* Escofet, 1971 (=sp. Ruffo 1956) (=*magellanicus* ID of Varela, 1983) [751–753].

Marine, Santos, Brazil to Magellan region, shallow water sands, 3 species.

Key to the Species of *Bathyporeiapus* and *Vadosiapus*

1\. Epimeron 2 not sinuate posteriorly, article 3 of mandibular palp lacking apicolateral ("A–B") setae, all setae on apical bevel, dactyl of gnathopod 2 well developed, telson broad, uropod 3 huge .... *V. copacabanus*

– Epimeron 2 sinuate posteriorly, article 3 of mandibular palp with apicolateral ("A-B") setae, apex poorly beveled, dactyl of gnathopod 2 weak, telson narrow, uropod 3 ordinary 2

2\. Rostrum strongly downturned apically, antennae and pereopods very setose, article 1 of primary flagellum (conjoint) as long as next 3 articles, apex of propodus on gnathopod 2 extremely setose and hiding vestigial dactyl, telson with 9–10 major apical and dorsal setae, dactyl of pereopod 7 with 15 articles .. *B. ruffoi*

– Rostrum not strongly downturned apically, antennae and pereopods moderately setose, article 1 of primary flagellum of antenna 1 not longer than succeeding articles, apex of propodus on gnathopod 2 well setose but not hiding small dactyl, telson with 6 or fewer major setae, dactyl of pereopod 7 with fewer than 11 articles 3

3\. Pereopods 3–4 (?with vestigial dactyl), telson with 6 apical setae increasing in length towards middle, dactyl of pereopod 7 with 8–10 articles, mandibular raker absent, uropodal spination sparse .... *B. magellanicus*

– Pereopods 3–4 lacking dactyl, telson with 2–4 short major apical setae, of subequal length, dactyl of pereopod 7 with 5–8 articles, mandibular rakers 2, uropodal spination strong, dense .... *B. bisetosus*

Vadosiapus, new genus

Type species.—*Vadosiapus copacabanus*, n. sp.

Etymology.—L., vadosi, shallower; L., apus, purulent, from the polluted type locality. Masculine.

Description.—Rostrum of moderate length, acute or downturned. Eyes bilateral, small. Article 3 of antenna 1 elongate, flagellar articles and armaments not diverse. Accessory flagellum "absent."

Cutting edge of mandible projecting and weakly toothed; molar large, weakly ridged; palp article 3 short, sublinear, apex beveled, all setae on apex. Inner plate of maxilla 1 lacking setae, outer plate with 7 spines. Plates

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Fig. 1. *Vadosiapus copacabanus:* unattributed figures = female holotype (USNM 195182), "i" 2.58 mm; k = male "k" 2.69 mm. Capital letters refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as described below: A, Antenna; B, Body; D, Dactyl; G, Gnathopod; H, Head; I, Inner plate or ramus; K, Seta; L, Labium; M, Mandible; P, Pereopod; R, Uropod; S, Maxilliped; T, Telson; U, Upper lip; W, Pleon; X, Maxilla; Y, Oostegite; Z, Gill; m, Medial; r, Right; t, Left.

of maxilla 2 strongly distinct in size, inner plate setose medially but without facial row of setae. Dactyl of maxilliped unguiform and long.

Coxae 1–4 large, coxa 5 scarcely shorter than coxa 4.

Gnathopods diverse, ?not sexually dimorphic, feeble, gnathopod 1 barely subchelate, carpus not lobate, much longer than propodus, latter expanded, palm oblique; gnathopod 2 much longer than gnathopod 1, simple, slender, carpus not lobate, very elongate, propodus also elongate; dactyl of gnathopod 2 moderately developed; palms without spine fields.

Dactyls of pereopods 3–4 vestigial or absent. Dactyls of pereopods 5–6 vestigial, of pereopod 7 multiarticulate; article 2 of pereopod 7 broad but scarcely lobate posteroventrally. Gill of pereopod 5 ordinary.

Epimera 1–2 with setae on margins, epimeron 2 lacking tooth, epimeron 3 naked. Extension of uropods 1–3 diverse; uropod 2 shortest; uropod 2 not exceeding end of peduncle on uropod 3. Uropod 3 very large, with 2 well developed rami, peduncle longer than rami of uropod 2. Telson broader than long, with single midapical armament.

Relationship.—Differing from *Exoediceros* and *Exoediceroides* in the feeble diverse gnathopods, with vestigial to moderate dactyl on gnathopod 2, lack of setae on the inner plate of maxilla 1, lack of facial row on the inner plate of maxilla 2, and the elongate article 3 of antenna 1.

Differing from *Bathyporeiapus* in the sublinear article 3 of the mandibular palp bearing only E setae on the bevel, in the lack of a tooth on epimeron 2, the enlarged uropod 3 which greatly exceeds the apex of uropod 2, the broad telson with a single midapical armament (versus bilateral armaments), and the much larger dactyl of gnathopod 2.

Species.—*copacabanus* Barnard & Thomas, herein [751].

Marine, shallow water sands, Rio de Janeiro, Brazil, 1 species.

Vadosiapus copacabanus, new species
Figs. 1–3

Holotype.—Deposited in the National Museum of Natural History (USNM), Washington, D.C., USNM 195182, female "i" 2.58 mm.

Type locality.–Brazil, Rio de Janeiro, Copacabana Beach, 3 May 1985, 45 m seaward from swash zone, depth 3.5 m, coarse quartz sediment, coll. J. D. Thomas and J. L. Barnard.

Material.—Type locality, paratypes, female "j" 2.47 mm, female "k" 2.69 mm, female "n" 2.52 mm and 2 other female specimens.

Etymology.—From the beach in Rio de Janeiro.

Diagnosis (in comparison to species of *Bathyporeiapus*).—Rostrum not strongly downturned apically; article 1 on primary flagellum of antenna 1 not conjoint; right and left mandibles each with large, linguiform lacinia mobilis, no rakers; article 3 of mandibular palp linear, apically beveled, all setae situated on bevel; dactyl of gnathopod 2 better developed than in other species; dactyls of pereopods 3–4 extremely vestigial; dactyl of pereopod 7 with about 8 articles; epimeron 2 convex posteriorly; telson broader than long, with stout apical spine in middle, with pair of lateral setae on each side.

Description (of holotype, female "i" 2.58 mm).—Eyes in alcohol purplish, with few clear ommatidia. Apex of upper lip truncate and scaled. Right and left mandibles almost identical. Mandibular lobes of lower lip very short. Inner plate of maxilla 1 small, naked, outer plate with 7 spines, palp article 2 with 8 setae. Inner plate of maxilla 2 narrower than outer plate, sparsely but fully setose medially, outer plate with 2 apicolateral setae. Inner plate of maxilliped with 7 setae, no locking spine; outer plate with 7 main medial spines and groups of ventral clavate setae, dactyl unguiform, with short nail.

Coxae 1–4 strongly increasing in size con-

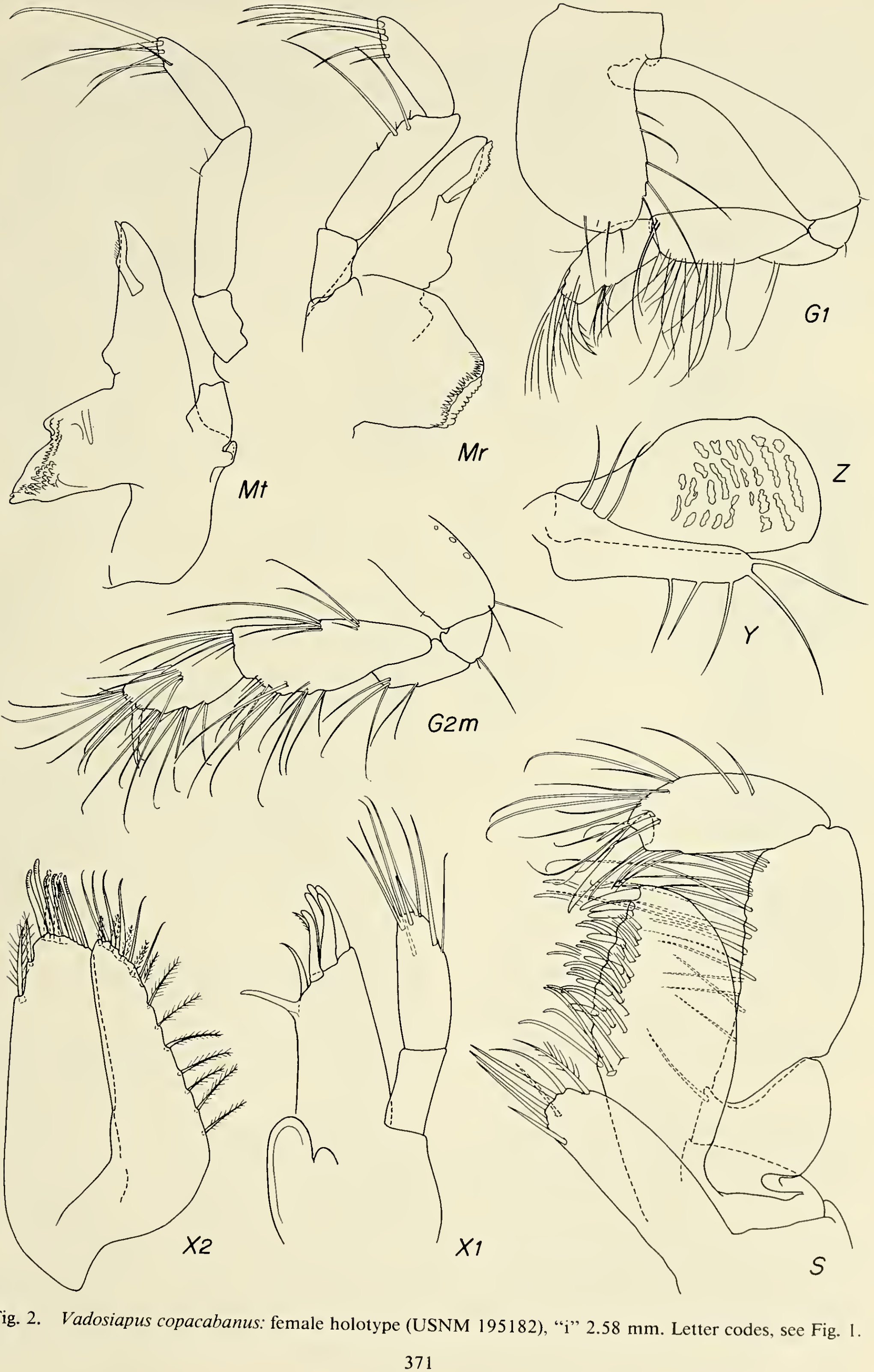

Fig. 2. *Vadosiapus copacabanus:* female holotype (USNM 195182), "i" 2.58 mm. Letter codes, see Fig. 1.

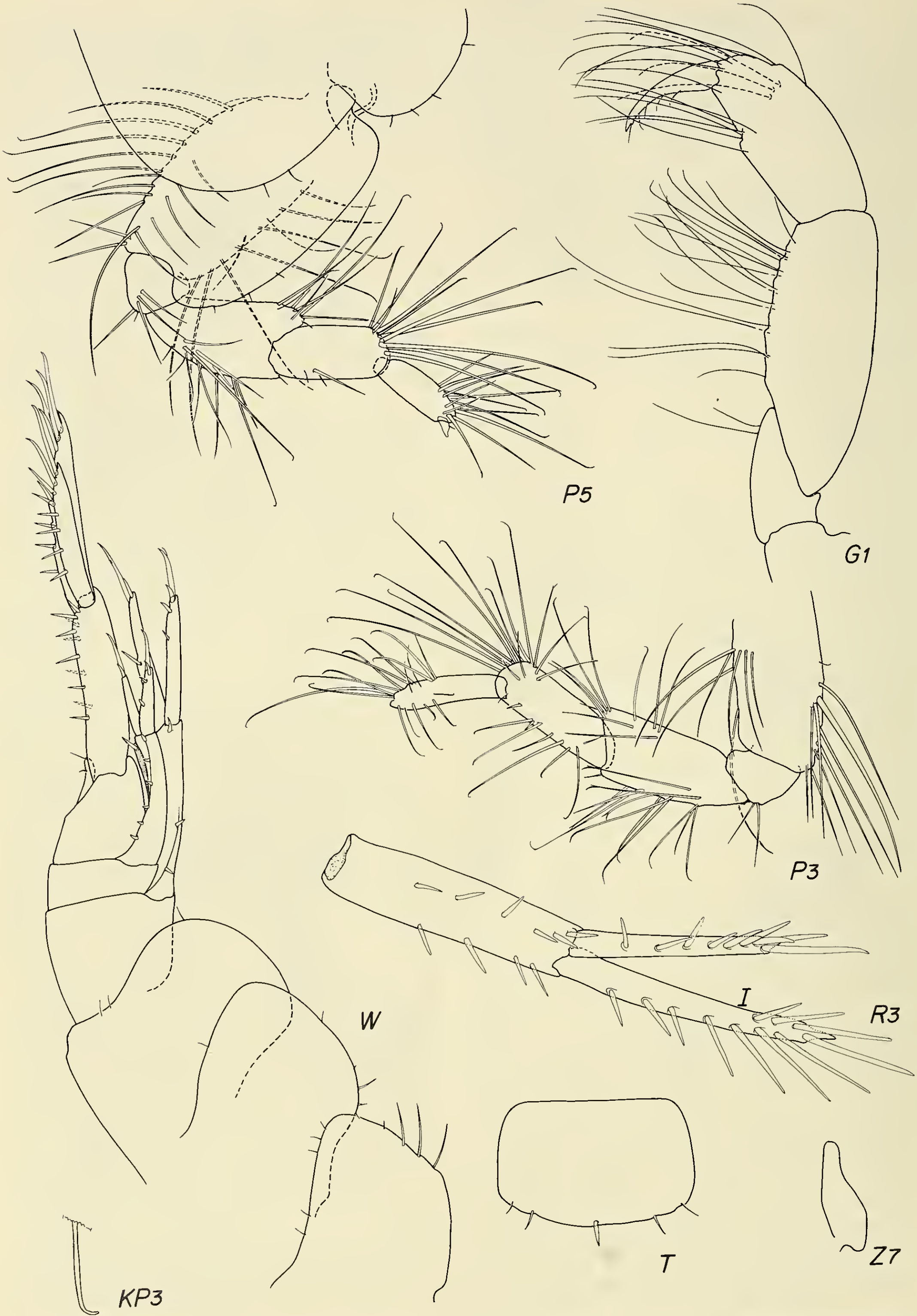

Fig. 3. *Vadosiapus copacabanus:* female holotype (USNM 195182), "i" 2.58 mm. Letter codes, see Fig. 1.

secutively, with sparse posterior setae, coxa 4 weakly excavated posteriorly, coxa 5 almost as long as 4. Gnathopods feeble, shapes weakly distinct, setation patterns strongly distinctive, gnathopod 1 simple, carpus anteriorly naked; gnathopod 2 scarcely subchelate, with propodal hump distal to dactyl, carpus setose anteriorly.

Dactyls of pereopods 3–4 vestigial or absent, pereopod 4 like 3 (thus 4 not illustrated). Dactyls of pereopods 5–6 very small, pereopod 6 like 5 but larger. Dactyl of pereopod 7 divided into 8 parts (articules). Gills on coxae 2–7, gill of coxa 7 very small (illustrated same magnification as pereopod 7); oostegites very thin and sparsely setose, present on coxae 2–5.

Pleopods well developed, similar to each other, peduncles about 2.8 times as long as wide, rami equal to each other in length, about 1.20 times as long as peduncle, outer rami with 10–11 articles, inner with 11, each peduncle with 2 coupling hooks, peduncle of pleopods 1–2 with apicolateral cusp. Epimera 1–2 rounded quadrate, 3 rounded posteroventrally, epimeron 1 with 5 ventral setae, epimeron 2 with 4 weak ventral setae, epimeron 3 naked ventrally. Peduncle of uropod 1 with 3 dorsolateral spines, medially with 3, of uropod 2 with 6 lateral spines, medially with one; each ramus of uropods 1–2 with 2 apical spines, outer rami with 2 marginal spines, inner with 1 and 0. Peduncle of uropod 3 with 6 dorsolateral and 4 dorsomedial spines, rami styliform or rod-like, outer much shortened, both richly spinose continuously to apex. Telson much shorter than broad, with single midapical spine and 2 penicillate setules in tandem on each side.

Female "j".—Palp article 2 of maxilla 1 with 7 elements, outer plate with 8 spines.

Female "k".—Palp article 2 of maxilla 1 with 5 elements, outer plate with 8 spines.

Male.—Unknown.

Relationship.—Differing from the species in *Bathyporeiapus* also in the dominant armament of the telson being a single medial spine, and the large lacinia mobilis on each mandible.

Couplet 2 of the key above lists characters for *B. ruffoi* all of which also differentiate it from *V. copacabanus.*

The species is perplexing in the condition of article 3 on the mandibular palp and departs most radically from "typical" *Bathyporeiapus* in that character.

Distribution.—Brazil, Rio de Janeiro, 3 m.

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NEW FOSSIL CRABS, *PLAGIOPHTHALMUS IZETTI, LATHETICOCARCINUS SHAPIROI,* AND *SAGITTIFORMOSUS CARABUS* (CRUSTACEA, DECAPODA), FROM THE WESTERN INTERIOR CRETACEOUS, U.S.A.

Gale A. Bishop

Abstract.—Collections of the U.S. Geological Survey (Denver) yielded three new species of crabs from the Cretaceous rocks of the Western Interior. *Plagiophthalmus izetti,* n. sp. and *Latheticocarcinus shapiroi,* n. gen., n. sp. are primitive crabs assigned to the Dromiacea. *Plagiophthalmus izetti* extends the geographic range of *Plagiophthalmus* from Europe (Albian-Cenomanian-Danian) into North America (Campanian). *Latheticocarcinus shapiroi* (Maastrichtian) is an enigmatic species which may be a descendant of *Dakoticancer. Sagittiformosus carabus* is a primitive dorippid with highly aberrant carapace morphology.

Recent studies of the Cretaceous crabs of North America have included examination of the Cretaceous paleontologic collections of the United States Geological Survey in Denver (USGS). In that collection were found the three species of Western Interior crabs described herein (Fig. 1). A second collection of specimens comprising *Latheticocarcinus shapiroi,* n. sp. was made available by a private collector, Mr. Robert Shapiro of New York City.

These three new species join the previously described Western Interior decapod faunas (Rathbun 1917; Bishop 1973, 1976, 1978, 1981, 1982, 1983a, b, c, 1985a, b, 1986b; Feldmann, Bishop, & Kammer 1977; Feldmann & Maxey 1980; Kues 1980; Bishop & Williams 1986). In contrast to the decapod-dominated Assemblages, including the *Dakoticancer* Assemblages, the Heart Tail Ranch Assemblage, and the Carlile *Linuparus* Assemblage, these crabs occur as isolated remains in faunas dominated by molluscs.

Systematic Paleontology

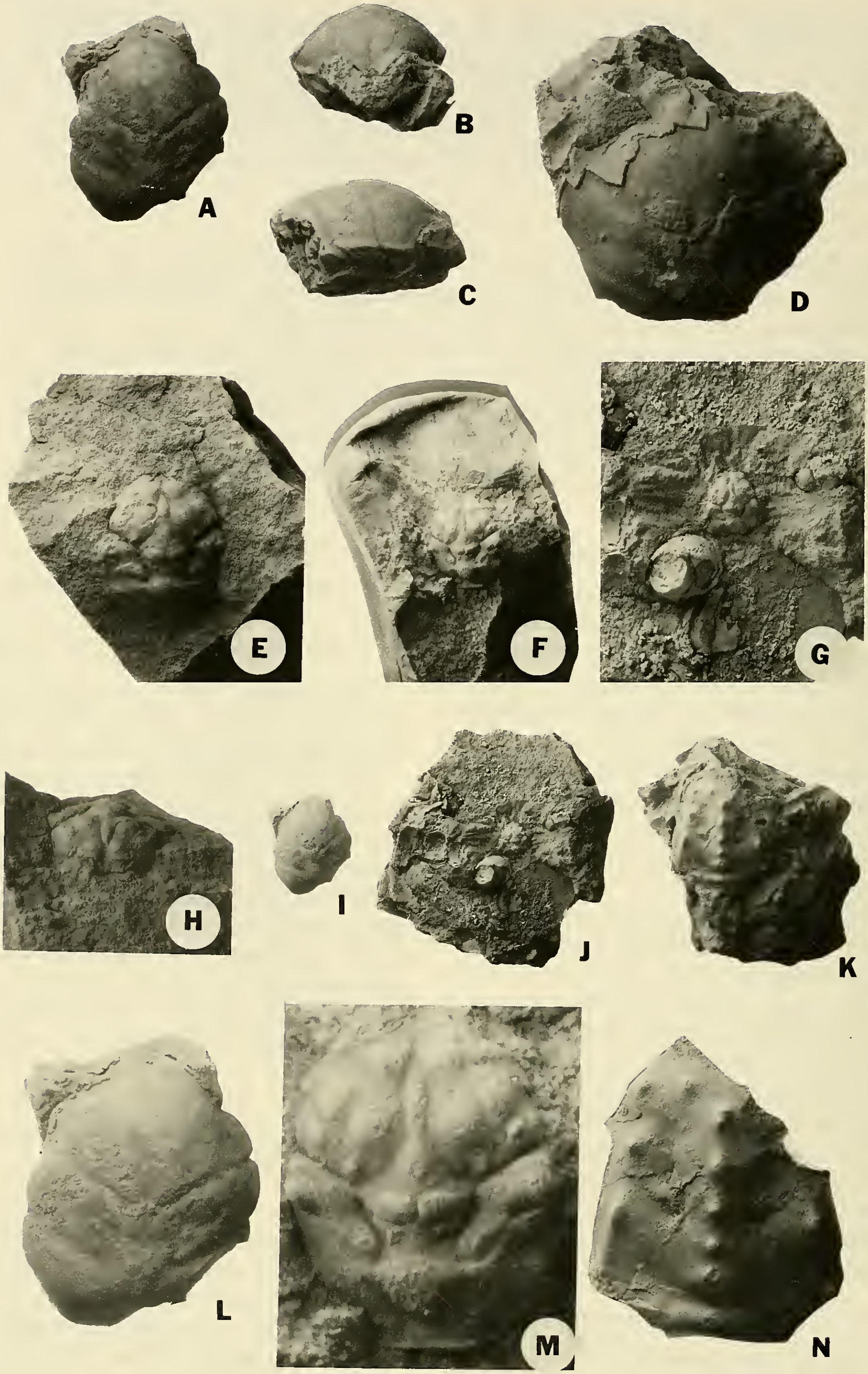
Superfamily DROMIOIDEA de Haan, 1833
Family PROSOPIDAE von Meyer, 1860
Subfamily PITHONOTINAE Glaessner, 1933
Genus *Plagiophthalmus* Bell, 1863

Type species.—The type species of *Plagiophthalmus* Bell, 1863, is *Plagiophthalmus oviformis* Bell, 1863, by monotypy.

Diagnosis.—Cephalothorax varying from broad with convex lateral margins to elongate with straight lateral margins; widest near middle; longitudinally and transversely arched. Lateral margins distinct, sometimes with prominent lateral spines. Rostrum short, downturned, broadly bilobed. Cervical and branchiocardiac furrows equal, well marked; carapace finely pitted. No emarginations in carapace for last pereopods.

Plagiophthalmus izetti, new species
Fig. 1A–C, D, I, L

Diagnosis.—Carapace elongate, ovate; arched longitudinally and transversely; smooth except for tumid branchial ridges, prominent frontal ridges, and subtle mesogastric groove. Cervical and branchiocardiac grooves deep, anterior of branchiocardiac shallow, swinging back to anterolateral


A
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margin. Cervical notch on anterolateral margin deep; carapace widest on mesobranchial lobe near midpoint; branchiocardiac groove forms marginal notches, posterolateral margin convergent; posterior of carapace missing.

Occurrence.—The holotype (Fig. 1A–C), deposited in the National Museum of Natural History (USNM), Washington, D.C. (USNM 418272) was collected from the Pierre Shale by Glen A. Izett (Col. No. CD-71-50) in the NE ¼, NE ¼, Sec. 25, T.3 N., R. 17 W., Grand Co., Colorado (USGS Locality D8090) from the zone of the ammonite *Baculites scotti,* an index fossil to upper Campanian rocks. The paratype (Fig. 1D) (USNM 418273) was collected from the Pierre Shale in the SE ¼, SE ¼, SE ¼, Sec. 29, T.2 S., R. 70 W., Jefferson County, Colorado, on 4 Nov 1955 by G. R. Scott, R. Van Horn, and W. A. Cobban (USGS Locality D596) from the zone of *Didymoceras cheyennense.*

Description.—Carapace elongate (L/W = 1.2), widest through middle, arched transversely and longitudinally, regions poorly differentiated by grooves, smooth. Cephalic arch poorly differentiated, diamond-shaped, bounded by broadly bilobed rostrum, slightly sinuous anterolateral margins and slightly sinuous broad, deep cervical furrow; only anterior tongue of mesogastric region delimited; faint hints of posterior parts of mesogastric and hepatic grooves split off cervical groove. Sides of rostrum raised into anterolateral margins, passing through cervical notches, becoming parallel, passing through branchiocardiac notch, converging toward missing posterior margin. Scapular arch well differentiated by cervical and branchiocardiac furrows; anterior part of branchiocardiac furrow obsolete distally, not reaching carapace margin; posterior part deep, forming notch where it meets dorsal shield margin. Epibranchial and mesobranchial regions thus partly separated; both well separated from broad metabranchial region. Cardiac region transverse with a granule on each side; intestinal region not delineated.

Comparison.—Plagiophthalmus izetti differs from *P. oviformis* Bell, 1863, by having a more triangular anterior, a more rapidly narrowing posterior, a better defined mesobranchial-epibranchial groove and two granules on its cardiac region. *Plagiophthalmus izetti* differs from *P. nitonensis* Wright & Wright, 1950, by having a more triangular front, lacking lateral spines, and having a more complete mesobranchial-epibranchial groove. *Plagiophthalmus izetti* is relatively much longer than *P. tribolet* Wright & Collins, 1972, and lacks the numerous nodes and tubercles of *P. nodosus* Wright & Collins, 1972.

Types.—The holotype (USNM 418272) and paratype (USNM 418273) are deposited in the collection of the United States National Museum of Natural History, Washington, D.C. 20560.

Etymology.—Plagiophthalmus izetti is named in honor of G. A. Izett, who collected the type specimens.

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Fig. 1. New Western Interior Cretaceous crabs. A–D, *Plagiophthalmus izetti*: A–C, Holotype (USNM 418272) in dorsal, anterior, and right lateral views (×2.0); D, Paratype 1 (USNM 418273) in dorsal view (×2.0). *E–H, Latheticocarcinus shapiroi*: E, H, Holotype (USNM 418474) in dorsal and anterior views (×2.0); F, Paratype 1 replica of impression (USNM 418275) in dorsal view (×2.0); G, Paratype 2 (USNM 418276) in dorsal view (×2.0); *Sagittiformosus carabus*: K, N, Holotype (USNM 418277) in dorsal view. I–K, L–N, Comparative dorsal views of new species from the Western Interior Cretaceous at normal size (I–K) and enlarged (L, ×3.0; M, ×7.1; N, ×2.0): *Plagiophthalmus izetti* (Holotype USNM 418272); *Latheticocarcinus shapiroi* (Paratype 1, USNM 418275); and *Sagittiformosus carabus* (Holotype, USNM 418277).

Superfamily DAKOTICANCROIDEA Rathbun, 1917

Family DAKOTICANCRIDAE Rathbun, 1917

Latheticocarcinus, new genus

Type species.—The type species is *Latheticocarcinus shapiroi,* n. sp.

Diagnosis.—Carapace very small, elongate, front rounded, posterior is rectangular; widest just ahead of midpoint; regions well delineated by grooves, tumid with broad, low bosses. Rostrum short, downturned, medially grooved; orbits occupy over half carapace width, rims beaded with granules.

Etymology.—*Latheticocarcinus* is derived from the Greek *lathetikos* (likely to be forgotten or overlooked) + karkinos (crab), masculine.

Latheticocarcinus shapiroi, new species

Fig. 1E–H, J, M

Diagnosis.—Same as for the genus *Latheticocarcinus.*

Occurrence.—The holotype (USNM 418274) was collected in 1940 by W. A. Cobban (WAC #1) from the Maastrichtian Fox Hills Formation on the Grand River, Corson County, South Dakota. Two paratypes (USNM 418275 and 418276) were collected by Robert Shapiro, either near Red Bird, Wyoming, or from the Fox Hills of Central South Dakota. The age of the holotype is Maastrichtian and the paratypes either Campanian or Maastrichtian.

Description.—Carapace very small, widest anterior to middle, elongate (L/W = 1.21), front oval, posterior rectangular; arched longitudinally and transversely; well differentiated by grooves into tumid regions. Anterolateral borders rounded (except for slightly projecting rostrum) to cervical notch, widening to maximum width on epibranchial ridge; posterolateral margins slightly convex, rounding abruptly onto rather straight, slightly raised posterior margin.

Grooves between mesogastric, protogastric, and urogastric regions shallow but well defined; cervical groove deep, sinuous, incomplete across gastric ridge; continuous with branchiocardiac groove, distally obsolete between epibranchial and mesobranchial regions; posterior of branchiocardiac regions nearly obsolete at anterior of cardiac region, fairly well defined posteriorly, outlining cardiac and intestinal regions; groove between metabranchial and mesobranchial regions indistinct. Mesogastric region triangular with long, narrow anterior tongue; widening slightly, then decreasing in width to point, forming single anterior medial groove, surmounted by 2 transverse bosses at species behind and one boss at widened place on anterior tongue. Protogastric region with 4 bosses arranged in shape of a diamond, bosses progressively decrease in size in order of proximal-anterior-distal-posterior. Rostrum short?, downturned, medially grooved; swollen boss. Frontal region narrow; orbits 22% of front, not fissured, beaded with granulation; hepatic region mostly on carapace wall and one boss just ahead of cervical groove on dorsum; urogastric region narrow, crescentic, slightly tumid. Cardiac region large, triangular, with transverse anterior base, slight boss at posterior base. Intestinal region small, with subtle central boss. Branchial region divided into well defined epibranchial ridge, three bosses in shape of a triangle, base oblique running forward and outward, the distal and anterior bosses nearly a continuous ridge. Mesobranchial region a narrow ridge, almost continuous with cardiac region, with subtle boss proximally. Metabranchial region wide, swollen distally, small boss proximally.

Comparison.—*Latheticocarcinus shapiroi* is similar to *Vectis wrighti* Withers, 1945, in the elongate nature of the carapace but differs in being widest across the middle, wider across the front, and differently ornamented. *Latheticocarcinus shapiroi* is most similar to members of the Family Dakoticancridae, particularly to *Tetracarcinus subquadratus* Weller, 1905, but differs by being even more elongate and having tumid bosses on the carapace lobes. The geographic and stratigraphic proximity of *Dakoticancer* in rocks slightly older than the Fox Hills Formation makes the possibility that *L. shapiroi* is a descendant of *Dakoticancer* or *Tetracarcinus* an intriguing possibility.

Types.—The holotype (USNM 418274), paratype 1 (USNM 418275), and paratype 2 (USNM 418276) are deposited in the collection of the National Museum of Natural History, Washington, D.C.

Etymology.—*Latheticocarcinus shapiroi* is named in honor of Robert Shapiro who collected the two paratypes.

Superfamily DORIPPOIDEA de Haan, 1841

Family DORIPPIDAE de Haan, 1841

Subfamily DORIPPINAE de Haan, 1841

Sagittiformosus, new genus

Type species.—The type species of *Sagittiformosus* is *Sagittiformosus carabus.*

Etymology.—The generic name, *Sagittiformosus,* is derived from the arrow-like shape of the type species (Latin; *sagitta,* arrow; *formosus,* beautifully shaped). Gender masculine.

Diagnosis.—Carapace rounded-pentagonal, longer than wide (l/w = 1.12), widest near the posterior, flat, sides slanted, poorly differentiated by grooves, 3 longitudinal rows of spines, one median sagittal with 6 spines, 2 lateral with 3 spines each, and one convex forward cephalic row of 4 spines (including the anterior spine of each lateral ridge). Cervical furrow broad and shallow distally, obsolete medially; branchiocardiac grooves reduced to depression flanking median sagittal ridge; deep transverse furrow between cardiac and intestinal regions.

Sagittiformosus carabus, new species

Fig. 1K, N

Occurrence.—The only known specimen of *Sagittiformosus carabus* is a carapace steinkern preserved in calcite cemented sandstone with steinkerns of molluscs. The specimen was collected by E. A. Merewether, S. C. Hook, and W. A. Cobban 17 Jul 1978 (Coll. #BG-78-8; USGS D10669) from the Frontier Formation in Fremont County, Wyoming (NE ¼ SW ¼ Sec. 22, T. 33 N., R.94 W.).

Diagnosis.—Same as for genus *Sagittiformosus.*

Description.—Carapace rounded, pentagonal, longer than wide (l/w = 1.12), widest at posterolateral angles; fairly level. Anterior margin rounded, diverging onto slightly convex lateral margins to obtuse posterolateral angle; posterolateral margin short, straight, and convergent posteriorly. Hind margin slightly sinuous and slightly concave at midpoint. Carapace grooves poorly developed; regions poorly delineated. Cervical groove broad and shallow distally, obsolete medially. Branchiocardiac groove reduced to a depression with extremely subtle anterior and lateral troughs that persist for short distances. A distinct transverse groove parallels the posterolateral and posterior margins, becoming obsolete near the lateral margins. The posterior margin is raised into an upturned rim. Three longitudinal rows and one transverse row of spines ornament carapace. Six median sagittal spines: 2 mesogastric, one urogastric (?), 2 cardiac, and one intestinal (on ridge behind transverse groove) flanked by 2 rows of 3 spines each, one hepatic and 2 branchial, just inside lateral margins of dorsum and forming a straight line coinciding with slope break onto slanted carapace sides. A convex forward row of 4 spines, one each on hepatic and protogastric regions, originates with anterior spines of lateral rows. A pair of tiny granules flank fourth medial spine (anterior cardiac spine).

Comparison.—*Sagittiformosus carabus* exhibits the characteristics of the subfamily Dorippinae and is similar to *Dorippe* Weber, 1795, and *Goniochele* Bell, 1858, in carapace outline, differing significantly from all of them by being spinose and tuberculate.

Type specimen.—The holotype (USNM

418277) and only known specimen is deposited in the collection of the National Museum of Natural History, Washington, D.C.

Etymology.—The crab is named *Sagittiformosus* + *carabus,* Latin, a sea crab.

Conclusions

The description of these scarce decapod remains from molluscan assemblages from the Western Interior Cretaceous Seaway reemphasizes the rarity of fossil decapods preserved under "normal" conditions. Aside from decapod-rich or decapod-dominated assemblages, the chances of preserving and collecting fossil decapods are greatly diminished (Bishop 1986a). It is much to the credit of Western Interior paleontologists that such scarce remains are found and conserved.

Plagiophthalmus izetti represents a relict species finding refuge in the shallow Western Interior Sea long after its acme of development in the Tethys Sea of Europe in the Early and early Late Cretaceous. In this respect, *P. izetti* joins *Ekalakia lamberti* Bishop, 1976, and *Dioratiopus dawsonensis* Bishop, 1973.

It is expected that additional specimens of the diminutive crab, *Latheticocarcinus shapiroi,* found high in the Pierre Shale and Fox Hills Formation of South Dakota and Wyoming will be found as curators of collections from those rocks become aware of and search for these tiny remains. As with many new decapod taxa described from scarce material, substantiation of the correct taxonomic assignment of this species must await additional specimens and analysis of new data derived from them.

All three new species are endemic to the Western Interior Late Cretaceous. This pattern of distribution, however, is highly suspect because of the nature of preservation as single or but a few specimens. The problem of sample size can only be overcome by continued collecting.

Acknowledgments

I thank Dr. W. A. Cobban of the U.S. Geological Survey (Denver) for allowing me to describe specimens from the collections which he administers. I also thank the individuals responsible for collecting individual specimens, W. A. Cobban, G. A. Izett, E. A. Merewether, S. C. Hook, and Robert Shapiro. Direct support for this research was provided by the National Science Foundation (NSF grant DEB 8011570) and The National Geographic Society (NGS 1629). Indirect support was provided by the Department of Geology and Geography and the Faculty Research Committee, Georgia Southern College, and The National Geographic Society. The manuscript was typed by Mrs. Judith McQuaig of the Institute of Arthropodology and Parasitology.

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REDESCRIPTION, ECOLOGICAL OBSERVATIONS, AND DISTRIBUTION OF THE CARIDEAN SHRIMP *PLESIONIKA ESCATILIS* (STIMPSON, 1860) (DECAPODA, PANDALIDAE)

Rafael Lemaitre and Robert H. Gore

Abstract.—Thirty-four shrimp specimens of *Pandalus escatilis* Stimpson, 1860 were collected using a research submersible in the Bahama Islands and during trawling operations elsewhere. The taxon, heretofore considered of obscure identity, belongs in the genus *Plesionika* Bate, 1888. The species is redescribed, and observations on the ecology, color pattern, and affinities are included. The distribution of Stimpson's species and that of the similar *Plesionika narval* (Fabricius, 1787), is briefly discussed.

On 31 Mar 1981, several specimens of a brightly colored shrimp were obtained west of Nassau Harbor, Bahama Islands, by a lock-out diver working from a research submersible. These shrimps, collected from a depth of 143 m, initially were considered by one of us (RHG) to represent *Parapandalus narval* (Fabricius, 1787), a species not known from the western Atlantic. Subsequently, Lemaitre (1984) reported a damaged specimen from Cay Sal Bank, Bahama Islands, as *Parapandalus* sp. The latter specimen appeared similar to *P. narval,* but because of its condition it was not possible to identify it with certainty.

In order to clarify the identity of these specimens, we compared them with material from various institutions and found that the Bahamas' specimens actually represent *Pandalus escatilis,* a species briefly described by Stimpson (1860). Stimpson's species was placed subsequently in the genus *Parapandalus* Borradaile, 1899. Some carcinologists (e.g., Holthuis 1949, Crosnier & Forest 1973), however, questioned this arrangement and noted that Stimpson's species might belong in *Plesionika* Bate, 1888. The present study will show that Stimpson's taxon has been confused with *Plesionika narval* (=*Parapandalus narval*) on the western coast of Africa.

Recently, Chace (1985) synonymized these two genera based on his opinion that the genus *Parapandalus,* retained in the past for those pandalids that differ from *Plesionika* in lacking epipods on the pereöpods (e.g., Holthuis 1955), is of no phylogenetic significance. Because of the problems of identity and distribution that have existed with Stimpson's *Pandalus escatilis,* we redescribe his species. Ecological observations obtained by a lock-out diver are also included, as well as some brief remarks on the distribution of this species and *Plesionika narval.*

Specimens used for this study came from the collection of: British Museum (Natural History) (BMNH); Florida International University (FIU); Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida (FSBC I); National Museum of Natural History, Washington, D.C. (USNM); and Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). The abbreviation CL indicates carapace length excluding rostrum, measured from posterior dorsal margin of carapace to posterior margin of orbit.

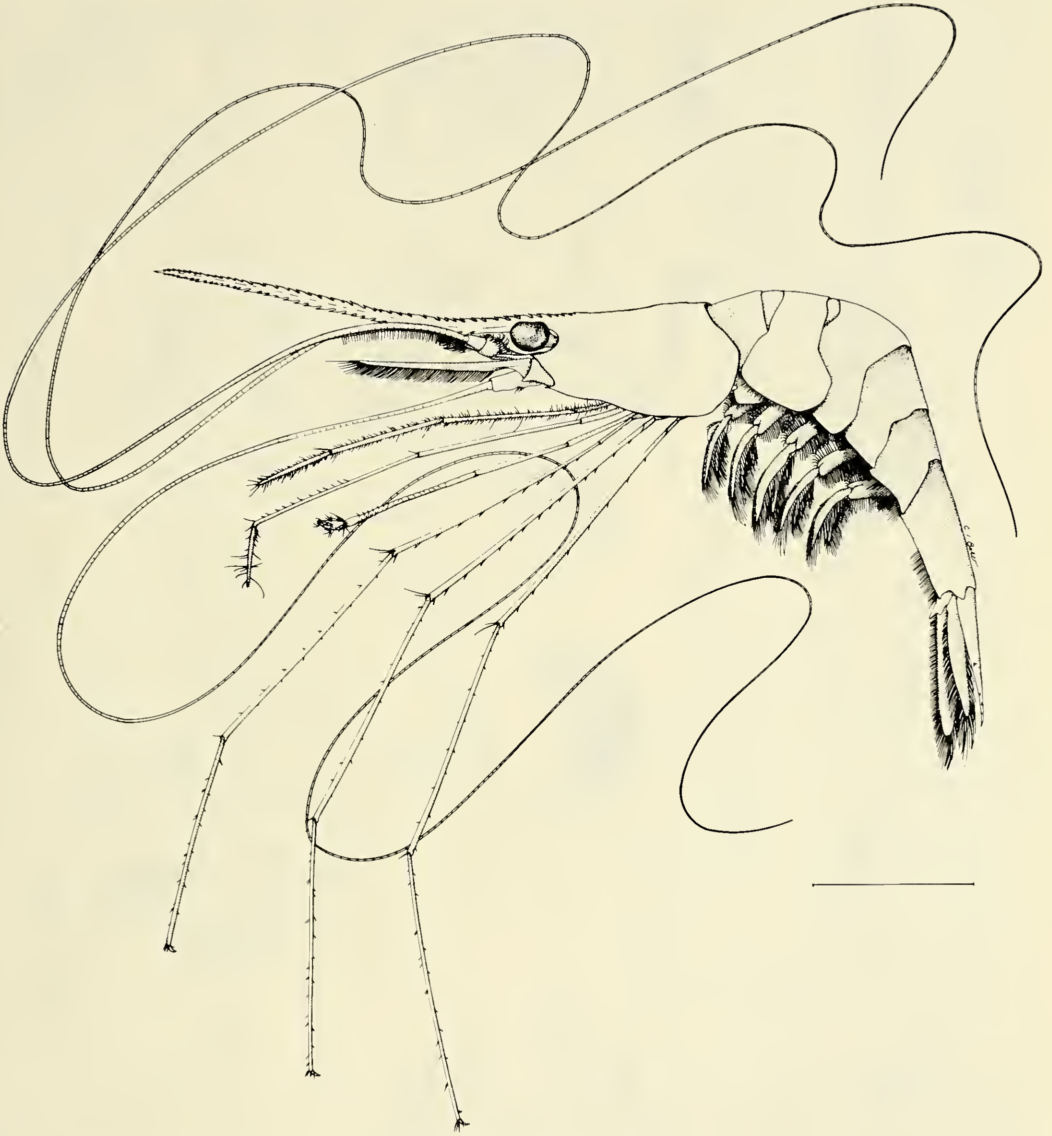

Fig. 1. *Plesionika escatilis* (Stimpson, 1860). ♂, USNM 204597. Scale equals 10 mm.

Plesionika escatilis (Stimpson, 1860), new combination
Figs. 1–4

Pandalus escatilis Stimpson, 1860:37.
Parapandalus escatilis: de Man, 1920:107.
Parapandalus narval: Crosnier & Forest, 1973:221, fig. 69a (in part, see Remarks).
Parapandalus sp.: Lemaitre, 1984:444.

Type material.—Two dry syntypes (sex undeterminable), off Madeira, BMNH 61.44.

Material examined.—Western Atlantic: 1 ♂ (CL = 16.4 mm), 1 ♀ ovig. (CL = 15.7 mm), off Mississippi River mouth, Jan 1976, USNM 155377.—1 ♀ ovig. (CL = 15.6 mm), west of Anna Maria Island, Manatee Coun-

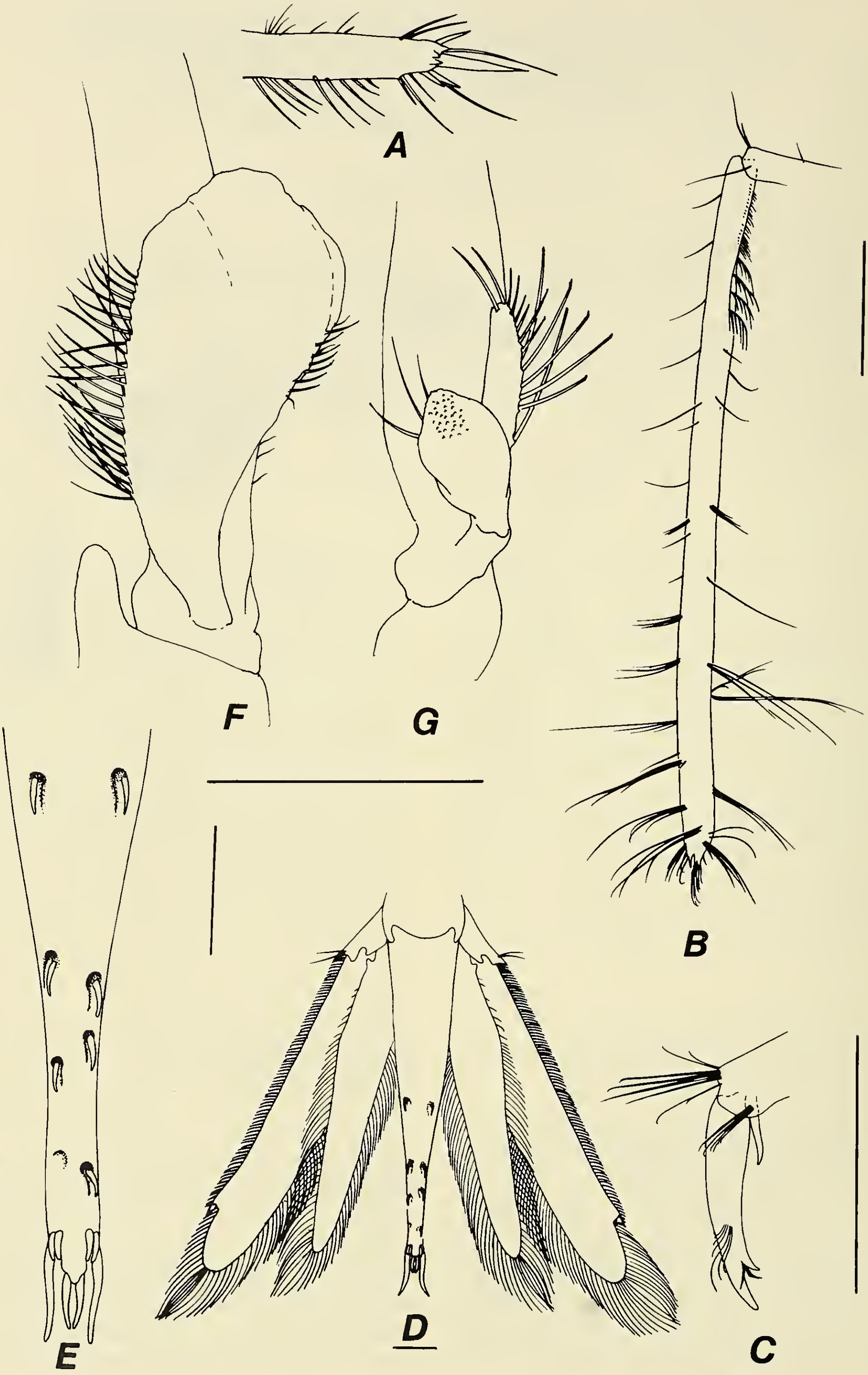
A
F
G
B
E
D
C

Fig. 3. A–J, *Plesionika escatilis* (Stimpson, 1860), ovig. ♀, USNM 172101. A–H, Mouthparts (left, external view): A, Mandible; B, Maxillule; C, Maxilla; D, first Maxilliped; E, second Maxilliped; F, third Maxilliped; G, Distal end of same; H, Basal part of same. I, Right antennular peduncle and eye (dorsal view); J, Right antennal scale (dorsal view). K–M, *Plesionika narval* (Fabricius, 1787), ♀, USNM 184993, right third maxilliped (external view): K, Distal segments; L, Basal part (arrow indicates epipod); M, Epipod. Scales equal 2 mm (A–E, I), 5 mm (F, J, K), 0.5 mm (G, M), and 1 mm (H, L).

←

Fig. 2. *Plesionika escatilis* (Stimpson, 1860). ♂, USNM 204597. A, Ultimate article of third maxilliped; B, Propodus and dactyl of left first pereopod; C, Dactyl of left third pereopod; D, Telson and uropods; E, Telson in dorsal view (posterior setae omitted); F, Endopod of right first pleopod; G, Endopod and appendix masculina of right second pleopod. Scales equal 1 mm.

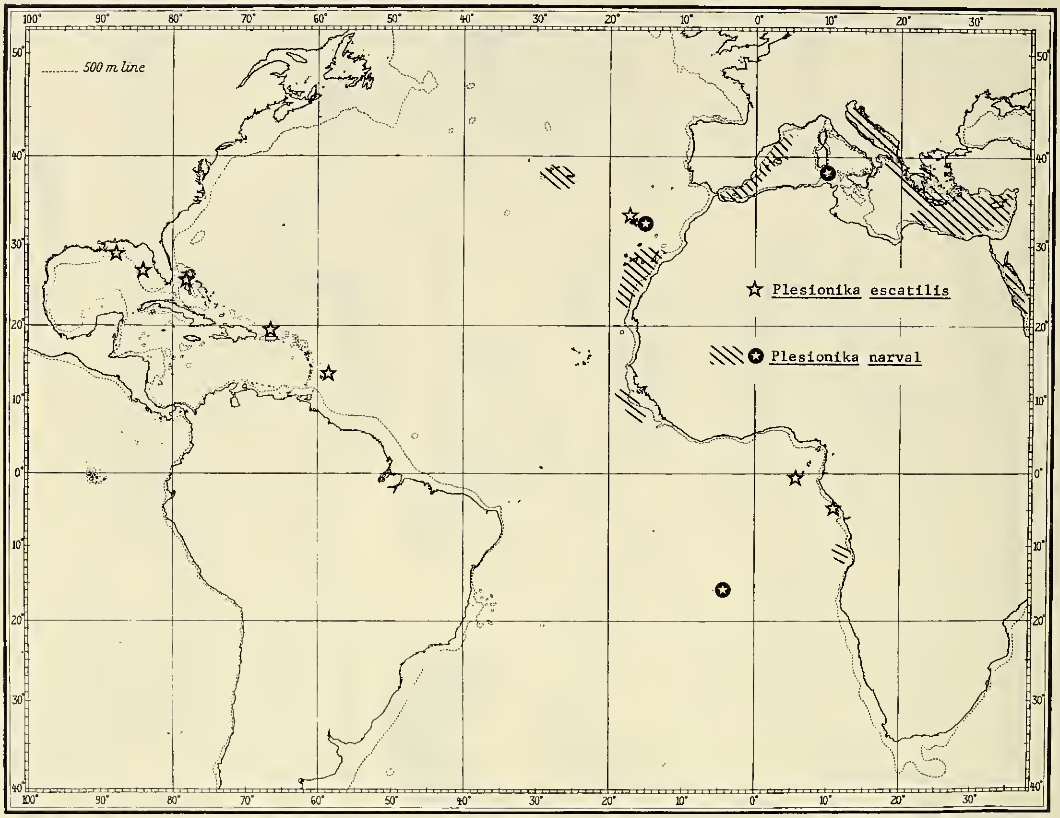

Fig. 4. Distribution of *Plesionika escatilis* (Stimpson, 1860), and *Plesionika narval* (Fabricius, 1787). [Hatched area based on Holthuis (1980). Circled stars based on the following material examined: 2 ♀, southern Sardinia, 70 m, 4 Nov 1978, USNM 184933.—5 ♀, 3 ♀ ovig., Funchal, Madeira (fish market), 29 Sep 1956, RMNH 11595.—2 ♂, 2 sex indet. (damaged), 3 ♀ ovig., James Bay, St. Helena, 17 Nov 1964, USNM 125502, 125503.]

ty, Florida, R/V *Hernan Cortez,* 27°31′N, 84°31′W, 136 m, 25 Apr 1981, FSBC I 29931.— 1 ♂ (CL = 9.3 mm), 5 ♀ (CL = 7.7–16.7 mm), *Johnson Sea Link,* 25°07′06″N, 77°26′06″W, 143 m, 31 Mar 1981, coll. R. S. Jones, RMNH D.33969; USNM 184577, 204597.—1 ♀ ovig. (CL = 13.2 mm), R/V *Bellows,* Cay Sal Bank, sta 79-13, 281 m, FIU.—7 ♂ (CL = 9.2–13.1 mm), 4 ♀ ovig. (CL = 12.7–14.2 mm), off San Juan, Puerto Rico, 18°30′N, 66°07′W, 90 m, from traps, 30 Aug 1978, coll. C. Boardman, USNM 172101.—1 ♂ (CL = 13.5 mm), 1 ♀ (CL = 14.5 mm), 1 ♀ ovig. (CL = 13.0 mm), off St. James, Barbados, from fish pots, Jan 1976, coll. J. Lewis, USNM 216172.—Eastern Atlantic: 3 ♂ (CL = 8.9–12.4 mm), 3 ♀ (CL = 11.0–13.6 mm), 2 ♀ ovig. (CL = 13.0–15.0 mm), R/V *Geronimo,* Gulf of Guinea, sta 184, 00°30.5′S, 08°43′E, 99 m, 1 Sep 1963, USNM 216173.—1 ♂ (CL = 13.0 mm), 1 ♀ (CL = 7.2 mm), off Congo, R/V *Geronimo,* sta 235, USNM 216174.

Description.—Rostrum (Fig. 1) directed dorsad, far overreaching antennal scale, 2–2.5 times as long as carapace, armed dorsally throughout length with 31–57 fixed teeth including 4–5 on carapace above or posterior to orbital margin, armed ventrally with 28–50 fixed teeth. Orbit sloping ventrally, concave posteriorly, nearly straight dorsally. Antennal spine stronger than pterygostomian spine. Carapace smooth, naked, usually with minute median dorsal tubercle on posterior sixth; median postrostral ridge extending posteriorly to about midlength of carapace.

Abdomen (Fig. 1) with third somite dorsally rounded, unarmed, without median dorsal carina. Pleura of anterior 3 somites rounded, those of fourth and fifth with acute posterolateral angle. Sixth somite 2–2.5 times as long as fifth, and 2.3–2.7 times as long as maximum height. Telson (Fig. 2D, E) subequal in length to sixth somite, or slightly shorter, with 2–3 pairs (rarely 4) of small movable spines dorsally; posterior process with 4 pairs of movable spines.

Eye (Fig. 3I) subpyriform, ocellus subcircular, in broad contact with cornea. Antennular peduncle (Fig. 3I) extending to about midlength of antennal scale; stylocerite not exceeding distal margin of first antennular segment, terminating in blunt or sharp tip; flagellum greatly exceeding body length. Antennal peduncle's basal segment with lateral ventrodistal spine; antennal scale (Fig. 3J) slightly exceeding carapace length, mesial margin with long setae, lateral margin with distal spine reaching to distal margin of blade; flagellum greatly exceeding body length.

Mouthparts as illustrated (Figs. 2A, 3A–H). Third maxilliped overreaching antennal scale by length of ultimate segment, or more; basal part with well developed coxal flange, lacking epipod; penultimate segment 1.3–1.6 times as long as ultimate; ultimate segment terminating in 1 or more long spines.

Pereopods (Fig. 1) long, slender, first and second distinctly shorter than others. First pereopod with minute chela (Fig. 2B); propodus with row of short setae on ventral margin proximally, and tufts of setae distally. Second pereopod chelate, reaching to about midlength of carpus of first pereopod; carpus subdivided into 19–31 articles (most frequently 24–28), not always consistent left to right in the same specimen. Third to fifth pereopods similar to each other, each exceeding first pereopods by at least length of propodus; merus with row of 9–17 spines ventrally; carpus with scattered setae; dactyl short, bifid.

Endopod (Fig. 2F) of first pleopod of male much wider distally than proximally, distal part unevenly convex. Appendix masculina on second pleopod (Fig. 2G) overreaching appendix interna, with long spines on anteromesial and distal margins. Uropod (Fig. 2D) elongate, setose; endopod shorter than exopod; exopod with short setae on lateral margin, and fixed distolateral spine.

Branchial formula:

	maxil-liped			pereopod				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	2	1	1	1	1	–
Podobranchs	–	1	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

Distribution (Fig. 4).—In the western Atlantic from the Gulf of Mexico and the Bahamas to the Antilles; in the eastern Atlantic from Madeira to off Congo, western Africa. Depth range: 90–400 m.

Coloration.—The following color pattern is based on the specimens (RMNH D.33969; USNM 184577, 204597) collected with the submersible. Body transparently white, streaked longitudinally with very clear, bright red stripes, and with 4 gilded yellow lines dorsally between the darker rays. Two dark red stripes extend longitudinally along the dorsal midline of the carapace and just below it, ending adjacent to the rostral spine and the dorsal margin of the orbit, respectively; 3 lighter stripes curve obliquely downward from the posterior carapace margin, extending to just behind the pterygostomian spine, about midway along the ventral margin of the carapace, and parallel to the posterolateral margin, respectively. This striping continues longitudinally along the abdominal somites. When the specimens were removed from formalin and placed in

70% ethanol, the stripes faded completely within 24 hours. A similar coloration has been described for *Plesionika narval* (as *Parapandalus narval*), by Dieuzeide (1931).

Affinities.—This species is morphologically very similar to *Plesionika narval.* The two can be differentiated however, by the following characters: 1) the third maxilliped in *Plesionika escatilis* lacks an epipod (Fig. 3F, H), whereas an epipod is present in *P. narval* (Fig. 3L, M); and 2) the number of dorsal teeth on the rostrum is fewer in *P. escatilis* (31–57), than in *P. narval* (58–70). *Plesionika escatilis* is also very similar to the Indo-Pacific *P. serratifrons* (Borradaile, 1899). But as Chace (1985) pointed out, the lack of an epipod on the third maxilliped in *P. escatilis* seems to be the only reliable means of separating this species from the Indo-Pacific one.

Ecological observations.—Plesionika escatilis, a relatively large deep-water shrimp, grows to about 100 mm total length, and inhabits continental and island shelf areas. It may be associated with rocky areas, as shown by the following observations made from a deep sea submersible in 143 m by Dr. Robert S. Jones. According to him, the shrimp became visible when the submersible light was switched on. At that time a dive was being made at the base of a limestone wall just above a talus slope off Nassau. This type of wall is characteristic of the offshore Bahamian plateau and rises nearly vertically toward the surface; the talus slope at the base drops off quickly toward extremely deep water. The wall itself is excavated with grooves and holes, and supports a varied epizoic and epiphytic community consisting predominantly of sponges and crinoids. The shrimp were standing on a sand covered ledge, and all were observed associated with some form of ledge or undercutting in the rock. The observer's attention was immediately drawn to the shrimp because they were "aligned in ranks, like soldiers, approximately 5–6 per rank in about 10 or so ranks." The shrimp assemblage exhibited a type of bouncing movement, in unison, which reminded the observer of a behavioral motion seen in harvestmen spiders inside terrestrial caves. It was not possible to determine whether feeding was occurring, or whether the shrimp were aligned toward or away from any water currents. Dr. Jones noted that the striking "candy-cane striping" was very apparent.

Remarks.—The synonymization of Stimpson's *Pandalus escatilis* with *Parapandalus narval* was questioned by Holthuis (1949), Crosnier & Forest (1973), and Chace (1985), all of whom suspected that Stimpson's taxon, although very similar to *Parapandalus narval,* might prove to be a distinct species. Subsequent examination of two of Stimpson's syntypes revealed that they lack an epipod on the third maxilliped, so that this character clearly sets Stimpson's species apart from *P. narval.* Crosnier & Forest (1973:221) eliminated Stimpson's name from the synonymy of *Parapandalus narval* because "l'avant-dernier article des troisièmes maxillipedes est plus court que le dernier" in *P. escatilis.* However, in his description Stimpson (1860:37) only indicated "Maxillipedes externi exognatho instructi; endognatho ei *P. annulicornis* simili" and noted in his final sentence, "A *P. priste* differt in maxillipedibus externis." From this description it is clear that the penultimate segment of the third maxilliped is shorter than the distal one in *Pandalus annulicornis* (=*P. montagui*). Unfortunately, Stimpson did not indicate how the appendages of the two species resembled each other. The measurement of Stimpson's syntypes has shown that the penultimate segment of the third maxilliped is longer than the ultimate, thereby indicating that Crosnier and Forest misinterpreted Stimpson's description. Examination of part of the material reported by them as *Parapandalus narval* from western Africa has shown that it actually represents *Plesionika escatilis.*

Distributional Remarks
Fig. 4

This study now clarifies the distribution of *Plesionika escatilis* and *P. narval*: *P. escatilis* is distributed in the eastern and western Atlantic, whereas the numerous reports of *P. narval,* summarized by Holthuis (1980), are only from the eastern Atlantic, Mediterranean, and Red Sea. *Plesionika escatilis* has been confused with *P. narval* on the west coast of Africa; therefore, records of the latter species from the area need to be reexamined. In fact, because *P. narval* has been found in the Atlantic only near oceanic islands (Madeira, Canary Islands, and St. Helena, Fig. 4), it appears that this species is distributed primarily in the Mediterranean. If Balss' (1915) record is correct it also occurs in the Red Sea.

The wide distribution of *P. escatilis* and *P. narval* may be a result of the oceanic dispersal of their pelagic larvae. However, the mode of life of these two species may also be a factor that has contributed to their distribution. Both species have been found living in close association with caves or other cryptic or stygobiont habitats (*P. escatilis*: this study; *P. narval*: Thessalou-Legaki & Hatzinikolaou 1985; Thessalou-Legaki et al. 1986).

In shrimps and other crustacean groups, the cryptic or crevicular way of life has recently been invoked to explain the wide distribution of closely related species in oceanic islands of the Atlantic and Pacific. According to this hypothesis, populations of these crevicular organisms are able to survive adverse ecological conditions by living in caves and crevasses which serve as refugia over long periods of time. The species may have subsequently achieved their present day distribution by means of the spreading of the sea floor (Iliffe et al. 1983, Hart et al. 1985, Manning et al. 1986). In the case of *P. escatilis* and *P. narval,* more information is certainly needed (e.g., degree of dependance on cryptic habitats and duration of pelagic larval development), before the effect of such hypothetical dispersal mechanism can be evaluated. It is conceivable, however, that the cryptic mode of life, in conjunction with enhanced larval survival of these two species, may have contributed to their present day distribution.

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THE CRAYFISH SUBGENUS *GIRARDIELLA* (DECAPODA: CAMBARIDAE) IN ARKANSAS, WITH THE DESCRIPTIONS OF TWO NEW SPECIES AND A KEY TO THE MEMBERS OF THE *GRACILIS* GROUP IN THE GENUS *PROCAMBARUS*

Horton H. Hobbs, Jr. and Henry W. Robison

Abstract.—The burrowing crayfish *Procambarus* (*Girardiella*) *ferrugineus* is described from two localities in the lower Arkansas River system, and *P.* (*G.*) *regalis,* from eight localities in the Ouachita and Red river basins of southwestern Arkansas. Their closest allies are *P.* (*G.*) *gracilis, P.* (*G.*) *liberorum,* and *P.* (*G.*) *reimeri. Procambarus* (*G.*) *regalis* may be distinguished from the others by possessing a rostrum with tapering, thickened lateral carinae and conspicuously thickened postorbital ridges; *P* (*G.*) *ferrugineus* differs from all except *P.* (*G.*) *regalis* and *P.* (*G.*) *reimeri* in exhibiting chelae with tuberculate palms, and from the last named species in having a very narrow or obliterated areola. Notes on, and spot maps depicting, the distribution of the eight members of *Girardiella* occurring in Arkansas follow a key to all of the members of the *gracilis* Group of the subgenus.

At least four handsome crayfish, the adult males of which sport a purplish red to brownish dorsum that is sharply delimited from a cream-to-buff ventrolateral section of the carapace, are known to occur in the Mississippi River basin: *P.* (*G.*) *gracilis* (Bundy 1876), reportedly a wide ranging species occurring in the prairie from southeastern Wisconsin southwestward into northern Texas (Hobbs III & Rewolinski 1985:22); *P.* (*G.*) *liberorum* Fitzpatrick (1978b), known largely from the upper Arkansas River basin; *P.* (*G.*) *ferrugineus,* n. sp., occupying at least part of the lower segment of the same basin; *P.* (*G.*) *reimeri* Hobbs (1979), apparently restricted to the upper Ouachita River watershed; and *P.* (*G.*) *regalis,* described herein from the Ouachita and Red river basins in southwestern Arkansas. Following the descriptions of the two new species is a key to all of the members of the *gracilis* Group of the subgenus. The first couplet, which defines the two currently recognized "groups" of *Girardiella,* provides a citation to the most recent key (Fitzpatrick 1978a) facilitating the recognition of the members of the *hagenianus* Group, one which is largely restricted to the prairie sections of western Alabama and eastern Mississippi. For each of the six additional species of the *gracilis* Group occurring in Arkansas, a summary statement of the range and a list of localities in the state are provided.

Procambarus (*Girardiella*) *ferrugineus,* new species
Figs. 1, 2, 12, 15

Diagnosis.—Body pigmented, eyes well developed. Rostrum of adults lacking marginal spines, tubercles, and median carina. Carapace with row of small cervical tubercles. Areola 38 to more than 100 times longer than broad in adults (as broad as 36 in one juvenile) and constituting 38.0 to 39.4 (average 38.7) % of total length of carapace (44.6 to 45.8, average 45.2, % of postorbital carapace length). Suborbital angle weak and obtuse. Hepatic area distinctly tuberculate; branchiostegal spine rudimentary. Antennal scale about 2.6 times as long as wide, widest distal to midlength. Ventral surface of chela strongly tuberculate, tubercles present along proximal fourth of ventral surface of dactyl. Ischium of third pereiopod in first form male with simple strong hook overreaching basioischial articulation; hook not opposed by tubercle on corresponding basis; coxa of fourth pereiopod lacking caudomesial boss. First pleopods of first form male reaching coxae of third pereiopods, symmetrical, bearing proximomesial, sclerotized spur and truncate cephalic shoulder at base of terminal elements, lacking lateral subterminal setae; setae on caudoproximal ridge flared; terminal elements (all at least partly cornified) consisting of (1) straight, long, tapering (occasionally bifid or bearing small spur) distally-directed mesial process projecting beyond other terminal elements; (2) short, acute, corneous-tipped, cephalodistally-directed cephalic process at cephalic base of mesial process; (3) strong, cornified, acute, cephalocaudally flattened, and laterally curved central projection situated between cephalic process; and (4) conspicuous, corneous caudal element consisting of distally rounded, caudally-concave lamelliform lobe partly shielding small, erect, subacute digitiform prominence. Lamelliform lobe and central projection reaching almost same level distally. Female with annulus ventralis freely movable, about 1.2 times as long as broad, subsymmetrical in outline, with cephalomedian trough curved at about midlength where leading to tilted sigmoid sinus ending on caudal wall of annulus near median line; anterior three-fourths of annulus lateral to trough multituberculate. Preannular plate and first pleopod present although somewhat reduced.

Holotypic male, form I.—Cephalothorax (Figs. 1, 2a, l) subovate, distinctly compressed laterally, even though greatest width of carapace only slightly less than height at caudodorsal margin of cervical groove (19.2 and 19.4 mm). Second segment of abdomen considerably narrower than thorax (13.8 and 19.2 mm). Areola almost linear, 54.3 times as long as broad, lacking punctations in narrowest part. Cephalic section of carapace 1.6 times as long as areola, latter comprising 39.1% of total length of carapace (45.8% of postorbital carapace length). Surface of carapace punctate dorsally, granulate laterally, tuberculate in hepatic region. Rostrum broad basally, tapering gradually anteriorly, but, approaching apex, margins contracting more rapidly, acumen not clearly defined basally; slightly upturned tip almost reaching base of ultimate podomere of antennular peduncle; margins slightly thickened, and dorsal surface rather deeply concave, lacking median carina, and with punctations scattered between those forming submarginal rows. Subrostral ridges moderately well developed and evident in dorsal aspect along basal two-fifths of rostrum. Postorbital ridges rather prominent, swollen caudally and merging gently with surface of carapace cephalically. Suborbital angle moderately prominent but obtuse. Branchiostegal spine absent; row of very small tubercles replacing cervical spine(s).

Abdomen distinctly shorter than carapace (35.5 and 42.7 mm). Pleura of third through fifth segments broadly rounded ventrally. Cephalic section of telson with 2 spines in each caudolateral corner, lateral ones fixed (Fig. 2m). Cephalic lobe of epistome (Fig. 2j) campanulate, thickened marginally and with low, irregular median carina; thickened marginal area bearing few setae; main body of epistome with spindle-shaped median depression exceeding dimensions of usual fovea; epistomal zygoma as illustrated. Ventral surface of proximal podomere of antennular peduncle with small spine near midlength. Antennal peduncle lacking spines on basis and ischium, but small lateral tubercle on lateral surface of latter in left member; flagellum broken, but in paratypic male, form I, reaching third abdominal tergum. Antennal scale (Fig. 2i)

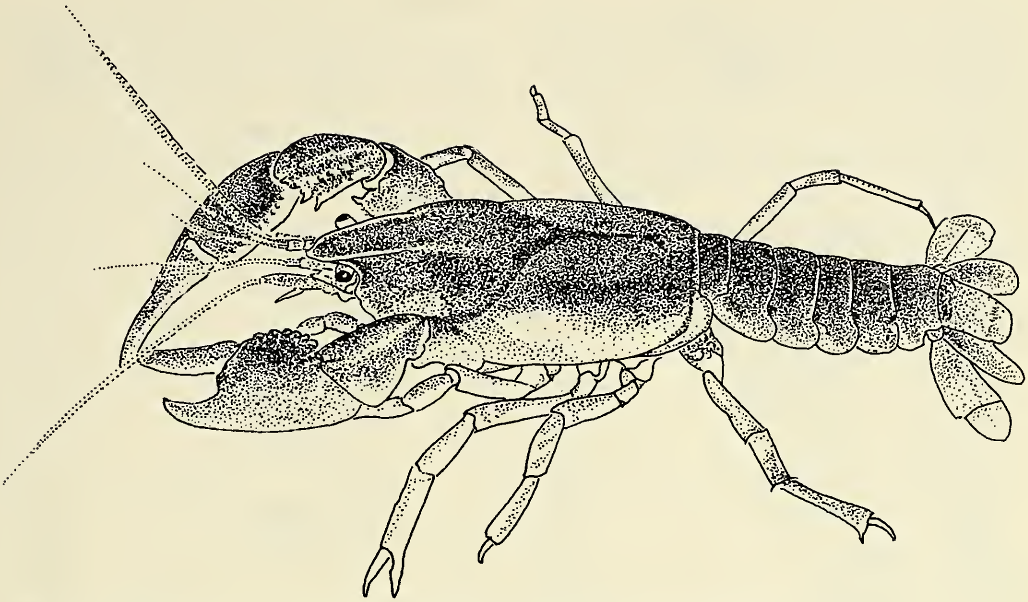


Fig. 1. *Procambarus* (*G.*) *ferrugineus*: dorsolateral view of holotypic male, form I.

about 2.5 times as long as broad, widest distal to midlength; greatest width of lamellar area about 1.5 times that of thickened lateral part.

Third maxilliped extending to level of ultimate podomere of antennule, ventral surface moderately setose, all conspicuous setae seemingly stiff some of which studded with short spiniform setules in area near midlength; merus not completely obscured in lateral aspect by long plumose setae extending distally from ischium and lateral surface of merus.

Right chela (left probably regenerated) (Fig. 2n) subovate in cross section, not strongly depressed; palm about 1.3 times as broad as length of mesial margin; latter about one-third total length of chela; entire palm except for proximolateral, lateral, and ventrolateral area studded with tubercles, those on dorsal surface becoming weaker and more withdrawn laterally. Mesial surface of palm with row of 7 tubercles (one reduced in earlier premolt injury) flanked dorso- and ventrolaterally by several sublinear rows of smaller ones; distalmost row of tubercles on ventral surface of palm extending, while diminishing in size, onto basal part of fixed finger. Both fingers with low median ridges dorsally and ventrally; ridges flanked proximally by squamous tubercles and along most of their lengths by setiferous punctations. Opposable margin of fixed finger with row of 4 prominent tubercles (fourth from base decidedly largest) along proximal fourth of finger followed by row of 8 smaller ones (several too small to be included in illustration) reaching level of large, more ventrally situated tubercle near base of distal fourth of finger; row of minute denticles extending between tubercles and forming narrow band between large distalmost tubercle and corneous tip of finger; lateral surface of finger rounded and bearing longitudinal row of setiferous punctations. Opposable margin of dactyl with conspicuous excision in basal third bearing row of 3 tubercles followed distally in same alignment by row of 8 of which proximalmost much larger than others (3 distalmost members too small to include in illustration); minute denticles arranged as on fixed finger; mesial surface of

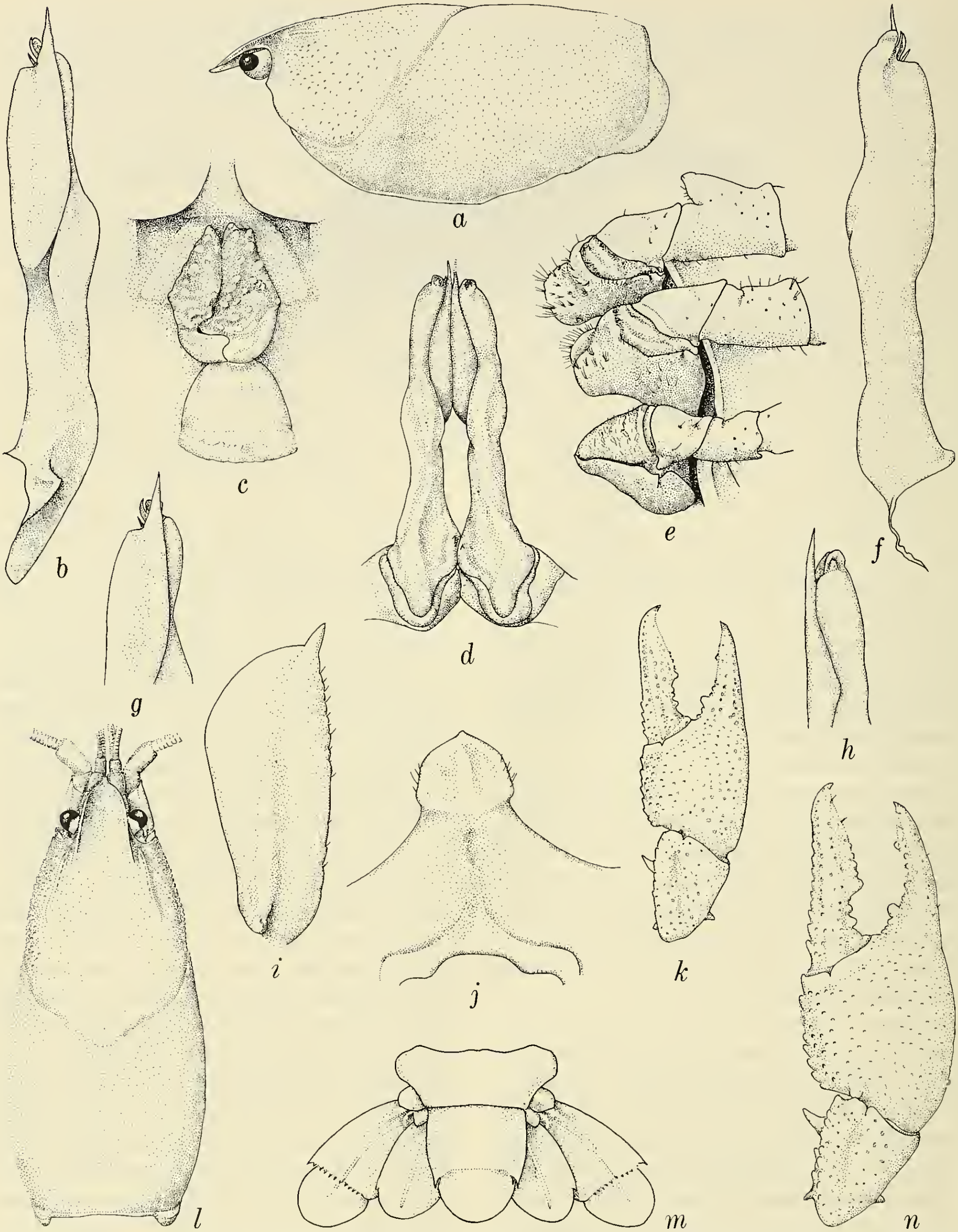


Fig. 2. *Procambarus* (*G.*) *ferrugineus* (all from holotype except c and k from allotype, and b and f–h from paratypic male, form I): a, Lateral view of carapace; b, Submesial view of first pleopod; c, Annulus ventralis and associated sclerites; d, Caudal view of first pleopods; e, Ventral view of basal podomeres of third, fourth, and fifth pereiopods; f, Sublateral view of first pleopod; g, Submesial view of distal part of first pleopod; h, Caudal view of same; i, Dorsal view of antennal scale; j, Epistome; k, Dorsal view of distal podomeres of cheliped; l, Dorsal view of carapace; m, Dorsal view of telson and uropods; n, Dorsal view of distal podomeres of cheliped.

finger with subserrate row of 9 tubercles along proximal two-thirds.

Carpus of cheliped longer than broad with oblique furrow dorsally; mesial surface with 1 large conical tubercle and several smaller ones proximal and ventral to it; dorsomesial margin bearing row of 8 tubercles preceding large one at distomesial angle; distoventral margin with row of 3 large tubercles.

Merus tuberculate along dorsodistal two-thirds of podomere; ventral surface with mesial row of 16 (left with 14) tubercles, and lateral with 10; several tubercles situated between rows, and 3 forming distal oblique row. Ischium with row of 3 tubercles ventromesially.

Hook on ischium of third pereiopod (2e) simple, heavy, overreaching basioischial articulation, not opposed by tubercle on corresponding basis. Coxae of neither fourth nor fifth pereiopods with caudomesial boss.

Sternum between third, fourth, and fifth pereiopods rather shallow; ventrolateral margins with plumose setae but obscuring only distal part of first pleopods.

First pleopods of paratypic first form male (Fig. 2b, d, f, g, h) as described in "Diagnosis." Left member in holotype with mesial process bifurcate, and right member of one paratypic male with same process bearing short acute spur.

Uropods (Fig. 2m) with neither lobe of basal podomere bearing spines; mesial ramus with distomedian spine small and situated proximal to distal margin.

Allotypic female.—Differing from holotype, other than in secondary sexual features, in following respects: second segment of abdomen proportionately broader (15.6 and 19.1 mm); right suborbital angle with acute, corneous apex; branchiostegal spine rudimentary, represented by very small obtuse angle; cephalic section of telson with single spine in right caudolateral corner; flagellum of antennae broken but probably reaching second abdominal tergum; chela (Fig. 2k) proportionately much smaller, mesial surface of palm with row of 7 or 8 (left) tubercles, opposable margin of fixed finger with row of only 3 prominent basal tubercles, that of dactyl with row of 7 or 10 tubercles instead of 11, minute denticles on both fingers limited to single rows, mesial margin of dactyl with row of 5 tubercles; merus of cheliped with only 9 tubercles in ventrolateral row, ischium of right cheliped with 4 tubercles. (Also see Table 1.)

Annulus ventralis (Fig. 2c) as described in "Diagnosis." Preannular plate inconspicuous, deeply embedded in sternum but forming calcified arch, anteromedian part of which fusing with sternite XIII, and lateral extremities with plates supporting lateral processes of sternal keel. Postannular sclerite about 1.5 times as broad as long and almost as wide as annulus, its ventral surface gently convex and rather smooth; calcified section shorter than annulus. First pleopod well developed, reaching cephalic margin of annulus when abdomen flexed.

In the allotype and one of the paratypes collected on 16 April, the cement glands were very well developed, suggesting that ovulation in these females would have occurred in the near future; thus females are likely to become ovigerous in late spring or early summer.

Color notes.—Holotype (Fig. 1): Dorsum of carapace basically brick red. Dorsal surface of rostrum and gastric region slightly paler than remainder; anterior flank of cervical groove very dark red. Rostral carinae and postorbital ridges orange; hepatic region dark red dorsally, fading ventrally, and bearing orange tubercles. Antennal and mandibular areas also fading ventrally, and entire lateral branchiostegal region cream suffused with pink. First abdominal tergum darker red than remaining terga which almost same hue as dorsum of thorax; red coloration fading across pleura. Telson dark red basally becoming paler to transverse suture; posterior section with basal dark brownish patches. Uropods reddish tan; mesial part of proximal section of lateral ramus and most of mesial ramus mottled with dark brown on reddish tan background. Antennules and antennae with

Table 1.—Measurements of adults of *Procambarus* (*G.*) *ferrugineus.*

	Holotype	Allotype	♂I	♀	♀	♀
Carapace:						
Entire length	41.7	42.1	38.1	38.7	38.1	30.3
Postorbital length	35.6	36.1	32.5	33.3	32.1	25.8
Width	19.2	19.1	17.6	17.7	17.5	14.3
Height	19.4	18.1	17.2	17.2	17.2	13.4
Areola:						
Width	0.3	0.2	0.1	0.3	0.2	0.1
Length	16.3	16.2	14.9	15.0	14.5	11.5
Rostrum:						
Width	5.8	5.9	5.3	5.4	5.6	4.4
Length	7.7	8.2	7.1	7.4	7.2	6.0
Chela:						
Length, palm mesial margin	11.2	7.6	9.2	7.1	7.4	5.1
Palm width	14.5	9.9	12.8	10.2	10.1	6.7
Length, lateral margin	32.9	23.2	28.8	21.8	22.4	15.7
Dactyl length	20.0	14.1	17.8	14.2	14.1	10.2
Abdomen:						
Width, second segment	13.8	15.6	12.5	14.7	14.8	10.7
Length, total	35.5	39.7	33.0	36.5	35.6	29.0

mottled peduncles, brown on greenish tan, and greenish brown flagella. Dorsal surface of distal podomeres of third maxilliped greenish brown with pink suffusion. Merus of cheliped pink mesially and laterally with triangular olive dorsal area bearing pinkish orange tubercles; carpus pink laterally, pinkish olive dorsally and mesially, also with pinkish orange tubercles; propodus mostly red dorsally but fading laterally to pink and darkest mesially where studded with very dark red (almost black) tubercles, but those forming mesialmost row with pinkish tips; finger becoming pale distally to base of dark, corneous tip; dactyl darker than fixed finger, with very dark tubercles proximally, but becoming lighter toward dark corneous tip; tubercles on opposable margins of fingers cream to white except for corneous tips. Remaining pereiopods pinkish tan, slightly darker on distal part of merus and over carpus and dorsal margin of propodus. Sternal area and basal parts of appendages grayish cream, ventral surface of more distal podomeres pink to orange.

Female differing from male chiefly in suppression of red coloration: dorsum basically brown with lavender suffusion and anterior flank of cervical groove very dark brown. Rostral carinae and postorbital ridges pinkish cream; hepatic region, dark and mottled with almost black splotches, fading ventrally and bearing pinkish cream tubercles; antennal area almost cream and mandibular area only slightly darker; entire branchiostegal region lavender cream. First abdominal tergum dark reddish purple suffused with tan; terga of second through fifth segments with reddish brown background on which are comparatively inconspicuous, slightly darker spots arranged in two paired rows: dorsolateral row of slightly obliquely placed rectangles, and lateral row, at base of pleura, of semicircular spots with dorsal side convex; tergum of sixth abdominal segment also reddish brown with pair of pinkish tan spots posteriorly; pleura of second through sixth segments paler reddish brown with cream submarginal slash and small dark spot caudodorsal to it. Telson with anteromedian subovate, transverse reddish brown spot and pair of rectangular ones immediately posterior to it; caudal section of telson and uropods paler than remainder of dorsal surface of abdomen and inconspicuously mottled, but no markings prominent. Fringe on pleura cream. Color pattern of chelipeds not differing from male, but reddish coloration reduced to pale pinkish orange. Antennae and antennules as in male. Third maxilliped and pereiopods similar but lacking pinkish suffusion, thus predominantly olive and cream.

Type locality.—Roadside ditch 10 miles (16 km) south of Lonoke on State Route 31, Lonoke County, Arkansas (T.1S, R. 8W, Sec. 6). There was no standing water in the ditch, and the burrows of this crayfish were marked by crude chimneys as much as 15 cm high. The simple or bifid galleries, with surface diameters no more than 8 cm, penetrated the watertable some 20 to 25 cm below the surface, and descended to depths of about 1 m. The soil consisted of a sandy clay over clay. Occurring in fewer numbers, but occupying adjacent burrows, in the ditch were members of *Cambarus* (*Lacunicambarus*) *diogenes* Girard (1852). Cultivated fields were adjacent to the grass-covered ditch, and members of the genera *Juglans, Prunus,* and *Quercus* were scattered along the fence rows.

Disposition of types.—The holotype and allotype are deposited in the National Museum of Natural History (Smithsonian Institution) (USNM), USNM 218841 and 218842 respectively, as are the paratypes consisting of 2 ♂I, 3 ♀, and 3 j♀.

Size.—The largest specimen available is the allotypic female which has a carapace length of 42.1 (postorbital carapace length 36.1) mm. The smaller of the two first form males has corresponding lengths of 38.1 and 32.5 mm. Ovigerous females or ones carrying young have not been collected.

Range and specimens examined.—Known from only two localities in Lonoke County, Arkansas; type locality, 2 ♂I, 4 ♀, 3 j♀, 16 Apr 1985, R. H. Gilpin and HHH, coll.; and roadside ditch 2.9 mi (4.6 km) S of Lonoke on St Rte 31 (T. 1N, R. 9W, Sec. 36), 1 ♂I, 11 Apr 1987, G. B. Hobbs and HHH.

Variations.—Noteworthy variations are few: the rostrum in all of the specimens, even in juveniles, reaches or almost reaches the base of the ultimate podomere of the antennule; none of the spines or tubercles, including the branchiostegal, is any better developed in the juvenile than in the adults; in none of the specimens does the antenna reach farther caudally than the tergum of the third abdominal segment. Even the areolae of the young are not appreciably wider than those of mature individuals; moreover, there is little variation in the number of tubercles adorning the several podomeres of the chelipeds of the adults: 3 or 4 on the ventromesial surface of the ischium; 12 to 16 in the ventromesial row on the merus and 8 or 9 in the lateral row; 6 to 8 present on the mesial margin of the palm, 7 to 9 on the opposable margin of the fixed finger, and 6 to 10 on the corresponding margin of the dactyl. Insofar as the secondary sexual characteristics are concerned, except for the variation noted above in the mesial process of the first pleopod in the holotype and one of the paratypic males, virtually no noteworthy variation exists; in one of the females, however, the annulus ventralis lies so close to sternite XIII that the preannular plate is scarcely visible.

Relationships.—In his study of *Procambarus* (*G.*) *hagenianus* and its allies, Fitzpatrick (1978a) recognized two species groups in the subgenus *Girardiella*: *gracilis* Group and *hagenianus* Group. Members of the former are readily recognized by lacking spines projecting from the caudal margin of the mesial ramus of the uropods, but possessing a cephalic process on the first pleopod of the male; they occur west and north of the Mississippi River. The members of the *hagenianus* Group, which Fitzpatrick treated in detail, possess two spines projecting from the caudal margin of the mesial ramus of the uropods and lack a cephalic process on the first pleopod of the male; all of them occur east of the Mississippi River in and near the prairie sections of Mississippi and Alabama. With the descriptions of *P.* (*G.*) *ferrugineus* and *P.* (*G.*) *regalis,* the *gracilis* Group, still poorly understood and the range of not one of its members clearly defined, encompasses ten species ranging from northeastern Mexico to Wisconsin. This new crayfish is similar to *P.* (*G.*) *gracilis, P.* (*G.*) *liberorum,* and *P.* (*G.*) *regalis* in color and in possessing a very narrow areola. It also shares much in common with *P.* (*G.*) *reimeri.* Its chela, with a tuberculate palm, is unlike that of two of the species just mentioned but in this respect similar to that of *P.* (*G.*) *regalis* and *P.* (*G.*) *reimeri.* Noteworthy is the presence of what is interpreted to be a preannular plate in the female, a character which, until discovered in the last-mentioned species, was thought to be a unique feature of the members of the subgenus *Austrocambarus.* Features that serve to distinguish *P.* (*G.*) *ferrugineus* from these and other close relatives are noted in the key herein.

Remarks.—In re-examining the species related to *P.* (*G.*) *ferrugineus,* we are unable to recognize any material between the range of typical *P.* (*G.*) *simulans* and that of the Mexican subspecies, described by Villalobos, from Nuevo León that might be interpreted as intergrades between them. In view of our lack of knowledge of such populations, we propose that *Procambarus* (*Girardiella*) *regiomontanus* Villalobos (1954) be accorded specific rank and are so treating it in the key that follows.

Procambarus (*Girardiella*) *regalis,* new species

Figs. 3, 4, 14, 15

Diagnosis.—Body pigmented, eyes well developed. Rostrum lacking marginal spines, tubercles, and median carina. Carapace with 1 or row of up to 6 small cervical tubercles. Areola linear to 31 times as long as wide and constituting 38.2 to 43.6 (avg. 40.4) % of total length of carapace (44.9 to 49.0, avg. 46.2, % of postorbital carapace length). Suborbital angle weak and obtuse. Hepatic and mandibular areas strongly tuberculate; branchiostegal spine rudimentary to moderately well developed. Antennal scale about 2.4 times as long as wide, widest distal to midlength. Ventral surface of chela tuberculate mesially, punctate laterally, 0 to 2 tubercles on ventral surface of dactyl. Ischium of third pereiopod of first form male with simple strong hook overreaching basioischial articulation; hook not opposed by tubercle on corresponding basis; coxa of fourth pereiopod lacking caudomesial boss. First pleopods of first form male reaching coxae of third pereiopods, symmetrical, bearing rudiment of proximomesial spur, angular shoulder at base of terminal elements, and lacking lateral subterminal setae; terminal elements (all at least partly sclerotized) consisting of (1) almost straight, long, tapering, distally directed mesial process projecting beyond other terminal elements; (2) short, acute, cephalodistally directed cephalic process situated at cephalolateral base of mesial process; (3) strong, cornified, obliquely flattened, and caudolaterally curved central projection situated between cephalic process; and (4) caudal element, most conspicuous of four, consisting of distally rounded, lamelliform lobe disposed in same plane as central projection, and digitiform prominence on caudomesial angle adnate from base almost, or quite, to tip. Central projection and lamelliform lobe of caudal element reaching almost same level distally. Female with annulus ventralis freely movable, about 1.3 times as long as broad, subsymmetrical in outline, with cephalomedian trough leading to tilted sigmoid sinus ending on caudal wall of annulus near median line, anterolateral prominences smooth or comparatively weakly tuberculate. Preannular plate and first pleopod present; long postannular sclerite tapering anteriorly.

Holotypic male, form I.—Cephalothorax (Figs. 1, 4a, l) subovate, distinctly compressed laterally even though greatest width

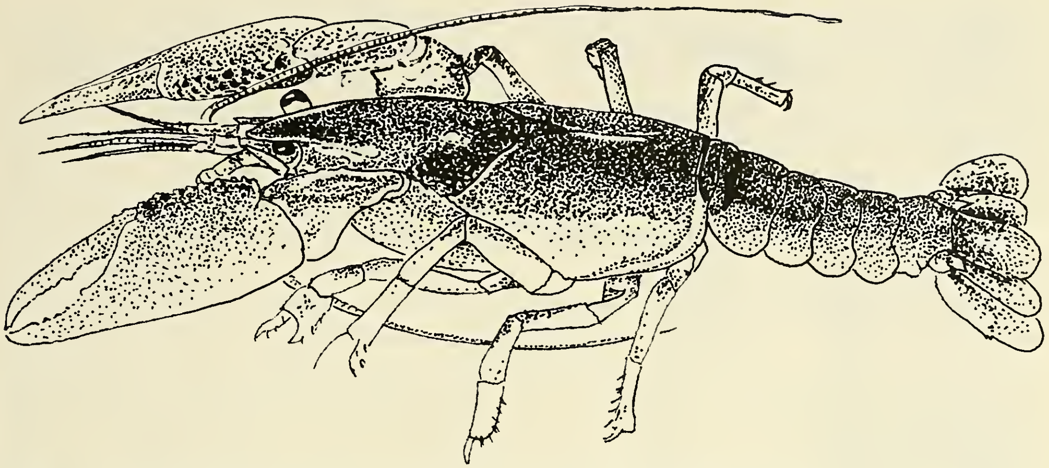


Fig. 3. *Procambarus* (*G.*) *regalis*: dorsolateral view of morphotypic male, form II.

of carapace slightly greater than height at caudodorsal margin of cervical groove (18.3 and 17.9 mm). Second segment of abdomen considerably narrower than thorax (13.2 and 18.3 mm). Areola very narrow, about 80 times as long as broad, lacking punctations in narrowest part. Cephalic section of carapace 1.4 times as long as areola, latter comprising 41.3% of total length of carapace (46.9% of postorbital carapace length). Surface of carapace punctate dorsally, granulate laterally, strongly tuberculate in hepatic and mandibular regions. Rostrum broad basally, gradually tapering anteriorly from base, margins contracting more rapidly toward apex; acumen, however, not clearly delimited basally; rostral tip slightly upturned, reaching midlength of penultimate podomere of antennular peduncle; margins distinctly thickened, particularly basally, and dorsal surface concave, lacking median carina, and with punctations scattered between those forming submarginal rows. Subrostral ridges rather weak and barely evident in dorsal aspect to base of acumen. Postorbital ridges very prominent, swollen caudally, and merging abruptly with surface of carapace cephalically, but lacking spines or apical tubercles. Paired posterior gastric prominences conspicuous. Suborbital angle obtuse. Branchiostegal spine rudimentary; row of 4 (left) or 5 (right) tubercles representing cervical spines.

Abdomen distinctly shorter than carapace (35.7 and 39.7 mm). Pleura of third through fifth segments broadly rounded ventrally. Cephalic section of telson with 2 spines in each caudolateral corner, lateral ones fixed. Cephalic lobe of epistome (Fig. 4i) thickened marginally and with median elevated area basally; main body of epistome lacking fovea; epistomal zygoma arched. Ventral surface of proximal podomere of antennular peduncle with strong spine near midlength. Antennal peduncle lacking spines and prominent tubercles on proximal three podomeres; flagellum reaching first abdominal tergum. Antennal scale (Fig. 4k) about 2.4 times as long as broad, widest distal to midlength; greatest width of lamellar area about 1.7 times that of thickened lateral part.

Third maxilliped extending to level of ultimate podomere of antennule, ventral surface moderately setose, conspicuous setae with short, densely set branches; merus not completely obscured in lateral aspect by long, plumose setae extending distally from ischium and lateral surface of merus.

Right chela (left regenerated) (Fig. 4m) subovate in cross section, rather strongly depressed; width of palm about 1.2 times

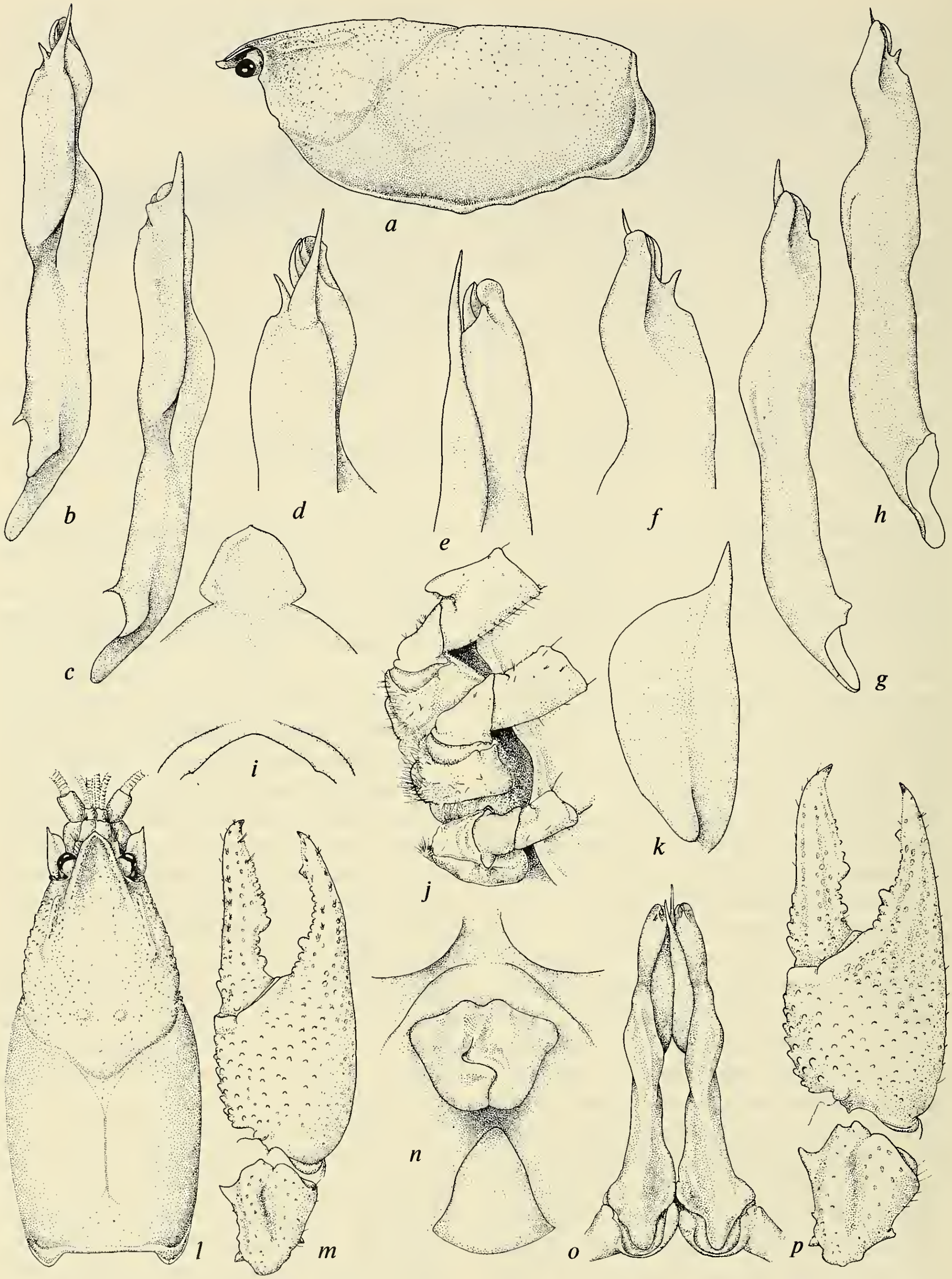


Fig. 4. *Procambarus* (*G.*) *regalis* (all from holotype except n and p from allotype, and c and g from morphotype): a, Lateral view of carapace; b–d, Mesial view of first pleopod; e, Caudal view of distal part of first pleopod; f–h, Lateral view of first pleopod; i, Epistome; j, Ventral view of basal podomeres of third, fourth, fifth pereiopods; k, Dorsal view of antennal scale; l, Dorsal view of carapace; m, p, Dorsal view of distal podomeres of cheliped; n, Annulus ventralis and associated sclerites; o, Caudal view of first pleopods.

length of mesial margin; latter slightly more than one-third total length of chela; palm except for dorso- and ventrolateral fourths, tuberculate, more lateral ones on both surfaces weaker and progressively withdrawn. Mesial surface of palm with row of 8 cream-colored tubercles flanked dorsolaterally by irregular row of 7 almost black ones and ventrolaterally by row of 7 smaller cream-colored ones. Both fingers with weakly elevated, rounded, median longitudinal ridges dorsally and ventrally; ridges flanked along most of their lengths by setiferous punctations. Opposable margin of fixed finger with row of 4 prominent tubercles (fourth from base decidedly largest) along proximal fourth of finger, followed by row of 7 smaller ones almost reaching level of large more ventral tubercle near base of distal fourth of finger; single row of minute denticles extending between 7 more distal tubercles and continuing, dorsal to distalmost tubercle, to corneous tip of finger; lateral surface of finger rounded and bearing row of widely spaced setiferous punctations. Opposable margin of dactyl with conspicuous excision in basal third bearing row of 3 tubercles followed distally in same alignment by row of 8, of which proximalmost much larger than others; single row of minute denticles extending distally from distal base of second tubercle in excised area; mesial surface of finger with 2 tubercles at base followed by row of setiferous punctations.

Carpus of cheliped longer than broad with oblique furrow dorsally; mesial surface with 1 large conical tubercle and 4 smaller ones proximal to it; dorsomesial surface with irregular row of 3 small, withdrawn tubercles; ventral surface with arc of 6 tubercles leading to more mesial one of 2 situated on ventrodistal margin of podomere.

Merus of cheliped with dorsal row of 9 tubercles of increasing size distally, all except 2 distalmost subsquamous; ventral surface with mesial row of 14 tubercles and lateral one of 9; several tubercles situated between rows. Ischium with row of 3 tubercles ventromesially.

Hook on ischium of third pereiopod (Fig. 4j) simple, heavy, overreaching basioischial articulation, not opposed by tubercle on corresponding basis. Coxae of neither fourth nor fifth pereiopods with caudomesial boss, but mesial caudoventral angle of that of left fifth with prominent tubercle; tubercle on right inconspicuous.

Sternum between third, fourth, and fifth pereiopods rather shallow; ventrolateral margins with plumose setae obscuring much of first pleopods.

First pleopods like those of paratype (Fig. 4b, d–f, h, o) described in "Diagnosis" except mesial process of right member regenerated: shorter and bifid. In addition, unlike arrangement of setae at caudal base of these appendages in many, if not most, crayfishes, setae of both pleopods splayed, disposed both distomesially and distolaterally, reminding one of caudal aspect of spread tail of fantail pigeon.

Uropods with mesial lobe of basal podomere produced in distally projecting spine; mesial ramus with distomedian spine small and situated much proximal to distal margin; lateral spine present on both mesial and lateral rami.

Allotypic female.—Differing from holotype, other than in secondary sexual features, in following respects: areola linear, even narrower than in holotype; tip of rostrum almost reaching base of ultimate podomere of antennular peduncle; rostral margins and postorbital ridges less conspicuously thickened; left branchiostegal spine absent, right one better developed than those in holotype; cervical spines represented by row of 6 minute tubercles on left and 5 on right; small lateral tubercle present on ischium of antennal peduncle; width of palm of chela (Fig. 4p) about 1.3 times length of mesial margin; mesial margin of left chela with row of only 7 cream-colored tubercles; ridges on fingers more distinctly elevated; more distal row of tubercles on opposable margin of fixed finger consisting of only 5 on both chelae; dactyl of right chela with row of 5 tubercles distal to excision, left with

Table 2.—Measurements of the primary types of *Procambarus* (*G.*) *regalis.*

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	39.7	33.1	35.3
Postorbital length	35.0	28.8	30.9
Width	18.3	15.1	14.7
Height	17.9	14.5	15.5
Areola:			
Width	0.2	0.1	0.4
Height	16.4	14.5	14.3
Rostrum:			
Width	5.9	5.1	5.1
Length	6.2	5.5	5.8
Chela:			
Length, palm mesial margin	12.0	7.8	10.6
Palm width	14.9	10.2	12.7
Length, lateral margin	35.2	21.8	29.5
Dactyl length	21.2	13.7	18.0
Abdomen:			
Width, second segment	13.2	12.7	11.3
Length, total	35.7	31.4	29.7

4; mesial surface of dactyl with row of 4 tubercles extending along basal two-fifths; ventral surface of carpus of cheliped with arc of 5 tubercles leading to 2 on ventrodistal margin; tubercles on dorsal margin of merus of cheliped forming single row proximally but more scattered distally, row of 9 on left but fewer, 7 or 8, on right; ventral surface of merus with mesial row of 13 tubercles, lateral rows of 10 on right and 8 on left. For measurements, see Table 2.

Annulus ventralis (Fig. 4n) as described in "Diagnosis." Moderately well developed calcified preannular plate present; postannular sclerite subtriangular, tapering anteriorly, slightly longer than broad, longer than annulus, and completely calcified. First pleopods comparatively well developed, almost reaching cephalic margin of annulus when abdomen flexed.

Morphotypic male, form II.—Differing from holotype in following respects: areola about 40 times as long as broad, and with 1 punctation in narrowest part; branchiostegal spine better developed and more acute than in holotype; 5 very weak cervical tubercles on each side; spine on ventral surface of proximal podomere of antennular peduncle smaller; palm of chela lacking ventrolateral row of tubercles flanking mesial row; opposable margin of fixed finger with row of 5 tubercles (fifth from base largest) along proximal fourth of finger followed by row of 7 (right) or 8 (left); dactyl of chela with 4 tubercles in excised area and 5 (left) or 6 (right) in row beyond excision; mesial surface of dactyl with row of 3 (left) or 4 (right) tubercles at base; other than large conical tubercle, those on mesial and dorsomesial surfaces of carpus quite inconspicuous; ventral surface of podomere with 3 (right) or 5 (left) tubercles forming arc leading to 2 larger tubercles on ventrodistal margin of palm; except for 1 (right) or 2 (left) tubercles on dorsal surface of merus, all much smaller than those of holotype; ventral surface of merus of left cheliped with mesial row of 13 tubercles and lateral one of 6, right with 14 and 7, respectively; hook on ischium of third pereiopod not reaching basioischial articulation. Proximal podomere of uropod with spine on mesial lobe less strongly produced.

First pleopod (Fig. 4c, g) differing from that of first form male described in "Diagnosis" in exhibiting more robust, less acute mesial process, rudimentary cephalic process, and more inflated, shorter central projection, none of terminal elements corneous; in spite of differences, lateral aspect markedly similar to that of first form male.

Color notes (based on morphotype).—Dorsum of carapace (Fig. 3) predominately brownish red; lateral rostral ridges and postorbital ridges, in striking contrast, orange to cream orange; mandibular adductor, extreme posterior gastric areas, and anterior areolar triangle dark reddish brown. Orbital region adjacent to postorbital ridges dark brown fading rapidly ventrally over remainder of orbital and hepatic regions to pale pink with cream tubercles; ventral half of branchiostegites, including anteroventral branchiostegal region and caudal ridge, pale tannish cream. First abdominal segment dark reddish brown, remainder of abdomen with broad brownish red, laterally undulating stripe terminating caudally at transverse suture of telson; stripe fading laterally on each segment with margins of pleura matching ventral halves of branchiostegites; caudal section of telson and both rami of uropods similarly pale tannish cream, latter with red median longitudinal ridges. Antennules and antennae (including flagella) pale olive green; setal clusters at apices of podomeres of peduncle grayish cream; third maxillipeds similarly olive with pale orange blush. Dorsum of merus and carpus of chelipeds reddish to olive brown with cream-tipped tubercles; chela tannish orange laterally, gradually increasingly tinged with olive toward mesial margin, most mesial row of tubercles pinkish cream and two parallel, more dorsolateral rows very dark blue, almost black; fixed finger lateral to median longitudinal ridge pinkish orange; more mesial part and entire dorsum of dactyl olive; ventral surface of chela pinkish orange. Basal podomeres of cheliped and remaining pereiopods, including most surfaces of ischia, very pale pinkish to lavender cream; dorsal surfaces of more distal podomeres with very pale bluish olive suffusion.

Dorsal surface of abdomen of juveniles and of some adult females with pale median longitudinal stripe flanked by pair of dark greenish gray or greenish brown ones.

Size.—The largest specimen available is a first form male having a carapace length of 40.8 mm (postorbital length 36.3 mm). The smallest first form male has corresponding lengths of 31.7 and 27.6 mm. Measurements are not available for either ovigerous females or ones carrying young; for those of the primary types, see Table 2.

Type locality.—De Ann Cemetery, about 1 mile (1.6 km) west of the junction of State Routes 19 and 24 on latter at western city limit of Prescott, Nevada County, Arkansas (T. 11S, R. 22W, Sec. 8). Specimens were collected from simple burrows which descended to a depth of approximately 1 m and were topped by chimneys from 8 to 12 cm high. Soils in the grass-covered, treeless field consisted of sandy clay, and no standing water was in the area inhabited by the crayfish.

Disposition of types.—The holotypic male, form I, allotype, and morphotypic male, form II, are deposited in the National Museum of Natural History, USNM 219244, 219245, and 219246, respectively, as are the paratypes consisting of 4 ♂I, 3 ♂II, 11 ♀, 3 j♂, and 1 j♀.

Range and specimens examined.—All of the specimens available were collected in southwestern Arkansas as follows (Those lots or specimens noted by an asterisk are excluded from the type series.). Ouachita River Basin: Nevada County; (1) type locality, 3 ♂I, 5 ♀, 16 Mar 1982, Elaine Laird, 1 ♀, 6 May 1979, EL; *65 very small juveniles, 28 Feb 1981, HWR. Red River Basin: Howard County; (2) Mineral Springs, 2 ♂I, May 1986, Kyle Erwin, Jason Erwin, 1 ♀, L. Tate, 1985. (3) 2 mi S of Mineral Springs, 1 ♂II, LT, 1985. (4) 1.4 mi S of St Rte 27 on 317, *1 j♀, 2 May 1986, HWR. Sevier County; (5) roadside wet area 5.1 mi E of Oklahoma state line on US Hwy 70, 21 Apr 1973, J. E. Pugh, G. B. Hobbs, HHH., 2j ♂, *5 j♀, 9 Apr 1982, HWR and D. Koym (6) field 1.5 mi N of Paraloma (T.11S, R. 28W, Sec. 8), 1 ♀, 1 Apr 1987, Eddie Daniels, KE, JE, HWR. (7) seepage area 1.6 mi S.W. of jct. on St Rtes 27 and 234, 1 ♂II, 3 ♀, 2 j♂, 1 j♀, 20 Apr 1987, GBH, HHH. (8) roadside ditch 0.4 mi E of Oklahoma state line, *1 ♂I, *1 ♂II, *2 ♀, *10 j♂, *12 j♀, 21 Apr 1973, JEP, GBH, HHH.

Variations.—Most conspicuous among the variations noted are those in specimens from localities 5 and 8, both in the Little River basin. They exhibit features that set them distinctly apart from specimens from the more eastern localities. Whereas most features of the first pleopod of the single first form male and the general mien are not conspicuously unlike those of males from the other localities, the shoulder on the pleopod is much more prominent and produced distally; in all of the specimens, the rostrum has weaker and decidedly less strongly convergent lateral ridges. Moreover in the first form male, there exists a weak, but distinct beard on the mesial surface of the palm of the chela similar to, but much less conspicuous than, that in *P.* (*G.*) *tulanei.* The crayfish from these localities are tentatively assigned to *P.* (*G.*) *regalis,* but further study of more material from the Little River basin will be required to ascertain their status.

Relationships.—Procambarus (*Girardiella*) *regalis* has its closest affinities with *P.* (*G.*) *gracilis* and *P.* (*G.*) *liberorum,* living specimens of the three resembling one another not only in their coloration, but also in most morphological features. The comparatively short (not overreaching the caudal process) central projection of the first pleopod of first form males differs from that of *P. gracilis,* and the more slender rostrum with thickened lateral carinae, more prominent postorbital ridges, and obliquely oriented caudal process of the first pleopod are among the features that distinguish it from members of *P. liberorum.* The rather smooth anterolateral prominences of the annulus ventralis and the long subtriangular postannular sclerite serve to separate the female from those of the other two species.

Key to the Members of the *gracilis* Group of the Subgenus *Girardiella* (Based on First Form Males)

1. Mesial ramus of uropod with 2 spines projecting from distal margin; cephalic process of first pleopod lacking .... *hagenianus* Group ... (See Fitzpatrick, 1978a:95, for key to members.)

– Mesial ramus of uropod without spines projecting from distal margin; cephalic process of first pleopod present .. *gracilis* Group .. 2

2. Opposable margin of dactyl of chela with prominent angular excision in basal third; dorsolateral surface of palm punctate; color of first form male mostly red 3

– Opposable margin of dactyl of chela lacking or with weak excision in basal third; dorsolateral surface of palm tuberculate; color of first form male brown, tan or greenish. 6

3. First pleopod with central projection clearly overreaching caudal element (Fig. 5) .... *gracilis*

– First pleopod with central projection not overreaching distal extremity of caudal element (Figs. 11, 13) 4

4. Areola less than 30 times as long as broad .... *reimeri*

– Areola at least 38 times as long as broad, sometimes linear 5

5. Palm of chela punctate except for tubercles along and adjacent to mesial surface; setae on caudoproximal ridge of first pleopod directed caudolaterally ..... *liberorum*

– Palm of chela mostly tuberculate, especially on mesial halves of dorsal and ventral surfaces; setae on caudoproximal ridge of first pleopod splayed, directed distomesially and distolaterally 7

6. Rostral margins conspicuously thickened and tapering from base; ratio of length to width of rostrum never more than 1.2 .... *regalis*

– Rostral margins not thickened and subparallel to ill-defined base of acumen; ratio of length to width of rostrum greater than 1.2 .... *ferrugineus*

7. Central projection of first pleopod clearly overreaching distal ex-

tremity of caudal element (Figs. 6, 7) 8
- Central projection not, or rarely barely, overreaching distal extremity of caudal element (Figs. 8, 9, 10) 9

8. Mesial surface of palm of chela bearded; blade of caudal element of first pleopod broadly rounded to truncate distally (Fig. 7) .. *tulanei*
- Mesial surface of palm of chela never bearded; blade of caudal element of first pleopod tapering distally (Fig. 6) ..... *regiomontanus*

9. Blade of central projection of first pleopod directed distolaterally, and in caudal aspect extending lateral to caudal element (Fig. 10b) .... *curdi*
- Blade of central projection of first pleopod directed distally, and, in caudal aspect, situated mesial to caudal element (Figs. 8, 9) 10

10. Areola no more than 14 times as long as broad; blade of caudal element of first pleopod with broadest plane almost transversely oriented; in mesial view, caudodistal end of shaft of pleopod subtruncate, almost forming angle with caudal element (Fig. 8) .... *parasimulans*
- Areola more than 14 times as long as broad; blade of caudal element of first pleopod with broadest plane obliquely oriented; in mesial view, caudodistal end of shaft of pleopod tapering, lacking even suggestion of angle of base of caudal element (Fig. 9) ...... *simulans*

Notes on the Ranges of Other Members of the Subgenus *Girardiella* Occurring in Arkansas

In addition to the new species described above, five other members of the subgenus *Girardiella* occur in Arkansas. They are listed below, and for each of them a statement of its range is followed by a list of locality records within the state; those localities from which specimens have not been examined by one or both of us are noted by an asterisk. As nearly complete synonymies as we have been able to amass are provided for all of the species except *P.* (*G.*) *simulans.* Many of the references in the literature are almost certainly based on erroneous determinations, and the reported range (Hobbs 1974: 48, one of the more recent) must be recognized as possibly, if not likely, encompassing that of several taxa (including *P.* (*G.*) *parasimulans,* see below).

Procambarus (*Girardiella*) *curdi* Reimer

Figs. 10, 16

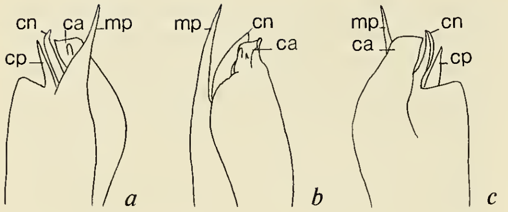
(?)*Procambarus simulans simulans.*—Penn & Hobbs, 1958:472 [in part].

Procambarus (*G.*) *curdi* Reimer, 1975:22–25, figs. 1–9 [type locality: Navasota River, NE of Bryan on US Hwy 190, Brazos County, Texas].—Bouchard, 1978a:451; 1980a:451.—Fitzpatrick, 1978b:538; 1983:206.—Bouchard & Robison, 1981: 28.—Hobbs & Robison, 1982:551, 552.

Procambarus curdi.—Bouchard & Robison, 1981:26.

Range.—The only confirmed previously reported localities for this species are those of Reimer (1975:25) which lie in the Navasota and Trinity watersheds of Texas and the Red River basin in Arkansas and Oklahoma. It is highly probable that some of the localities cited for *P.* (*G.*) *s. simulans* by Penn & Hobbs (1958) were based on misidentifications of members of *P.* (*G.*) *curdi.* The localities listed here lie within the Red River basin of Arkansas and represent only minor extensions of the range of the species.

Arkansas records.—Little River County: (1*) 12.5 mi W of Ashdown (Reimer 1975: 25); (2) 4 mi N of cross roads, S of Little River Bridge on St Rte 41, 11 j♂, 20 j♀, 11 Apr 1982, B. Boyd, coll; (3) roadside ditch



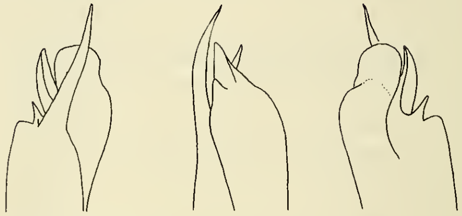
5. *P. (G.) gracilis*

6. *P. (G.) regiomontanus*

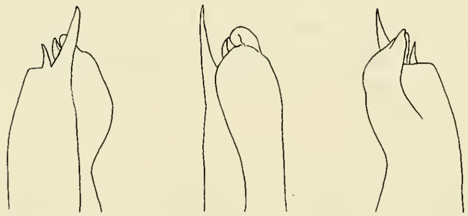
7. *P. (G.) tulanei*

8. *P. (G.) parasimulans*

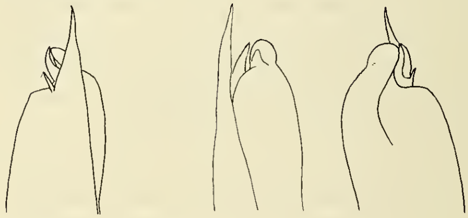
9. *P. (G) simulans*



10. *P. (G.) curdi*

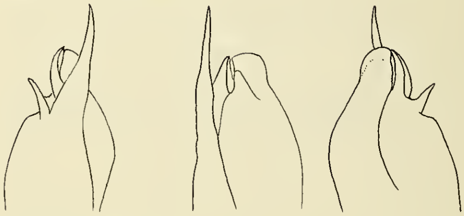


11. *P. (G.) reimeri*



12. *P. (G.) ferrugenius*

13. *P. (G.) liberorum*



14. *P. (G.) regalis*

Figs. 5–14. Distal part of first pleopods of first form males: a, Mesial view; b, Caudal view; c, Lateral view. (ca, caudal element; cn, central projection; cp, cephalic process; mp, mesial process.)

4.3 mi S of Ashdown, 1 ♂II, 25 j♂, 25 j♀, 11 Apr 1982, Boyd; (4) roadside ditch 1.9 mi W of Ashdown on St Rte 32, 1 ♂II, 14 j♂, 12 j♀, 27 Apr 1976, M. T. Kearney, HHH; 3 j♂, 3 j♀, 10 Apr 1982, HWR, D. Koym. (5) roadside ditch 7 mi N of Miller Co line on US Hwy 71, 1 ♀, 26 Apr 1976, MTK & HHH. Miller County: (6) 8.5 mi SW of Fouke, near Sulphur River, 1 ♀, 8 j♂, 8 j♀, 26 Mar 1982, C. Johnson; (7) 3 mi E of Fouke on St Rte 134, 2 j♂, 1 j♀, 28 Mar 1982, Thomason.

Procambarus (*Girardiella*) *liberorum* Fitzpatrick

Figs. 13, 15

Procambarus (*Girardiella*) *gracilis*.—Hobbs, 1974:47 [in part; and previous authors listing Arkansas within the range of the species].—Hobbs III & Rewolenski, 1985: fig. 1 [in part].—Page, 1985, fig. 99 [in part].

Procambarus (*G.*) *liberorum* Fitzpatrick, 1978b:533–538, figs. 1–14 [type locality: yard at 206 SW Seventh Street, Bentonville, Benton County, Arkansas]; 1983:206.—Bouchard, 1978b:14.—Hobbs, 1979:804, 810.—Bouchard & Robison, 1981:28.—Hobbs & Robison, 1982:552.

Procambarus liberorum.—Bouchard & Robison, 1981:28, 29.—Robison & Smith, 1982:54.—Mayden, 1985:200.—Page, 1985:371.

Range.—This crayfish is an inhabitant of the Arkansas River basin, occurring from Benton and Washington counties to Pope and Yell counties in Arkansas, and presumably will be found in the Oklahoma segment of the watershed.

Arkansas records.—Benton County: (1) type locality, 2 ♂I, 3 ♀, summer, 1976, Fitzpatrick family. Franklin County: (2) pond 8.3 mi S of Coombs, 1 ♂I, 1 ♀, 26 Feb 1955, E. Whatley. (3) 0.2 mi E of Branch on St Rte 22, 1 j♂, 15 Mar 1981, HWR. (4) seepage area 0.4 mi E of Branch on St Rte 22, 1 ♀, 7 j♂, 6 j♀, 16 Apr 1982, HWR, DK. (5) Prairie Creek, 2 mi N of Charleston on St Rte 217, 1 ♂I, 24 May 1980, G. L. Harp. Johnson County: (6) P. L. Hill Work Center on St Rte 21, N of Clarksville, 1 j♀, 1 Feb 1986, D. Ebert. Logan County: (7) 0.8 mi E of Midway city limits on St Rte 22, 1 ♂I, 1 j♂, 15 Mar 1981, HWR; 1 ♂I, 1 ♀, 1 j♀, 16 Apr 1982, HWR, DK. Pope County: (8) roadside ditch 1.3 mi N of Hector on St Rte 105, 1 ♂I, 2 ♀, 17 Apr 1973, JEP, GBH, HHH. (9) stream 2.6 mi NW of St Rte 7 on St Rte 164, 4 ♂II, 4 j♂, 8 j♀, 16 Apr 1973, JEP, GBH, HHH. (10) dry stream-bed 1.8 mi N of Hector on St Rte 105, 1 ♀, 42 j, 16 Apr 1982, HWR, DK. (11) 2 mi E of Scottsville on St Rte 27, 1 j♂, 20 Mar 1986, (molted to first form in September 1987) HWR; 2 ♂II, 1 ♀, 20 Mar 1987 (one of the males molted to first form in September 1987), HWR. Scott County: (12) roadside ditch 5 mi E of Waldron on St Rte 80, 1 ♂II, 3 ♀, 8 j♂, 6 j♀, 18 Apr 1973, JEP, GBH, HHH. Sebastian County: (13) seepage area 3 mi E of Central City on St Rte 22, 7 j♂, 9 j♀, 15 Mar 1981, HWR; 5 j♂, 7 j♀, 16 Apr 1982, HWR, DK; 3 ♀, 2 j♂, 16 Mar 1986, HWR. Washington County: (14) low area near University of Arkansas campus, Fayetteville, 1 ♂I, 1 ♀, 11 May 1949, D. W. Gray. Yell County: (15) roadside ditch 5.8 mi SW of St Rte 7 on Rte 27, 1 ♂I, 4 ♀, 3 j♂, 9 j♀, 17 Apr 1973, JEP, GBH, HHH. (16) roadside ditch 1.7 mi SW of St Rte 154 on St Rte 27, 1 j♂, 2 j♀, 17 Apr 1973, JEP, GBH, HHH. (17) roadside ditch 32 mi N of Story on St Rte 27, 1 ♀, 15 Mar 1981, HWR.

Procambarus (*Girardiella*) *parasimulans* Hobbs & Robison

Figs. 8, 16

Procambarus (*Girardiella*) *simulans simulans*.—Hobbs, 1974:48 [in part].

Procambarus (*G.*) *parasimulans* Hobbs & Robison, 1982:545–533, fig. 1 [type lo-

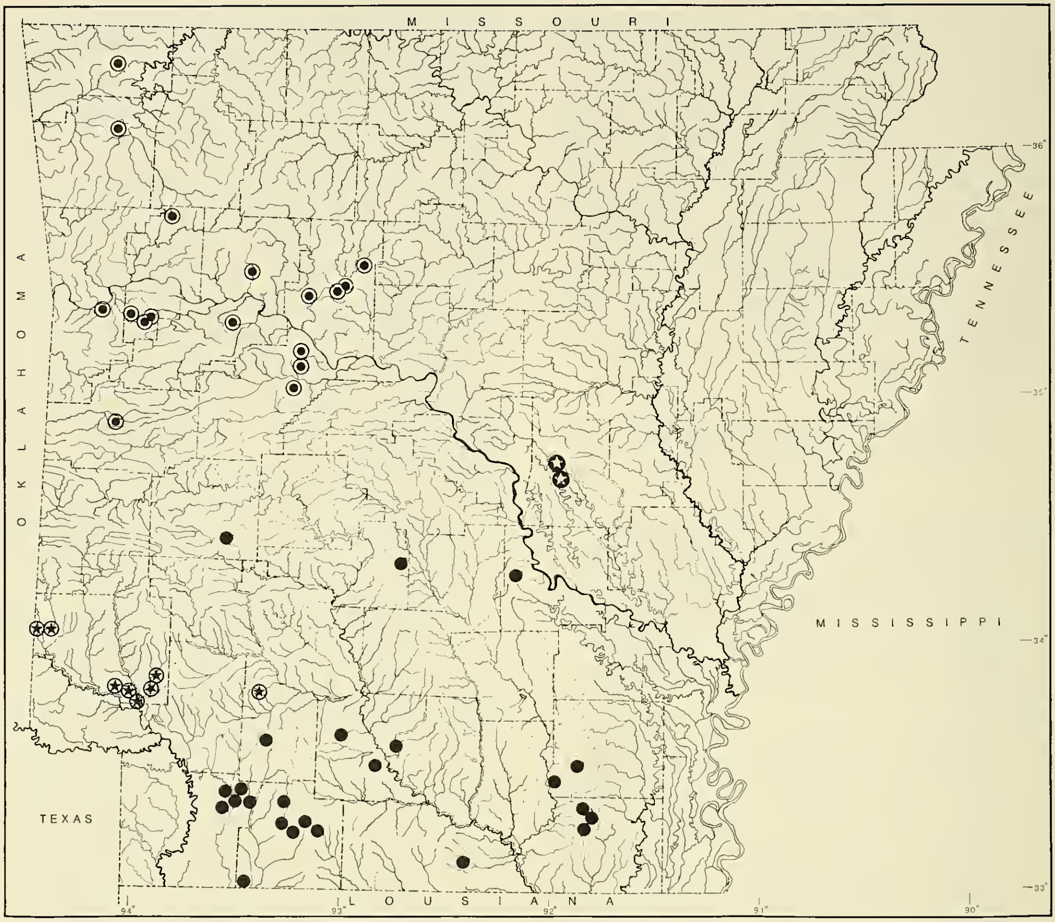


Fig. 15. Distribution of the members of the subgenus *Girardiella* in Arkansas: *P.* (*G.*) *ferrugineus* (white star on black background); *P.* (*G.*) *liberorum* (encircled dots); *P.* (*G.*) *regalis* (encircled black stars); and *P.* (*G.*) *tulanei* (black dots).

cality: tributary to Prairie Bayou, 10.2 miles E of Bismarck on St Rte 84, Hot Spring County, Arkansas (Sec. 35, R. 19W, T. 48)].

Procambarus parasimulans.—Mayden, 1985:196, 207.

Range.—This crayfish is one of the more common inhabitants of pools (largely juveniles) and burrows in the southwestern part of Arkansas where it has been found in the Red and Ouachita river basins and in three localities in the Arkansas watershed.

Arkansas records.—It was reported by Hobbs & Robison (1982:551) from 12 localities in the Red and Ouachita river basins in Clark, Grant, Hot Spring, Nevada, Ouachita, Pike, and Sevier counties, Arkansas. Additional localities are as follows: Clark County: (1) roadside ditch, 7.4 mi E of Amity Courthouse on St Rte 84, 1 j♀, 30 Apr 1976, MTK, HHH. Franklin County: (2) 0.2 mi E of Branch on St Rte 22, 1 ♂II, 7 j♂, 6 j♀, 15 Mar 1981, HWR; 1 ♂II, 1 j♂, 16 Apr 1982, HWR, DK. (3) roadside ditch 3.1 mi E of Charleston on St Rte 22, 28 j♂, 20 j♀, 15 Mar 1981, HWR. Hempstead

County: (4) Blevins, 1 ♂II, 20 Apr 1982, E. Laird; 1 j♂, 20 May 1983, EL. Hot Spring County: (5) roadside ditch 5.2 mi E of Clark Co line on St Rte 84, 1 j♀, MTK, HHH. (6) unnamed creek on Hwy 84, 2.1 mi W of Bismarck, 6 j♂, 8 j♀, 13 Mar 1981, HWR. Howard County: (7) several creeks in or near Nashville, 1 ♂II, 1 ♀, 10 Mar 1986, R. Smith; 1 ♂II, 2 ♀, 13 Mar 1986, RS; 2 j♂, 17 Mar 1986, A. Brown, D. Byers; 1 j♂, 1 j♀, 17 Mar 1986, B. Evans, T. Crabtree; 1 j♂, 1 j♀, 19 Mar 1986, BE, TC; 1 ♀, 20 Mar 1986, C. Farr; 8 j♂, 5 j♀, 2 Apr 1986, C. King; 1 ♀, 9 Apr 1986, B. Cooper; 1 ♀, 14 Apr 1985, L. Tate, B. Wallis; 1 ♀, 2 May 1986, W. Johnson. (8) Mineral Springs, 1 ♀, 1985, L. Newton; 1 ♂I, 1 ♀, 1985, LT; 2 ♀, 1985, LT; 1 ♀, 8 Nov 1986, M. Fox; 1 ♂II, 9 Nov 1985, D. Batson. (9) Blue Bayou Creek W of Nashville (T. 9S, R. 26W, Sec. 15), 1 j♂, 14 Apr 1985, LT, BW. (10) about 3 mi N of Nashville on Pump Springs Road, 1 ♂I, 2 ♂II, 2 ♀, 5 j♂, 4 j♀, 2 Apr 1986, D. Howard. (11) small creek 7.5 mi SW of Newhope, 3 j♂, 2 j♀, 11 May 1963, A. P. Blair. (12) stream and seepage area 1.8 mi E of Sevier Co line on St Rte 4, 4 j♂, 1 j♀, 29 Apr 1976, MTK, HHH. Montgomery County: (13) 0.9 mi W of Caddo Gap, 1 ♀, 23 Nov 1962, A. P. Blair. Nevada County: (14) Outskirts of Willisville, 6 j♂, 8 j♀, 11 Sep 1985, DK. Pike County: (15) Antoine Creek, 2.5 mi N of Kirby, 1 ♀, 21 Apr 1952, E. Lachner. (16) roadside ditch 2 mi NE of Daisy on US Hwy 70, 9 j♂, 6 j♀, 21 Apr 1973, JEP, GBH, HHH. (17) roadside ditch 2.6 mi W of St Rte 8 on Rte 84, 1 ♂II, 11 j♂, 11 j♀, 17 Mar 1980, HWR. Polk County: (18) West Creek 3.5 mi E of Wicks (T. 5S, R. 32W, Sec. 27), 1 j♀, 27 Sep 1975, HWR. Saline County: (19) Saline River at Benton, 1 ♂II, 28 Sep 1985, HWR. (20) flooded field just W of Saline River, S side of St Rte 291, 1 j♂, 19 Mar 1980, HWR. Sebastian County: (21) 3 mi E of Central City on St Rte 22, 1 ♀, 10 j♂, 6 j♀, 16 Apr 1982, HWR, DK.

Remarks.—We have found that many young males, particularly those with regenerated chelae (which cannot always be recognized as such in smaller individuals), and almost all females of this crayfish are virtually indistinguishable from those of *P.* (*G.*) *tulanei.* Therefore, many of the above localities and a few of those listed by Hobbs & Robison (1982:551) must be accepted provisionally.

Procambarus (*Girardiella*) *reimeri* Hobbs
Figs. 11, 16

Procambarus (*Girardiella*) *reimeri* Hobbs, 1979:804–811, 1 fig. [type locality: roadside ditch about 5 mi (8 km) NE of Mena on unnumbered road to Irons Fork River, Polk County, Arkansas].—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983: 206.—Hobbs & Robison, 1982:552.—Robison & Smith, 1982:53.

Procambarus reimeri.—Bouchard & Robison, 1981:26.—Mayden, 1985:196, 200.—Page, 1985:371.

Arkansas records.—The only localities in which this species is known to occur are the six in Polk County, Arkansas, cited by Hobbs, 1979:810.

Procambarus (*Girardiella*) *simulans* (Faxon)
Figs. 9, 16

Procambarus (*Girardiella*) *simulans* (Faxon, 1884:112–113) [type locality, Dallas, Texas].

Range.—Reported to occur in the following states: New Mexico, Texas, Louisiana, Oklahoma, Kansas, Arkansas, and Colorado; the limits of its range in them, however, have not been determined.

Arkansas records.—We have examined only one specimen referable to this species in Arkansas, that collected along with *P.* (*G.*) *regalis* in a pasture 1.5 mi (2.4 km) N of Paraloma, Sevier County. (See locality 6 under *P.* (*G.*) *regalis.*)

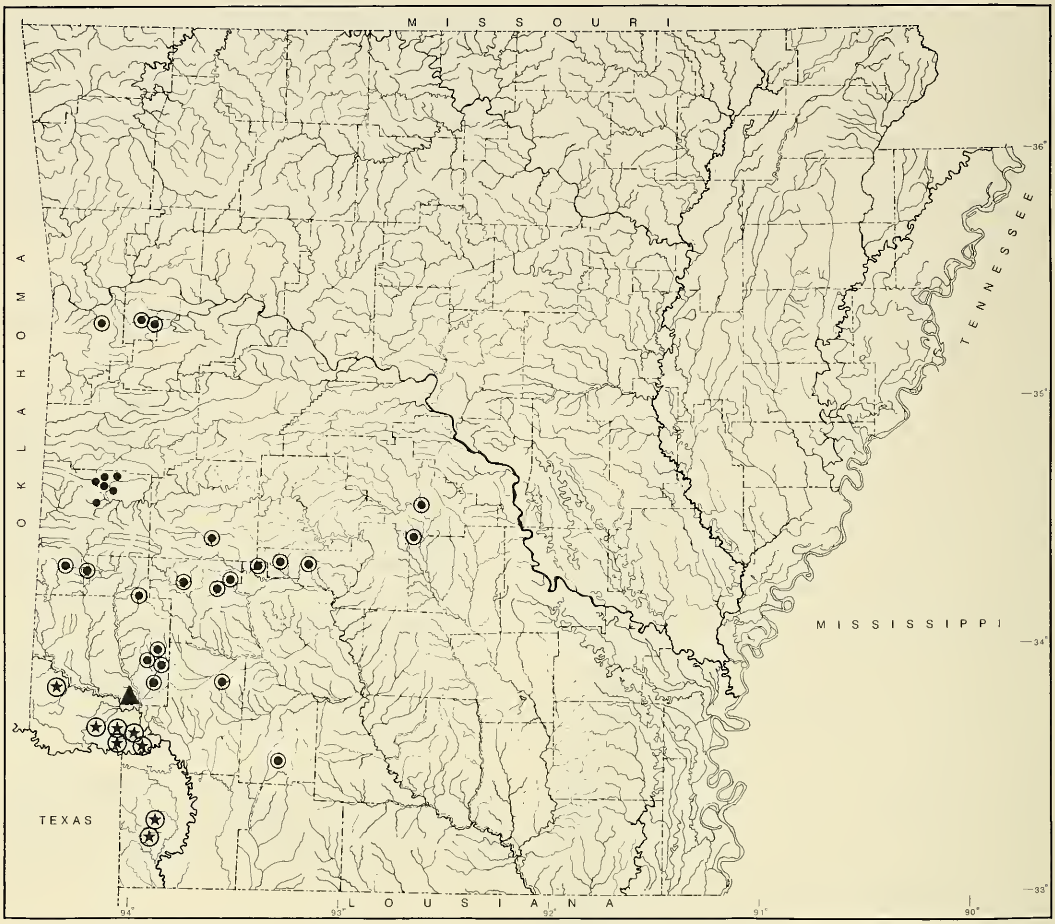


Fig. 16. Distribution of the members of the subgenus *Girardiella* in Arkansas: *P.* (*G.*) *reimeri* (small black dots); *P.* (*G.*) *parasimulans* (encircled dots); *P.* (*G.*) *simulans* (black triangle); *P.* (*G.*) *curdi* (encircled black stars).

Procambarus (*Girardiella*) *tulanei* Penn
Figs. 7, 15

Procambarus tulanei Penn, 1953a:163–166, 12 figs. [type locality: tributary of Bayou D'Arbonne, 4 mi W of Dubach on St Rte 288, Lincoln Parish, Louisiana]; 1953b: 6; 1956:420; 1959:5, 6, 12, 13, 17, figs. 11, 41.—Hobbs, 1959:887; 1968:K11, K25; 1971:466.—Walls, 1968:417.—Hart & Hart, 1974:30.—Bouchard, 1978b:fig. 2g.—Bouchard & Robison, 1981:26, fig. 2g.

Procambarus (*Girardiella*) *tulanei*.—Hobbs, 1972a:7; 1972b:45, 152, figs. 38a, 39e; 1974b:48, 127, fig. 189.—Fitzpatrick, 1975:53; 1976:384; 1978a:57, 59, 93, 95, fig. 121; 1978b:538; 1983:206.—Reimer, 1975:25.—Bouchard & Robison, 1981: 28.—Hobbs & Robison, 1982:552.

Range.—Previously known only from the Red and Ouachita river basins in southern Arkansas and Louisiana, it is reported below from the lower Arkansas River basin in Jefferson County, Arkansas.

Arkansas records.—Ashley County: (1) Fountain Creek, 8 mi N of Hamburg on St Rte 81, 15 j♂, 21 j♀, 16 Mar 1967, J. E. & M. R. Cooper. (2) North Fork of Fountain

Creek at St Rte 81, 5 j♂, 3 j♀, 16 Mar, 1967, JEC & MRC. (3) 8 mi N of Hamburg on St Rte 81, 15 j♂, 21 j♀, 16 Mar 1967, JEC & MRC. Columbia County: (4) 3.8 mi E of Magnolia on US Hwy 82, 6 j♂, 5 j♀, 23 Apr 1965, W. J. Harman & HHH. (5) Big Creek, 2 mi E of Lamartine on St Rte 98, 1 j♂, 14 Jun 1974, HWR. (6) Big Creek at US Hwy 82 bypass, 1 ♂II, 11 Jul 1974, L. Weaver, L. Calhoun; (7) Magnolia city limits, 1 ♂II, 2 Jun 1974, HWR. (8) Cornie Creek, 6 mi SE of Magnolia, 2 ♂II, 1 ♀, 1 Nov 1974, S. Pelt. (9) roadside ditch 2.3 mi N of Louisiana state line on St Rte 132, 1 ♂II, 25 Apr 1976 [molted to form I, 20 Sept 1976] MTK, HHH. (10) Magnolia, 2 j♂, 2 j♀, 12 Apr 1974, HWR, Patrick Robison; 1 ♂II, 19 Sep 1979, M. A. Bryan, Montgomery. Drew County: (1) north of county line [on St Rte 81 ?], 8 j♂, 4 j♀, 16 Mar 1967, JEC & MRC. (12) Saline River about 13 mi SE of Monticello at end of St Rte 172, 1 j♂, 26 Oct 1974, HWR. Hot Spring County: (13) roadside ditch 3.5 mi W of Poyen on US Hwy 270, 1 ♂II, 1 ♀, 17 Mar 1980, HWR. Jefferson County: (14) ditch on Holland Rd off US Hwy 270 W of White Hall, 2 ♀, 1 j♂, 22 Apr 1979, B. Lovorn; 9 j♂, 6 j♀, 25 Apr 1982, BL. Lafayette County: (15) Bodcaw Creek, 10 mi N of Stamps on Hope Rd, 1 ♀, 5 May 1975, M. Foster. (16) Creek in Stamps, 2 ♀, 13 j♂, 5 j♀, 3 May 1975, J. Turnage. (17) backwaters of Bayou Bodcaw 4 mi N of Lewisville on Sunray Rd off St Rte 29, 3 j♂, 26 Apr 1976, MTK, HHH. (18) Lewisville, 2 ♂II, 13 Jun 1974, C. Lathan. Montgomery County: (19) Trib. to Collier Creek 1 mi W of Caddo Gap, 1 j♂, 2 j♀, 11 May 1963, A. P. Blair. Nevada County: (20) Whitten Branch 0.75 mi S of Bodcaw, 1 ♀, 7 Dec 1974, P. Ross. Ouachita County: (21) Larkin Bayou 3 mi N of St Rte 4 on Co Rd near Camden, 1 j♂, 1 j♀, 6 May 1975, SP, J. Stephens. (22) Larkin Bayou 1 mi E of St Rte 57, 4 mi N of jct with Rte 4, 1 j♀, 25 May 1975, SP, J. Wilson. (23) trib to Two Bayou between St Rtes 4 and 24, 1 ♂II, 1 j♂, 4 j♀, 30 Mar 1975, SP. (24) trib to Little Bayou just off US Hwy 79 on Co Rd near Camden, 1 ♂II, 8 j♂, 8 j♀, 10 May 1975, SP. Union County: (25) roadside ditch 3 mi W of Strong on US Hwy 82, 1 ♂II, 1 ♀, 25 Apr 1986, HWR.

Remarks.—See "Remarks" under *Procambarus* (*G.*) *parasimulans.*

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We extend our appreciation to all of those persons cited herein who donated, or assisted us in collecting, the specimens on which this study was based. Special thanks are offered to Eddie Daniels, Linda Tate, and the students at Mineral Springs and Nashville high schools for their interest in this study. The Southern Arkansas University Faculty Research Fund provided travel funds to H. W. Robison for collecting crayfishes. For their criticisms of the manuscript we are grateful to Thomas E. Bowman of the National Museum of Natural History, J. F. Fitzpatrick, Jr., of the University of South Alabama, and Horton H. Hobbs III of Wittenberg University.

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TWO SPECIES OF GALATHEID CRUSTACEANS (DECAPODA: ANOMURA) NEW TO FLORIDA, *MUNIDA SPINIFRONS* HENDERSON, AND *MUNIDOPSIS KUCKI,* NEW SPECIES

Keiji Baba and David K. Camp

Abstract.—Two species of galatheid crustaceans are reported for the first time from off Florida. *Munida spinifrons* was known previously only from *Challenger* sta 113A in Brazilian waters. Extensive description of the holotype of that species is provided, and its affinities to *M. pusilla* are discussed. *Munidopsis kucki,* new species, is closely related to *M. sharreri.* Their relationships are discussed based upon an examination of the holotype of *M. sharreri.*

Personnel at the Florida Department of Natural Resources, Bureau of Marine Research, in conjunction with the National Marine Fisheries Service, have been collecting selected macroinvertebrates in depths of 9 to about 550 meters off the east coast of Florida since 1983, as part of the Southeast Area Mapping and Assessment Program (SEAMAP). Among numerous specimens representing over 250 species of decapod crustaceans found to date were four unusual specimens of small galatheid anomurans. Three of these specimens seemed to be *Munida spinifrons* Henderson, 1885, known previously only by the type specimen from Fernando de Noronha, Brazil (Henderson 1885, 1888). We could not identify the specimens with certainty, however, because of the brevity of Henderson's species accounts; therefore, the holotype was borrowed (by KB) from the British Museum (Natural History) (BMNH). Examination of that specimen confirmed that the specimens from off Florida are *M. spinifrons.* Some characters of *M. spinifrons* suggest that it is very close to *M. pusilla* Benedict, 1902. Their relationships are discussed based on examination (by KB) of syntypes of *M. pusilla* and examination (by DKC) of other material from off eastern Florida.

The fourth specimen from SEAMAP samples strongly resembled *Munidopsis sharreri* (A. Milne Edwards, 1880) from off St. Croix, Virgin Islands. Comparison of our specimen with the holotype of that species revealed that the Floridian specimen is a distinct species, described below.

Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the Florida Department of Natural Resources, Marine Invertebrate Collection, St. Petersburg (FSBC I).

Munida spinifrons Henderson, 1885
Fig. 1

Munida spinifrons Henderson, 1885:412; 1888:144, pl. 15, figs. 1, 1a, 1b.

Material.—*Challenger* sta 113A, Fernando de Noronha, 3°47′00″S, 32°24′30″W, 7–25 fm (13–46 m), volcanic sand and gravel: holotype, ♀ (BMNH 1888:33).—*Delaware II* cruise 83-05, sta 147, about 52.5 nmi E of St. Augustine, St. Johns County, Florida, 29°50′N, 80°15′–16′W, 49–50 fm (90–91 m), rock rubble, 23.2°C, coll. W. Lyons, D. Camp, & J. Quinn, Jr., 27 Apr 1983, 1806–1821 hr: 1 ♂ (USNM 234230).—*Delaware II* cruise 84-05, sta 091, about 52 nmi E of Jacksonville Beach, Duval County, Florida, 30°20.2′N, 80°23.9′W, 20–22 fm (36–40 m), Arca zebra reef, 25.9°C, coll. W. Lyons, D. Camp, J. Quinn, Jr. et al., 22 May 1984, 2318–2333 hr: 2 ♀ (1 ovigerous) (FSBC I 32355).

Description of holotype.—Carapace longer than wide, greatest width equaling length measured in midline between base of anterolateral spine and posterior margin of carapace. Dorsal ridges and cervical groove distinct. Gastric region convex; epigastric region with 6 spines in 3 pairs, median pair largest, directly behind supraocular spines; lateral protogastric spine [=parahepatic spine of Zariquiey Alvarez (1952)] on each side; anterior branchial region with tiny spine directly behind midlength of anterior bifurcation of cervical groove. No other spines on dorsal surface of carapace. Lateral margin oblique; anterolateral spine sharp, curved somewhat inward, followed by 6 spines: 1 in front of, and 5 behind cervical groove.

Rostrum markedly curved dorsad, laterally armed with 4 distinct and 2 tiny spines, dorsally provided with rounded ridge, length about ¾ of postrostral carapace length. Supraocular spines subparallel, close to rostrum, about ⅙ of rostral length and falling short of end of eyestalk.

Second abdominal tergum with 3 transverse ridges, anterior ridge with 2 tiny spines.

Eyes dilated, somewhat depressed, setae short.

Basal segment of antennule bearing well-developed mesial terminal spine twice as long as ventrolateral terminal one; 2 lateral spines, distal one somewhat longer than ventrolateral terminal one. Antennal peduncle composed of 4 segments, first segment with distomesial spine only, second segment with distolateral spine, third segment unarmed.

Merus of third maxilliped with 4 small, subequal, mesial marginal spines and distinct distodorsal spine. Ischium bearing distomesial and distodorsal spines, distomesial one larger. Distal 2 segments slender, carpus unarmed.

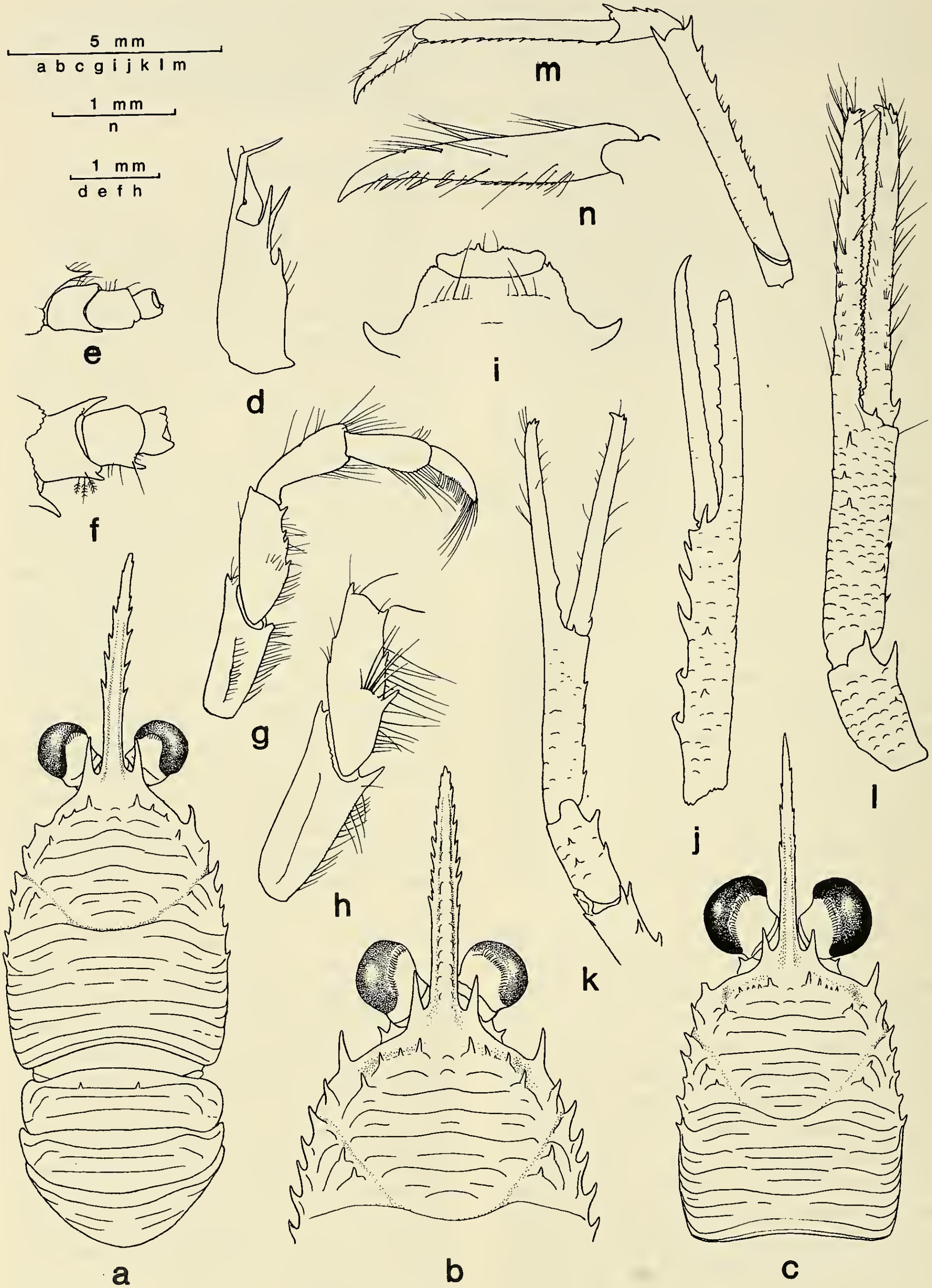
Anterior part of sternal segments as illustrated (Fig. 1i); third thoracic sternum with denticles on anterior margin; fourth thoracic sternum not triangular, anteriorly contiguous with whole posterior margin of preceding sternum.

Chelipeds dissimilar; right one larger but broken, only incomplete chela remaining; palm 5 times as long as wide, armed with 5 acute mesial marginal, 3 dorsal, 3 ventral, and 2 lateral spines; distodorsal and distoventral spines pronounced; fingers not gaping, movable finger distally curved, lacking mesial marginal spine, immovable finger distally broken, opposable margin with several distinct processes, opposing margin with smaller processes. Left cheliped slenderer and shorter than right one, subcylindrical, spination weaker; merus with 3 rows of 6 spines each including terminal one; carpus with 2 mesial marginal, 2 dorsal, and 3 ventral spines; palm about 5 times as long as wide, shorter than movable finger, mesially with small spines in 2 rows, 4 somewhat dorsal, 9 somewhat ventral; distodorsal and distoventral spines at junction with movable finger small; fingers not gaping, each ending in spine directed inward and 2 tiny spines laterally; opposable margins lacking pronounced tubercles, bearing 2 low processes on immovable finger; movable finger with distinct spine at mesial proximal margin.

Second and third pereopods slender, sparsely setose except for dactyli; meri with 10 dorsal and 1 distoventral spines, distal spines on both margins pronounced; carpi with 4 dorsal spines; propodi 10 times as long as wide, twice as long as dactyli, bearing 15 ventral spinelets on second pereopod, 17 on third pereopod; dactyli curved, without distinct serration ventrally, bearing 13 spinelets on second pereopod, 17 on third pereopod, spinelets gradually diminishing in size toward base of segment. Fourth pereopods missing.

Epipods absent from all pereopods.

Measurements.—Postrostral carapace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length of female holotype, 6.3 mm; of male, 6.6 mm; of ovigerous female, 5.8 mm; of nonovigerous female, 8.1 mm.

Remarks.—The Floridian specimens differ from each other and from the holotype in the following details: the front margin of the male is less oblique than those of the females, whereas the margins of the Floridian females are less oblique than that of the holotype female (Fig. 1a, b, c). Epigastric spines are more numerous in the male (Fig. 1c). Branchial regions in all the Floridian specimens bear two spines behind the anterior bifurcation of the cervical groove, instead of a single spine as in the holotype. The strong upward curve of the rostrum of the holotype is rather weakly expressed on the Floridian specimens. The lateral margin of the rostrum bears about nine small spines in the nonovigerous female, but only three in the male (Fig. 1b, c). The ovigerous female lacks a rostrum. Distomesial spines on the second and third segments of the antennal peduncle are distinct on the Floridian specimens, but are absent from the holotype (Fig. 1e, f). Chelipeds in the females are more granular than in the male, and the fingers are longer than the palm, as in the left cheliped of the holotype; in the male, the fingers and the palm are of equal length. The very spinose palm and lack of mesial marginal spines on the movable finger of the right cheliped of the holotype are found on only one Floridian specimen, the ovigerous female. The meri of the third maxillipeds of the Floridian specimens bear three equidistant mesial marginal spines (Fig. 1h), the proximal one being consistently larger, usually accompanying coarse, iridescent setae on the lateral face. Spination of meri of the fourth pereopods is not exactly the same in the holotype and the Floridian specimens, if the illustration in Henderson (1888: pl. 15, fig. 1) is correctly depicted; in the Florida specimens the distodorsal spine is completely absent. Unfortunately, the fourth pereopods are no longer with the holotype. Finally, the two tiny spines on the second abdominal tergum are absent in the Floridian specimens.

Several features displayed to a greater or lesser extent by the Floridian specimens of *M. spinifrons,* including the less oblique front margin, the absence of spines on the second abdominal segment, and weaker spination of the rostrum, strongly suggest that *M. spinifrons* approaches *M. pusilla,* previously known in the western Atlantic between Cape Lookout, N.C., and Trinidad (Benedict 1902, Williams 1984). Because of the brevity of available accounts of *M. pusilla,* 19 specimens (15 males, 4 ovigerous females) were kindly selected for our examination by Austin B. Williams from more than 230 syntypes in the collection of the National Museum of Natural History (USNM 140191). Most of the features once thought to be characteristic of *M. spinifrons,* i.e., shapes of the antennular basal segments, antennae and anterior parts of sternal segments, and spination of pereopods, are shared with *M. pusilla.* Furthermore, the two species occur together off east Florida. The two females of *M. spinifrons* (FSBC I 32355) were in the same sample with 21 specimens (13 males, 7 females, 1 fragment) of *M. pusilla.* The latter specimens were also examined for this discussion.

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Fig. 1. *Munida spinifrons* Henderson, 1885; a, d, e, g, i, j, k, m, n, female holotype from *Challenger* sta 113A (BMNH 1888:33); b, f, h, l, female from *Delaware II* cruise 84-05 sta 091 (FSBC I 32355); c, male from *Delaware II* cruise 83-05 sta 147 (USNM 234230): a, Carapace and abdomen; b, Anterior half of carapace; c, Whole carapace; d, Basal segment of left antennule, ventral view; e, Antennal peduncle, left, ventral view; f, Same, right; g, Endopod of right third maxilliped; h, Same, distal three segments omitted; i, Anterior part of sternal segments; j, Cheliped, right; k, Same, left; l, Same; m, Left second pereopod; n, Dactylus of same.

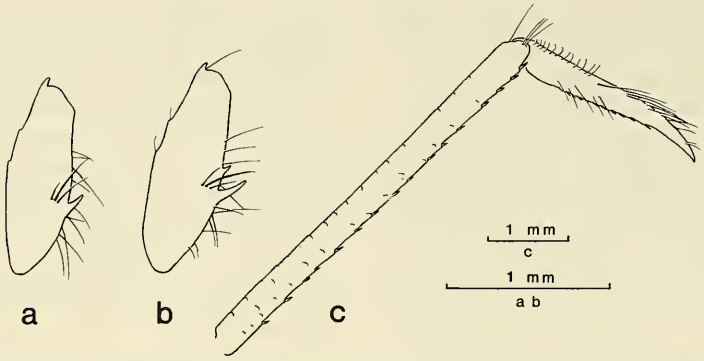

Fig. 2. *Munida pusilla* Benedict, 1902, syntypes (USNM 140191): a, Merus of third maxilliped, male, cl (postrostral carapace length) 4.5 mm; b, Same, male, cl 5.3 mm; c, Distal two segments of right second pereopod, male, cl 5.3 mm.

The two species are so morphologically similar to each other that careful examination of the following is needed for discrimination: 1) The rostrum of *M. spinifrons* is relatively longer than that of *M. pusilla.* In the intact Floridian specimens of *M. spinifrons,* the rostrum is 1.14 and 1.33 times the length of the rostrocervical distance; i.e., the distance between the level of the rostral base and the midcervical groove. In the holotype, the rostrum is 1.46 times the rostrocervical distance. By contrast, the rostral length in *M. pusilla* is far less than the rostrocervical distance (0.47–0.82, average 0.70 in the syntypes; 0.61–0.94, average 0.77 in 14 intact SEAMAP specimens). Also, lateral spination of the rostrum is barely discernible in *M. pusilla,* even under high magnification. 2) The postcervical spine on the dorsum of the carapace is absent in *M. spinifrons,* but is consistently present in *M. pusilla* (although one of the SEAMAP specimens of the latter species had the spine on one side of the carapace, but lacked the spine on the other side). 3) Meri of the third maxillipeds in both species are similar, having coarse, iridescent setae near the mesial spine at midlength. However, the three or four mesial marginal spines present in *M. spinifrons* are usually reduced in *M. pusilla* to a single large median spine and are rarely accompanied by a much smaller spine distal to it (found on only two of the 19 syntypes and on five of the 21 east Florida specimens) (Fig. 2a, b). 4) The second to fourth pereopods are much more slender in *M. pusilla* (Fig. 2c). 5) Finally, chelipeds in the two species are similar in spination, but the fingers are as long as the palm or much longer in *M. spinifrons,* whereas they are distinctly shorter in *M. pusilla.* The finger-to-palm ratio in 15 syntypes of the latter species ranges from 0.67 to 0.93, average 0.80; in 12 intact Floridian specimens the ratio is 0.67–0.90, average 0.79. The fingers of female *M. pusilla* are also relatively longer (average ratio 0.85) than those of males (average 0.76), which is statistically a highly significant difference ($t_{0.01[10]}$ = 3.91**).

Munidopsis kucki, new species
Fig. 3

Type material.—Delaware II cruise 84-05, sta 129, about 59 nmi NE of St. Augustine Inlet seabuoy, St. Johns County, Florida, 30°10.1′N, 80°10.4′W, 124 fm (227 m), with black coral, sponges, and alcyonarians, coll. W. Lyons, D. Camp, J. Quinn, Jr. et al., 25 May 1984, 2256–2326 hr: holotype (sex indeterminate) (USNM 234229).

Description.—Carapace dorsally covered with spinules, nearly smooth, posterior por-

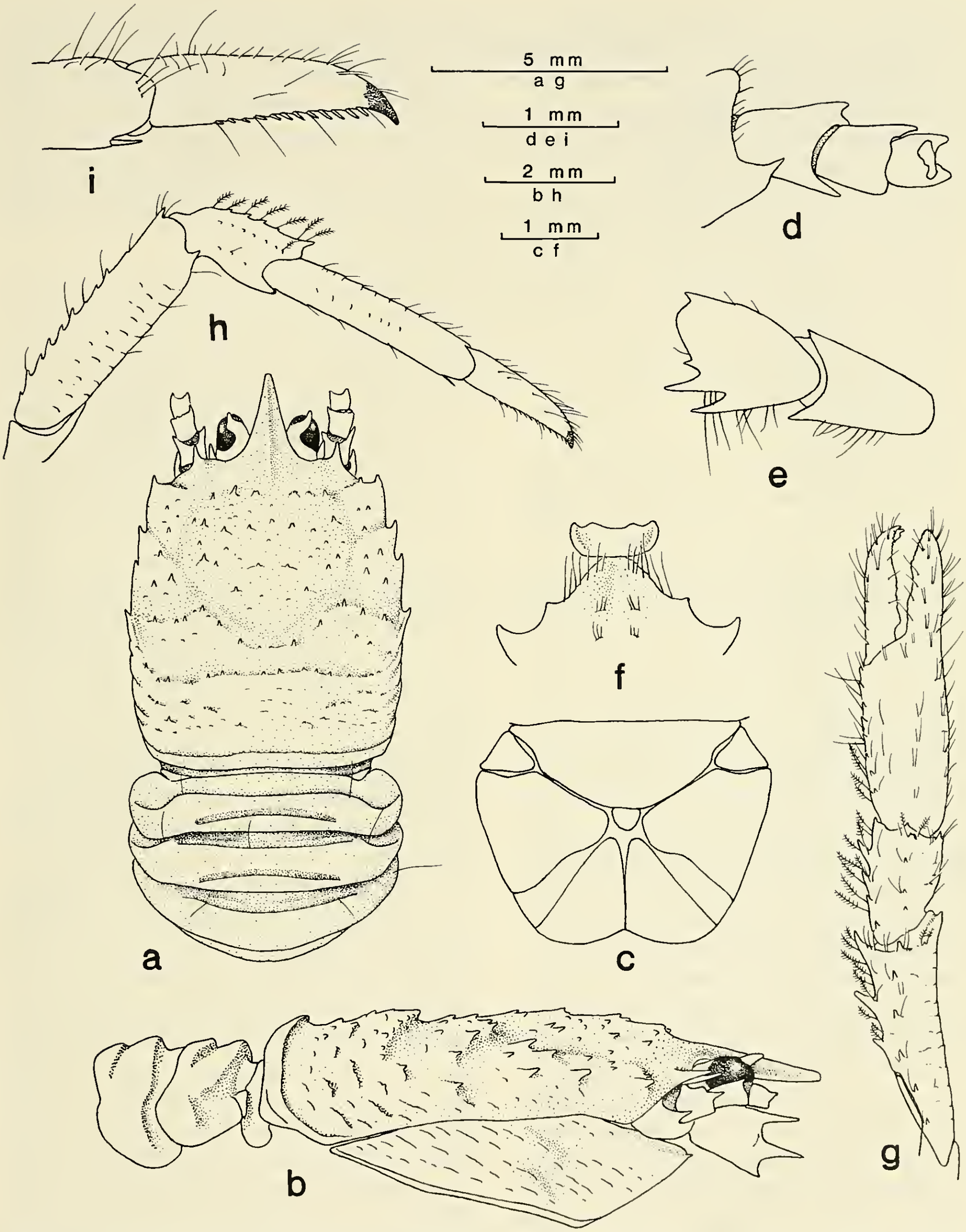

Fig. 3. *Munidopsis kucki,* new species, holotype from *Delaware II* cruise 84-05 sta 129 (USNM 234229): a, Carapace and abdomen, dorsal view; b, Same, lateral view; c, Telson; d, Left antennal peduncle; e, Merus and ischium of left third maxilliped; f, Anterior part of sternal segments; g, Right cheliped; h, Right second pereopod; i, Distal part of same.

tion sparsely covered with interrupted, reduced rugae, areas not well-delineated; gastric region convex, anterior transverse ridge of cardiac region moderately elevated. Lateral margins armed with 4 similar spines, 3 of them behind cervical groove. Front margin armed with distinct antennal spine larger than anterolateral spine. Sharp spine ventral to front margin between eyestalk and antennal peduncle. Posterior transverse ridge lacking spines, but fine denticles discernible under high magnification.

Rostrum triangular, feebly directed ventrad, dorsally carinate, 0.28 as long as postrostral carapace.

Abdomen polished, very sparsely provided with long setae; second and third segments each with 2 transverse ridges, both moderately elevated; margin of pleuron of second segment not curved dorsad. Telson divided into 8 plates.

Eyes basally relatively wide, distomesially with short, blunt eyespine; cornea wide, length more than that of peduncle.

Basal segment of antennule with 2 terminal spines, distomesially unarmed. Antennal peduncle relatively stout; first segment rounded on distomesial margin, armed with short, strong spine on distolateral margin; second segment with both distomesial and distolateral spines, distolateral larger; third segment with distomesial spine.

Ischium of third maxilliped with small distodorsal and well-developed distomesial spines; mesial ridge with 21 denticles. Merus with 3 mesial marginal spines, distalmost small, proximal 2 very strong; distodorsal margin with small, distinct spine. Anterior part of sternal segments as illustrated (Fig. 3f); third thoracic sternum relatively wide, contiguous with following sternum.

Chelipeds similar, 1.9 times as long as carapace including rostrum, somewhat massive, distally moderately depressed. Meri with 3 rows of spines: dorsal row of 6 spines, mesial row of 3 pronounced spines, ventral row of 2 (right) or 3 (left) spines; lateral margin with single distal spine. Carpal spination as illustrated (Fig. 3g), 2 ventromesial spines invisible from above. Palms medially somewhat widened, twice as long as wide, 1.3 times as long as movable finger, mesially armed with 8 (left) or 7 (right) small spines. Fingers with sinuous opposable margins, distally fitted with few intermeshing teeth when closed.

Pereopods intact, shortened posteriorly, relatively stout, sparsely setose, and ventrally polished. Dorsal margins of meri with 9 small spines on second and third pereopods, feebly cristate without distinct spines on fourth pereopod; distoventral margin produced. Carpi dorsally with 3 or 4 denticles and 1 distinct terminal spine on second and third pereopods, none on fourth pereopod. Propodi 5 times as long as wide, ventrally with 2 terminal spinelets. Dactyli relatively stout, nearly straight excepting corneous distal claw, more setose than remaining segments, ventrally with 11-13 spinelets, length more than half that of propodus.

Epipods absent from all pereopods.

Measurements.—Postorbital carapace length, 6.3 mm; length of cheliped, 15.6 mm (right).

Remarks.—The scattered dorsal spinules and four lateral marginal spines of the carapace, the dorsally carinate rostrum, the presence of an eyespine, and the absence of epipods from all pereopods, suggest a relationship of *M. kucki* with *Munidopsis sharreri,* previously known from Blake Station 134 off St. Croix, Virgin Islands, in 454 m and off Carriacou, Windward Islands, in 298 m (A. Milne Edwards & Bouvier 1897). Comparison of the present specimen from off eastern Florida with the holotype of *M. sharreri,* now deposited in the Museum of Comparative Zoology at Harvard University (MCZ 4751), disclosed that the former specimen belonged to a new species. The holotype of *M. sharreri* is now more incomplete than when it was described originally: the left posterior part of the carapace and

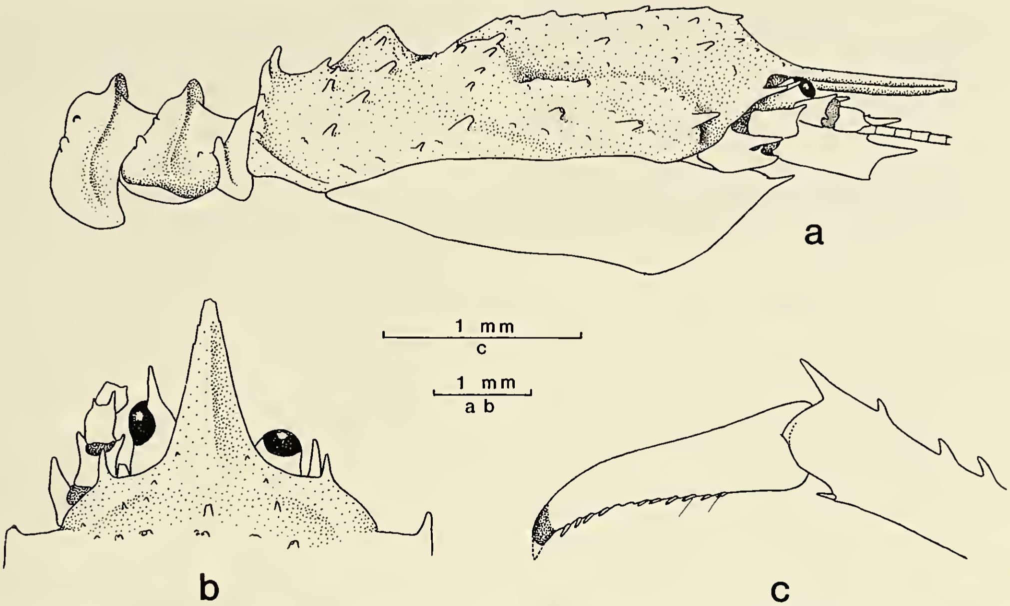

Fig. 4. *Munidopsis sharreri* (A. Milne Edwards, 1880), holotype from *Blake* sta 134 (MCZ 4751): a, Carapace and anterior part of abdomen, lateral view; b, Anterior part of carapace; c, Distal part of left pereopod (detached from body, possibly third pereopod).

telson are broken; some of the mouthparts are missing (the left third maxilliped and, with the exception of a mandible, all right appendages are lost, having been removed for examination and not replaced); both chelipeds are detached from the body, but the right one is broken, and only its chela remains in the jar; one detached left pereopod, possibly the third pereopod, is present, but the remaining pereopods are lost. The short right eye, lacking an eyespine, is abnormal, possibly regenerated.

The following characters of *M. sharreri* differentiate it from the Floridian new species (see Fig. 4): 1) The carapace has a strong cardiac elevation, a pronounced concavity between the anterior and posterior branchial regions near the cervical groove, and distinct spines on the posterior transverse ridge; 2) the second and third abdominal segments bear only one cristate transverse ridge, and the anterior pleuron is turned upward marginally; 3) the pterygostomian flap bears a very sharp anterior spine; 4) the eyestalk is relatively narrow, the eyespine is more prominent and distomesial in position, and the cornea is lateral; 5) the antennal peduncle is relatively more slender, the first segment bearing a very strong distolateral spine; 6) carpi and meri of the chelipeds are subcylindrical, more spinous, and have an additional row of lateral marginal spines; 7) meri in the following pereopods (walking legs) have ventral marginal spines, propodi bear dorsal marginal spines, and dactyli are more slender and curved.

Etymology.—It is our pleasure to name this species in honor of Hans G. Kuck, who made preliminary identifications on the majority of the crustacean material collected during the SEAMAP cruises off eastern Florida.

Acknowledgments

We thank R. W. Ingle of the British Museum (Natural History); Austin B. Williams of the National Marine Fisheries Service, Washington; and Ardis B. Johnston of the Museum of Comparative Zoology, Harvard University, for lending the type materials. Austin Williams kindly reviewed a draft of the manuscript, as did Thomas H. Perkins, James F. Quinn, Jr., and Llyn French of the Florida Department of Natural Resources.

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EVIDENCE FOR A TRANSIENT DIGESTIVE TRACT IN VESTIMENTIFERA

Meredith L. Jones and Stephen L. Gardiner

Abstract.—A medial process has been observed at the base of the branchial plume of juvenile vestimentiferans; this structure persists for only a short period in early developmental stages of the worms. In the youngest specimens observed, there is a continuity from the distal, ciliated opening of the process to a posterior basal opening. This complete apparatus appears to be the mouth-gut-anus of the Vestimentifera, heretofore not observed. The ciliated opening (mouth) of the process connects with a ciliated duct (esophagus/foregut) which, in turn, leads to the presumptive trophosome (midgut), then into a spacious, thin-walled region (hindgut) and, finally, opens to the exterior via a posterior, terminal anus. In later stages the midgut is filled with presumptive endosymbiotic bacteria; its communication with the hindgut is lost, and the anal opening disappears. In still later stages the medial process, with its oral opening, also is lost and the endosymbionts of the midgut are isolated internally in tissue that will become the trophosome; the foregut persists in later stages, even in adults, as a rudimentary strand of tissue traversing the brain. We suggest that free-living bacteria pass through the mouth of early juveniles to the midgut where they come to lodge in epithelial cells, the bacteriocytes of the future trophosome. We further suggest that the side of the worm with the medial process, the nerve trunks and a prominent vestimental ciliated field is ventral, as has been suggested previously; the side with the excretory and genital pores and the pulsatile blood vessel (heart) is dorsal. Such an orientation, coupled with the aspect of the septa and medial mesentery of the opisthosome, emphasizes more clearly the close relationship of the phylum Vestimentifera to the phylum Annelida.

Bacteria have been demonstrated in the trophosome of vestimentiferans (Cavanaugh et al. 1981, Cavanaugh 1983b) and pogonophorans (Southward et al. 1981, Southward 1982), in the ctenidia of certain bivalves (Cavanaugh 1983b) and in association with the body wall of certain marine nematodes (Ott et al. 1982), turbellarians (Ott et al. 1982) and oligochaetes (Giere 1981). These and other studies have suggested a chemoautotrophic role for these bacteria that provides or augments the nutrition of their hosts (Cavanaugh et al. 1981; Felbeck et al. 1981, 1983; Southward et al. 1981; Cavanaugh 1983b; Felbeck 1983; Fisher & Hand 1984; Dando et al. 1985). Among numerous ultrastructural and biochemical studies of the relationships of these symbionts with their hosts, however, there are few suggestions as to the source of the bacteria or how they gain access to their ultimate location in the body of the host (for extensive bibliography see Jones & Bright 1985).

It has been suggested: (1) that a possible endocytosis of bacteria into bivalve epithelia is followed by phagocytosis into vacuoles (Southward 1986); (2) that bacteria of pogonophores are probably derived from free-living species in muds of the sea bottom

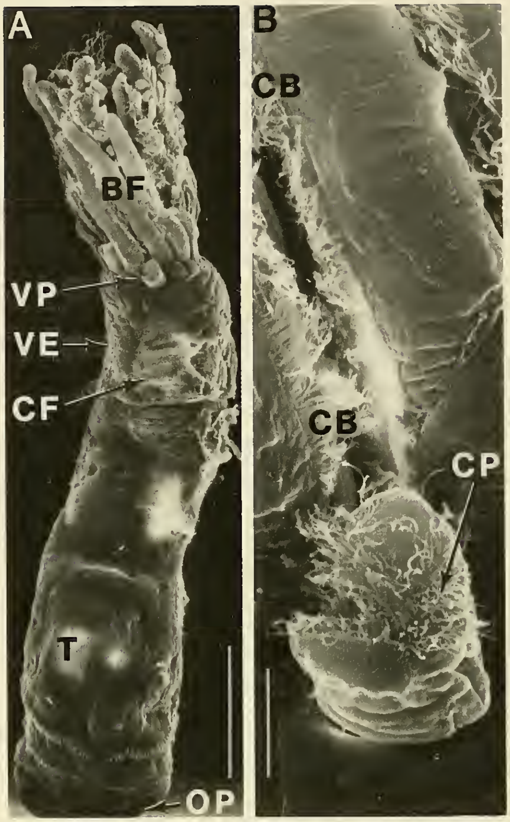

Fig. 1. *Riftia pachyptila* Jones, juvenile, SEM; *Alvin* Dive 984, Rose Garden, Galapagos Rift, 2451 m depth. A, Ventral view, showing medial process (VP) at base of branchial filaments (BF); B, Same, enlargement of medial process. Scale bars: A = 200 μm; B = 20 μm; CB, cilia of branchial filaments; CF, ciliated field; CP, cilia of process; OP, opisthosome; T, trunk; VE, vestimentum.

(Flügel & Langhof 1983); and (3) that, in the case of *Solemya reidi* Bernard, eggs of adult females are infected by bacteria. These bacteria develop in the tests of brooded larvae and following ingestion of test fragments, the larval gut degenerates at metamorphosis and releases bacteria into the hemocoel, whence they are presumed to pass to the ctenidia [this sequence of events is suggested in a dissertation by Gustafson (Reid & Brand 1986)]. Bacteria have not been observed in developing eggs of *Riftia pachyptila* (SLG, personal observations using TEM) or in developing sperm (Jones & Gardiner 1985, Gardiner & Jones 1985), suggesting that some method other than a direct parental inoculation may be operative.

In worms of the phylum Vestimentifera (Jones 1985) there is a transient access to the interior of juveniles (and larvae?) (Jones, in press). In *Riftia pachyptila* Jones, *Oasisia alvinae* Jones and juvenile vestimentiferans from Axial Seamount, Juan de Fuca Ridge (probably *Ridgeia piscesae* Jones), a medial process arises at the boundary of the obturacular (branchial) and vestimental regions on the so-called neural side (Figs. 1, 2, VP; for methods for scanning microscopy see Jones & Gardiner 1985). The process is present on specimens of *R. pachyptila* up to at least 15.5 mm total length. In larger specimens (for example, 111 mm total length) the process has disappeared.

In small juveniles of *R. pachyptila, O. alvinae* and ?*R. piscesae* the medial process possesses a ciliated aperture that leads to an internal ciliated duct; this traverses the brain and excretory organ, passes posteriorly through the vestimentum between the two major longitudinal blood vessels (Fig. 3D) and, at least in *R. pachyptila,* communicates with the trophosome via paired structures noted as trophosomal chambers (Jones, in press). In larger specimens the duct has atrophied such that its course through the excretory organ to the trophosome cannot be followed. Jones (in press) suggested that free-living bacteria from the microenvironment of the larvae/juveniles are taken up, at random, by the medial process and are transported to the presumptive trophosomal tissue via the ciliated duct; here the bacteria are acquired by putative bacteriocytes, perhaps by phagocytosis. Once associated with the internal milieu of the young *Riftia,* those bacteria that can survive do so as endosymbionts.

Examination by transmission electron microscopy (TEM; for methods see Gardiner & Jones 1985) reveals that the luminal

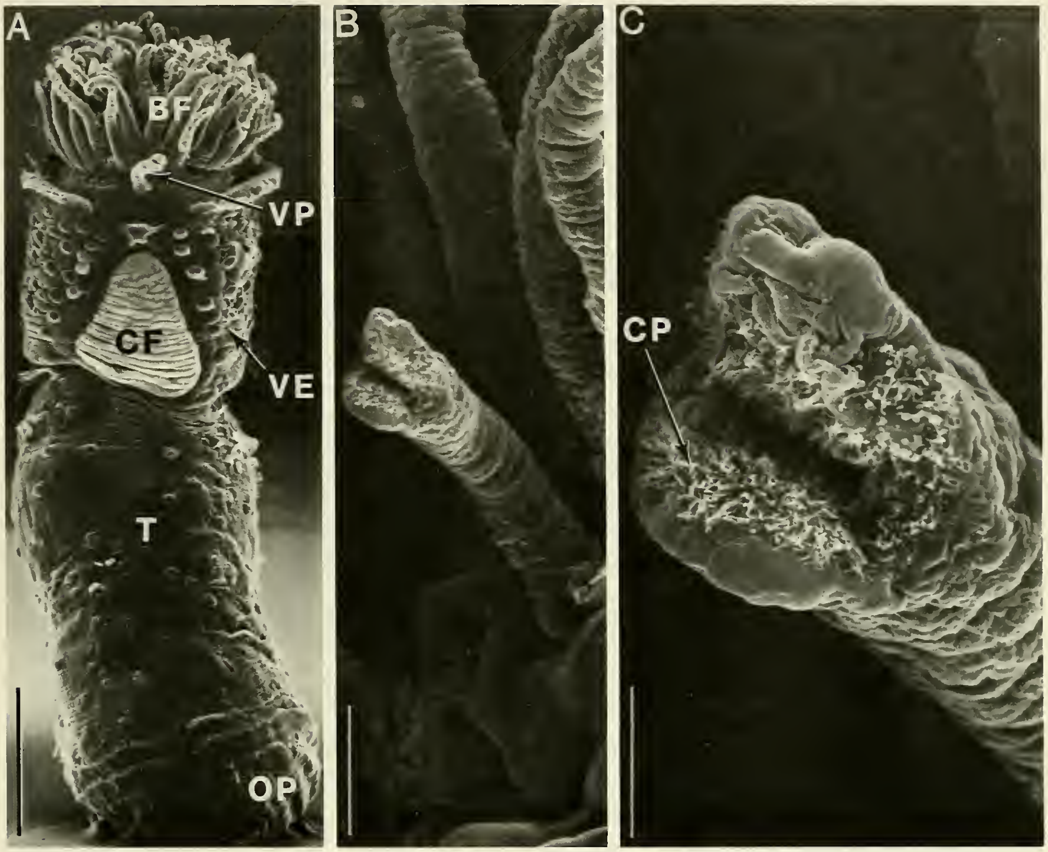

Fig. 2. ?*Ridgeia piscesae* Jones, juvenile, SEM; *Alvin* Dive 1413, Axial Seamount, Juan de Fuca Ridge, 1546 m depth. A, Ventral view, showing medial process (VP) at base of branchial filaments (BF); B, Same, enlargement of distal end of medial process; C, Same, further enlargement of medial process, showing cilia surrounding opening leading to ciliated duct. Scale bars: A = 400 μm; B = 50 μm; C = 20 μm; CF, ciliated field; CP, cilia of process; OP, opisthosome; T, trunk; VE, vestimentum.

wall of the duct in the anterior region of the vestimentum comprises at least three or four multiciliated cells about 4–5 μm in thickness (Fig. 4A). The lumen of the duct, which is obscured by cilia, is about 5–7 μm in diameter. A thin basement lamina separates the luminal wall from an outer wall that consists of approximately 10 longitudinal muscle cells (Fig. 4A, single arrow). A second basement lamina is situated between the layer of muscle cells and the epithelium of the body wall (Fig. 4A, double arrows). In the region of the brain, the duct appears somewhat triangular in shape when viewed in cross-section (Fig. 4B). However, it displays the same organization as anteriorly, except that approximately 15 muscle cells occur in the outer layer. The cells of the luminal wall display a complex pattern of interdigitation that prevents an accurate estimate of the number of cells present (Fig. 4C). As the duct passes posteriorly from the brain to the excretory organ, the outer muscular wall loses its integrity. Only the inner luminal wall remains (approximately 3.5–12 μm thick) surrounding the ciliated lumen (about 7 × 20 μm), which, in the present case, is compressed frontally (Fig. 4D).

In the course of its traverse of the muscles and connective tissue of the vestimentum,


D
DV
VV
B
P

the lumen of the duct undergoes variation in its dimensions (8 × 22 μm, 8 × 11 μm, 4 × 9 μm), as does the thickness of its wall (1–10 μm, 4.5–5.5 μm, 3–19 μm). This variation is probably an artifact of fixation, based on the compression and asymmetry of the duct lumen and duct wall. In the region of the anterior extension of the trunk and trophosome onto the vestimentum, the duct is situated between the ventral blood vessel and the well-muscularized dorsal blood vessel (Fig. 3, VV, DV). The lumen and wall of the duct appear irregular in shape. It has not yet been possible to trace the duct into the trunk region using TEM.

The bulk of the trophosome of *R. pachyptila,* and, by extension, that of other vestimentiferan species, consists of endosymbiotic bacteria in bacteriocytes (Fig. 5A). Only blood vessels and their associated muscle cells, the peritoneum of the trophosomal lobules, and the cell membranes and cytoplasm of the bacteriocytes that house the endosymbionts, are structures of the vestimentiferan host (Cavanaugh et al. 1981; Jones 1981a, b, 1984; Cavanaugh 1983a; Bosch & Grassé 1984a, b; de Burgh 1986). Plasma membranes of adjacent bacteriocytes are shown by TEM observations to have a junctional complex characteristic of those invertebrate epithelia that line outer surfaces and luminal surfaces such as gut, gonoducts, etc. (Green & Bergquist 1982, Lane et al. 1987). This complex consists of a belt desmosome (*zonula adhaerentes*) and an accompanying region of septate junction (Fig. 5B, C). The occurrence of such a junctional complex between bacteriocytes, coupled with the probability that bacteria are transported to the presumptive trophosomal tissue via a ciliated duct with an anterior external opening is suggestive of a heretofore unobserved characteristic of the Vestimentifera, that, during early development a temporary mouth and gut are present.

Early juvenile stages of vestimentiferans from the Juan de Fuca Ridge have been observed in which trophosomal bacteria are present, as well as still earlier stages in which trophosomal bacteria have not yet been acquired; in these latter stages a complete gut can be demonstrated (see below).

The distal end of the medial process is provided with a ciliated vestibule that is continuous with an internal ciliated duct passing posteriorly through the brain (Fig. 6A). Based on the extension of the external cuticular covering as a lining for the vestibule and its abrupt proximal termination (MLJ, pers. observ.), we propose that the vestibule represents the stomodeum of the developing worm and thus its mouth. Internal to the cuticular termination, epithelial cells with staining properties different from those of the vestibular epithelium, line a ciliated duct (Fig. 6B). This layer of cells, at this stage about 10 μm thick with a lumen diameter of about 12 μm, may be the beginning of the foregut (Fig. 7C, FG). The foregut passes through the brain and connects to the midgut (Fig. 7C, MG). The midgut, with a lumen diameter of about 4 μm at this stage, has a layer, from 6 to 8 μm thick, of dark-staining epithelial cells; these cells have fewer cilia than those of the foregut. The midgut leads to a spacious, thin-walled hindgut (Fig. 7C, HG), which opens externally through a posterior, terminal anus (Fig. 7A–E, A).

In later stages of development the midgut accumulates bacteria, presumably within the

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Fig. 3. *Oasisia alvinae* Jones, juvenile, TEM; *Alvin* Dive 1221, Clam Acres, 21°N on East Pacific Rise, 2618 m depth. Montage of cross-section in posterior region of vestimentum, showing ciliated duct (D) between ventral blood vessel (VV) and muscularized dorsal blood vessel (DV). Scale bar: 10 μm; B, bacteria in trophosomal lobule; P, peritoneal cell of trophosome.

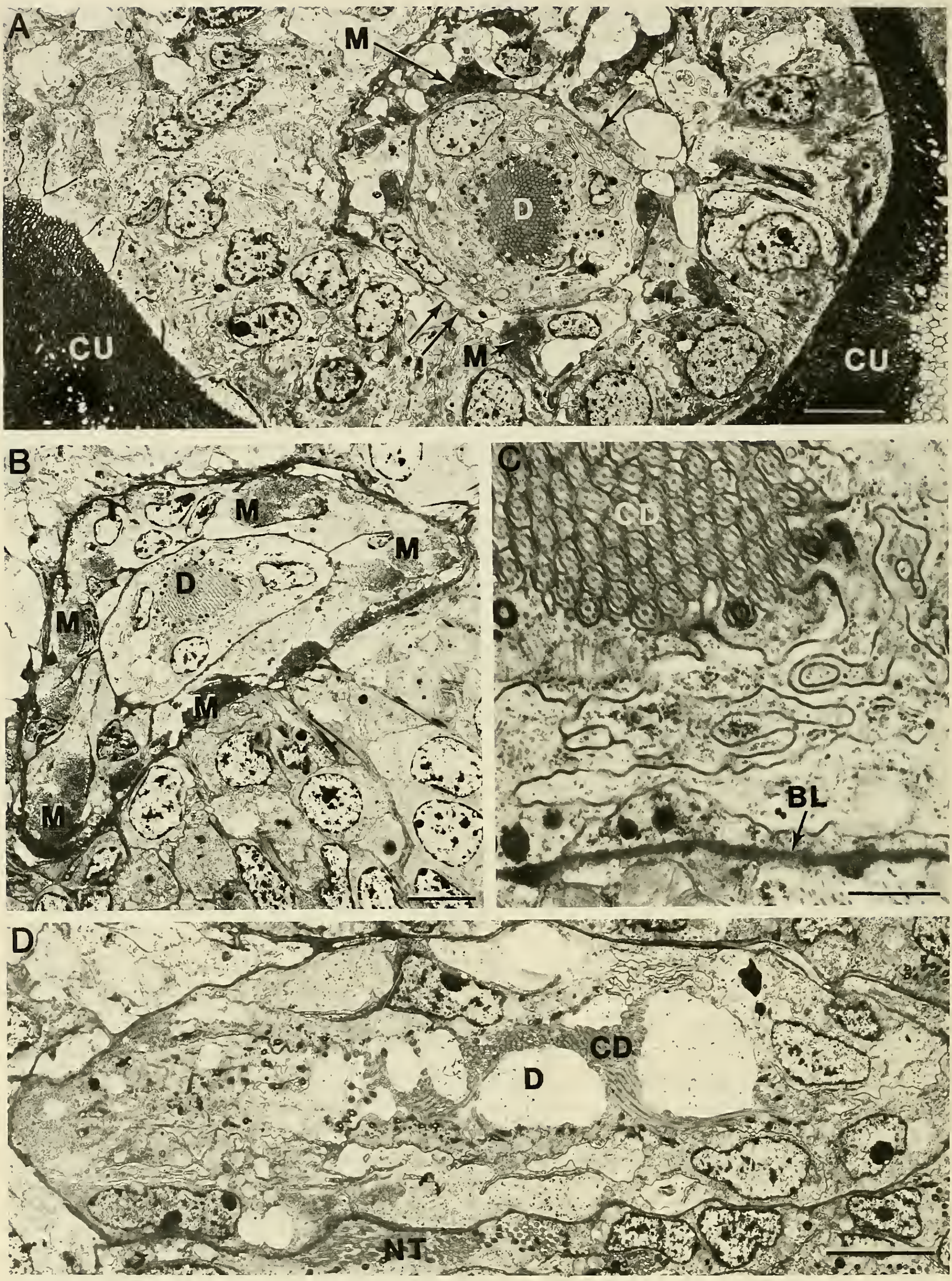

Fig. 4. *Oasisia alvinae* Jones, juvenile, TEM; *Alvin* Dive 1221, Clam Acres, 21°N on East Pacific Rise, 2618 m depth. A, Duct (D) in anterior region, showing basement lamina (single arrow) surrounding ciliated cells of

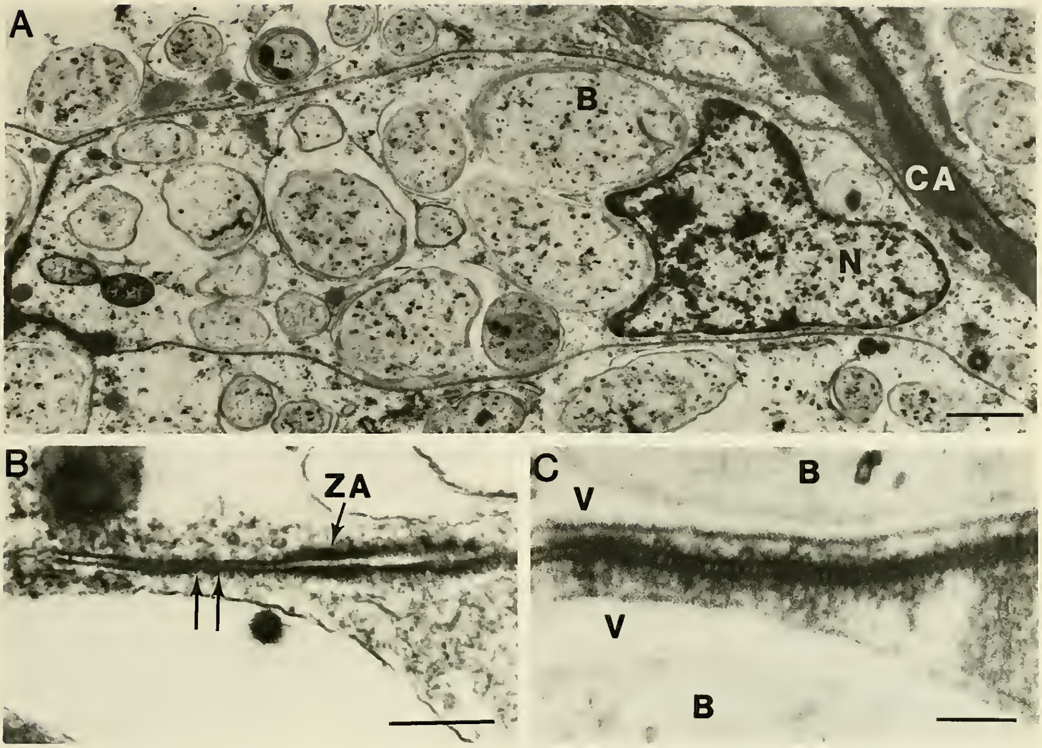

Fig. 5. *Riftia pachyptila* Jones, adults, TEM, bacteriocytes in trophosome; A, C: *Alvin* Dive 1221, Clam Acres, 21°N on East Pacific Rise, 2618 m depth; B: *Alvin* Dive 990, Rose Garden, Galapagos Rift, 2451 m depth. A, Bacteriocyte adjacent to capillary (CA). Note amount of space in bacteriocyte occupied by bacteria (B). B, Junctional complex between bacteriocytes, showing *zonula adhaerentes* (ZA) and region of septate junction (double arrows). C, Enlargement of portion of septate junction. Scale bars: A = 1 μm; B = 0.3 μm; C = 0.1 μm; N, nucleus of bacteriocyte; V, vacuole containing bacteria.

epithelial cells (Fig. 7B, TR); these cells are the original bacteriocytes of the presumptive trophosome. We postulate that the bacteria are incorporated into the bacteriocytes by phagocytosis. The later development from this original state to the well-vascularized, lobular condition of the adult trophosome is not known nor is the status of the "trophosomal chambers" found in somewhat older juveniles of *Riftia pachyptila* (Jones, in press).

The presence of a gut in juvenile vestimentiferans is anatomically and phylogenetically significant. In the past, there has

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←

luminal wall and second basement lamina (double arrows) separating layer of longitudinal muscle cells (M) from epithelium of body wall. B, Duct at level of brain. C, Enlargement of ciliated cells of luminal wall of duct, showing interdigitation of plasma membranes. D, Slightly oblique cross-section of duct in region of excretory organ (NT). Scale bars: A, B, D = 5 μm; C = 1 μm; BL, basement lamina; CD, cilia of duct; CU, cuticle of body wall.

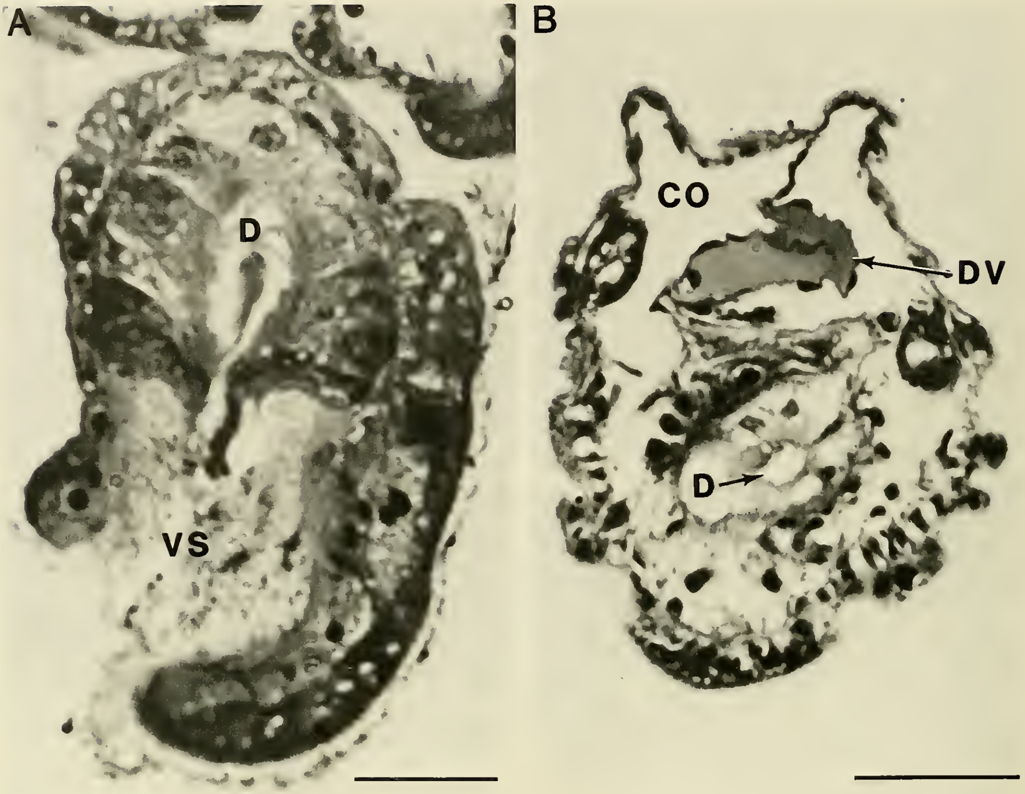

Fig. 6. ?*Ridgeia piscesae* Jones, juvenile, light micrographs of semi-thin sections (1.5 μm thick); *Alvin* Dive 1413, Axial Seamount, Juan de Fuca Ridge, 1546 m depth. A, Oblique cross-section through anterior end, showing ciliated duct (D); B, Cross-section through trunk region, showing dorsal vessel (DV) and ciliated duct (D). Scale bars: A = 20 μm; B = 30 μm; CO, coelom; VS, vestibule.

been controversy concerning the dorsal-ventral orientation of the pogonophorans and vestimentiferans (Jones 1981a). The opinion of one of us (MLJ) that "dorsal" and "ventral" of Vestimentifera (and Pogonophora) were defined by the location of a pulsatile, well-muscled blood vessel (heart) and of the nerve cord, respectively, was based on the assumption of a close affinity to the Annelida (Jones 1981a). The present observations strengthen this assumption; that is, the ciliated opening (mouth) of the medial process leads to a ciliated duct (esophagus/foregut) that passes through the brain (supraesophageal and subesophageal ganglia and commissures) and leads to the trophosome (midgut). In later stages this passage atrophies to a thin strand of tissue. This arrangement supports annelidan affinities and suggests a possible homology between bacteriocytes and the gut epithelium of a common ancestor to the Annelida and Vestimentifera. Further, the side of the animal with the medial process, the nerve cord and the extensive ciliated field of the vestimentum is ventral. Because a similar morphological arrangement has not yet been observed in the Pogonophora, their affinities and orientation remain unclear; however, we do feel that the phyla Vestimentifera and

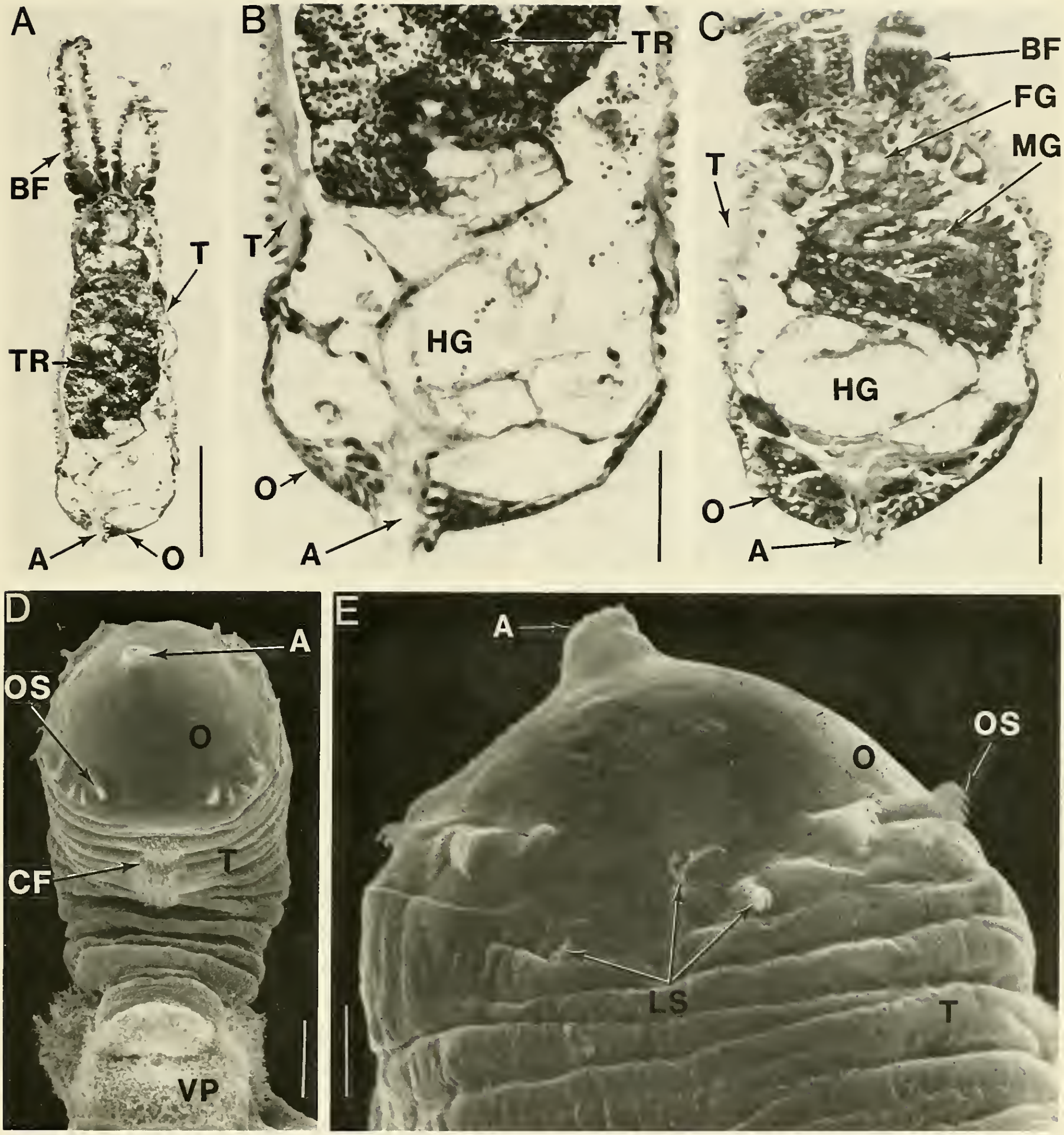

Fig. 7. ?*Ridgeia piscesae* Jones, juveniles, A–C, light micrographs of semi-thin sections (2 μm thick), D–E, scanning electron micrographs; *Alvin* Dive 1413, Axial Seamount, Juan de Fuca Ridge, 1546 m depth. A, Frontal section, showing internal organization; B, Same, enlargement of posterior region, showing presumptive trophosome (TR), hindgut (HG) and anus (A); C, Frontal section of second specimen, lacking trophosomal bacteria, showing regions of foregut (FG), midgut (MG) and hindgut (HG) and anal opening (A); D, Specimen mounted with anterior end down, ventral view; Same, lateral view of left side of opisthosomal region. Scale bars: A = 100 μm; B = 50 μm; C, D = 25 μm; E = 10 μm; BF, branchial filament; CF, ciliated field; LS, larval setae; T, trunk; O, opisthosome; OS, opisthosomal setae; VP, medial process.

Pogonophora are relatively closely related to each other and both are related to the phylum Annelida.

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We thank Cheryl F. Bright, National Museum of Natural History, for her technical assistance, insight and stimulating discussions throughout the course of this investigation. We thank J. C. Harshbarger, Registry of Tumors of Lower Animals for assistance in certain histological procedures, W. R. Brown and S. Braden, Scanning Electron Microscope Laboratory, for the operation of their equipment, both of these units being in the National Museum of Natural History, and M. Peters, Bryn Mawr College, for assistance in sectioning procedures. For material used in this study, we thank J. F. Grassle, Woods Hole Oceanographic Institution, Chief Scientist for the expedition to the Galapagos Rift in Dec 1979, Dr. A. Malahoff, University of Hawaii, Chief Scientist for the expedition to the Juan de Fuca Ridge in Jul 1984, Dr. K. L. Smith, Scripps Institution of Oceanography, Chief Scientist for the *Oasis* expedition to the East Pacific Rise at 21° North and A. Flerchinger, Smithsonian Oceanographic Sorting Center, for sorting wash-samples that contained some study materials. We thank Dr. K. Fauchald, National Museum of Natural History, for his review of the manuscript. This is Contribution No. 80 of the Galapagos Rift Biology Expedition, supported by the National Science Foundation, and a contribution of the *Oasis* Expedition.

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A NEW SPECIES OF *POGONOPHRYNE* (PISCES: ARTEDIDRACONIDAE) FROM THE SOUTH SHETLAND ISLANDS, ANTARCTICA

Richard R. Eakin

Abstract.—*Pogonophryne dewitti* is described from a 55.0 mm SL juvenile specimen collected from between 800 and 900 m in the Bransfield Strait, South Shetland Islands, Antarctica. This species belongs to the unspotted group of the genus, but is from shallower water. It is distinguished from other members of the unspotted group in having a long mental barbel (22% SL), the terminal expansion with short, rounded, unbranched processes; 18 gill rakers on the first gill arch; and about 19 tubular scales in the upper lateral line. A key to the unspotted group of *Pogonophryne* is provided.

Among the unidentified specimens of *Pogonophryne* collected by the USNS *Eltanin* from 1963–1968, two juveniles were distinguished from all other known species of the genus by the absence of any dark markings (Eakin 1977). One of these (*P.* sp. 1b, Eakin 1977) was described as a new species, *P. albipinna,* a particularly deepwater form with white fins (Eakin 1981a). The other specimen (*P.* sp. 1a, Eakin 1977) differs significantly from *P. albipinna* and is described below as a new species, *P. dewitti.* Recent collecting has yielded additional undescribed species of *Pogonophryne*; descriptions of those and a complete key to the known species of the genus will appear in a forthcoming paper (Eakin, 1987). Presented here is a key to the unspotted group to which *P. dewitti* belongs.

Measurements and counts follow those of Eakin (1977) and Eakin & Kock (1984). Measurements are presented as percentages of standard length unless otherwise indicated.

LACM refers to the Los Angeles County Museum of Natural History, Los Angeles, California. USC-*Eltanin* refers to the University of Southern California Antarctic Biological Research Program conducted aboard the USNS *Eltanin.*

Pogonophryne dewitti, new species
Figs. 1–2

Holotype.—LACM 10485-3; juvenile, 55.0 mm SL; USC-*Eltanin* sta 432, Bransfield Strait, South Shetland Islands, Antarctica (from 62°52′S, 59°27′W to 62°55′S, 59°15′W), 884–915 m; 5-foot Blake trawl; 7 Jan 1963.

Diagnosis.—This species of *Pogonophryne* is unspotted and has a long mental barbel, the terminal expansion of which is covered with short, rounded, unbranched processes.

Description.—Body stout anteriorly, tapering to caudal peduncle. Length of head 36.4; posttemporal ridges not pronounced, depth of head at this level 17.3; width of head at preoperculars 21.8. Depth of body at origin of second dorsal fin 17.3; depth of body at origin of anal fin 12.2; width of body at origin of anal fin 6.7; depth of caudal peduncle 6.9.

Snout (curve of jaws) in dorsal view slightly flattened at midline; internostril distance 8.4; length of snout 9.0; diameter of orbit 8.4; snout to orbit ratio 1.09. Interorbital region rather wide, fleshy measurement 10.0; bony measurement 6.0. Opercular-subopercular distance 14.5; snout to

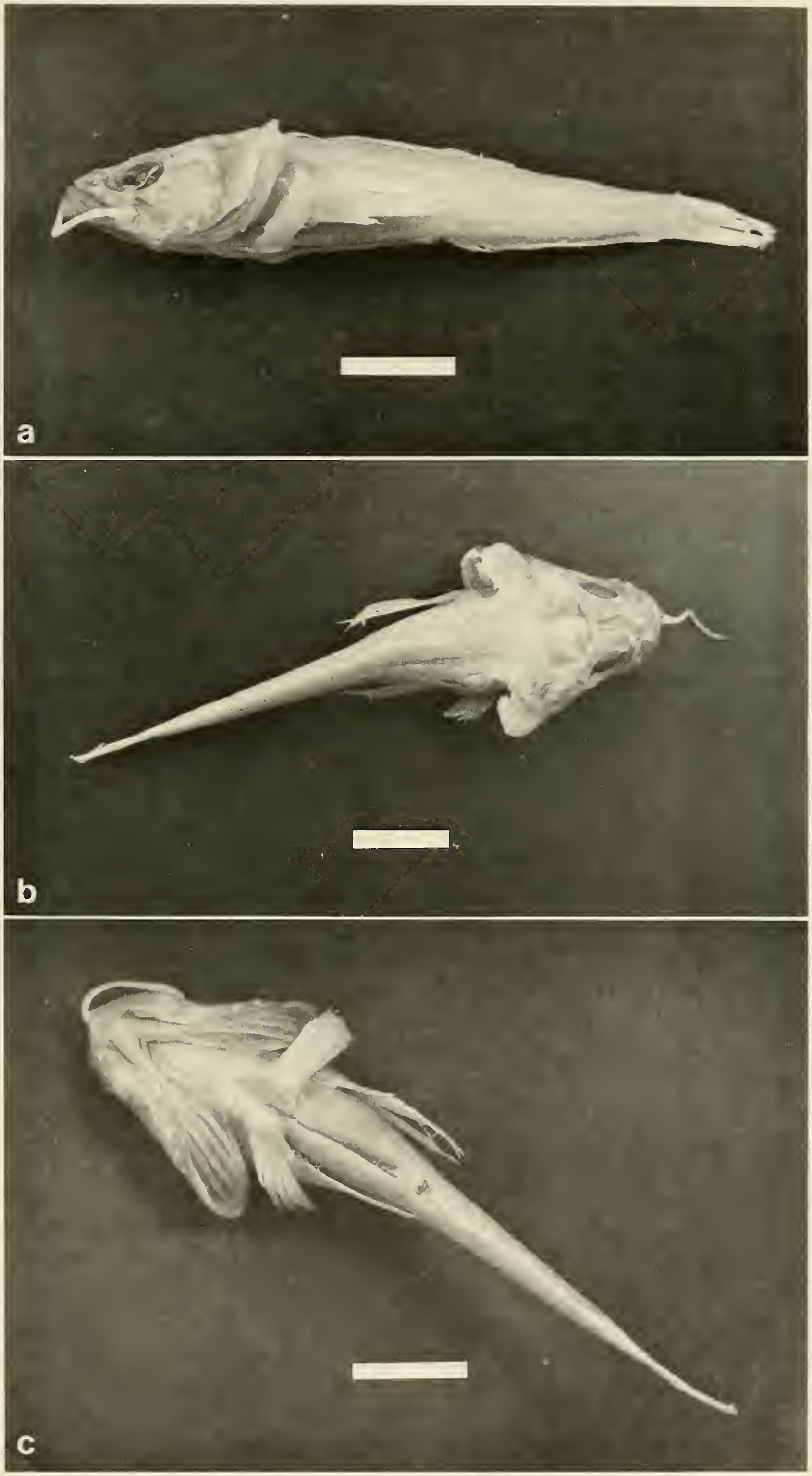

Fig. 1. *Pogonophryne dewitti,* holotype, LACM 10485-3; juvenile, 55.0 mm; a, lateral view; b, dorsal view; c, ventral view; scale = 1 cm.

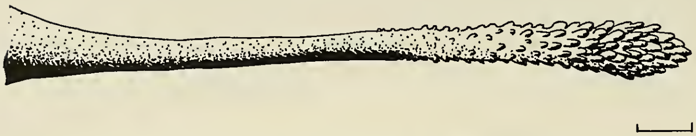

Fig. 2. Mental barbel of *Pogonophryne dewitti,* holotype; dorsal view; scale 1 mm.

opercular-subopercular ratio 0.625. Postorbital length of head 19.6. Width of jaws 18.2. Length of upper jaw 14.5; lower jaw projecting beyond upper a distance 3.0 of head length. Tooth patterns: (indistinct due to small size of specimen) upper jaw with 2 to 3 broadly curved, irregular rows of teeth (2 rows posteriorly, 2 to 3 rows near symphysis); lower jaw with 1 to 2 irregular rows of teeth in V-shaped pattern. Mental barbel very long, 22.7; terminal expansion comprising about 40% of barbel length, less than twice as wide as stalk, and covered with short, rounded, unbranched processes (Fig. 2). Anterior gill rakers on first arch 2 + 0 + 8 = 10; posterior gill rakers 1 + 0 + 7 = 8; total 18.

First antedorsal distance 34.5; second antedorsal distance 40.2; anteanal distance 61.8. Length of second dorsal-fin base 52.7; length of anal-fin base 34.0; length of caudal fin 20.0; length of pectoral fin 26.7; width of pectoral-fin base 7.3; length of pelvic fin 21.8. Interdorsal distance 5.5. First dorsal fin with two spines of equal length, 9.1. Second dorsal fin with 27 rays; length of longest (fifth) ray 12.5. Ratio of longest first dorsal-fin spine to longest second dorsal-fin ray 0.725. Anal-fin rays 17. Pectoral-fin rays 19 (left) and 20 (right). Upper lateral line with 19 pores (tubular scales) on both sides, ending under about seventeenth (left) and fifteenth (right) rays of second dorsal fin. Middle lateral line with about 17 (left) and 19 (right) disc-shaped scales; no tubular scales visible, but several posterior scales appear to be partially closed tubes. Cephalic lateral-line pores typical for *Pogonophryne*: preoperculo-mandibular canal with 9 pores; infraorbital canal with 7 pores; supraorbital canals with 2 nasal pores, 2 interorbital pores, and 1 unpaired coronal pore; temporal canal with 6 pores; and supratemporal canal incomplete across occiput (one pore on each side). Vertebrae 15 + 22 = 37.

Color.—Head, body, and fins, in alcohol, uniform yellowish brown with no dark markings (under magnification, very small brown pigment spots covering most of head and body visible).

Etymology.—I take pleasure in naming this species for Hugh H. DeWitt who not only provided the specimen but who has for many years contributed immeasurably to our knowledge of Antarctic fishes. He has inspired and guided me in my ichthyological research since my graduate study in his laboratory at the University of Maine.

Remarks.—This species, without dark markings and having relatively high numbers of vertebrae (37) and second dorsal-fin rays (27), belongs to the unspotted group together with *P. albipinna* (Eakin, 1981a) and *P. immaculata* (Eakin, 1981b). It differs from these species, however, in having been collected at a relatively shallow depth (less than 1000 m vs. about 1500 m for *P. albipinna* and 2500 m for *P. immaculata*). It is represented only by the juvenile holotype collected in the South Shetland Islands.

Key to the Unspotted Species of *Pogonophryne* Regan

1. Head and body with dark markings .... spotted groups
– Head and body without dark markings 2
2. Fins light in color; first gill arch with total of 18–21 gill rakers; jaw width about 18% SL 3
– Fins dark basally, light distally; first

gill arch with total of 12 gill rakers; jaw width about 25% SL .... *P. immaculata* Eakin, 1981

3. Fins largely white; first gill arch with total of 21 gill rakers; upper lateral line with about 12 pores (tubular scales); mental barbel about 17% SL, terminal expansion about three times as wide as stalk; deepwater form (greater than 1500 m) .... *P. albipinna* Eakin, 1981

– Fins not white; first gill arch with total of 18 gill rakers; upper lateral line with about 19 pores (tubular scales); mental barbel about 22% SL, terminal expansion about twice as wide as stalk; not a deepwater form (less than 1000 m) ....*P. dewitti* n. sp.

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ROBINSICHTHYS ARROWSMITHENSIS, A NEW GENUS AND SPECIES OF DEEP-DWELLING GOBIID FISH FROM THE WESTERN CARIBBEAN

Ray S. Birdsong

Abstract.—*Robinsichthys arrowsmithensis* is described from Arrowsmith Bank in the western Caribbean. The genus is among the deepest dwelling gobiids with some specimens taken below 240 m. The diagnostic characters and monophyly of the tribe Gobiosomini are discussed. *Robinsichthys* is assigned to the Gobiosomini; however, its relationship to other gobiosominines is unclear.

The difficulty and expense of collecting on deep, rough-bottom habitats makes their faunas among the most poorly known in the sea. In 1967–1968, the University of Miami research vessels R/V *John Elliott Pillsbury* and R/V *Gerda* made two brief collecting forays, comprising five 3 m otter-trawl stations, in depths ranging from about 90 to 585 m on Arrowsmith Bank. The bank, a submarine prominence northeast of the island of Cozumel off the coast of Yucatan, is centered at approximately 21°05′N, 86°30′W. Along its western margin, the bank drops precipitously from depths of approximately 20 m to over 4000 m in the adjacent Yucatan Channel. The waters are of tropical oceanic clarity and it is apparent that the live-bottom habitat extends to a considerable, but undetermined, depth. The limited material obtained includes an unusually large proportion of undescribed or poorly known species of fishes, crustaceans, and mollusks. Among the fishes collected was the gobiid, *Robinsichthys arrowsmithensis,* herein described as new.

Methods and materials.—Counts and measurements were made following Böhlke & Robins (1968) except as noted. Measurements are straight-line distances made with an ocular micrometer and converted to the nearest 0.1 millimeter. Morphometric data are presented in thousandths of standard length (SL). Gill-raker counts are from the first ceratobranchial plus first epibranchial. Vertebral counts, spinous dorsal-fin pterygiophore formulae (DF), and number of anal pterygiophores preceding the first haemal spine (AP) were determined from radiographs or cleared and stained material and follow the conventions and notational procedures of Birdsong et al. (1988). Institutional abbreviations used are: UMML, University of Miami, Rosenstiel School of Marine and Atmospheric Sciences; USNM, National Museum of Natural History, Washington, D.C.

Robinsichthys, new genus

Diagnosis.—Vertebrae 11 + 17 = 28; 7 spinous dorsal-fin pterygiophores, the last with or without a spine; cephalic lateralis pores absent; pelvic fins separate to base, rays branched with fifth ray longest; caudal fin with hypurals 1–2 fused to each other but free from hypurals 3–4 and the terminal vertebral element; one epural; body scaled posterior to pectoral axil with 25–28 caducous scales; caudal fin with at least one highly modified scale (Fig. 1) on base of upper primary rays, lower base probably also with a modified scale but none remain in the specimens; two anal pterygiophores preceding first haemal spine (vertebra 12); epipleural ribs present on vertebrae 1–9, pleural ribs on vertebrae 3–10; metapterygoid

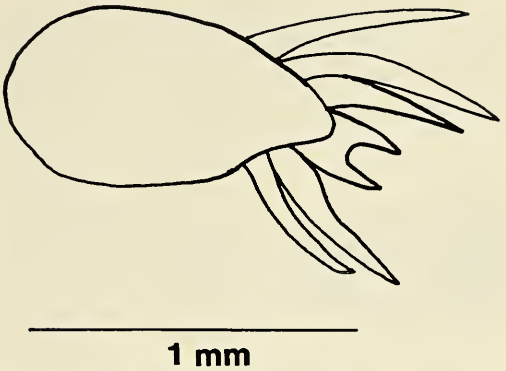

Fig. 1. Modified basicaudal scale of *Robinsichthys arrowsmithensis*; ctenii oriented posteriad.

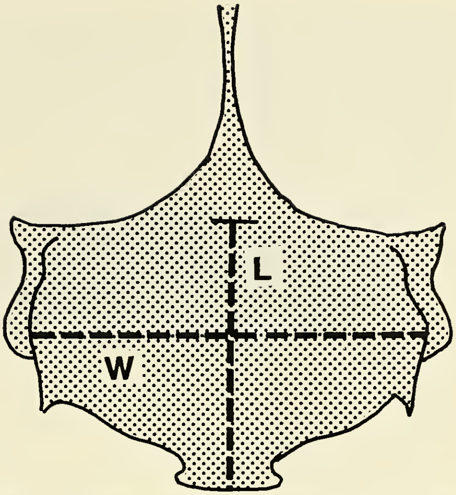

Fig. 2. Diagrammatic dorsal view of the brain case of *Robinsichthys arrowsmithensis* illustrating the measurements used in calculating the length/width ratio; anterior toward the top.

separated from quadrate by cartilage, not anteriorly expanded; ossified basihyal spatulate with anterolateral cartilagenous extensions making tongue emarginate; all vertebrae with reduced neural arches that lack lateral foramina; brain case broad, length/width approximately 0.7 (Fig. 2); frontals very narrow between orbits; both nostrils opening at the ends of short tubes; upper lip with free dorsal margin. The genus is further characterized by those features given below for *R. arrowsmithensis,* the single included species and type by monotypy and original designation.

Etymology.—In recognition of his many contributions to our knowledge of American gobies, the generic name is derived from the surname of C. Richard Robins and *ichthys*. The gender is masculine.

Robinsichthys arrowsmithensis, new species

Figs. 1–3, Tables 1–3

Holotype.—USNM 290207, male (21.8 mm SL), 21°02′N, 86°26′W, R/V *Gerda* sta 952, beginning depth 586 m, ending depth 92 m, 28 Jan 1968.

Paratypes.—USNM 290208, male (22.4 mm SL) and female (20.4 mm SL), same data as holotype; UMML 34393, female (23.2 mm SL), 20°59′N, 86°24′W, R/V *Gerda* sta 897, beginning depth 293 m, ending depth 210 m, 10 Sep 1967; UMML 34392, two females (23.5 mm SL, cleared and stained, and 15.2 mm SL), 21°10′N, 86°21′W, R/V *Gerda* sta 893, beginning depth 242 m, ending depth 320 m.

Description.—In addition to those characteristics given for the genus, the species is characterized by: 6 or 7 spines in the D_1 and spinous dorsal-fin pterygiophore formula of 3-22111*0 (holotype and one paratype), 3-221110 (two paratypes), and 3-22111*00 (one paratype); D_2 = I,10 (I,9 in one specimen); A = I,10 (I,9 in one specimen; P_1 = 21–24 (usually 22–23); P_2 rays with moderately enlarged tips in holotype but not apparent in other specimens; caudal fin with 31–33 total rays, 9/8 or 8/8 segmented rays, 7/7, 8/7, or 8/8 procurrent rays; gill rakers 9+1; gill opening extending from upper pectoral base ventrally to point below posterior preopercular margin; teeth caninoid, in two rows in both jaws; lower jaw with outer row comprising 4–7 slightly enlarged, anteriorly placed teeth, inner row comprising about 40 smaller teeth; upper jaw with outer row comprising about 20

Fig. 3. Holotype of *Robinsichthys arrowsmithensis,* USNM 290207, male, 21.8 mm SL.

slightly enlarged, widely spaced teeth, inner row of about 60 smaller teeth; sensory papillae pattern too damaged to be described.

Individual morphometric data given in Table 2. Average values in thousandths of SL are: head length 333; snout length 70; eye diameter 106; interorbital distance 15, upper jaw length 138; P_1 length 244; P_2 length 190; caudal-fin length 234; longest D_1 spine (the second) 185; greatest body depth 176.

The following description of the pigmentation pattern of alcohol preserved specimens is based on photographs of the holotype (Fig. 3) and two paratypes taken a few months after capture. The material is now faded such that little of the pattern remains. Ground color pale with the pattern formed by concentrations of large discrete melanophores in varying densities. Body and caudal-fin base marked by four vertical, dusky bars; anterior bar the most prominent and extends dorsad from the belly to the D_1 and well onto dorsal spines 4–6 or 7; second bar extends from the anal-fin origin onto the anterior rays of the D_2 fin; third bar, the least conspicuous of the four, extends from the area just above the anal-fin terminus onto the posterior rays of the D_2 fin; posteriormost bar lies on the caudal-fin base, with some melanophores extending anteriad onto the caudal peduncle, especially along the midline. On the dorsum, between the vertical bars, lie a series of dusky blotches or saddles that extend onto the dorsal fins. These saddles located as follows: one at the D_1 terminus, one at the middle of D_2 base, and two (the two coalesced in the holotype) on the dorsal surface of the caudal peduncle. Venter along anal-fin base bears scattered melanophores.

Ventral rays of caudal fin dusky, espe-

Table 1.—Frequency distribution of meristic features in *Robinsichthys arrowsmithensis.*

	Lateral scale pockets				D_2 elements		Anal elements		P_1 elements (left and right)			
Count	25	26	27	28	9	10	9	10	21	22	23	24
Number of specimens	2	1	1	1*	1	5*	1	5*	2	4*	5*	1

* Condition in holotype.

Table 2.—Morphometrics of *Robinsichthys arrowsmithensis.* Standard lengths expressed in mm, other measurements in thousandths of standard length.

	USNM 290207*	USNM 290208	USNM 290208	UMML 34393	UMML 34392	UMML 34392
Sex	M	M	F	F	F	F
Standard length (mm)	21.8	22.4	20.4	23.2	15.2	23.5
Head length	316	321	320	333	370	340
Snout length	63	62	72	79	73	—
Eye diameter	105	107	99	107	103	115
Interorbital distance	12	16	14	16	18	—
Upper jaw length	139	132	131	147	158	123
P_1 length	270	226	—	—	242	238
P_2 length	186	173	158	187	224	209
Caudal-fin length	234	—	—	—	—	—
Longest D_1 spine	186	210	171	187	170	—
Greatest body depth	177	181	180	171	170	—

* Holotype.

cially near their tips, and dorsal half of caudal fin bears two dark slashes. Anal fin dusky along the distal margin and pelvic fins uniformly dusky.

Head has triangular dusky blotch below the eye (the apex pointing ventrad) and scattered melanophores along the margin of the upper lip. Operculum bears large, widely spaced melanophores that extend ventrad onto the branchiostegal membranes, dorsad across the nape, and posteroventrad to the pectoral axil.

Etymology.—The specific epithet, *arrosmithensis,* is taken from the name of the type locality in the western Caribbean, Arrowsmith Bank.

Discussion.—The affinities of *Robinsichthys,* though enigmatic, clearly lie with the American seven-spined gobies. Birdsong (1975) proposed the Tribe Gobiosomini to encompass the American seven-spined gobies and several apparently allied genera also endemic to the New World, to wit, *Aruma, Barbulifer, Bollmannia, Chriolepis, Eleotrica, Enypnias, Evermannichthys, Ginsburgellus, Gobiosoma* (including *Elacatinus* of some authors), *Gobulus, Gymneleotris, Microgobius, Nes, Palatogobius, Pariah, Parrella, Psilotris, Pycnomma, Risor,* and *Varicus.* The primary characters used to unite these endemic American genera were a DF of 3-221110 (in all but *Evermannichthys, Pariah,* and *Risor*), an uncommon vertebral count of 11+16−17 (in all but *Evermannichthys* and *Pariah*), and the fusion of hypurals 1–2 with hypurals 3–4 and the terminal vertebral element (in all but *Bollmannia, Microgobius, Palatogobius,* and *Parrella*). Subsequently, Hoese (1976) allied the monotypic Chilean genus *Ophiogobius* on the basis of overall similarity. *Ophiogobius* has the typical hypural fusion of the group but is divergent in DF (3-2211110 or 3-2121110) and in vertebral number (13+18−19).

Birdsong et al. (1988) inferred that the Gobiosomini, as originally conceived, was not monophyletic. However, a subset, referred to by them simply as the "Gobiosoma Group," and including *Ophiogobius* but excluding *Bollmannia, Microgobius, Palatogobius,* and *Parrella* was hypothesized as monophyletic based on the unusual hypural fusion. Among gobiids (sensu Hoese 1984) a similar hypural fusion is known to occur only in the Indo-Pacific six-spined genera *Eviota, Gobiodon, Gobiopterus, Kelloggella, Monishia,* and *Trimmatom,* all

Table 3.—Comparison of *Robinsichthys* with phenetically similar genera.

Character	*Robinsichthys*	*Chriolepis*	*Varicus*	*Pycnomma*	*Parrella*	*Palatogobius*	*Microgobius*
D_2	9–10	10–12	9–12	10–11	11–12	19–20	14–21
Anal fin	9–10	10–11	8–11	9–10	12–13	20	14–22
Vertebrae	11+17	11+16	11+16	11+16	11+16	11+16	11+16
AP	2	2*	1*	2	2	2	2
Hypural fusion	absent	present	present	present	absent	absent	absent
Neural arches	reduced	normal	normal	normal	normal	normal	normal
Vomerine teeth	absent	absent	absent	absent	absent	present	absent
Cephalic LL pores	absent	absent	absent	present	present	present	present
Pelvic fins	separate	separate	separate	separate	united	united	united
Modified basicaudal scales	present	present	present	present	absent	absent	absent

* Condition of the type species.

probably unrelated to the Gobiosomini. The four excluded genera were sequestered as the "Microgobius Group" and were only phenetically associated on the basis of DF and vertebral osteology.

Despite the comments of Birdsong et al. (1988), and at the risk of appearing to argue with myself, I remain convinced of the validity of the Gobiosomini, including the "Microgobius Group" and *Robinsichthys,* even though it is supported by the single synapomorphy, DF = 3-221110, a character in which *Robinsichthys* shows some variation and four genera (*Evermannichthys, Ophiogobius, Pariah,* and *Risor*) display divergent autapomorphous conditions probably derived from 3-221110. This pterygiophore pattern is known outside the group only in the monotypic Philippine genus *Tukugobius,* a genus that appears unrelated on the basis of most other characters.

The preceding resumé has been presented to provide the required background for comments on the relationships of *Robinsichthys. Robinsichthys,* like the "Microgobius Group," lacks the diagnostic hypural fusion found in all other Gobiosomini, but in the possession of modified basicaudal scales it resembles the "Gobiosoma Group" (Table 3). Many species scattered among at least seven genera of the "Gobiosoma Group" have modified basicaudal scales, whereas none in the "Microgobius Group" do. Additionally, such scales are not present in any other gobioids and I, therefore, consider them to be apomorphic within some subset of the Gobiosomini. The value of the character in establishing relationships within the tribe is diminished, however, by the apparent independent loss of the scales in a number of species and genera.

Excepting the absence of hypural fusion (which may represent a reversal), *Robinsichthys* is most similar overall to the "Gobiosoma Group" genera *Chriolepis, Varicus,* and *Pycnomma.* The limits of *Chriolepis* and *Varicus* are poorly defined and, as noted by Birdsong et al. (1988), it is likely that both genera are polyphyletic. *Robinsichthys* shares with *Varicus* and *Chriolepis* the absence of cephalic lateralis pores and canals, and with these two genera plus *Pycnomma,* the loss of a pelvic frenum and the loss or near loss of a membrane uniting the inner pelvic rays, the presence of modified basicaudal scales, and the absence of a quadrate process on the metapterygoid. Also, expanded pelvic-ray tips, present in the holotype of *R. arrowsmithensis,* are known among the Gobiosomini only in *Varicus. Robinsichthys, Chriolepis,* and *Varicus* are among the deepest dwelling gobies, each having some species recorded below 175 m. The similarities exhibited may represent convergent adaptations to a deep habitat and, thus, carry no phylogenetic information.

The reduction of the neural arches in *Robinsichthys* appears to be an autapomorphy. Such reductions are common in fishes and have been noted by Pezold (pers. comm.) in several oxudercine and gobionelline genera of gobies, two groups that do not appear to be closely related to the Gobiosomini. A survey of some 75 species representing all other genera of Gobiosomini has failed to find a similar condition in any of them.

In the possession of modified basicaudal scales and the lack of fusion of hypurals 1–2 with 3–4 and the terminal vertebral element, *Robinsichthys* appears to bridge the gap between the "Gobiosoma Group" and the "Microgobius Group" of Birdsong et al. (1988). However, the loss of cephalic lateralis pores, lack of fusion of the pelvic fins, and reduction of the neural arches are all apomorphic states within the Gobiosomini thus rendering *Robinsichthys* an unlikely candidate as the sister group of any large portion of the "Gobiosoma Group." If the lack of hypural fusion prepresents a reversal, it seems likely that the closest relatives of *Robinsichthys* will be found among those species presently assigned to *Varicus* or *Chriolepis*.

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MINIATURIZATION IN SOUTH AMERICAN FRESHWATER FISHES; AN OVERVIEW AND DISCUSSION

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Abstract.—Miniature species within the South American freshwater fish fauna are listed and their phylogenetic and ecological distribution is analyzed. Criteria used in identifying miniature South American freshwater fishes are briefly discussed and eighty-five such fishes of five ordinal groups, Clupeiformes, Characiformes, Siluriformes, Cyprinodontiformes and Perciformes, are listed. Approximately eighty-eight percent of these miniatures are characiforms and siluriforms, all primary division ostariophysan fishes. Phylogenetic information on the relationships of these miniatures indicates that such species have arisen in the freshwaters of South America about sixteen times within the Characiformes, twelve in Siluriformes, four in the Cyprinodontiformes and once each in the Clupeiformes and Perciformes. Miniatures of most groups occur in lentic or slow-flowing waters, but the one pimelodid and some trichomycterid catfish miniatures are cryptobenthic in swift-flowing streams.

Resumo.—Peixes miniatura de água doce da América do Sul são definidos e uma lista contendo 85 espécies miniatura, pertencentes â cinco diferentes ordens de teleósteos, é fornecida. Peixes miniatura de água doce sul americanos são arbitrariamente definidos como aqueles que, até onde se sabe, não excedem 26 milímetros de comprimento padrão, sendo que a maioria atinge a maturidade sexual com menos de 20 milímetros de comprimento padrão. As espécies incluídas entre estes limites tem em comum vários caracteres pedomórficos (redutivos) quando comparadas com táxons relacionados. Duas espécies miniatura são conhecidas dentre os Clupeiformes, 49 dentre os Characiformes, 26 dentre os Siluriformes, cinco dentre os Cyprinodontiformes e três dentre os Perciformes. Aproximadamente 88% destes peixes miniatura são Ostariophysi da divisão primária.

A informação disponível sobre as relacões filogenéticas da maioria dos peixes miniatura é de qualidade questionável; no entanto, nós provisoriamente estimamos que espécies miniatura surgiram independentemente pelo menos 34 vezes na fauna de peixes de aqua doce da América do Sul; 16 dentre os Characiformes, 12 dentre os Siluriformes, quatro dentre os Cyprinodontiformes e uma única vez dentre os Clupeiformes e dentre os Perciformes.

A informação sobre a ecologia de peixes miniatura é também escassa mas, como seria de se experar no caso de peixes diminutos, a maioria ocorre em aguas lênticas ou de fluxo lento. No entanto, um pimelodídeo miniatura e alguns tricomicterídeos miniatura são criptobênticos em riachos de fluxo rápido.

The South American freshwater fish fauna is one of the most diverse in the world, with numerous species unknown to science being continually discovered, and a large percentage of the fauna still undescribed (Böhlke et al. 1978). The early collectors and researchers engaged in studies of the ichthyofauna of that continent failed to appreciate the degree of this diversity, particularly among smaller species, and as a consequence often focused on the more obvious species of larger adult body size (Myers 1947: 13–14). Subsequent research by various authors has resulted in a better appreciation of the large number of species of smaller body size, but it is only in the last few decades that a number of species of very small size as adults have been described. The pace of description of such miniature species has quickened in the last decade and recent collecting efforts in various regions of South America revealed the existence of many interesting miniature species (Stewart 1985, 1986; M. Weitzman 1985; Weitzman & Fink 1985; Géry & Uj 1986; Weitzman 1986, 1987; Fernandez & Weitzman 1987; Weitzman & Vari 1987). The comparative studies associated with the description of some of those species (Weitzman & Vari 1987) disclosed that the number of miniature species is much greater than commonly recognized. Indeed, during the twelve decades that have passed since the Thayer Expedition about 85 freshwater South American species (Table 1) that are miniature as adults, or not known to exceed 25 to 26 mm in standard length in nature, have been described from the freshwaters of South America.

In the present paper we discuss the phylogenetic distribution of miniatures in the Neotropical freshwater ichthyofauna, and provide an estimate of the number of miniaturization events within this fauna. The available information on the ecology of South American miniature fishes is summarized, and we evaluate a previous concept of the predominance of secondary freshwater fishes among the miniature species known from South American drainages.

Miniature Fishes in South American Freshwaters

The range in body sizes among fishes, bony and cartilaginous, is remarkable, covering the spectrum from diminutive fishes under 26 mm standard length (SL), such as those discussed in this paper, to species such as the whale shark which achieves lengths of over 12 m and possibly up to 21.4 m (Campagno 1981). Whereas the larger species of fishes are typical of open waters, particularly in marine environments, smaller species, especially miniatures, are usually, although not exclusively, associated with more complex substrates and ecosystems. This correlation is reflected in the ichthyofaunas of South American streams and rivers, and of Indo-Pacific coral reefs, which are the most diverse in the freshwater and marine environments respectively. Correlated with that high species diversity is the presence in those habitats of a large number of species of small fishes of approximately 25 to 70 or 80 mm SL as adults, together with many miniature species. In Table 1 we list 85 nominal species not known to exceed 26 mm SL, many of which are known to mature at under 20 mm SL. These are considered to be miniature fishes in this paper. Although the term "miniature" implies a very small body size, our primary criterion for distinguishing miniature fishes is not solely size related. Rather it involves the presence in such miniatures of a large number of apparently paedomorphic morphological features including the degree of development of the laterosensory canal system of the head and body, reductions in the number of fin rays and body scales, and a diminution of the sculpturing on the surface bones of the head. Such paedomorphic features in fishes are commonly referred to as reductive in the systematic ichthyological literature and are considered to be due to

Table 1.—Miniature Neotropical freshwater fishes arranged by order, family and some cases by subfamilies and tribes following sequence of discussion in text. Species arranged alphabetically within families, subfamilies or tribes. Maturity is given as minimum known body length at maturity. Maximum is maximum known body length.

Name, author, date	Maturity	Maximum	Reference
Clupeiformes			
Engraulidae			
Amazonsprattus scintilla Roberts, 1984	19.0	19.5	Roberts 1984:318
Anchoviella manamensis Cervigón, 1982	17.5	25.0	Cervigón 1982:220
Characiformes			
Lebiasinidae			
Nannostomus anduzei Fernandez & Weitzman, 1987	11.2	16.2	Fernandez & Weitzman 1987:165
Nannostomus marginatus Eigenmann, 1909	17.0	23.0	Weitzman & Cobb 1975:25
Nannostomus minimus Eigenmann, 1909	16.0	23.0	Weitzman & Cobb 1975:21
Characidae			
Characinae			
Priocharax ariel Weitzman & Vari, 1987	11.8	17.1	Weitzman & Vari 1987:642
Priocharax pygmaeus Weitzman & Vari, 1987	?	16.4	Weitzman & Vari 1987:642
Glandulocaudinae			
Iotabrycon praecox Roberts, 1973b	14.2	21.8	Weitzman & Fink 1985:105
Scopaeocharax atopodus (Böhlke, 1958)	17.8	22.0	Weitzman & Fink 1985:107
Scopaeocharax rhinodus (Böhlke, 1958)	19.2	25.0	Weitzman & Fink 1985:107
Tyttocharax cochui (Ladiges, 1950)	<16.0	22.0	Ladiges 1950:308; Weitzman & Fink 1985:108, 110
Tyttocharax madeirae Fowler, 1913	13.5	17.5	Weitzman & Fink 1985:108
Xenurobrycon heterodon Weitzman & Fink, 1985	13.6	20.1	Weitzman & Fink 1985:88, Weitzman 1987:113
Xenurobrycon macropus Myers & Ribeiro, 1945	12.0	19.8	Weitzman & Fink 1985:7, 75
Xenurobrycon polyancistrus Weitzman, 1987	11.0	13.1	Weitzman 1987:113
Xenurobrycon pteropus Weitzman and Fink, 1985	13.5	13.8	Weitzman & Fink 1985:85
Tetragonopterinae			
Axelrodia lindeae Géry, 1973	?	20.6	Géry 1973:111
Axelrodia riesei Géry, 1966	?	16.7	Géry 1966:112
Axelrodia stigmatias (Fowler, 1913)	?	20.5	Géry 1966:117
Cheirodon luelingi Géry, 1964	?	17.6	Géry 1964:19
Hemigrammus iota Durbin, 1909	?	21.0*	Durbin 1909:60
Hyphessobrycon amandae Géry & Uj, 1986	16.0	19.5	Géry & Uj 1986:59
Hyphessobrycon catableptus (Durbin, 1909)	?	18.0*	Durbin 1909:55
Hyphessobrycon diancistrus Weitzman, 1977	23.2	23.9	Weitzman 1977:349, 351
Hyphessobrycon elachys Weitzman, 1985	12.0	17.9	Weitzman 1985:800

Table 1.—Continued.

Name, author, date	Maturity	Maximum	Reference
Hyphessobrycon flammeus Myers, 1924	14.5	25.0	M. Weitzman pers. comm.
Hyphessobrycon georgetii Géry, 1961b	14.4	16.7	Géry 1961b:124
Hyphessobrycon gracilior Géry, 1964	?	21.5	Géry 1964:12
Hyphessobrycon griemi Hoedemann, 1957	14.2	25.7	M. Weitzman pers. comm.
Hyphessobrycon loretoensis Ladiges, 1938	?	24.0	Géry 1961a:35
Hyphessobrycon minimus Durbin, 1909	?	21.0*	Durbin 1909:68
Hyphessobrycon minor Durbin, 1909	?	25.0*	Durbin 1909:65
Hyphessobrycon tukunai Géry, 1965a	19.0	20.6	Géry 1965a:25
Megalamphodus rogoaguae Pearson, 1924	16.5	23.0	Pearson, 1924:33; personal observation
Microschemobrycon elongatus Géry, 1973	?	25.0	Géry 1973:97
Oxybrycon parvulus Géry, 1964	?	15.7	Géry 1964:16
Paracheirodon innesi (Myers, 1936)	17.2	22.2	Personal observation
Paracheirodon simulans (Géry, 1963)	17.0	19.6	Weitzman & Fink 1983:358
Spintherobolus broccae Myers, 1925a**	17.6	23.5	Myers 1925a:144; personal observation
Tyttobrycon dorsimaculatus Géry, 1973	19.0	20.5	Géry 1973:118
Tyttobrycon hamatus Géry, 1973	14.1	16.9	Géry 1973:129
Tyttobrycon spinosus Géry, 1973	17.0	20.5	Géry 1973:121
Tyttobrycon xeruini Géry, 1973	17.7	22.6	Géry 1973:126
Characidiinae			
Elachocharax geryi Weitzman & Kanazawa, 1978	?	15.5	Weitzman & Kanazawa 1978:173
Elachocharax junki (Géry, 1971)	?	22.4	Weitzman & Géry 1981:892
Elachocharax mitopterus Weitzman, 1986	?	13.9	Weitzman 1986:738
Elachocharax pulcher Myers, 1927	?	22.1	Weitzman & Géry 1981:890
Jobertina bahiensis (Almeida, 1971)	16.0	23.3	Almeida 1971:112
Jobertina eleotrioides Géry, 1960	?	21.0	Géry 1960:4
Klausewitzia aphanes Weitzman & Kanazawa, 1977	13.0	16.5	Weitzman & Kanazawa 1977:151, 158
Klausewitzia ritae Géry, 1965b	<20.0	25.0	Géry 1965b:199
Siluriformes			
Trichomycteridae			
Trichomycterinae			
Trichomycterus hasemani Eigenmann, 1914	?	18.0*	Eigenmann 1918b:326
Trichomycterus santaeritae Eigenmann, 1918b	?	24.0*	Eigenmann 1918b:341
Trichomycterus johnsoni Fowler, 1932	?	16.0	Fowler 1932:368
Glanapterygiinae			
Pygidianops eigenmanni Myers, 1944	?	23.0	Myers 1944:593

Table 1.—Continued.

Name, author, date	Maturity	Maximum	Reference
Vandeliinae			
Paravandellia bertonii (Eigenmann, 1918a)	?	24.0*	Eigenmann 1918b:368
Paravandellia magdalenae (Miles, 1943a)	?	22.0	Miles 1943b:369
Paravandellia oxyptera A. Miranda-Ribeiro, 1912	?	23.0	P. Miranda-Ribeiro 1947:4
Tridentinae			
Miuroglanis platychephalus Eigenmann & Eigenmann, 1889	?	17.0*	Eigenmann & Eigenmann 1889:56
Tridensimilis brevis (Eigenmann & Eigenmann, 1889)	?	21.0*	Eigenmann & Eigenmann 1889:54
Tridensimilis venezuelae Schultz, 1944	?	20.5	Schultz 1944:267
Tridentopsis pearsoni Myers, 1925b	18.0	23.0	Myers 1925b:86
Tridentopsis tocantinsi LaMonte, 1939	?	23.0	LaMonte 1939:1
Sarcoglanidinae			
Malacoglanis gelatinosus Myers & Weitzman, 1966	18.2	19.9	Myers & Weitzman 1966:282
Sarcoglanis simplex Myers & Weitzman, 1966	?	19.6	Myers & Weitzman 1966:279
Loricariidae			
Microlepidogaster lophophanes (Eigenmann & Eigenmann, 1889)	?	18.0	Eigenmann & Eigenmann 1889:42
Callichthyidae			
Aspidoras brunneus Nijssen & Isbrücker, 1976b	?	21.3	Nijssen & Isbrücker 1976b:116
Aspidoras carvalhoi Nijssen & Isbrücker, 1976b	?	25.4	Nijssen & Isbrücker 1976b:116
Aspidoras pauciradiatus Weitzman & Nijssen, 1970	?	23.2	Weitzman & Balph 1979:10–11
Corydoras gracilis Nijssen & Isbrücker, 1976a	?	23.2	Nijssen & Isbrücker 1976a:91
Corydoras habrosus Weitzman, 1960a	15.5	20.1	Weitzman 1960a:141–145
Corydoras hastatus Eigenmann & Eigenmann, 1888	18.2	20.1	Personal observation
Corydoras pygmaeus Knaack, 1966	18.3	23.7	Nijssen & Isbrücker 1986:52, personal observation
Aspredinidae			
Dupouyichthys sapito Schultz, 1944	?	23.0	Schultz 1944:245; Stewart 1985:10
Hoplomyzon papillatus Stewart, 1985	?	16.9	Stewart 1985:8
Scoloplacidae			
Scoloplax dicra Bailey & Baskin, 1976	?	13.8	Bailey & Baskin 1976:5, 7
Pimelodidae			
Horiomyzon retropinnatus Stewart, 1986	23.3	23.3	Stewart 1986:50
Cyprindontiformes			
Poeciliidae			
Fluviphylacinae			
Fluviphylax pygmaeus (Myers & Carvalho), in Myers, 1955	12.5	22.0	Roberts 1970:10, Weitzman 1982:191

Table 1.—Continued.

Name, author, date	Maturity	Maximum	Reference
Poeciliinae			
Poeciliini			
Poecilia hasemani (Henn, 1916)	?	23.0	Jacobs 1969:287
Poecilia minor (Garman, 1895)	9.5	15.0	K. Hartel pers. comm.
Heterandriini			
Neoheterandria elegans Henn, 1916	16.5	18.0	Henn 1916:118
Cnesterodontini			
Phallotorynus jucundus von Ihering, 1930	14.9	24.9	C. Ferraris pers. comm.
Perciformes			
Eleotrididae			
Microphilypnus amazonicus Myers, 1927	?	17.1	Personal observation***
Microphilypnus macrostoma Myers, 1927	?	20.0	Myers 1927:135***
Microphilypnus ternetzi Myers, 1927	?	20.0	Myers 1927:134***

* Total length taken from cited literature.

** Research in progress by the senior author indicates that *Spintherobolus broccae* Myers (1925a) is not a synonym of *Phoxinopsis typicus* Regan (1907) as proposed by Myers in Anonymous (1970).

*** The largest *Microphilypnus* specimen examined (of an unidentified species) is 25.5 mm SL.

the loss of terminal stages in the developmental sequence. Myers (1958:29) discussed various characters commonly demonstrating paedomorphic features in South American freshwater fishes, and those features will be discussed and evaluated in greater detail in a future paper. For the purposes of this paper, the miniature South American fishes listed in Table 1 satisfy either of two criteria. They are either species which mature sexually at under 20 mm SL and may sometimes reach somewhat larger sizes, or species for which maturity data are unknown but which are not reported to exceed 25 to 26 mm SL in the wild. Species examined by us or reported in the literature as getting larger than that size, even though they may mature at lengths somewhat shorter than 20 mm SL are not included. This cut-off point for "miniatures" is arbitrary and the listing is meant as a preliminary guide to future studies of miniature fishes in South America rather than as a definitive enumeration of such species.

The size limitation used in the present study was adopted because all listed species that have been examined in detail which mature under 20 mm SL, and do not grow to longer than 25 to 26 mm SL, have in common numerous apparently paedomorphic morphological reductions. A few species in Table 1 are known to somewhat exceed 26 mm SL when raised and kept in aquaria. These include *Corydoras habrosus* Weitzman, *Paracheirodon innesi* (Myers), *Hyphessobrycon flammeus* Myers, *Hyphessobrycon griemi* Hoedemann, and *Hyphessobrycon loretoensis* Ladiges. Some of these species may exceed this length in nature, but that remains unconfirmed. Geisler & Annibal (1984:77–78) have discussed aquarium versus wild lengths for *Paracheirodon axelrodi* (Schultz), a fish that exceeds our size limit, but which displays paedomorphic features (Weitzman & Fink 1983:354–357). Geisler & Annibal believed that individuals of this species rarely live more than one year in the wild, and that poor nutrition in its natural habitat further limits the adult size of the species. Most miniatures probably live less than one year in the wild, perhaps considerably less.

The apparent paedomorphic nature of miniature species in Table 1 at maturity, and the reductive nature of some characters are recognized within the context of the developmental sequences of the characters in apparently related outgroups maturing at longer lengths. The phylogenetic hypotheses available for most taxa are of an imprecise nature. Thus the documentation of paedomorphosis with respect to proximate sister groups involves general rather than specific phylogenetic comparisons. Precise information on morphology and size at maturity is not available for some taxa, a number of which are known only from limited series. In those instances we extrapolate that the correlations between a body size under 25 to 26 mm SL and the presence of paedomorphic features that are characteristic of other more inclusive taxa also applies to the species we have been unable to examine critically. It is also necessary to note that maturity data are absent for a number of the listed species. It is possible that future studies may reveal that adults of some of these taxa achieve sizes greater than the cutoff used to delimit miniatures in this paper.

The size criterion for miniatures in this study is not completely satisfactory when applied to some unlisted species with elongate bodies. For example the trichomycterid catfishes *Typhlobelos ternetzi* Myers and *Glanapteryx anguilla* Myers, have small heads displaying many paedomorphic features of miniatures, although the fishes exceed 30 mm SL. Similarly *Tomeurus gracilis* Eigenmann, an elongate poeciliid, is in many ways a miniature fish, but we have examined both males and females of 26.5 mm SL from Surinam (USNM 225463), and as a consequence do not include the species in our list. These three species are in actuality elongate miniatures in which the head length, but not body length agrees with that of the species in Table 1. The concept of an elongate miniature is perhaps even more appropriate for the South American freshwater needlefishes of the genus *Belonion* Collette. Collette (1966:9, 15–21) in his description of the genus and contained species detailed numerous reductive characters for the genus relative to outgroup needlefishes involving the epipleurals, fourth upper pharyngeal tooth bones, laterosensory canal system and other features. Although *Belonion dibranchodon* Collette matures at 24.5 mm SL and members of the genus reach 41.8 mm SL (Collette 1966:12–13), the species are very elongate. In fishes of such shapes it might be more appropriate to compare species on the basis of the bony head length (exclusive of the elongate lower jaw in *Belonion*) rather than focusing on standard length. In such a framework more species such as *Belonion dibranchodon* would be listed as miniatures. A criterion of size using such a portion of the body with numerous paedomorphic features could be similarly used to delimit miniature species regardless of their actual standard length.

Although the data from *Belonion* and some characiform groups suggests that some alternative standard for miniature fishes might be appropriate, morphological data on paedomorphic features are unfortunately largely absent for many relatively small species of some major groups of South American freshwater fishes (e.g., Gymnotiformes, Cichlidae) slightly longer than 26 mm SL. Similarly there is a paucity of data on how and whether paedomorphic characters correlate with standards such as absolute head size in most groups. Thus for the sake of consistency we prefer to use standard rather than head length or another measurement as the benchmark for our discussion until more data are available.

If the concept of miniature fishes of this paper can be extended to other groups of fishes, then the majority of the miniature fishes, in both freshwater and marine environments, have been described within the last 40 years. Böhlke & Robins (1968), Jewett & Lachner (1983), Lachner & Karnella (1978, 1980), Winterbottom (1983), and Winterbottom & Emery (1981, 1986) provide many examples of miniature marine gobies, and references in those publications will lead to other descriptions of such species. Springer (1983), in describing a new miniature species of western Pacific goby, has documented several skeletal modifications, of which some appear paedomorphic to us. More recently Whitehead and Teugels (1985) have described apparently paedomorphic features in *Sierrathrissa leonensis* Thys van den Audenaerde a species of African freshwater clupeid that reaches a slightly greater length, 26.7 mm SL, than the 26 mm SL limit on miniature fishes. Finally, Roberts (1986:332–340) reported many similar reductions in a miniature Asian cyprinid, *Danionella translucida* Roberts (1986:233).

Phylogenetic Lineages of South American Freshwater Fishes

The large number of species of miniature fishes within the South American freshwater ichthyofauna is striking, but a true sense of the possible significance of this phenomenon can only be achieved by examining miniaturization within a phylogenetic framework. In other words, in which major groups of fishes is miniaturization found, and how many times has it independently evolved?

Not surprisingly, the two largest groups of South American fishes, the ostariophysan orders Characiformes and Siluriformes, account for the vast bulk (88%) of the miniatures, while the Clupeiformes, Cyprinidontiformes and the Perciformes which are less speciose on that continent cumulatively include only about 12% of the miniatures. These five orders are each monophyletic and the evolution of miniatures in each of these clades has clearly proceeded independently. The question of how many times miniatur-

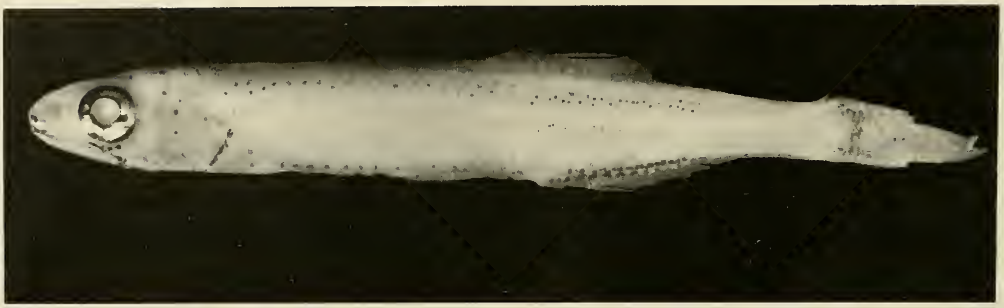

Fig. 1. *Amazonsprattus scintilla* Roberts, a miniature clupeiform fish, family Engraulidae, from the Amazon basin, AMNH 57371, 24.3 mm SL; Brazil, state of Amazonas, Rio Urubaxi, tributary of Rio Negro, south of east end of Ilha Tamaquari (01°32′N, 64°59′W).

ization has evolved within each lineage cannot be answered with the same precision, but we will address the issue to the extent possible within the context of available phylogenetic data. We must preface our general discussion with the observation that there are relatively few rigorous phylogenetic studies of components of the South American freshwater fish fauna, and many traditionally accepted taxa have not been critically reviewed with respect to their possible monophyly. In light of this lack of precision we conservatively do not hypothesize multiple miniaturization events within a genus unless phylogenetic data indicate that reduced size and its attendant paedomorphic features have independently evolved more than once in the taxon.

Only two species of miniature clupeiformes are described from South American freshwaters. Roberts (1984:321) withheld judgement on the phyletic associations of *Amazonsprattus* Roberts (Fig. 1), but further study by Gareth Nelson (pers. comm.) indicates that it is a member of the Engraulidae, as is *Anchoviella* Fowler, the other South American clupeiform genus with a described miniature species. A phylogenetic hypothesis that would provide insight into the relationships of the two miniature South American engraulids is not available, and currently it is not appropriate to hypothesize more than a single evolutionary miniaturization event in the group.

Interestingly no miniature species are known to occur in ten of the twelve Neotropical characiform families recognized by Greenwood et al. (1966:395–396), although in at least one, the Gasteropelecidae, there are several species of *Carnegiella* Eigenmann displaying numerous apparently paedomorphic features (Weitzman 1954, 1960b). Many of the characiform families without known miniatures demonstrate marked morphological adaptations for specialized feeding methods (e.g., Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae, Vari 1983:7–33, 43–46; in press), which may be incompatible functionally with a pronounced reduction in overall body size. Miniatures are rather found only in the Lebiasinidae and Characidae among the South American characiforms. Within those families the miniatures are distributed among eighteen genera, one lebiasinid and seventeen characid, most of which are poorly understood in terms of intrageneric phylogenetic relationships.

Lebiasinids show a considerable range in overall standard lengths with *Pyrrhulina* Valenciennes and *Lebiasina* Valenciennes each having species reaching 100 mm SL, and species of *Piabucina* Valenciennes growing to about 200 mm SL. The three species of *Nannostomus* Günther listed in Table 1 are members of a genus of 15 species that includes numerous species of about 25 to 35 mm SL and it is not surprising that several miniatures are found in that taxon. According to Weitzman (1964:152–153) *Nannostomus* forms a derived clade within the Lebiasinidae. That hypothesis along with the larger body sizes in the lebiasinid outgroups, and the small but not minute body size of other *Nannostomus* species indicates that the minute size of the miniature *Nannostomus* is derived. Attempts to resolve the relationships within *Nannostomus* have not proved feasible (Weitzman & Weitzman 1982:417–419; Fernandez & Weitzman 1987:165). In the absence of that data we are unable to reasonably hypothesize whether the miniaturization process in that genus has occurred one, two, or three times, but conservatively assume that it took place only once.

The absence of reliable hypotheses of relationships among the vast majority of subfamilies and genera in the Characidae similarly does not permit us to advance any critically evaluated hypothesis on the exact number of evolutionary events represented by the occurrence of miniatures in 17 genera within the family. These genera are currently assigned to four subfamilies, Characinae, Glandulocaudinae, Tetragonopterinae (including Cheirodontinae) and Characidiinae. We prefer not to recognize a Cheirodontinae separate from the Tetragonopterinae in light of the difficulties in advancing an unambiguous diagnosis of the Cheirodontinae that were discussed by Fink & Weitzman (1974:1), Géry (1977:543) and particularly Weitzman & Fink (1983:341–353).

The uncertainties associated with hypotheses of the exact phylogenetic relationships of *Priocharax* Weitzman & Vari within the Characinae were discussed by Weitzman & Vari (1987:648–651). Nonetheless, the data demonstrate that the two species form a monophyletic group within the Characinae, a putative group of typically larger size fishes, although some taxa (*Gnathocharax* Fowler, *Heterocharax* Eigenmann and *Hoplocharax* Géry) are in the 25 to 35 mm SL size range. Thus, the minute size of the *Priocharax* species is considered to be the consequence of a single ancestral miniaturization.

The next two subfamilies, the Glandulocaudinae and Tetragonopterinae (including Cheirodontinae), both of which contain many miniatures, are apparently closely related groups, neither of which has, however, been shown to be monophyletic (Weitzman & Fink 1983:341–346; Weitzman et al. in Weitzman & Fink 1985:112-117). The phylogenetic relationships of the miniature glandulocaudine genera *Iotabrycon* Roberts, *Xenurobrycon* Myers & Miranda-Ribeiro, *Scopaeocharax* Weitzman & Fink, and *Tyttocharax* Fowler (Table 1) were analyzed phylogenetically by Weitzman & Fink (1985:12–70) who hypothesized with considerable evidence that they form a monophyletic unit. The sister taxon to that assemblage, the genus *Argopleura* Eigenmann, has adults that range from 35 to 53 mm SL and the miniaturization in the four cited xenurobryconin genera is apparently the product of a single evolutionary event.

Few tetragonopterine genera have been the subject of comparable studies, and for most it is only possible to tentatively presume monophyly for multispecific taxa. One exception is the genus *Paracheirodon* Géry hypothesized to be monophyletic by Weitzman & Fink (1983:347–357), but of uncertain phylogenetic relationships within the Tetragonopterinae. The genus consists of three species, *P. simulans* Géry and *P. innesi,* both miniatures, and *P. axelrodi* which reaches an adult size of 33.1 mm SL in the wild, although Geisler & Annibal (1984:32) report an old aquarium specimen that reached 51.0 mm SL. Thus the genus evidently represents a single evolutionary shift to reduced body size with subsequent miniaturization. The hypothesis of the monophyly of *Paracheirodon* as proposed by Weitzman & Fink has been challenged by Géry (1984:59) and Géry & Mahnert (1986:49) who maintain that *P. simulans* belongs to the large tetragonopterine genus *Hyphessobrycon* Durbin. A reanalysis of the data of Géry (1984) and Géry & Mahnert (1986) by Weitzman & Fink (1987) has reconfirmed the placement of *P. simulans* in the monophyletic clade *Paracheirodon*.

The lack of information on phylogenetic relationships within and among the remaining tetragonopterine taxa containing miniatures precludes any indepth critical discussion of the number of times that miniaturization arose among these taxa. We prefer to take a conservative course and assume that miniatures in genera with two or more species arose from single ancestral miniaturization events. That assumption may be disproved when the necessary phylogenetic studies are undertaken, indicating multiple independent miniaturization events in some of the taxa. Alternatively, such analyses may also reveal presently unsuspected sister group relationships between some of the genera, with a consequent reduction in the number of hypothesized miniaturization events. The involved tetragonopterine genera and the number of included species (in parentheses) are as follows: *Hyphessobrycon* (12), *Tyttobrycon* Géry (4), *Axelrodia* Géry (3), *Oxybrycon* Géry (1), *Megalamphodus* Eigenmann (1), *Microschemobrycon* Eigenmann (1), *Cheirodon* Girard (1), *Hemigrammus* Gill (1), and *Spintherobolus* Eigenmann(1) (Fig. 2). Although we only count the miniature species of *Hyphessobrycon* as being the result of a single ancestral miniaturization, the genus is relatively speciose (over 60 nominal species) and includes a number of species in the 26 to 35 mm SL range (Weitzman 1977:355–356; M. Weitzman 1985:805) increasing the likelihood that miniaturization may have occurred multiple times in the genus. It has also been suggested that *Hyphessobrycon* may be polyphyletic (Weitzman & Fink 1983:342), a possibility that further complicates the question of the number of miniaturization events in the genus. All species of *Tyttobrycon* are miniatures (Géry 1973:117) as is the case with *Axelrodia* (Géry 1965a:31–35, 1966:111–118, 1973:111–115) and *Oxybrycon* (Géry 1964:15). *Microschemobrycon,* in contrast, contains a number of species of 30 to 35 mm SL (Eigenmann 1915:53; Géry 1973: 86–101, 1977:598).

The last characid subfamily to be considered and one containing eight described miniatures in three genera (*Elachocharax* Myers, *Klausewitzia* Géry and *Jobertina* Pellegrin) is the Characidiinae. Once again the information on relationships within the subfamily is limited, with only *Elachocharax* having been the subject of phylogenetic treatment (Weitzman & Géry 1981; Weitzman 1986). *Elachocharax* is hypothesized to be monophyletic with four known species, all miniatures, and the reduced adult size assumed to be a consequence of a single evolutionary event. The situation in *Klausewitzia* is more equivocal, with the two described species, both of which are miniatures, perhaps united by a single character, the presence of a maxillary tooth, a character that may be either plesiomorphous or a derived reversal (Weitzman & Kanazawa 1977:157–159).

The phylogenetic problems associated with *Jobertina* and the evidently most closely related genus, *Characidium* Reinhardt are complex and we neither have data on whether *Jobertina* is monophyletic nor on whether the two known miniatures are sister species. We can only note that some of the species of *Characidium* achieve adult body sizes of over 110 mm SL and that the reduced size of the two *Jobertina* species is apparently a derived feature. Miniaturization in the Characidiinae is thus counted as having occurred three times, once each in *Elachocharax, Klausewitzia* and *Jobertina*. We note, however, that most of the miniature species of these genera have in common various features (e.g., elongate pectoral fin rays, Weitzman & Kanazawa 1978:160) that may represent synapomorphies for those taxa. If that is the case, miniaturiza-

Fig. 2. *Spintherobolus broccae* Myers, a miniature characiform fish, family Characidae, from southeastern Brazil, USNM 287324: (A) mature female, 22.0 mm SL, (B) mature male, 18.5 mm SL; Brazil, state of Rio de Janeiro, small tributary of Rio Macacu, about 1–2 km from town of Cachoeiros de Macacu (approx. 22°29′S, 42°41′W).

tion may have arisen only once in the Characidiinae, but the problem requires more study.

Phylogenetic analyses of South American freshwater siluriform families and genera are very rare. According to present classifications (Myers 1944, Myers & Weitzman 1966, Bailey & Baskin 1976, Isbrücker 1980, Stewart 1985) the miniature siluriforms listed in Table 1 are distributed among six family group taxa, although some authors disagree on the placement of *Scoloplax* Bailey and Baskin. Under all the classificatory schemes, miniatures are found in the Aspredinidae, Callichthyidae, Loricariidae, Pimelodidae and Trichomycteridae. *Scoloplax,* originally placed in the Loricariidae by Bailey & Baskin (1976), was removed from that family by Isbrücker (1980) who placed it in the monotypic Scoloplacidae. That shift fails to elucidate the phylogenetic relationships of the single contained species, but that classification is followed for the purposes of this discussion since the alternative proposed alignment is no more satisfactory.

The eight genera of miniature Trichomycteridae are found in five subfamilies, Trichomycterinae (*Trichomycterus* Valenciennes), Glanapterygiinae (*Pygidianops* Myers), Vandelliinae (*Paravandellia* Miranda-Ribeiro), Tridentinae (*Tridensimilis* Schultz, *Miuroglanis* Eigenmann & Eigenmann, and *Tridentopsis* Myers (Myers 1944: 599) (Fig. 3)) and Sarcoglanidinae (*Sarcoglanis* Myers & Weitzman, and *Malacoglanis* Myers & Weitzman (Myers & Weitzman 1966:279)). The Trichomycterinae

Fig. 3. *Tridentopsis* sp., a miniature South American siluriform fish, family Trichomycteridae, 23.8 mm SL; aquarium specimen, no definite collecting locality information.

contains species ranging from 16.0 to over 260 mm SL as adults (Eigenmann 1918b: 286, 326; Fowler 1932:368). The phylogenetic relationships of the three described miniatures of that subfamily are unresolved and we assume that they represent a single miniaturization event. Four subfamilies contain only miniatures (Sarcoglanidinae) or mostly miniatures and small species (Glanapteryginae, Vandelliinae, Tridentinae) but belong to separate and divergent clades within the Trichomycteridae (J. N. Baskin, pers. comm.) and thus represent distinct miniaturization events. Miniaturization in the Trichomycteridae thus arose at least five times.

Miniature species in the Callichthyidae are limited to three species of *Aspidoras* von Ihering and four species of *Corydoras* Lacepède. Although Weitzman & Balph (1979: 16–18) raised questions about the distinctiveness of these genera, they noted (1979: 20) that reduced size in *Corydoras* and *Aspidoras* was apparently independently derived. The relationships of the four miniature *Corydoras* species are unresolved and the genus is very speciose raising the possibility that miniaturization arose several times in that taxon. We prefer nonetheless to be conservative and to hypothesize only a single miniaturization within each genus. Miniaturization is consequently considered to have arisen at least twice in the Callichthyidae.

Two miniatures, one each in *Hoplomyzon* Myers and *Dupouyichthys* Schultz, occur in the Aspredinidae. According to Stewart (1985:4) the species occur in separate monophyletic taxa containing other small species. Thus miniatures are presumed to have arisen twice in the Aspredinidae. There is only one described miniature in the Pimelodidae, *Horiomyzon retropinnatus* Stewart (1986), and a single such species is tentatively identified for the Loricariidae, *Microlepidogaster lophophanes* (Eigenmann & Eigenmann). As noted above, the phylogenetic relationships of *Scoloplax,* the only genus of the Scoloplacidae, are the subject of some controversy, but under either proposed classification it probably represents an independent miniaturization event since no miniatures are known in likely sister groups to that genus. In summary miniatures have arisen at least twelve times in the South American members of the Siluriformes.

The five miniature species in the Cyprin-

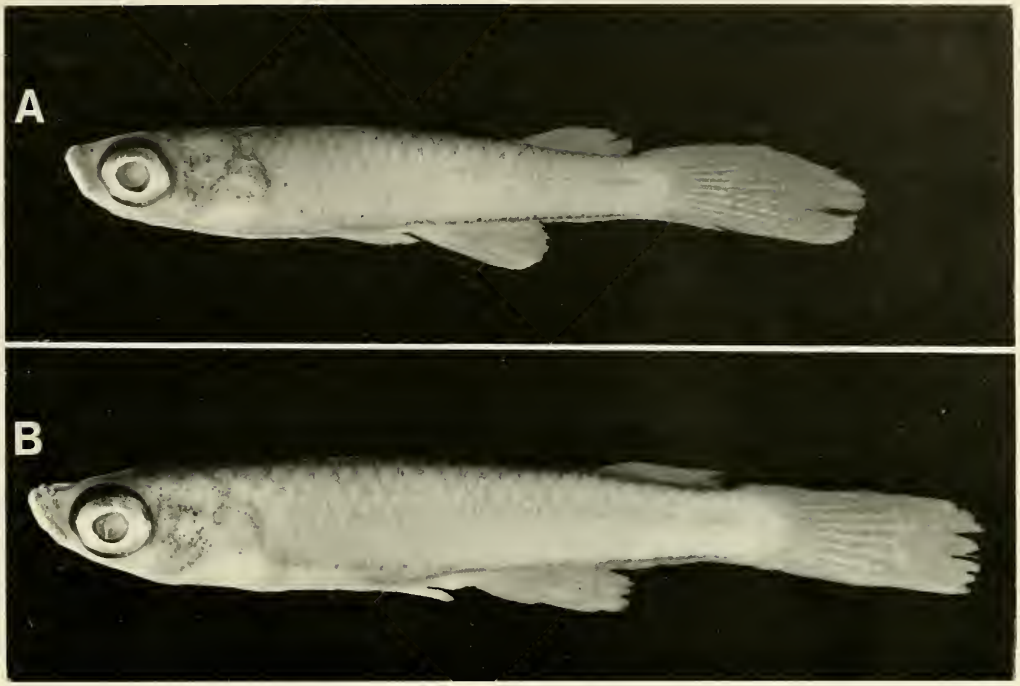

Fig. 4. *Fluviphylax pygmaeus* (Myers & Caravalho), a miniature cyprinodontiform fish, family Poeciliidae, from the Amazon basin, USNM 227730: (A) mature male, 10.3 mm SL, (B) mature female, 13.1 mm SL; Brazil, state of Amazonas, Rio Negro, Lago Sirola, Anavilhanas Archipelago (approx. 03°10–15′N, 60°40–45′W).

idontiformes belong to two subfamilies of the Poeciliidae according to Parenti (1981: 451, 463). *Fluviphylax pygmaeus* (Myers & Carvalho) (Fig. 4) is the only described member of the Fluviphylacinae and is an independent evolution to small size. The four other diminutive cyprinidontiform species are distributed in three tribes of the Poeciliinae in the classification proposed by Rosen & Bailey (1963:3, 39, 61, 116). The two species of *Poecilia* Bloch & Schneider are placed in the Poeciliini, *Neoheterandria* Henn in the Heterandriini, and *Phallotorynus* Henn in the Cnesterodontini. If these tribes represent monophyletic groups, then miniatures have evolved at least three times in the Poeciliidae and a total of four times in the Cyprinodontiformes.

The final miniatures known in the South American freshwater ichthyofauna, the eleotridids of the genus *Microphylipnus* Myers (Fig. 5) have not been studied since described by Myers (1927). Although of uncertain relationship to other members of that family, and not shown to be monophyletic, they represent at least one evolutionary miniaturization event.

On the basis of present information we can reasonably estimate that miniaturization within the South American freshwater fish fauna has taken place independently sixteen times in the Characiformes, on at least twelve occasions in the Siluriformes, in four instances in the Cyprinidontiformes and once in each of the Clupeiformes and Perciformes, for a total of about thirty-four events.

Ecology of South American Miniature Freshwater Fishes

There are currently 85 described species of miniature or putatively miniature fishes from forested regions of South America (Table 1), a number that will undoubtedly increase. Fewer miniature fish species have

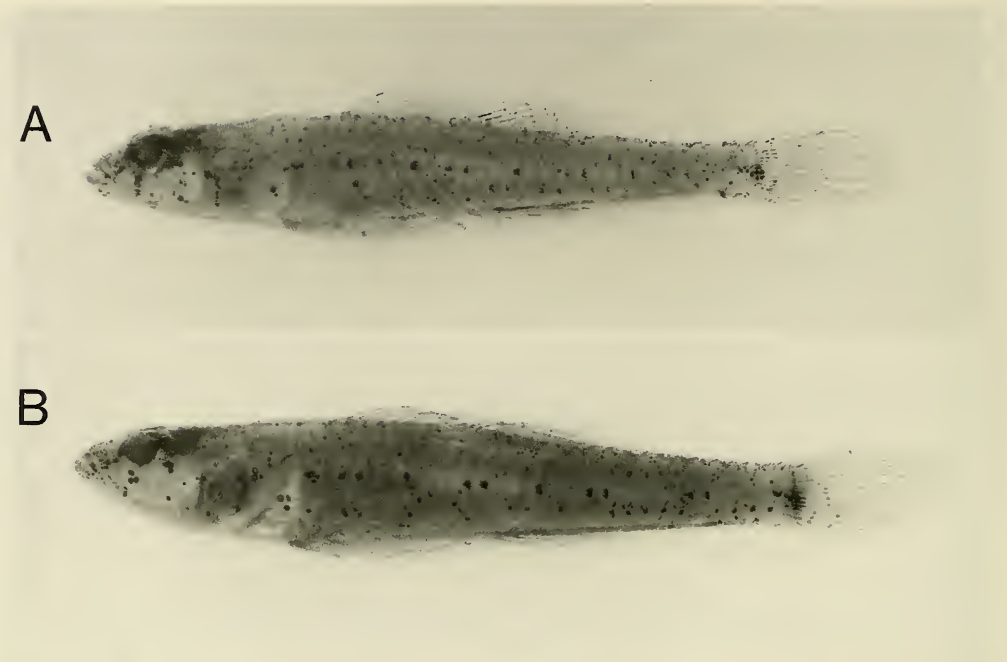

Fig. 5. *Microphilypnus* sp., a miniature perciform fish, family Eleotrididae, from the Amazon basin, USNM 290836: (A) mature male, 20.8 mm SL, (B) mature female, 21.7 mm SL; Brazil, state of Amazonas, Rio Urubaxi, tributary of Rio Negro, south of east end of Ilha Tamaquari (01°32′N, 64°59′W).

been reported from other tropical freshwater regions. If we use the same standard for a miniature, approximately one dozen miniature fish species are known from the freshwaters of Africa (Daget et al. 1984, 1986) and a comparable number seem to have been reported from the Asiatic tropics, totals admittedly likely to increase in the future. Reasons for the current differences in the numbers of miniature species from the three continental tropical regions are obscure. In part the larger number of miniatures in South American freshwaters may simply reflect the richness of the overall fish fauna on that continent; however, our knowledge of the ichthyofauna is so poor (Böhlke et al. 1978:667–670) that it is premature to speculate further at this time.

The diversity and composition of the miniature fish fauna in South America was previously discussed by Roberts (1973a: 247–248), who stated that "Excepting the catfishes, all diminutive (Amazonian) species are secondary freshwater fishes and belong to groups whose presence can be thought of as 'marginal'." More recently (1984:320) he has further suggested that "In the Amazon, where community structure of freshwater fishes may be more complex than anywhere else, minute body size seems to have arisen primarily in response to biotic factors." He continued that, "this in my opinion, is the general reason why so many of the smallest Amazonian fishes belong to secondary freshwater fish groups which in terms of relative numbers of species represent an insignificant fraction of the fauna." He also notes that miniatures in various other groups may be discovered in the future. Secondary freshwater fishes as defined by Myers (1937:344–345) are those fishes belonging to teleost groups ordinarily of marine or euryhaline habit, or those groups with members commonly entering an euryhaline habitat. In South American freshwaters the known miniatures belong to five major groups, three of which, the Cyprinodontiformes, Clupeiformes and Perciformes (only Eleotrididae) are secondary freshwater fish groups according to Myers' concepts. The other two groups, the Characiformes and Siluriformes are primary freshwater groups, that is teleost groups typically of freshwater habits. Of the 85 listed species of South American miniatures, about 88% belong to the primary freshwater groups, the characiforms and siluriforms (Table 1). The secondary freshwater groups, cyprinidontiforms, clupeiforms, and perciforms in contrast, together represent only ten of the 85 miniature freshwater fishes known from South America (Table 1). Increased collecting with specialized techniques, and future revisionary studies may change the relative contribution of these major taxonomic units to the fauna of miniature fishes. Current data indicate, however, that contrary to Roberts, it is the primary rather than secondary freshwater groups that predominate among miniature fishes of the Amazon basin, the area of occurrence of the majority of characiform and siluriform fishes listed in Table 1.

The degree to which ecological factors (? the biotic factors of Roberts (1984:320)) show a correlation with, and may have been involved in the evolution of miniature fishes in South American freshwaters is difficult to determine at this time. The possibility that acidic waters of low productivity may result in reduced poring of the laterosensory system of the body, and perhaps of overall body size was noted by Collette (1962:179–191) relative to the North American percid fish *Etheostoma fusiforme* Girard. Black acidic waters are quite common in South America, and many of the species listed in Table 1 occur in that environment (pers. observ.). In-depth studies of the ecology of most freshwater fishes is South America are rare and very little is known about the habits or life histories of small and miniature freshwater fishes in that region. The reasons for this lack of information about miniatures are myriad, many revolving around the diminutive size of the species in question. Such species are not often noted while making general collections. Those sampling efforts are, furthermore, usually not focused at the microhabitat level necessary to delimit those ecological parameters possibly idiosyncratic to miniature species.

Miller (1979:271–274) briefly discussed the habitats of small fishes, but did not specifically refer to miniatures as defined herein. Our own observations and the limited pertinent literature reveal one general ecological parameter common to many miniatures—their repeated occurrence in still or slow-flowing shallow waters. This association is not unexpected given the difficulties small or miniature fishes have in maintaining position in a rapidly moving water column. Miniature Neotropical fishes living in less turbulent habitats are detailed below. This listing is based on personal observations supplemented by personal communications and literature information.

Among the miniature clupeiforms, only *Amazonsprattus scintilla* Roberts is known to live in still or slow-flowing waters. The more speciose characiform miniatures we have seen in, or which have been reported from that habitat include the characidiines *Elachocharax mitopterus* Weitzman & *Elachocharax pulcher* Myers, the characinines *Priocharax ariel* Weitzman & Vari and *Priocharax pygmaeus* Weitzman & Vari, the glandulocaudines *Xenurobrycon polyancistrus* Weitzman (Weitzman 1987:118–119), species of *Tyttocharax* Fowler (Saul 1975: 111; D. J. Stewart, pers. comm.), and *Iotabrycon praecox* Roberts (Roberts 1973b: 501–502), the tetragonopterine *Hyphessobrycon elachys* M. Weitzman (1985:799), and the lebiasinids *Nannostomus anduzei* Fernandez & Weitzman and *N. marginatus* Eigenmann. The siluriform species *Corydoras hastatus* Eigenmann & Eigenmann (Myers 1953:269; I. Sazima, pers. comm.)

and *Scoloplax dicra* Bailey & Baskin (R. M. C. Castro, pers. comm.) also are found in that habitat. The cyprinodont *Fluviphylax pygmaeus* (Myers & Carvalho) has been observed at or near the water surface by us and others in still waters, attached and detached floating meadows, and slow-flowing river margins both with and without plant cover (Weitzman 1982:193–195). An unidentified species of *Microphylipnus* of the Eleotrididae has been observed in quiet waters of small and large rivers, usually on or near the bottom, both over sand and mud, in areas with and without plant cover (C. J. Ferraris, Jr., pers. comm.). It is likely that the remaining miniatures in these groups will also share comparable habitats.

The catfish family Trichomycteridae has many members parasitic on the gills of large fishes, and perhaps as a consequence of that unusual habit does not neatly fit the above characterization of the habitats of miniatures. During feeding the miniature parasitic trichomyterids (e.g., *Paravandellia bertonii* Eigenmann (A. Miranda-Ribeiro 1923: 11–12) and *P. magdalenae* Miles (1947:99) attach to the gills of larger fishes, a feeding habit that also serves to insulate them from the currents of the surrounding stream. *Trichomycterus santaeritae* Eigenmann (1918b:341; see also Eigenmann 1911:350, locality number 56) of the Trichomycterinae and *Malacoglanis gelatinosus* Myers & Weitzman (1966:286) of the Sarcoglanidinae both live in relatively still waters, and their morphology indicates that they are not parasitic. As noted by Eigenmann (1918b: 269) most non-parasitic members of the Trichomycterinae (=Pygidiinae of Eigenmann), in contrast, live in moderately to swiftly flowing streams, but avoid the water currents by being cryptobenthic. Thus on a microhabitat level the two species of *Trichomycterus* listed in Table 1 can be considered to inhabit water conditions typical of other miniatures.

Stewart (1985) noted that although the miniature catfish species of Aspredinidae live in streams with strong currents, they are actually benthic, occupying an area of reduced current flow. The same is apparently true for the one pimelodid catfish species in Table 1 (Stewart 1986:48).

Although we note an association of miniature fishes with still or slow-flowing waters, this does not imply that such environmental parameters have been the prime selective agents for miniaturization, a process that undoubtedly is the result of many different factors. Further studies are necessary to determine the generality of the correlation between still waters and miniatures, and to study the degree to which these relate to physical environmental parameters.

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PROC. BIOL. SOC. WASH.
101(2), 1988, pp. 466–470

CUORA MCCORDI, A NEW CHINESE BOX TURTLE FROM GUANGXI PROVINCE

Carl H. Ernst

Abstract.—*Cuora mccordi* (Emydidae: Batagurinae), a new species of box turtle from Guangxi Province, China is described and compared to other members of the genus.

Recent collecting trips by Mr. Oscar Shiu to Yunnan and Guangxi provinces, China, to find the turtle *Cuora yunnanensis,* which has not been taken since 1905 (Boulenger 1906), have instead revealed two new species of the genus *Cuora.* The first, *C. chriskarannarum* from Yunnan, has been described by Ernst & McCord (1987). The second is described below.

Methods and materials.—Straight-line measurements of each specimen were taken with dial calipers accurate to 0.1 mm of the greatest carapace length, carapace width and depth at the level of the seam between vertebrals 2 and 3, marginal width (the difference between the carapace width and the width across the pleurals taken between the points of juncture of the marginals and pleurals at the level of the seam between vertebrals 2 and 3), greatest plastron length, greatest width and length of both plastral lobes, least bridge length, greatest width and length of vertebrals 1 and 2 and pleural 2, and the medial seam length and greatest width of all plastral scutes. Notes and drawings were made of head, neck, limb, carapace, plastron, and bridge patterns. Colors were recorded from living turtles and color transparencies. Shell proportions are expressed as ratios of one measurement to another. Sixteen ratios proved useful in discriminating between taxa of *Cuora* (abbreviations used in the text are given in parentheses): width/length of cervical scute (W/L CS), width/length of first vertebral (W/L 1st V), width/length of second vertebral (W/L 2nd V), width/length of second pleural (W/L 2nd Pl), marginal width/carapace width (MW/CW), marginal width/carapace length (MW/CL), carapace width/carapace length (CW/CL), carapace depth/carapace length (D/CL), carapace depth/carapace width (D/CW), plastron length/carapace length (PL/CL), bridge length/plastron length (B/PL), bridge length/carapace length (B/CL), length of anterior plastron lobe/plastron length (APL/PL), width of anterior plastron lobe/plastron length (APW/PL), length of posterior plastron lobe/plastron length (PPL/PL), and width of posterior plastron lobe/plastron length (PPW/PL). The number of rows of large scales at the lateral edge of the antibrachium between the claw of digit V and the first horizontal skin fold proximal to the elbow (presented in text as foreleg scale rows) was recorded.

Specimens from the following collections were examined: William P. McCord, Hopewell Junction, New York, personal collection of living turtles (WPM), National Museum of Natural History, Smithsonian Institution (USNM).

Cuora mccordi, new species

Holotype.—USNM 281850, adult male; highland near Paise, Guangxi Province, China (23°54′N, 106°37′E); purchased from locals by Oscar Shiu, Aug 1986.

Diagnosis.—A moderately domed species of *Cuora* with a yellow head having a greenish crown, an orange black-bordered postorbital stripe, soft parts varying from yellow to orange, a reddish-brown carapace, a medial carapacial keel most pronounced on vertebrals 2–4, vertebral 1 extending laterally no farther than the seam separating marginals 1–2, a yellow plastron with a large medial black pattern, the plastron with a shallow anal notch, and the interanal seam complete.

Description (from twelve specimens examined).—Carapace length to 134 mm (males 131, females 134), elliptical, moderately domed (D/CL 0.38–0.46, $\bar{x} = 0.418$; D/CW 0.54–0.65, $\bar{x} = 0.582$; CW/CL 0.66–0.77, $\bar{x} = 0.719$); widest at marginals 8, highest at seam separating vertebrals 2–3. Carapace sides straight, posterior rim slightly to nonserrated with a very small medial notch. Anterior and posterior marginals usually flared (more in mature individuals); lateral marginals vertical with reverted rims (MW 8.9–16.3 mm, $\bar{x} = 12.98$; MW/CW 0.01–0.19, $\bar{x} = 0.140$; MW/CL 0.07–0.14, $\bar{x} = 0.107$). Marginal 1 widest, marginals 4–6 smallest. Scute texture rough with growth annuli. Cervical rectangular to triangular, longer than wide (W/L CS 0.44–0.87, $\bar{x} = 0.621$). Vertebrals 1, 3–5 wider than long, vertebral 2 longer than wide in 9 of 11 specimens (81.8%); vertebrals 4 and 5 widest, vertebral 5 posteriorly flared, vertebral 1 anteriorly flared, barely reaching seam separating marginals 1–2. Low medial keel most pronounced on vertebrals 2–4. Color reddish-brown, rim to marginals 7 or 8 yellow, seams outlined with dark brown or black. Dark posteriorly directed wedge near rim on dorsal surface of each marginal; undersides of marginals yellow laterally, orange medially.

Plastron length to 134 mm (males 123, females 134), shorter than carapace in 9(82%) specimens (PL/CL 0.90–1.03, $\bar{x} = 0.950$), slightly upturned anteriorly, movable hinge between pectoral and abdominal scutes. Posterior lobe longer and wider than anterior lobe (APL/PL 0.40–0.43, $\bar{x} = 0.419$; PPL/PL 0.56–0.61, $\bar{x} = 0.580$; APW/PL 0.53–0.57, $\bar{x} = 0.554$; PPW/PL 0.57–0.64, $\bar{x} = 0.618$; APW/CW 0.69–0.81, $\bar{x} = 0.727$; PPW/CW 0.74–0.88, $\bar{x} = 0.810$). Anterior lobe rounded anteriorly; posterior lobe with shallow anal notch. Sides of anal scutes taper toward midline. Bridge moderate (B/CL 0.26–0.35, $\bar{x} = 0.312$; B/PL 0.28–0.36, $\bar{x} = 0.331$); 1–2 axillaries; 1 small inguinal. Average plastral formula Abd. > Pect. > An. > Gul. > Fem. > Hum.; 5 (45% had this formula, but 4 other formulae occurred; all variation occurred in the relative lengths of Abd., Pect., and An.; Gul., Fem., and Hum. never varied in position. Interanal seam present and complete. Plastron is yellow with a distinctive black pattern (gulars totally black, humerals with posterior portion 25–50% black, other plastral scutes medially to 90% black); bridge with two black blotches.

Head narrow; snout slightly projecting; upper jaw neither hooked nor notched. Laterally yellow with an orange, black bordered postorbital stripe, and a narrow, black bordered stripe between the orbit and nostril. Crown green. Iris yellow to yellow-green; tympanum, jaws, and chin immaculate yellow. Neck yellow-orange dorsally and laterally, cream to yellow ventrally; a faint, narrow middorsal stripe may be present.

Digits partially webbed. Forelimbs with large scales (8–11 rows, $\bar{x} = 9.9$); outer surface reddish-brown to brown, inner surface and sockets yellow to orange. Hindlimbs with smaller scales; hindfoot brown with large scales at heel; inner surface and sockets yellow to orange. Tail yellowish orange with a black middorsal stripe.

Males with moderately concave plastra, and longer, thicker tails with the vent beyond the carapacial rim. Females with flat plastra, and smaller tails with the vent beneath the posterior marginals.

Other material.—WPM 1–11 (live; 3 males, 8 females); from locality of type specimen.

Etymology.—The name *mccordi* honors Dr. William P. McCord, who first realized the uniqueness of this turtle, and whose hus-

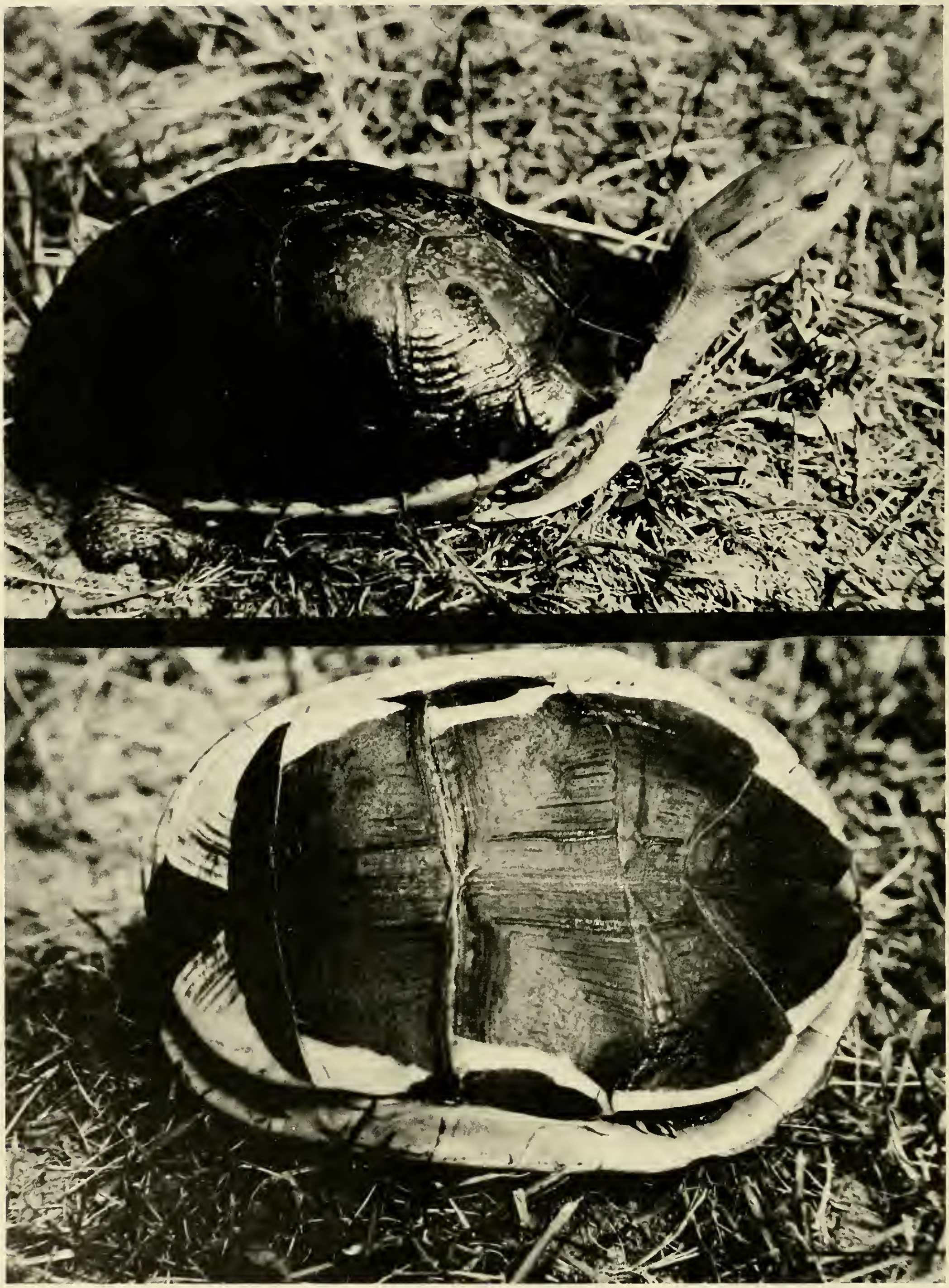

Fig. 1. *Cuora mccordi,* new species (WPM 1); carapace above, plastron below.

Table 1.—Comparison of species of *Cuora* characterized by complete interanal seams.

Character	*mccordi*	*amboinensis**	*chriskarannarum*	*pani*	*trifasciata*	*yunnanensis*
Greatest carapace length (mm)						
Male	131	206	113	120	170	126
Female	134	194	160	156	166	140
Mean depth/carapace length	0.42 (0.38–0.46)	0.45 (0.41–0.51)	0.35 (0.29–0.42)	0.35 (0.30–0.39)	0.38 (0.33–0.44)	0.35 (0.33–0.39)
Carapace keels	1	1 (3 in juvenile)	1	1	3	3
Carapace color pattern	red-brown, yellow anterior rim,dark seams	black stripe	olive-brown, dark medial vertebrals	olive-brown, red-brown vertebrals, yellow rim	brown, three black stripes	brown, dark seams
Plastron pattern	large dark medial blotch	large dark spot at outside of each scute	broad dark seam borders	large triangular shaped dark blotches	large dark medial blotch	dark seams
Head color						
Dorsal	green	olive to dark brown	olive	yellow	olive	brown
Lateral	yellow	dark brown to black	olive	yellow	black	brown
Lateral head stripes	1	3	2	2	1	1
Chin pattern	none	none	none	none	none	large cream colored blotches
Extent of 1st vertebral width	marginals 1	marginals 1	seam marginals 1–2, or marginal 2	marginal 1; occasionally marginal 2	marginals 1	marginals 1

* = mainland Asia only.

bandry efforts involve freshwater turtles of the world.

Remarks.—Cuora mccordi (Fig. 1) belongs to the species group within *Cuora* characterized by plastrons with anal notches and complete interanal seams. The other members of this group are *C. amboinensis, C. chriskarannarum, C. pani, C. trifasciata,* and *C. yunnanensis* (Table 1). *Cuora mccordi* is intermediate in shell depth between the highly domed *C. amboinensis* and the four flattened species. It shares its dark plastron with *C. trifasciata*: Only *C. chriskarannarum, C. trifasciata,* and *C. yunnanensis* are presently known to occur in this region. *Cuora trifasciata* has been recorded 200 km downstream from the type-locality of *C. mccordi* in the Yu Jiang basin at Nanning (Fang 1930), and *C. trifasciata* is also known from the lower reaches of the Red River in Vietnam (Iverson 1986), while *C. chriskarannarum* occurs upstream in the same basin in Yunnan (Ernst & McCord 1987). *Cuora yunnanensis* has only been found in the upper Yangtze basin in Yunnan province (Boulenger 1906). *Cuora chriskarannarum* is a green species with a yellowish-green, black-bordered postorbital stripe, an oblique yellowish-green stripe extending from the upper jaw below the tympanum to the neck, the first vertebral scute extending laterally at least to the seam separating marginals 1–2, and a broad black seam-following plastral pattern (Ernst & McCord 1987). *Cuora yunnanensis* has a brown head with a narrow yellow stripe extending from the nostril through the eye to the neck, a unique mottled chin pattern, a brown carapace with dark seams, the first vertebral not extending to the seam separating marginals 1–2, and a yellow or light brown plastron with narrow dark seams (Ernst 1988).

Acknowledgments

Drs. William P. McCord and George R. Zug critically reviewed the manuscript.

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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15 February 1988

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A revised and updated edition of the *Official Lists and Indexes of Names and Works in Zoology* has been published. For the first time all the names and works on which the International Commission on Zoological nomenclature has ruled since it was set up in 1895 are brought together in a single volume. Entries are arranged in four sections giving in alphabetical order the family-group names, generic names, specific names and titles of works which have been placed on the Official Lists or the Official Indexes. There are about 9,900 entries of which 134 are for works. In addition, there is a full systematic index and a reference list to all relevant Opinions and Directions. The volume is 366 pages, size A4, casebound.

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15 February 1988

The following Opinions have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature,* volume 44 (1987), parts 3 and 4:

Opinion No.

1447 *Trichomonas* Donné, 1836 (Protista, Mastigophora): spelling confirmed.
1448 *Dryophthorus* Germar, 1824 (Insecta, Coleoptera): conserved.
1449 *Cholus* Germar, 1824 (Insecta, Coleoptera): conserved.
1450 *Zygops* Schoenherr, 1825 (Insecta, Coleoptera): conserved.
1451 *Lachnopus* Schoenherr, 1840 (Insecta, Coleoptera): conserved.
1452 *Nemocestes* Van Dyke, 1936 (Insecta, Coleoptera): conserved and *Geoderces incomptus* Horn, 1876 designated as type species.
1453 *Strongylaspis* Spaeth, 1936 and *Strongylocassis* Hincks, 1950 (Insecta, Coleoptera): *Cassida atripes* LeConte, 1859 designated as type species.
1454 *Nomadacris* Uvarov, 1923 (Insecta, Orthoptera): conserved.
1455 *Clausilia* Draparnaud, 1805 (Mollusca, Gastropoda): *Pupa rugosa* Draparnaud, 1801 designated as type species.
1456 *Ammonites* (currently *Euaspidoceras*) *perarmatus* J. Sowerby, June 1822 (Cephalopoda, Ammonoidea): conserved despite the senior primary homonym *Ammonites* (currently *Peronoceras*) *perarmatus* Young & Bird, [May] 1822.
1457 *Astacilla falclandica* Ohlin, 1901 (Crustacea, Isopoda): confirmed as type species of *Neastacilla* Tattersall, 1921.
1458 *Tylocidaris* Pomel, 1883 (Echinodermata, Echinoidea): *Cidaris clavigera* Mantell, 1822 designated as type species.
1459 *Carcharias* Rafinesque, 1810 (Chondrichthyes, Lamniformes): conserved.
1460 *Dasyurus hallucatus* Gould, 1842 (Mammalia, Marsupialia): conserved.
1461 A ruling on the authorship and dates of the text volumes of the *Histoire naturelle* section of Savigny's *Description de l'Egypte.*
1462 CAECILIIDAE Rafinesque-Schmaltz, 1814 (Amphibia, Gymnophiona) and CAECILIIDAE Kolbe, 1880 (Insecta, Psocoptera): a ruling to remove the homonymy.
1463 De Lacépède, 1788–1789, *Histoire Naturelle des Serpens* and later editions: rejected as a non-binominal work.

J D D SMITH
Scientific Administrator

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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15 February 1988

The following applications have been received by the Commission and have been published in volume 44, parts 3 and 4 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is welcomed for publication in the *Bulletin* and should be sent to the Executive Secretary, ICZN, % British Museum (Natural History), Cromwell Road, London, SW7 5BD, U.K.

Applications

Sorites Ehrenberg, 1839 (Foraminiferida): proposed designation of *Nautilus orbiculus* Forskål, 1775 as type species.

Discocyclina Gümbel, 1870 (Foraminiferida): proposed designation of *Orbitolites prattii* Michelin, 1847 as type species.

EUGLENIDAE Stein, 1878 (Protista, Flagellata) and EUGLENIDAE Seidlitz, 1875 (Insecta, Coleoptera): proposals to remove the homonymy, with conservation of ADERIDAE Winkler, 1927 (Insecta, Coleoptera).

Dysidea Johnston, 1842 (Porifera, Keratosa): proposed conservation.

Hypsibius Ehrenberg, 1848 (Tardigrada): proposed designation of *Macrobiotus dujardini* Doyère, 1840 as type species.

Dioctophyme Collet-Meygret, 1802 (Nematoda): proposed confirmation of spelling (CIOMS Case No. 7).

Disculiceps Joyeux & Baer, 1935 (Cestoidea): proposed conservation.

Avicula gryphaeoides J. de C. Sowerby, 1836 (Mollusca, Bivalvia): proposed conservation.

Haminoea Turton & Kingston, 1830 (Mollusca, Gastropoda): proposed confirmation of original spelling.

Cryptocoeloma Miers, 1884 (Crustacea, Decapoda): proposed designation of *Cryptocoeloma haswelli* Rathbun, 1923, as type species.

Loxoconchella Triebel, 1954 (Crustacea, Ostracoda): proposed confirmation of type species.

Chelonus Panzer, 1806 (Insecta, Hymenoptera) and *Anomala* Samouelle, 1819 (Insecta, Coleoptera): proposed conservation.

Curculio assimilis Paykull, 1792 (currently *Ceutorhynchus assimilis*; Insecta, Coleoptera): proposed conservation of the specific name.

Dytiscus cinereus Linnaeus, 1758 (currently *Graphoderus cinereus*; Insecta, Coleoptera): proposed replacement of neotype.

Dytiscus ater De Geer, 1774 (currently Ilybius ater) and *Dytiscus planus* Fabricius, 1781 (currently *Hydroporus planus*; Insecta, Coleoptera): proposed conservation of the specific names.

Parasigara Poisson, 1957 (Insecta, Heteroptera): proposed confirmation of *Corisa transversa* Fieber, 1848 as type species.

Dacus parallelus Wiedemann, 1830 (currently *Anastrepha parallela*; Insecta, Diptera): proposed replacement of lectotype.

Pararatus Ricardo, 1913 (Insecta, Diptera): proposed designation of *Pararatus ricardoae* Daniels, 1987 as type species.

Glabellula Bezzi, 1902 (Insecta, Diptera): proposed designation of *Platygaster arcticus* Zetterstadt, 1838, as type species.

ETHMIIDAE Busck, 1909 (Insecta, Lepidoptera): proposed precedence over AZINIDAE Walsingham, 1906.

Chelifer Geoffroy, 1762 (Arachnida, Pseudoscorpionida): proposed conservation.

Asterias squamata Delle Chiaje, 1828 (currently *Amphipholis squamata*; Echinodermata, Ophiuroidea): proposed conservation of the specific name.

Climacograptus manitoulinensis Caley, 1936 (currently *Paraclimacograptus manitoulinensis*; Graptolithina): proposed conservation of the specific name.

Heliases ternatensis Bleeker, 1856 (currently *Chromis ternatensis*; Osteichthyes, Perciformes): proposed conservation, and adoption of the name *Chromis viridis* (Cuvier, 1830) for the fish commonly called *C. caerulea* (Cuvier, 1830).

Neamia octospina Smith & Radcliffe, 1912 (Osteichthyes, Perciformes): proposed conservation of the specific name.

Sarotherodon melanotheron Rüppell, 1852 (Osteichthyes, Perciformes): proposed conservation of the specific name.

Megaloceros Brookes, 1828 (Mammalia, Artiodactyla): proposed emendation of the original spelling.

Platanista Wagler, 1830 (Mammalia, Cetacea): proposed conservation.

Anabas oxyrhynchus Boulenger, 1902 (currently *Ctenopoma oxyrhynchum*; Osteichthyes, Perciformes): proposed conservation of the specific name.

J D D SMITH
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Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

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CONTENTS

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GEOGRAPHIC VARIATION AND PROBABLE SOURCES OF THE NORTHERN MOCKINGBIRD IN THE BAHAMA ISLANDS

Donald W. Buden

Abstract.—Northern Mockingbirds in the extreme northern Bahamas on the Little Bahama Bank mensurally and chromatically are more similar to examples from Florida than to those from the more southern Bahamas. They are included in *Mimus polyglottos orpheus,* whereas the Bahaman populations south of the Little Bank and those in the Greater Antilles are considered *M. p. orpheus.* The Northern Mockingbird probably colonized the Bahamas by natural dispersal overwater from both the north (southeastern United States) and the south (Greater Antilles). Birds captured on Jamaica and Great Inagua were released on New Providence, but several decades after the species was first recorded there. Introductions by man from North America have been claimed but are unconfirmed. The Northern Mockingbird has increased in number markedly since the late 1800s probably in large measure as a result of man-induced alteration of natural habitats.

The Northern Mockingbird, *Mimus polyglottos,* is widespread and locally common to scarce in the Bahamas, including the Turks and Caicos Islands (Fig. 1). It occurs mainly in the settlements and in open areas (e.g., fields and widely scattered trees, and sparse, coastal scrub), and has a somewhat spotty distribution, apparently being absent where seemingly suitable habitat is available. Recent reports suggesting it first arrived on New Providence, or in the Bahamas, generally during the early 1900s (Brudenell-Bruce 1975; Campbell 1976, 1978; Green 1977) are contradicted by earlier records (Table 1). Paulson (1966) and Miller (1978) alluded to a recent spread of *M. polyglottos* southward in the chain to Cat and San Salvador islands, respectively, but they did not discuss its distribution elsewhere in the archipelago. The present paper includes a chronology of the first records of *M. polyglottos* on 45 Bahama Islands, and it reviews geographic variation, taxonomy, and probable sources of Bahaman populations.

Methods.—The linear measurements (in mm) are wing length (wing flat against rule), tail length (from base to tip of longest rectrix), bill length (exposed culmen), bill depth and bill width (both at the level of the anterior halves of the nares), and tarsus length (from the posterior surface of the proximal end of the tarsometatarsus to the last undivided scute near the base of the toes); the bill, tail, and tarsus were measured with dial calipers. Measurements were submitted to a single classification analysis of variance and to a-posteriori testing for differences between paired means using the GT2-method (Sokal & Rohlf 1981).

Color comparisons were made largely by eye, but ventral coloration in selected samples was measured also with an Applied Color System Spectro-Sensor II Reflectance Spectrophotometer coupled to a DEC PDP 11/23 Mini Computer, the data processed via an ACS proprietary Chroma-Pac program. Values on the "L" scale (0 = black to 100 = white) were obtained for the upper part of the breast and the lower part of the

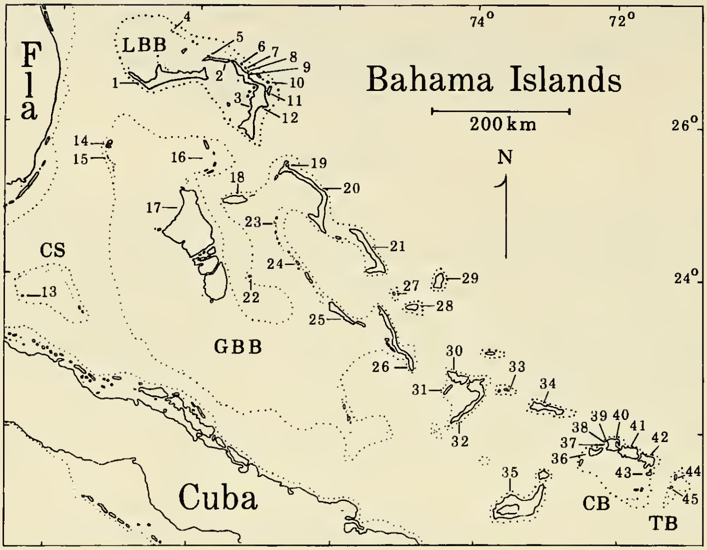

Fig. 1. Map of the Bahama Islands showing where *Mimus polyglottos* has been recorded in the archipelago; LBB = Little Bahama Bank, CS = Cay Sal Bank, GBB = Great Bahama Bank, CB = Caicos Bank, TB = Turks Bank. See Table 1 for place names.

abdomen. Among the specimens examined by spectrophotometry, all those from Florida and Jamaica, all but two from Great Inagua, and all but two from the Little Bahama Bank were collected during the late 1800s. Those from the Turks and Caicos Islands were collected in 1961 and 1972, and those from the Great Bahama Bank were taken in different years from 1890 to 1961.

The amount of white on the fourth and fifth rectrices (third and second, respectively, in the older literature, with the outermost the first) is the estimated percent of surface area covered; frequency distributions were tested for association using Fisher's Test (Armsen 1955, Langley 1970). Rectrices were examined unilaterally on each specimen, but not necessarily all on the same side across samples.

Unless stated otherwise, the Hispaniolan sample includes specimens from the satellite islands Vache, Gonave, Tortue, and Saona, and the locality "Florida" refers to the peninsula only; the Keys are treated separately. Sexes have been treated separately in all comparisons.

Distribution.—The Northern Mockingbird was first recorded in the Bahamas by Bryant (1866). He considered it "abundant" in the southern Bahamas on Great Inagua during the winter of 1865/66, but did not see it elsewhere in the archipelago on 12 other islands and island groups visited during the mid-1800s (Bryant 1859, 1866). Cory (1880) also saw many on Great Inagua, and none on any of the other Bahama Islands he visited in 1879—Andros, New Providence, the Exumas, Long Island, and the Mira Por Vos Cays.

The first record of *M. polyglottos* on the Little Bahama Bank is a specimen taken on [Great] Abaco in Mar 1886 (Ridgway 1891) during apparently the first ornithological survey of the bank. Allen (1905) stated that the Northern Mockingbird seemed to be a recent arrival to the Northern Bahamas, and went on to say that a resident on Little Abaco had noticed an increase in the mockingbird population there over several years in the very early 1900s. But 32 specimens in the FMNH collected on Grand Bahama by D. J. Sweeting, 11 Dec 1891 to 28 Jan 1892,

Table 1.—First records of *Mimus polyglottos* on different Bahama Islands. Sources of unpublished data are given as the names of observers and collectors enclosed in brackets. B & S = Buden and Schwartz, JCD = J. C. Dickinson, Jr., S & K = Schwartz and Klinikowski, T & W = Todd and Worthington.

Island	Date and reference	Island	Date and reference
1. Grand Bahama	1891 (Cory, 1891a)	24. Staniel Cay	1977 [T. Schoener]
2. Little Abaco	1902 (Bonhote, 1903)	25. Great Exuma	1964 (Bond, 1964)
3. Great Abaco	1886 (Ridgway, 1891)	26. Long Id.	1909 (T & W, 1911)
4. Grand Cays	1976 [T. Schoener]	27. Conception Id.	—— (Riley, 1905)
5. Hawksbill Cays	1976 [T. Schoener]	28. Rum Cay	1976 [M. H. Clench]
6. Powell Cay	1976 [M. H. Clench]	29. San Salvador	1973 (Miller, 1978)
7. Nun Jack Cay	1942 [A. C. Twomey]	30. Crooked Id.	1976 (Bond, 1978)
8. Green Turtle Cay	1886 [A. H. Jennings]	31. Fortune Id.	1972 [D. W. Buden]
9. Sand Bank Point Cay	1976 [T. Schoener]	32. Acklins Id.	1957 (?) (Bond, 1958)
10. Man of War Cay	1976 [M. H. Clench]	33. West Plana Cay	1976 [M. H. Clench]
11. Elbow Cay	1904 (Allen, 1905)	34. Mayaguana	1891 (Cory, 1892a)
12. Cherokee Sound Cays	1976 [T. Schoener]	35. Great Inagua	1866 (Bryant, 1866)
13. Cay Sal	1968 (B & S, 1968)	36. Providenciales	1970 [D. W. Buden]
14. Bimini Ids.	1891 (Cory, 1891b)	37. Pine Cay	1974 [JCD]
15. Cat Cay	—— (Bond, 1950)	38. Dellis Cay	1972 [D. W. Buden]
16. Berry Ids.	1891 (Cory, 1891b)	39. Parrot Cay	1972 [D. W. Buden]
17. Andros	1890 (Northrop, 1891)	40. North Caicos	1971 [D. W. Buden]
18. New Providence	1898 (Bonhote, 1899)	41. Middle Caicos	1972 [D. W. Buden]
19. Harbour Id.	1952 (Bond, 1952)	42. East Caicos	1978 [D. W. Buden]
20. Eleuthera	—— (Bond, 1950)	43. South Caicos	1961 (S & K, 1963)
21. Cat Id.	1958 (Bond, 1959)	44. Grand Turk	1959 (Bond, 1959)
22. Green Cay	1976 [M. H. Clench]	45. Salt Cay	1979 [D. W. Buden]
23. Allan's Cays	1974 [T. Schoener]		

indicate that *M. polyglottos* was well-established on the Little Bank, at least locally, in the late 1800s.

The first record for the Great Bank was provided by Northrop (1891), who considered *M. polyglottos* "common" at Nichols Town, northern Andros Island, in 1890. One slightly earlier record for New Providence is questionable and another probably is a typographical error: Moore (1877) mentioned a female "Mimus polyglottos (?)" killed on 28 Feb [1877?], and Jennings (1888) reported *M. polyglottos* on "Green Turtle Cay, NP" probably intending Abaco for NP = New Providence. Jennings included several Abaco records in his "New Providence list," and USNM 275024 is a Northern Mockingbird labeled as having been collected on Green Turtle Cay by him, 3 Jun 1886. Green Turtle Cay, which lies off the eastern coast of Great Abaco (locality number 8 in Fig. 1), is the only island of that name known to me; it was settled very early in Bahaman history (Durrell 1972) and thus is unlikely to have been confused with any other island. The first confirmed record for New Providence is an adult female collected on 30 September 1898 by J. L. Bonhote, who stated it was "the only specimen of this species" he saw during his stay of "about a year" (Bonhote 1899).

By 1898, the Northern Mockingbird had been recorded on nine different islands and island groups in the Bahamas (Great Inagua and Mayaguana in the south; Grand Bahama, Great Abaco, Green Turtle Cay, Bimini Islands, Berry Islands, Andros, and New Providence in the North), but it was still unconfirmed from the central part of the chain. W. W. Worthington (*in* Todd and Worthington 1911) considered *M. polyglottos* "common at Clarence Town," Long

Table 2.—Selected measurements (in millimeters) of Northern Mockingbirds from eight localities (Loc.) in Florida, the Bahamas, and the Greater Antilles; FL = Florida, LB = Little Bahama Bank, GI = Great Inagua, TC = Turks and Caicos Islands, CU = Cuba, HI = Hispaniola,[1] JA = Jamaica, PR = Puerto Rico.

	Males			Females		
Loc.	n	Mean ± SD	(Range)	n	Mean ± SD	(Range)
			Wing length			
FL	22	111.5 ± 3.4	(105–119)	22	109.2 ± 3.6	(104–116)
LB	7	112.4 ± 3.1	(108–117)	3	112.0 ± 4.4	(109–117)
GI	9	106.4 ± 3.6	(101–112)	1	104.0	
TC	5	111.4 ± 2.2	(110–115)	1	99.0	
CU	15	108.6 ± 4.3	(102–117)	12	101.8 ± 3.4	(96–106)
HI	24	110.9 ± 3.6	(103–116)	14	103.6 ± 3.5	(97–109)
JA	21	108.9 ± 3.3	(100–113)	24	101.4 ± 2.5	(96–106)
PR	18	110.4 ± 3.1	(105–115)	11	103.1 ± 2.8	(98–107)
			Tail length			
FL	21	114.7 ± 5.1	(104.2–121.2)	22	112.7 ± 4.3	(103.0–119.8)
LB	14	110.8 ± 5.5	(97.7–119.0)	14	111.8 ± 3.7	(104.5–119.8)
GI	8	107.1 ± 4.0	(99.2–112.5)	7	106.3 ± 4.0	(102.3–114.3)
TC	5	110.4 ± 3.7	(105.0–113.6)	1	108.8	
CU	14	109.5 ± 4.9	(98.5–116.5)	12	104.5 ± 3.9	(97.4–110.0)
HI	23	110.5 ± 5.1	(101.4–118.0)	13	103.3 ± 3.3	(98.0–109.3)
JA	21	110.3 ± 4.2	(101.0–116.2)	23	102.8 ± 3.1	(97.3–109.0)
PR	16	111.3 ± 2.7	(107.7–117.5)	9	104.7 ± 3.3	(99.5–110.5)
			Bill length			
FL	22	16.2 ± 0.8	(14.8–17.4)	20	15.9 ± 0.9	(14.4–18.0)
LB	19	15.7 ± 1.0	(14.0–17.5)	15	15.3 ± 0.8	(14.2–16.8)
GI	20	15.8 ± 0.9	(14.1–17.7)	14	15.8 ± 0.7	(14.3–16.9)
TC	5	16.0 ± 0.8	(15.3–17.3)	1	15.3	
CU	14	15.9 ± 1.1	(14.4–18.3)	13	15.7 ± 0.7	(15.2–17.4)
HI	26	16.5 ± 1.0	(14.3–18.5)	20	16.3 ± 1.1	(14.4–18.1)
JA	20	16.6 ± 0.6	(15.2–17.6)	21	16.2 ± 0.5	(15.5–17.0)
PR	18	16.5 ± 1.1	(15.0–18.7)	11	15.8 ± 0.6	(14.8–17.0)

[1] Including satellite islands Vache, Gonave, Tortue, and Saona.

Island, in 1909, although as early as 1879, local villagers told Cory (1880) that a small kind of mockingbird (not the Bahama Mockingbird, *M. gundlachii*) was seen there occasionally, at least in summer. *M. polyglottos* was unknown on other islands in the more central part of the archipelago until Bond (1950) recorded it on Eleuthera, presumably based on sight records by J. Van Tyne and H. Mayfield during the mid-to-late 1940s (see Bond 1950:ix).

Mimus polyglottos has become much more numerous and widespread in the archipelago since the early 1900s. However, that nearly half the records in Table 1 are from 1970 and later probably is due largely to sampling and not necessarily to recent colonizations. Many of the islands were inadequately surveyed and, in most cases, approximate dates of colonization cannot be established. Among the possible exceptions is San Salvador, which has been visited by ornithologists fairly frequently over the past 100 years. *M. polyglottos* was not encountered there during field observations in 1963 (Paulson 1966), nor during earlier explorations, but has been present in small number "at least since December 1973" (Miller 1978). Also, the Northern Mockingbird probably colonized the Turks and Caicos

Table 3.—Wing and tail measurements (in millimeters) and amount of white (D = dark, <25%, I = intermediate, 25–75%, P = pale, >75%) on rectrices of 21 Northern Mockingbirds from the Cay Sal, Great Bahama, Turks, and Caicos banks. AN = Andros, BE = Berry Islands, BI = Bimini Islands, CS = Cay Sal, EL = Eleuthera, GT = Grand Turk, LI = Long Island, NP = New Providence, SC = South Caicos. m = male, f = female, ? = sex unidentified.

				Amount of white								
				4th rectrix inner web			5th rectrix inner web			5th rectrix outer web		
Locality	Sex	Wing length	Tail length	D	I	P	D	I	P	D	I	P
Cay Sal												
Bank: CS	f	101	104.8		X				X		X	
Great Bahama												
Bank: BI	?	–	–		X				X	X		
BE	m	–	118.7			X			X			X
	m	–	117.5	X				X			X	
AN	m	109	106.7			X			X	X		
	m	107	107.9		X				X	X		
NP	m	109	109.7			X			X	X		
	m	115	121.9		X				X	X		
	f	110	107.0		X				X	X		
EL	m	110	109.3		X				X		X	
	m	114	117.5		X				X		X	
	f	102	106.5		X				X	X		
	f	100	105.1	X					X		X	
LI	m	102	103.6			X			X		X	
	m	104	111.1		X				X		X	
Turks												
Bank: GT	m	110	105.0	X					X			X
	m	112	113.6		X				X		X	
	m	110	108.5	X					X		X	
	m	115	113.8		X				X			X
Caicos												
Bank: SC	m	110	111.0			X			X		X	
	f	99	108.8		X				X	X		

Islands after 1930. It was not mentioned in earlier expedition reports and there is no evidence it was encountered by Paul Bartsch and expedition members who visited at least 22 of the islands in July and August 1930 (Bartsch, unpublished field notes; USNM bird catalog). Bond (in litt.) found it widespread on Grand Turk in 1959.

Breeding doubtless occurs on most of the islands, but is confirmed only for Grand Bahama (nestling — MCZ 17142, collected on 14 Apr 1936 by J. C. Greenway, Jr.), Little Abaco (Bonhote 1903), Great Abaco (King et al. 1979), Elbow Cay (Allen 1905), Bimini Islands (Vaurie 1953), Cat Island (Buden 1987b), Great Inagua (fledgling—USNM 323717, collected on 10 Aug 1930 by P. Bartsch), and Providenciales (Aldridge 1984).

Size comparisons.—Northern Mockingbirds from Florida, the Bahamas, and the Greater Antilles overlap broadly in most measurements and the females tend to be smaller than the males (Tables 2 and 3). On the average, the specimens from Great Inagua (southern Bahamas) are the smallest, whereas those from the Little Bahama Bank (northernmost Bahamas) and Florida are among the largest. At the 0.05 level of significance, the Little Bank and Florida sam-

Table 4.—Probability of difference (* = $P < 0.05$) between paired means in six sets of measurements of Northern Mockingbirds using the GT2-method (Sokal and Rohlf 1981) and data in Tables 2 and 4 (X = combinations excluded from comparisons). Males are above the diagonal and females are below in each set. Localities are listed from north to south generally; FL = Florida, LB = Little Bahama Bank, GI = Great Inagua, CU = Cuba, HI = Hispaniola, JA = Jamaica.

Wing length

	FL	LB	GI	CU	HI	JA
FL	—		*			
LB[1]	X	—	*	*		*
GI[2]	*	X	—		*	
CU	*	X		—		
HI	*	X			—	
JA	*	X				—

Tail length

	FL	LB	GI	CU	HI	JA
FL	—		*	*		
LB		—				
GI	*	*	—			
CU	*	*		—		
HI	*	*			—	
JA	*	*				—

Bill length

	FL	LB	GI	CU	HI	JA
FL	—					
LB		—			*	*
GI			—			
CU				—		
HI		*			—	
JA		*				—

Bill depth

	FL	LB	GI	CU	HI	JA
FL	—		*			
LB		—	*			
GI	*	*	—		*	
CU	*	*		—		
HI					—	
JA	*	*				—

Bill width[3]

	FL	LB	GI	CU	HI	J
FL	—					
LB		—				
GI			—			
CU				—		
HI					—	
JA	*				*	—

Tarsus length

	FL	LB	GI	CU	HI	JA
FL	—		*			
LB		—	*			
GI	*		—	*	*	*
CU				—		
HI					—	
JA	*					—

[1] The small sample of three females excluded from these comparisons averaged (112.4 mm) closer to the Florida sample (111.5) than to the one from Inagua (106.4).

[2] The measurements of six females from the Bahamas south of the Little Bahama Bank were pooled: Cay Sal (1), New Providence (1), Eleuthera (2), Great Inagua (1), South Caicos (1).

[3] A single classification analysis of variance of measurements of males revealed no significant difference at the 0.05 level and the GT2-method was not applied.

ples do not differ from each other in wing, tail, bill, and tarsus measurements (Table 4). On the other hand, males from the Little Bank are significantly larger than those from Inagua in wing length, bill length, bill depth, and tarsus length, and the females are significantly larger in tail length and bill depth, and probably (see footnote, Table 4) in wing length as well. Inaguan males are smaller ($P < 0.05$) than those from Cuba, Hispaniola, and Jamaica in tarsus length and smaller than Hispaniolan males also in bill depth; no statistically significant differences were found between Inaguan females and those from Cuba, Hispaniola, and Jamaica.

Measurements of birds from Puerto Rico were not submitted to testing, but they tend to average larger than other Antillean samples in most cases (Table 2). Wing and tail measurements of birds from the Cay Sal, Great Bahama, Turks, and Caicos banks (Table 3) overlap broadly with those from the other samples, but there is little comparative material from these islands. Specimens from the Florida Keys tend to average smaller than those from the peninsula (e.g., wing 110.8 in 4 males, 105.0 in 6 females; tail 112.9 in 4 males, 106.1 in 6 females).

Color comparisons.—Northern Mockingbirds from Florida and the Little Bahama Bank are darker (more gray, less white) on the venter than those from the southern Bahamas and the Greater Antilles, the females being the same as, or very slightly darker than, males. The whitest birds are from the Turks and Caicos Islands, but this condition may be due in part to their having been collected relatively recently (see "Methods"). Examples from the Great Bank are somewhat intermediate in ventral coloration but average closer to samples from the southern Bahamas and the Antilles than to those from Florida and the Little Bank. The four specimens from Eleuthera are subadults faintly spotted on the upper part of the breast and on the sides of the throat and the transition between the darker coloration of the breast and paler abdomen is more abrupt than in most other Bahaman specimens. Visual impressions of differences in ventral coloration are confirmed by reflectance spectrophotometry in selected samples (Fig. 2). Three males and three females from Puerto Rico are anomalous in being much darker on the breast than the others in the series (the males also being at or near the upper extreme in most measurements). All six (FMNH 28659, 28661–65) were collected at an unspecified locality by C. P. Streator in Oct and Nov 1888. I found no appreciable geographic differences in dorsal coloration, nor in the amount of white on the wing, among Bahaman samples.

Variation in the amount of white on the tail tends to be more uniformly clinal than does ventral coloration, also with the "darkest" birds in the north and the "whitest" in the south, the females usually with less white than the males (Table 5). I found no significant differences ($P > 0.05$, Fisher's Test) in frequency distributions for "tail color" between Florida and Little Bank samples. But compared with specimens from Inagua, both sexes from the Little Bank have less white on the inner web of the fourth rectrix, and the males also have less white on the outer web of the fifth rectrix ($P < 0.05$), the Inaguan birds being more like those from the Antilles. Among Antillean samples, specimens from Cuba and Puerto Rico tend to have less white on the tail than those from Hispaniola or Jamaica.

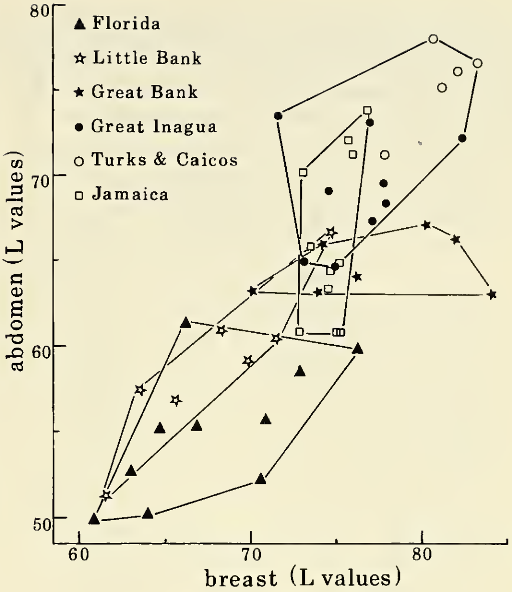

Fig. 2. Spectrophotometry L values (0 = black to 100 = white) of the upper part of the breast and lower part of the abdomen in males of *Mimus polyglottos* from Florida, the extreme northern Bahamas (Little Bahama Bank), the Great Bahama Bank, the southern Bahamas (Great Inagua, Turks and Caicos), and Jamaica.

Nine of ten males from six different islands and island groups on the Great Bahama Bank have more than 75% of the inner web of the fifth rectrix white, thus, as a group, resembling the southern Bahaman-Antillean samples in this character. But they are more nearly intermediate between Florida-Little Bank samples and those from the southern Bahamas in the amount of white on the outer web of the fifth and the inner web of the fourth rectrices. Of these nine, the specimen with the least amount of white on the tail is from the extreme north, in the Berry Islands. Specimens from the Florida Keys are similar to those from the peninsula in coloration.

Table 5.—Distribution of the amount of white on rectrices of Northern Mockingbirds from six localities in Florida, the Bahamas, and the Greater Antilles with results of Fisher's Test (FT) for association between selected paired samples (an asterisk indicates $P \leq 0.05$). Localities are listed from north to south generally; FL = Florida, LB = Little Bahama Bank, GI = Great Inagua, CU = Cuba, HI = Hispaniola, JA = Jamaica, PR = Puerto Rico. Numbers in parentheses are percentages.

	Males					Females				
		Amount of white					Amount of white			
Locality	n	<25%	25–75%	>75%	FT[1]	n	<25%	25–75%	>75%	FT[1]
				4th rectrix, inner web						
FL	22	12 (55)	10 (45)		LB	21	16 (76)	5 (24)		LB[2]
LB	18	6 (33)	11 (61)	1 (6)	GI*	12	6 (50)	6 (50)		GI*
GI	19	2 (10)	6 (32)	11 (58)	FL*	14	2 (14)	7 (50)	5 (36)	FL*
CU	15		1 (7)	14 (93)	GI*	15	2 (13)	7 (47)	6 (40)	GI
HI	25		1 (4)	24 (96)	GI*	18	1 (6)	3 (17)	12 (67)	GI
JA	21		1 (5)	20 (95)	GI*	20			20 (100)	GI*
PR	19		5 (26)	14 (74)	GI	11		5 (45)	6 (55)	GI
				5th rectrix, inner web						
FL	22		7 (32)	15 (68)	LB	21		10 (48)	11 (52)	LB
LB	18		5 (28)	13 (72)	GI	12		4 (33)	8 (67)	GI
GI	19		1 (5)	18 (95)	FL*	14		3 (21)	11 (79)	FL
CU	15			15 (100)	GI	15		1 (7)	14 (93)	GI
HI	25			25 (100)	GI	18			18 (100)	GI
JA	21			21 (100)	GI	20			20 (100)	GI
PR	19			19 (100)	GI	11			11 (100)	GI
				5th rectrix, outer web						
FL	22	20 (91)	2 (9)		LB[2]	21	20 (95)	1 (5)		LB
LB	18	14 (78)	4 (22)		GI*	12	10 (84)	1 (8)	1 (8)	GI*
GI	19	2 (11)	4 (21)	13 (68)	FL*	14	2 (14)	6 (43)	6 (43)	FL*
CU	15	1 (7)	5 (33)	9 (60)	GI	15	9 (60)	6 (40)		GI
HI	25		3 (12)	22 (88)	GI	18	3 (17)	1 (6)	14 (78)	GI
JA	21	1 (5)		15 (95)	GI	20	1 (5)	1 (20)	15 (75)	GI
PR	19	3 (16)	1 (5)	15 (79)	GI	11	4 (36)	3 (28)	4 (36)	GI

[1] The two categories <25% and 25–75% have been pooled.

[2] Both samples fall into one and the same color-category or have the same ratio and are considered not different; the test is not applicable.

Taxonomy.—Slight differences in size and coloration among local populations of *Mimus polyglottos* in the Bahamas have led to diverse taxonomic interpretations. Sharpe (1881) proposed the name *Mimus elegans* for the birds on Great Inagua; his list of specimens included only one of that form. Cory (1891c) included all Bahaman populations along with those of Jamaica, Cuba, Grand Cayman, and Hispaniola under *M. p. orpheus* (Linnaeus). Later, he (Cory 1892b) considered Inaguan birds an endemic subspecies (*M. p. elegans*) and included "northern birds" (from Abaco, Bimini, and Andros) under *M. p. polyglottos* (Linnaeus), as did Ridgway (1907), who previously (Ridgway 1891) reported a specimen from Abaco tentatively under *M. p. elegans.* The nominate race is widespread in eastern North America. Riley (1905) listed all records of Northern Mockingbirds in the Bahamas under *M. p. polyglottos.* Todd (*in* Todd & Worthington 1911) considered the birds from Inagua *M. p. orpheus* and those in the northern Bahamas *M. p. polyglottos.* Bangs (1916) proposed the name *M. p. delenificus* for Northern Mockingbirds in the northern Bahamas (at least on Andros and

Little Abaco), and his description indicated this race to be somewhat intermediate chromatically between "*elegans*" and the nominate subspecies.

Hellmayr (1934), after examining 135 FMNH specimens from the Bahamas (including 38 from Grand Bahama and 88 from Great Inagua) included all Bahaman populations under *M. p. elegans.* He stated "Bahaman birds are easily told from typical *polyglottos* by their much whiter underparts with very little, if any, grayish suffusion on the chest." He said he was "unable to split them into two races, since the lesser amount of white on the third rectrix, which served as the principal character for the discrimination of *M. p. delenificus* (from Andros Island), proves to be exceedingly variable." He reported also that the amount of white on the wing was variable among Bahaman samples and that although Inaguan birds tended to have more white on the tail and averaged smaller in size than those elsewhere in the archipelago, they were insufficiently distinct "to justify their retention as a separate race." Hellmayr (1934) did not compare Bahaman birds with those from the Antilles, but he considered the latter *M. p. orpheus.* More recent authors (e.g., Bond 1956, Davis & Miller 1960) include all Bahaman and Antillean populations together under *M. p. orpheus.*

I agree with the more recent taxonomic treatment generally, but differ in including the Little Bahama Bank within the range of *M. p. polyglottos.* Specimens from the Little Bank are grayer on the venter and have less white on the tail than those from the more southern Bahama Islands; they more closely resemble specimens from Florida (including the Keys) in these characters. They also tend to average slightly larger (wing length, bill depth, and tarsus length in males; wing length, tail length, and bill depth in females) than those from Great Inagua in the southern Bahamas, but they are not significantly different ($P > 0.05$) from peninsular Florida birds in any of the measurements. I tentatively include all of the Great Bahama Bank (together with the Cay Sal Bank) in the range of *M. p. orpheus,* mainly on the basis of ventral coloration and the amount of white on the tail in the relatively few specimens examined, but in some characters examples from the Great Bank are more nearly intermediate, and occasionally closer to the Florida-Little Bank samples.

Discussion.—The avifauna of the Bahamas was derived overwater largely, if not entirely, from the Antilles and (to a lesser degree) the southeastern United States (Buden 1987a). In the case of *Mimus polyglottos,* the occurrence of the nominate subspecies on the Little Bahama Bank, and *M. p. orpheus* on the more southern islands suggests colonization via both routes.

Campbell (1976, 1978) suggested *M. polyglottos* was introduced to the Bahamas from North America, and Brudenell-Bruce (1975) stated it was "introduced on New Providence only 60 or 70 years ago." But there is no evidence to support these claims and no need to hypothesize an introduction to account for its presence in the Bahamas. *M. polyglottos* is vagile, as indicated by its widespread distribution in the archipelago and its occurrence on many of the small, remote, and largely uninhabited islands (e.g., Grand Cays, Cay Sal, Green Cay, West Plana Cay). That the nominate race probably reached the northern Bahamas from Florida by natural means is very likely and does not exclude the possibility that birds also were introduced to the islands from eastern North America. Many *M. p. orpheus* were introduced to New Providence from Great Inagua and Jamaica in the early 1930s (Bond fide Miller 1978), and Bond (1952) stated Northern Mockingbirds "inhabiting New Providence, Harbour Island and Eleuthera may be descendants of those introduced from Jamaica following the 1928 hurricane."

The "Antillean race" (*M. p. orpheus*) was well established in the southern Bahamas on Great Inagua at the time of the first ornithological explorations in the mid-1800s (Bryant 1866). In all probability, it colonized the southern Bahamas from Cuba or Hispaniola, or both. The abundance of Northern Mockingbirds at opposite ends of the archipelago (Inagua and the Little Bank) when they were absent or very rare on many intervening islands also suggests a bipartite route of colonization.

Land development (e.g., housing and road construction) probably has contributed greatly to the spread and population growth of the Northern Mockingbird in the Bahamas by providing an abundance of open, sparsely vegetated habitats and additional sources of food and freshwater. In the Bahamas, *M. polyglottos* is much more numerous in edificarian and ruderal habitats than in the broad expanses of scrublands and woodlands, and it has become one of the most common "yard-birds" in Nassau and immediate vicinity, the most densely populated area in the Bahamas. Jehl & Parkes (1983) reported increased availability of freshwater at a new military base on Socorro Island, Mexico, as probably a key factor responsible for the recent successful colonization of *M. polyglottos*. Bond (1984) reported *M. polyglottos* evidently has increased in number in Hellshire Hills, Jamaica, as a result of a recently constructed road, and it may be displacing a relict population of the Bahama Mockingbird (*M. gundlachii*) there. The Bahama Mockingbird occurs sympatrically with *M. polyglottos* on many Bahama Islands, but it prefers the more densely vegetated scrublands and woodlands. Its numbers are likely to decrease in the wake of further land development and the degradation of natural habitats. *M. polyglottos,* on the other hand, has adapted well to urban environments and land modification in the islands, and it may be expected to become increasingly more numerous in the archipelago.

Specimens examined.—Mimus polyglottos orpheus.—Florida: peninsula, MCZ (22M 22F); Keys, FMNH (3F), MCZ (4M 5F). Bahama Islands: Grand Bahama, AS (1F), FMNH (12M 12F), MCZ (2M); Great Abaco, FMNH (3M 2F 1?), USNM (1M); Little Abaco, MCZ (1M); Green Turtle Cay, USNM (1M).

Mimus polyglottos orpheus.—Bahama Islands: Cay Sal, AS (1F); Bimini Islands, FMNH (1?); Berry Islands, FMNH (2M); Andros Island, AMNH (1M), MCZ (1M); New Providence, AMNH (1M), AS (1F), LSUMZ (1M); Eleuthera, AS (2M 2F); Long Island, MCZ (2M); Great Inagua, AS (1M), FMNH (16M 14F), MCZ (3M 3?), USNM (1M 1F 1?). Turks and Caicos Islands: South Caicos, AS (1M 1F); Grand Turk, AS (1M), LSUMZ (3M). CUBA (by province): La Habana, MCZ (1M), USNM (2M 1F); Matanzas, MCZ (3F), USNM (1M); Cienfuegos, USNM (1F); Holguin, MCZ (3M 2F), Santiago de Cuba, MCZ (1M), USNM (1M 3F); Guantanamo, USNM (6M 5F). Hispaniola: Haiti, MCZ (2M), USNM (3M 3F); Dominican Republic, FMNH (5M 6F), MCZ (7M 5F), USNM (2M 2F). Île-à-Vache: USNM (1M 2F). Île de la Gonâve: USNM (2M 2F). Île de la Tortue: USNM (2M 1F). Isla Saona: MCZ (2M). Jamaica: MCZ (21M 24F). Puerto Rico: FMNH (10M 6F), USNM (9M 6F).

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A NEW SUBSPECIES AND NEW RECORDS OF *PAPASULA ABBOTTI* (AVES: SULIDAE) FROM ARCHEOLOGICAL SITES IN THE TROPICAL PACIFIC

David W. Steadman, Susan E. Schubel, and Dominique Pahlavan

Abstract.—An extinct new subspecies of *Papasula abbotti, P. a. costelloi,* is described from seven bones found in archeological sites on Tahuata and Hiva Oa islands, Marquesas. *Papasula a. costelloi* differs from the extant *P. a. abbotti* in size and qualitative features. From an archeological site on Tikopia in the Solomon Islands we report two bones of *P. a. abbotti,* known previously only from Christmas and Assumption islands in the Indian Ocean. The former presence of *P. a. costelloi* in the Marquesas and *P. a. abbotti* in the Solomons suggests that this species was widespread in the Pacific until the human disruptions of the past several thousand years.

The late Holocene record of birds from Polynesian archeological sites has revealed many extinct species and new island records of land birds (Steadman, in press). Herein we report the first undescribed, extinct form of seabird from these sites.

Materials and methods.—Comparative skeletons are from the Division of Birds, National Museum of Natural History (USNM). Skeletons examined include *Sula sula* (USNM 491921, 498134, 498275, 498364), *S. leucogaster* (USNM 289139, 298137, 488048, 499909), *S. dactylatra* (USNM 498028, 498133, 498270, 498271), *Morus serrator* (USNM 18770), *M. capensis* (USNM 558367), and *Papasula a. abbotti* (USNM 560682, 560683). The fossils are from the Vertebrate Zoology Collection, Bernice P. Bishop Museum (BPBM). Osteological terminology usually follows Baumel et al. (1979). Measurements were taken with dial calipers with 0.05 mm increments, rounded to the nearest 0.1 mm.

Systematic Paleontology

Order Pelecaniformes

Family Sulidae

Genus *Papasula* Olson and Warheit

The specimens to be described are referred to *Papasula* (monotypic; contains only *P. abbotti*) rather than to the other two genera of Sulidae, *Sula* and *Morus,* because of the following characters.

Axis vertebra—processus ventralis short, wide, and blunt in lateral aspect (long, narrow, and blunt in *Morus,* long, narrow, and pointed in *Sula*); dorso-medial process large and stout (small in *Morus,* large but not flattened dorsally in *Sula*); facies articularis caudalis wider in dorsal half than in ventral half in *Papasula* and *Morus* (ventral half is wider than dorsal half in *Sula*); lateral portions of facies articularis caudalis more expanded dorsally; lateral portions of facies articularis caudalis expanded ventrally less in *Papasula* and *Morus* than in *Sula*; foramen vertebrale nearly circular in cross-section, with a small process interrupting the dorso-medial surface of the circle (more perfectly circular in *Morus,* dorso-ventrally elongated in *Sula*).

Fourth cervical vertebra—in dorsal or ventral aspect, the entire vertebra is nearly square, with straight lines on all margins (narrower, more elongated cranio-caudally, and more laterally constricted in the midsection in *Morus* and *Sula*); facies articularis larger and more dorsally oriented (small and dorso-medially oriented in *Sula,* intermediate in *Morus*); processus dorsalis stout,

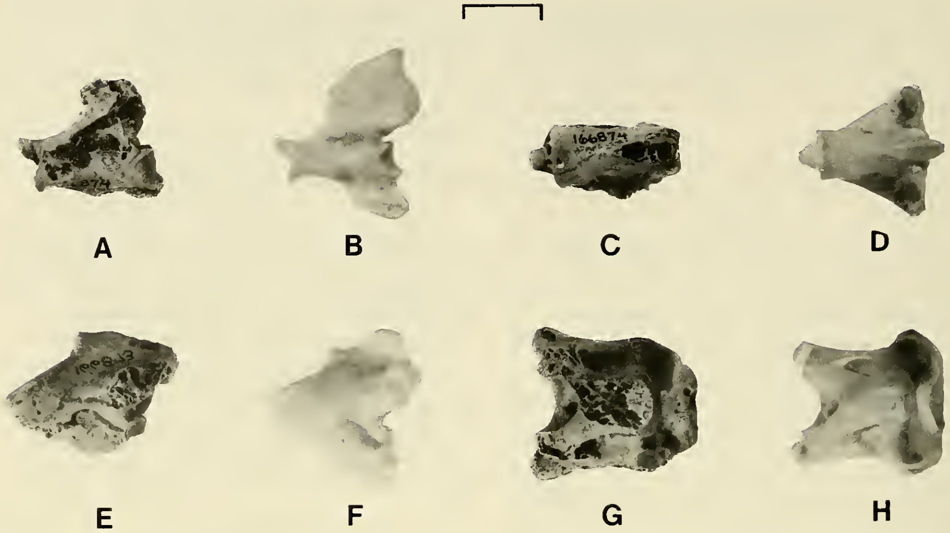

Fig. 1. The axis vertebrae of *Papasula* in left lateral (A, B) and ventral (C, D) aspects. A, C. *P. a. costelloi,* BPBM 166874, Tahuata. B, D. *P. a. abbotti,* USNM 560683, Christmas Island. The fourth cervical vertebra of *Papasula* in left lateral (E, F) and ventral (G, H) aspects. E, G. *P. a. costelloi,* BPBM 166873, Tahuata. F, H. *P. a. abbotti,* USNM 560683, Christmas Island. Image reversed in E, F. Scale bar = 1 cm.

dorsally extended, and rounded (narrow, short, and sharp in *Morus* and *Sula*); dorso-caudal margin straight (with medial indentation in *Morus* and *Sula*); medial facet of dorso-caudal surface larger than in *Sula,* and comparable in size with *Morus* but less expanded laterally; medial facet of dorso-caudal surface oriented more cranially (less ventrally); foramen transversarium smaller in *Papasula* and *Sula* than in *Morus*; facies articularis cranialis more ventrally flared.

Coracoid—sterno-lateral corner of facies articularis humeralis more squared and pointed in *Papasula* and *Morus* than in *Sula*; facies articularis humeralis narrower and less concave in *Papasula* and *Sula* than in *Morus*; shaft more concave on the immediate sternal side of facies articularis humeralis; sterno-medial portion of facies articularis humeralis extends less far sternally (relative to processus procoracoideus); processus procoracoideus stouter, straighter, and more pitted than in *Sula.*

Tibiotarsus—distal junction of fibula and tibiotarsus very bulbous (laterally expanded), short, and located more distally; disto-lateral portion of shaft more cranio-caudally compressed; lateral portion of pons supratendineus more constricted; sulcus extensorius and canalis extensorius shallower; condylus lateralis wider and more cranio-caudally compressed; incisura intercondylaris shallower in *Papasula* and *Sula* than in *Morus*; epicondylus medialis smaller in *Papasula* and *Sula* than in *Morus*; medial margin of epicondylus medialis sharper in *Papasula* and *Sula* than in *Morus.*

Tarsometatarsus—cotyla lateralis shallow; sulcus extensorius much more deeply excavated, extending down the shaft to the foramen vasculare distale; foramina vascularia proximalia smaller in *Papasula* and *Morus* than in *Sula*; foramina vascularia proximalia penetrate straight through to plantar side in *Papasula* and *Sula,* but not in *Morus*; crista lateralis hypotarsi large with a sharp plantar surface; crista medialis hypotarsi narrower in *Papasula* and *Morus* than in *Sula*; crista lateralis hypotarsi and crista intermedialis hypotarsi incompletely fused, resulting in only one hypotarsal canal (two hypotarsal canals in *Morus* and *Sula*);

Fig. 2. The tibiotarsus of *Papasula* in cranial (A–C) and caudal (D–F) aspects. A, D. *P. a. costelloi,* BPBM 166872, Tahuata. B, E. *P. a. costelloi,* BPBM 167105, Holotype, Tahuata. C, F. *P. a. abbotti,* USNM 560683, Christmas Island. A, D = right side. B, C, E, F = left side. Scale bar = 1 cm.

plantar surface of the shaft more sculptured with crista plantaris mediana especially distinct, long, and located more laterally on the shaft (plantar surface especially smooth in *Morus*); fossa parahypotarsalis medialis deep, angular, and non-pneumatic (very shallow, less angular, and non-pneumatic in *Morus,* shallow, less angular, and pneumatic in *Sula*); in lateral aspect, proximal margin of lateral trochlea metatarsi joins the shaft nearly perpendicularly (more obtusely in *Morus* and *Sula*); in dorsal aspect, medial groove of middle trochlea metatarsi shallower; in medial and lateral aspects, the middle trochlea metatarsi protrudes less dorsally from the plane of the shaft; in distal aspect, the medial margin of inner trochlea metatarsi is nearly straight (deeply incised in *Morus* and *Sula*); inner trochlea extends farther distally relative to middle trochlea in *Papasula* and *Sula* than in *Morus*; ridge from inner trochlea metatarsi to fossa metatarsi I more prominent and continuous; distal foramen smaller than in *Sula*; dorsal surface of shaft more excavated, especially on lateral side; dorso-lateral margin of shaft thin and sharp.

Among the characters used by Olson & Warheit (1988) in recognizing *Papasula* as distinct from *Sula* and *Morus* were certain of those used here for the coracoid, tibiotarsus, and tarsometatarsus. We agree with the generic distinction of *Papasula,* finding this genus to be no more similar osteologically to *Sula* than to *Morus,* at least in the five elements we have as fossils. Especially profound are the differences between the vertebrae of *Papasula* and those of *Sula* and *Morus.*

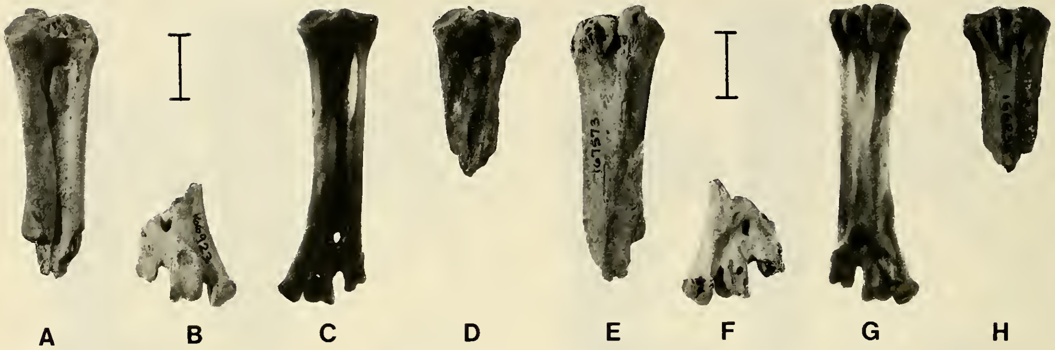

Fig. 3. The tarsometatarsus of *Papasula* in dorsal (A–D) and plantar (E–H) aspects. A, E. *P. a. costelloi,* BPBM 167573, Hiva Oa. B, F. *P. a. costelloi,* BPBM 166923, Tahuata. C, G. *P. a. abbotti,* USNM 560683, Christmas Island. D, H. *P. a. abbotti,* BPBM 166234, Tikopia. A, C, D, E, G, H = left side. B, F = right side. Scale bar = 1 cm.

Papasula abbotti costelloi, new subspecies
Figs. 1–3

Holotype.—Complete tibiotarsus, BPBM 167105, Hanamiai Site, Tahuata, Marquesas, square L12, Layer H35, depth 255–260 cm; B. Rolett, 1985.

Paratypes.—Hanamiai Site, Tahuata, Marquesas, collected in 1985 by B. Rolett: axis vertebra, BPBM 166874, fourth cervical vertebra, BPBM 166873, and tibiotarsus, BPBM 166872, square N13, Layer H30, depth 245–250 cm; tarsometatarsus, BPBM 166923, square L13, Layer H27, depth 240–245 cm. Hanatekua Beach Site (MH-3-13, formerly known as MH-12), Hiva Oa, Marquesas, P. Bellwood, 1967: coracoid, BPBM 167758, test pit 2; tarsometatarsus, BPBM 167573, test pit 23, depth 30+ cm.

Diagnosis.—Differs from *Papasula a. abbotti* in being larger in all known elements (Tables 1–5) and as follows. Axis—in cranial aspect, ventral surface of facies articularis atlantica convex rather than concave. Tibiotarsus—crista fibularis shorter; lateral portion of pons supratendineus more constricted than in adult of *P. a. abbotti* but similar to that of immature individual of *P. a. abbotti.* Tarsometatarsus—dorso-lateral margin of shaft thicker in dorsal aspect; dorsal surface of shaft more deeply excavated just distal to foramina vascularia proxi-

Table 1.—Measurements (in mm) of the axis vertebra in *Papasula.* All specimens are unsexed. CE = cranial end. FAC = facies articularis caudalis. FV = foramen vertebrale.

	Length from FAC through dens	Width of FAC at midpoint	Maximum depth of FAC	Maximum width of FV (CE)	Depth through CE	Length of dens	Depth of dens
P. a. abbotti USNM 560683, adult, Christmas Island	14.9	5.5	4.3	5.2	6.0	2.2	2.6
P. a. abbotti USNM 560682, immature, Christmas Island	14.4	5.2	4.6	5.4	5.8	2.4	2.7
P. a. costelloi BPBM 166874, adult, Tahuata	18.1	6.6	5.6	5.2	7.2	2.9	3.4

Table 2.—Measurements (in mm) of the fourth cervical vertebra in *Papasula.* All specimens are unsexed. CE = cranial end. FAC = facies articularis caudalis. FACR = facies articularis cranialis. FV = foramen vertebrale.

	Total length	Dorsal length at midline	Cranial width	Maximum width FV (CE)	Maximum depth FV (CE)	Maximum width of FACR	Maximum width of FAC	Width at midpoint
P. a. abbotti USNM 560683, adult, Christmas Island	19.9	12.1	16.1	5.4	5.8	7.3	7.2	14.1
P. a. abbotti USNM 560682, immature, Christmas Island	20.5	13.0	18.4	5.9	7.4	8.0	7.5	14.6
P. a. costelloi BPBM 166873, adult, Tahuata	21.8	13.1	20.3	6.1	6.4	9.3	8.2	16.3

malia; middle trochlea with more deeply excavated groove on dorsal and ventral surfaces; inner trochlea extends farther distally relative to middle trochlea; distal foramen relatively smaller.

Etymology.—Named for Lou Costello (1906–1959) of the popular comedy team "Abbott and Costello" of the 1940's and 1950's. The name *costelloi* complements the name *P. abbotti,* which honors, however, ornithologist W. L. Abbott rather than Lou Costello's partner, Bud Abbott. Tropical islands figured in two of Abbott and Costello's movies, "Pardon My Sarong" and "Abbott and Costello Meet Captain Kidd" (C. Costello 1981).

Remarks.—Our classification of *costelloi* as a distinct subspecies rather than a full species is based in part on the level of quantitative difference between *costelloi* and *abbotti* (Tables 1–5), which corresponds with that found between different subspecies of modern species of *Sula* (K. I. Warheit, pers. comm.). The difference in size between *costelloi* and *abbotti* exceeds that attributable to sexual dimorphism in species of *Sula.* While some of the non-quantitative differences between *abbotti* and *costelloi* (see Diagnosis) would seem to indicate a species-level distinction, we prefer a more conservative approach for now, pending an increase in the sample sizes of fossil and modern specimens of *Papasula.*

Papasula abbotti abbotti (Ridgway 1893)

Material.—Kiki Site (SE-TK-4), Tikopia, Solomon Islands: coracoid, BPBM 166283, test pit N1, Layer II, P. V. Kirch and D. E. Yen, 1977–1978; tarsometatarsus, BPBM

Table 3.—Measurements (in mm) of the coracoid in *Papasula.* All specimens are unsexed. CS = cotyla scapularis. FAH = facies articularis humeralis. SE = sternal end.

	Width of FAH at midsection	Length of FAH	Width of SE of FAH	Width of CS
P. a. abbotti USNM 560683, adult, Christmas Island	7.8	11.0	9.4	8.6
P. a. abbotti USNM 560682, immature, Christmas Island	6.9	10.3	9.1	7.9
P. a. abbotti BPBM 166283, adult, Tikopia	—	10.5	—	—
P. a. costelloi BPBM 167758, adult, Hiva Oa	7.9+	—	10.7	9.3

Table 4.—Measurements (in mm) of the tibiotarsus in *Papasula.* All specimens are unsexed. For the modern skeletons from Christmas Island, measurements are given for both the right and left tibiotarsus. CC = cristae cnemialis cranialis et lateralis.

	Total length without CC	Proximal width	Length of crista fibularis	Least width of shaft	Least depth of shaft	Distal width at juncture of fibula	Distal width through condyles	Depth of medial condyle	Depth of lateral condyle
P. a. abbotti USNM 560683, adult, Christmas Island	79.0, —	10.5, —	19.2, 19.9	5.8, 5.9	4.0, 4.1	11.2, 11.3	11.2, 11.3	10.9, 11.0	8.1, 8.1
P. a. abbotti USNM 560682, immature, Christmas Island	81.6, 82.2	10.4, 10.6	18.0, 18.8	5.7, 5.7	3.7, 3.7	11.9, 12.0	11.8, 11.8	10.1, 10.2	8.2, 8.4
P. a. costelloi BPBM 167105, adult, Tahuata	87.0	12.5	13.7	7.3	4.8	13.3	13.7	11.9	9.7
P. a. costelloi BPBM 166872, adult, Tahuata	—	—	—	—	—	13.3	13.7	12.0	—

166234, grid 019I, Layer II, depth 30–40 cm, P. V. Kirch and D. E. Yen, 14–15 Jun 1977.

Remarks.—These two specimens are referred to *P. a. abbotti* rather than to *P. a. costelloi* because of these characters: small size (Tables 3, 5); BPBM 166234 (Fig. 3) has a thin dorso-lateral margin of the shaft and a more shallowly excavated dorsal surface of the shaft just distal to the foramina vascularia proximalia.

Discussion

Based mainly upon osteological characters, Olson & Warheit (1988) described the new genus *Papasula* to accommodate *abbotti,* noting that this species is as distinct from *Sula* Brisson (the "boobies") as it is from *Morus* Leach (the "gannets"). We agree, and find each of the five elements we have studied to be very different from those of both *Sula* and *Morus.* Nelson (1971) found the behavior of *P. abbotti* also to be aberrant within the Sulidae.

Papasula a. abbotti occurs today only on Christmas Island, south of Java in the Indian Ocean, although it was described (Ridgway 1893) from a specimen taken on Assumption Island in the western Indian Ocean, 6300 km west of Christmas Island. Subsequently, *P. a. abbotti* has been extirpated on Assumption Island (Nelson 1974, Bourne 1976, Stoddart 1981). The record of *P. a. abbotti* from Tikopia, a Polynesian outlier in the Solomon Islands, is an eastward range extension of 6400 km from Christmas Island. Considering the innumerable islands between Assumption and Tikopia, it is likely that *P. a. abbotti* has suffered a population decline much more severe than previously recognized. The true distribution of *P. a. abbotti* can be approximated only by the discovery of additional Holocene fossils.

Papasula a. costelloi is known thus far only from Hiva Oa and Tahuata, Marquesas Islands. This is a 4800 km eastward range

Table 5.—Measurements (in mm) of the tarsometatarsus in *Papasula*. All specimens are unsexed. For the modern skeletons from Christmas Island, measurements are given for both the right and left tarsometatarsus. DF = distal foramen. IT = inner trochlea. MT = middle trochlea. OT = outer trochlea.

	Total length to DF	Proximal width	Proximal depth	Minimum width of shaft	Distal width	Depth of OT	Depth of MT	Depth of IT	Width of MT	Length from DF through MT
P. a. abbotti										
USNM 560683, adult, Christmas Island	34.4, 34.7	12.5, 12.6	9.1, 9.1	7.7, 7.8	13.4, 13.5	7.2, 7.7	6.0, 6.2	4.8, 4.9	4.6, 4.8	9.8, 10.1
P. a. abbotti										
USNM 560682, immature, Christmas Island	33.6, 34.1	12.7, 12.8	9.0, 9.2	7.5, 7.5	13.3, 13.4	7.1, 7.3	6.2, 6.2	5.0, 5.1	4.4, 4.5	—
P. a. abbotti										
BPBM 166234, adult, Tikopia	—	13.6	10.0	—	—	—	—	—	—	—
P. a. costelloi										
BPBM 166923, adult, Tahuata	—	—	—	—	15.5	8.0+	7.1	5.8	5.3	10.9
P. a. costelloi										
BPBM 167573, adult, Hiva Oa	39.9	14.6+	10.9	9.1	—	—	—	—	—	—

extension for *P. abbotti.* We believe that *P. a. costelloi* nested in the Marquesas, for the holotype tibiotarsus (BPBM 166872) is filled with medullary bone, indicating a female either laying eggs or preparing to do so. Whether *P. a. costelloi* occurred outside of the Marquesas is unknown but seems likely. We also do not know where or if the ranges of *P. a. costelloi* and *P. a. abbotti* once met in the Pacific. We have examined bones of sulids from archeological sites on Lifuka (Tonga), Huahine (Society Islands), Henderson (Pitcairn Group), and Nuku Hiva and Ua Huka (Marquesas), finding all to be referable to modern species of *Sula.*

Slud (1967) repeatedly sighted several individuals of an unusual sulid on Cocos Island, between Costa Rica and Galapagos. These birds, which did not agree in plumage with any living species of booby, were reminiscent of Abbott's Booby in several aspects, such as the white wing patches, bluish skin behind the eye, tree-perching habits, and deep, croaking voice. The discovery of Abbott's Booby in the Marquesas raises the possibility that the unknown species of sulid on Cocos Island might be *P. abbotti.*

Many extinct species of land birds have been discovered in the archeological sites on Tahuata and Hiva Oa (Steadman 1988, in press; Steadman & Zarriello 1987). *Papasula a. costelloi* is the first extinct seabird to be reported from these sites, although study of the seabird bones is in preliminary stages and the faunas do include locally extirpated procellariids.

The initial human settlement of the Marquesas occurred at least 2000 years ago (Kirch 1986). Evidence from the Hanamiai Site on Tahuata suggests that *P. a. costelloi* survived into the second millenium of human occupation. The bones of *P. a. costelloi* from Hanamiai were recovered only from the lowest stratigraphic levels. Radiocarbon dates for these levels indicate a maximum age of around 920 ± 80 B.P. (Rolett 1988). The stratigraphic contexts of the two bones of *P. a. costelloi* from the Hanatekua Beach Site on Hiva Oa have not been correlated with artifactual assemblages. There are no radiocarbon dates for this site. The archeology of Hiva Oa has been described by Bellwood (1972), Sinoto (1979), and Kirch (1986).

On Tikopia, *Papasula a. abbotti* may not have survived long after the first humans arrived. The Kiki Site, from which both bones of *P. a. abbotti* were found, contains the richest sample of archeological materials from the initial occupation of Tikopia (Kirch & Yen 1982:111). Both of these bones are from Layer II, which is the lowest cultural layer at the site and is radiocarbon dated (on charcoal) at 2680 ± 90 years B.P. (Kirch & Yen 1982:313).

The apparent vulnerability of Abbott's Booby to human activities is probably related to two factors. First, boobies provided a readily accessible food source for Polynesians, as shown by the occurrence of booby bones in archeological kitchen middens. Second, the clearing of forests removed nesting habitat. Unlike other species of sulids, Abbott's Booby is known to nest only in tall trees.

The distribution of *Papasula,* as presently understood, is extremely scattered (Assumption and Christmas islands in the Indian Ocean; Tikopia, Hiva Oa, Tahuata, and perhaps Cocos islands in the Pacific). We presume that some combination of hunting and habitat destruction has removed these sulids from a significant number of the thousands of intervening islands.

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LEIOGNATHUS PAN, A NEW PONYFISH (PISCES: LEIOGNATHIDAE) FROM THAILAND, WITH COMMENTS ON THAI LEIOGNATHIDS

Thosaporn Wongratana

Abstract.—*Leiognathus pan,* n. sp., is described from ten specimens from the Gulf of Thailand and the Andaman Sea. It is chiefly distinguishable from its congeners in having: scaly breast, a dark blotch on nape, four series of broken longitudinal lines on sides dorsally (vs. vertical zig-zag lines or vermiculations), upper half of spinous dorsal fin between second and sixth spines with a prominent dark patch. Leiognathids are important in the fisheries of Thailand; seventeen species are known in the fauna.

Fishes of the genus *Leiognathus* Lacepède are widely distributed in the Indo-Pacific from Australia to Japan through the Malay Peninsula to the east coast of Africa and to the Red Sea, as well as the Persian Gulf (Tiews & Caces-Borya 1965; Kühlmorgen-Hille 1974; James 1978, 1984). They are a dominant element of the coastal fish fauna of Thai waters.

In the 1970's, I discovered an apparently undescribed species of *Leiognathus* in the Bangkok Wholesale Fish Market. Six specimens from the Gulf of Thailand purchased in 1973 and four specimens from Ranong Province on the Andaman Sea, collected in 1975, provide the basis for the following description. Two specimens, not treated herein, were collected from the Andaman Sea in 1984 by Mr. Hiroshi Senou and are housed in the Department of Marine Sciences, University of Ryukyus, Japan.

Type specimens of the new species have been deposited in the British Museum (Natural History), London (BMNH); the Center for Thai National Reference Collection, Bangkok (CTNRC); the Chulalongkorn University Museum of Zoology, Bangkok (CUMZ); the Kasetsart University Museum of Fisheries, Bangkok (KUMF) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

In describing this new species, data presented in parentheses refer to paratypes (when different from the holotype). Additional measurements and counts are given in Table 1.

Leiognathus pan, new species
Table 1, Figs. 1, 2

Holotype.—CUMZ 2528.2.9.1, 65.0 mm standard length (SL), trawled from the Gulf of Thailand, via Bangkok Wholesale Fish Market, 15 Apr 1973; T. Wongratana.

Paratypes.—Eight specimens, BMNH 1974.11.20.1, (1, 52.8), CTNRC 2621, (1, 62.0), CUMZ 2528.2.9.2, (1, 54.2), KUMF 2750, (1, 64.5), and USNM 276536, (1, 53.0), same data as for holotype. CUMZ 2528.2.9.3, (1, 50.0), Ranong Province, Andaman Sea, via Bangkok Wholesale Fish Market, 26 Feb 1975; T. Wongratana. USNM 276537, (2, 54.0–59.0), same data as preceding specimen, 31 Mar and 30 Apr 1975; T. Wongratana.

Non-type.—BMNH (uncat.), (1, 58.0 cleared and stained), Ranong Province, Andaman Sea, via Bangkok Wholesale Fish Market, 26 Feb 1975; T. Wongratana. Badly damaged when collected.

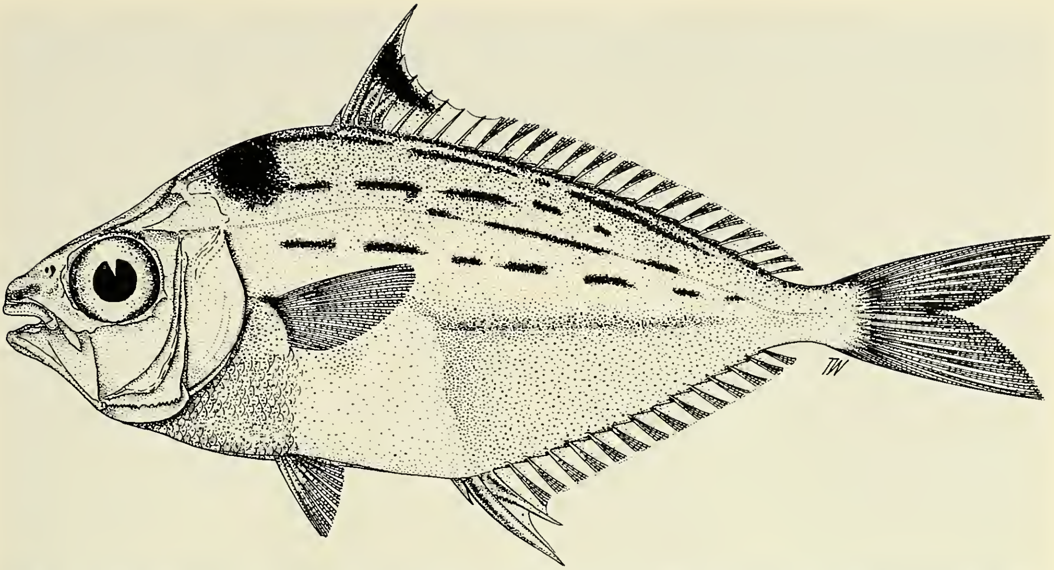

Fig. 1. *Leiognathus pan,* holotype, CUMZ 2528.2.9.1, 65.0 mm SL, Gulf of Thailand, collected at the Bangkok Wholesale Fish Market, on 15 Apr 1973. Scales on breast are shown, those on body omitted.

Diagnosis.—A species of *Leiognathus,* with oblong body, chiefly differing from congeners (see also "Remarks") in having in combination: scaly breast, dark blotches on nape, 4 series of broken longitudinal lines on sides of body dorsally (vs. vertical zigzag lines or vermiculations in most known species), and upper half of spinous dorsal fin between second and sixth dorsal spines with a prominent dark patch.

Description.—Meristics and morphometrics are presented in Table 1. Body slightly elongate and moderately compressed, depth at dorsal-fin origin 39.2 (34.2–42.6)% SL, dorsal and ventral profiles evenly curved, tapering slightly to caudal peduncle. Snout pointed, followed by indistinct supraorbital depression and slightly convex curvature to dorsal-fin origin. Eye relatively large, horizontal diameter 9.5 (8.8–10.9)% SL, scarcely nearer to snout tip than to posterior opercular margin. Supraorbital ridges smooth, converging posteriorly to form triangular space. Nuchal spine with distinct median keel, tip reaching just over half distance from occipital to dorsal-fin origin. One or two prominent, curved postnasal spines on lateral ethmoid (number varies among specimens and between sides of a single specimen). Mouth small, terminal, horizontal when closed, and level with lower edge of eye; posterior tip of maxilla reaching to vertical at anterior orbital margin. Mouth, when protuded, directed obliquely downwards. Mandible very slightly concave and ascending at an angle of 36 (35–38) degrees. Teeth fine, villiform, in a single series in each jaw. Lower preopercular margin with about 27 (22–32) serrations.

Scales small, absent only on head and in pectoral area. Lateral line co-arching with dorsal profile and terminating just anterior to caudal-fin base; tubed scales 50 (48–54). Gill rakers spinescent, 5 on upper arch and 15 (15–17) on lower arch, longest raker half or little more than half length of corresponding gill filament.

First dorsal-fin spine minute, second longest, 16.1 (18.1–20.6)% SL and slightly longer than second anal-fin spine; last dorsal-fin spine slightly shorter than first dorsal segmented ray. Anal fin similar to but shorter than dorsal fin, inserted under seventh or eighth dorsal spine. Pelvic fins short, only

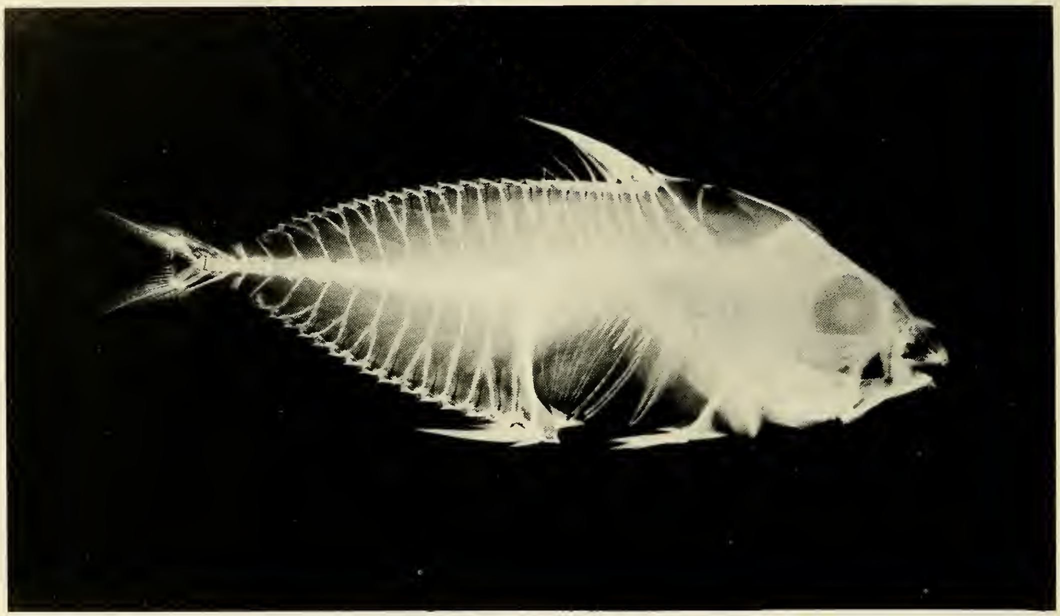

Fig. 2. Negative print made from radiograph of *Leiognathus pan,* paratype, USNM 276536, 53.0 mm SL, same data as for Fig. 1.

slightly larger than horizontal eye diameter. Pectoral fins somewhat pointed, reaching below base of sixth or seventh dorsal-fin spine. Caudal forked, with 8 (upper)+7 (lower) branched fin rays.

Fresh specimens with head and body iridescent blue-green dorsally, silvery laterally, brilliant silvery white, washed with very pale orange ventrally from pectorals to above middle of anal-fin base. Snout with dense melanophores. Iris of eye white, dusky dorsally. Upper half of body with four longitudinal rows of elongate, greenish blue spots, third row on lateral line, fourth below. Body contour along dorsal-fin base with black line. Prominent greenish-blue blotch across nape. Inner surface of gill cover largely white with scattered melanophores. All fins hyaline. Spinous dorsal fin with large black blotch on upper half from second to sixth spines; caudal washed with very pale orange near inner edge of fin; pectoral-fin base darkish posteriorly.

Preserved specimens light brown on body and head; markings on back and sides obscure, blotch on nape diffuse. Snout and pectoral-fin axil dusky. Inner surface of opercle dotted with dark. Breast dusky; lower sides conspicuously paler below pectoral fins, dusky posteriorly. Black blotch on spinous dorsal fin distinct.

Etymology.—The specific epithet, *pan,* is derived from the Thai word for a small, flat, platelike, more or less shining object, and is the Thai vernacular name commonly used for all leiognathids.

Remarks.—*Leiognathus pan* has a prominent dark blotch on the nape, which is also present on four congeners: *L. argentea* Houttuyn from China and Japan, *L. blochii* (Valenciennes) and *L. brevirostris* (Valenciennes) from India to the western central Pacific and Australia, and *L. nuchalis* (Temminck & Schlegel) from Japan, China and Queensland. However, *L. argentea, L. brevirostris,* and *L. nuchalis* are readily distinguishable from the new species by lacking scales on the breast. *Leiognathus blochii* and

Table 1.—Measurements and counts of the types of *Leiognathus pan,* standard length in mm; all other measurements expressed as percentage of standard length. Abbreviations: tb, tip broken; nc, not counted.

	Holotype	Paratypes							
Character	CUMZ 2528.2.9.1	BMNH 1974.11.20.1	CTNRC 2621	CUMZ 2528.2.9.2	CUMZ 2528.2.9.3	KUMF 2750	USNM 276536	USNM 276537	
Standard length, mm	65.0	52.8	62.0	54.2	50.0	64.5	53.0	54.0	50.0
Body depth	39.2	40.7	39.5	50.2	39.2	36.3	42.6	38.9	34.2
Greatest width at pectoral region	14.3	15.1	12.1	14.8	15.8	12.1	13.3	—	11.9
Least depth of caudal peduncle	6.1	6.6	6.9	6.8	6.8	6.0	7.1	7.0	6.6
Length of head	28.3	27.6	27.1	27.3	29.5	28.7	32.4	29.4	28.1
Length of snout	8.5	8.7	8.1	9.2	9.3	9.3	9.4	9.2	8.5
Horizontal diameter of eye	9.5	9.3	8.9	8.8	9.5	9.4	10.9	9.4	10.5
Length of postorbital	10.0	9.8	10.5	10.1	10.3	10.5	10.4	10.7	10.3
Interorbital breadth	10.1	9.3	10.0	8.7	10.7	9.6	10.9	10.0	10.2
Predorsal length	44.6	42.4	42.7	42.6	42.5	43.4	43.4	42.6	42.0
Preanal length	56.1	52.5	54.2	53.5	53.2	53.9	43.2	55.4	52.2
Prepelvic length	36.1	35.6	36.6	34.9	35.8	35.6	36.2	39.1	34.9
Prepectoral length	30.5	29.9	29.8	30.4	31.0	31.0	32.1	32.0	30.8
Dorsal base length	53.1	55.1	51.3	54.8	52.5	52.2	56.0	53.7	52.7
Anal base length	40.0	43.6	40.3	42.6	43.7	41.1	45.1	42.0	42.0
Length of longest (2nd) dorsal spine	16.1	19.5	18.1	20.5	18.3	20.1	20.4	20.6	20.0
Length of longest (2nd) anal spine	14.5	16.1	15.8	16.4	14.9	15.5	17.0	18.3	15.9
Length of 3rd anal spine	11.5	tb	tb	tb	tb	tb	tb	1.5	tb
Length of pelvic fin	11.1	12.3	11.3	12.9	12.5	11.6	13.2	12.8	10.3
Length of pectoral fin	17.1	21.0	19.8	19.4	19.0	18.6	22.6	20.4	16.8
Dorsal-fin rays	VIII,16	VIII,16	VIII,16	VIII,16	VIII,16	VIII,16	VIII,16	VIII,16	VIII,16
Anal-fin rays	III,14	III,14	III,14	III,14	III,14	III,14	III,14	III,14	III,14
Pelvic-fin rays	I,5	I,5	I,5	I,5	I,5	I,5	I,5	I,5	I,5
Pectoral-fin rays	16	16	16	17	17	16	16	17	17
Branched caudal-fin rays	15	15	15	15	15	15	15	15	15
Tubed scales on lateral lines	50	54	49	51	51	49	48	51	51
Gillrakers	5+15	nc	5+16	nc	nc	5+16	nc	5+17	4+15
Precaudal and caudal vertebrae	10+14	nc	nc	10+14	10+14	nc	10+14	10+14	10+14

L. spilotus, doubtfully distinct from each other (Weber & De Beaufort 1931, James 1978), have scaly breasts and are separable from *L. pan* by not having interrupted dorsolateral streaks.

The holotype (ANSP 27529) of *L.* (*Eubleekeria*) *spilotus* is a small specimen, 26 mm SL. It was illustrated by Fowler (1904), who noted that it has "several rows of brownish blotches, two or three blotches to a row, and line of demarcation distinct." Fowler's illustration has a body depth of 48.2% SL, where my measurement of the holotype indicates the depth is 43.5% SL. No markings are now evident. James (1978) and Böhlke (1984) referred *L. spilotus* to the synonymy of *L. blochii* and I concur with their actions. The fact that the young of most leiognathid fishes normally have several dark blotches on the flanks and a relatively deeper body than adults is further evidence that the holotype of *L. spilotus* is a juvenile. Many specimens of *L. blochii* (in ANSP, USNM and also the California Academy of Sciences, San Francisco) of a size equivalent to that of specimens of *L. pan* also show the irregular vertical lines on sides. Absence of these markings in the latter specimens confirms that they do not represent the young of *L. blochii* or other species.

Comments on Thai Leiognathids

In Thailand, Leiognathidae, including members of the genera *Gazza* Rüppell, *Leiognathus* Lacepède, and *Secutor* Gistel, are of economic importance, mainly the bottom trawl fishery (Tiews 1965, Wongratana 1968); and smaller quantities are caught by a variety of other inshore methods, e.g., set-bag nets, bamboo-stake traps, push-nets, beach seines and dip-nets. Some species are commonly found also in coastal shrimp or fish ponds. At present, the numbers and average size available to the fishery are greatly diminishing, undoubtedly due to over fishing resulting from unenforced regulations. Formerly, the best catches were obtained at depths of 20–40 m while catches on the deeper fishing grounds were normally very poor (Tiews 1965, Ritragsa et al. 1969, Ritragsa et al. 1970). The local economic value of leiognathids varies according to size of the fishes. Excess catches, as well as small fishes in great quantities, are utilized as animal food or fish meal whereas larger individuals of certain species, e.g., *L. equulus* (Forskål), *L. splendens* (Cuvier), *L. fasciatus* (Lacepède), *L. smithursti* (Ramsay & Ogilby), *L. blochii* (Valenciennes), *L. daura* (Cuvier) and *Gazza minuta* (Bloch) are consumed locally (Wongratana 1982). Despite their economic importance, several problems remain, including the validity of several nominal forms and their distributions.

Seventeen species of leiognathids are reported from Thai waters, including those reported by the following: Weber & De Beaufort 1931; Fowler 1934, 1935, 1937, 1939; Suvatti 1950; Rofen 1963; Banasopit & Wongratana 1967; Wongratana 1968, 1972, 1982; and Kühlmorgen-Hille 1968, 1974. Previously reported species confirmed by my collections are: *L. berbis* (Valenciennes), *L. bindus* (Valenciennes), *L. blochii* (Valenciennes), *L. brevirostris* (Valenciennes) (as *L. decorus* (De Vis) according to Sainsbury et al. 1985), *L. daura* (Cuvier), *L. elongatus* (Günther), *L. equulus* (Forskål), *L. fasciatus* (Lacepède), *L. leuciscus* (Günther), *L. lineolatus* (Valenciennes), *L. smithursti* (Ramsay & Ogilby), and *L. splendens* (Cuvier). Among these species, *L. equulus* is the largest member, attaining 170 mm SL (Rofen 1963). *Leiognathus berbis* and *L. lineolatus,* previously redescribed and figured from Thailand by Fowler (1935, 1937), seem to be very rare, and I have collected very few specimens during the past 20 years. Interestingly, *L. berbis* appears to be the first species of the Leiognathidae recorded from Thailand (Weber & De Beaufort 1931).

My recent examination of Fowler's (1939) Thai specimens of *L. dussumieri* (ANSP

76828; 118,119 and 120 mm SL, from Krabi Province, Andaman Sea), for which he gave total lengths of 157–161 mm, revealed them to be specimens of *L. equulus* (Forskål). They have no scales on the breast, very deep body (1.6 vs. 2.0–2.3 in SL in *L. dussumieri*) and their length exceed the maximum size of *L. dussumieri* given by James (1984, 140 mm TL). No substantiated records of *L. dussumieri* exist for Thailand, although overall distribution suggests it may occur there.

Other leiognathid species recorded from Thai waters are *Secutor ruconius* (Hamilton-Buchanan), *S. insidiator* (Bloch) and *Gazza minuta* (Bloch). The name *G. equulaeformis* Rüppell which appeared in Fowler's (1935, 1937) reports from Sriracha, Paknam and Rayong, is evidently a junior synonym of *G. minuta* (Weber & De Beaufort 1931, Herre 1953). An additional species of *Secutor, S. indicius* was described by Mongkolprasit (1973) from the Gulf of Thailand. These fishes are very common throughout the year along the coasts of Thailand.

Gazza achlamys (Jordan & Starks), reported from the Philippines (Tiews & Caces-Borya 1965) and India (James 1978, 1984, 1985a, b), may eventually be found in Thai waters.

Acknowledgments

This article is dedicated to the late Dr. Robert H. Gibbs, Jr., of the USNM, who passed away 3 April 1988. I was warmly welcomed and continuously encouraged by him during my stay at the museum.

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SEMAPROCHILODUS VARII, A NEW SPECIES OF PROCHILODONTID FISH (OSTARIOPHYSI: CHARACIFORMES) FROM THE MAROWIJNE RIVER, SURINAM

Ricardo M. C. Castro

Abstract.—*Semaprochilodus varii* is described from localities in the lower and upper portions of the Marowijne River, Surinam. The species is distinguished from all other *Semaprochilodus* species by its lower number of pored scales in the lateral-line (40 or 41). In addition the combination of the low lateral-line count and other meristic characters outlined in the text further distinguish *S. varii* within the genus.

Resumo.—*Semaprochilodus varii,* uma nova espécie da família Prochilodontidae, é descrita de duas diferentes localidades na bacia do rio Marowijne, Suriname. *S. varii* pode ser separada das outras espécies do gênero por possuir um baixo número de escamas perfuradas na linha-lateral (40 ou 41). Além disso, o baixo número de escamas na linha-lateral em combinação com outros caracteres merísticos descritos no texto também distingue *S. varii* dentro do gênero.

During ongoing phylogenetic and revisionary studies of the family Prochilodontidae, specimens of a new species belonging to the genus *Semaprochilodus* Fowler were found in the collections of the American Museum of Natural History and the Instituut voor Taxonomische Zoölogie (Zoölogish Museum). The specimens originated in two different localities in the Marowijne River system in Surinam; one in the upper reaches and another near the mouth of the river, with the species presumably widely distributed throughout the basin. *Semaprochilodus* specimens from the Marowijne River system were previously wrongly identified as *S. insignis* (Schomburgk), due to the present confused state of prochilodontid taxonomy.

Methods and materials.—The methods of counting and measuring specimens in this paper are those outlined in Fink & Weitzman (1974:1–2). Standard length (SL) and other body measurements were taken in mm and are expressed as percentages of the standard length or, in the case of subunits of the head, as percentages of the bony head length. Ranges of counts include all specimens, with the values in square brackets being those of the holotype. Counts of total vertebrate are from radiographs and include the four vertebrae of the Weberian apparatus, with the fused $PU_1 + U_1$ of the caudal skeleton counted as a single element. All perforate lateral-line scales were counted. In counts of fin rays, lower case Roman numerals indicate unbranched fin rays, and Arabic numbers indicate branched fin rays. In the dorsal-fin ray counts the predorsal spine is treated as an unbranched ray. Tooth counts were taken from the left side of the jaws.

Specimens examined for this study are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); National Museum of Natural

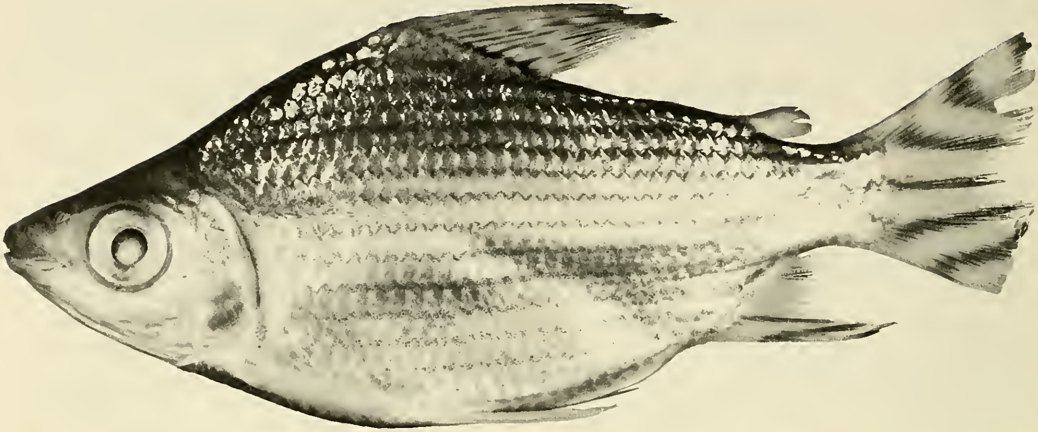

Fig. 1. *Semaprochilodus varii,* new species, holotype ZMA 106.222, SL 66.3 mm, Surinam, Marowijne River, about 25 km south of Albina, 17 Jun 1966.

History, Washington, D.C. (USNM); and Instituut voor Taxonomische Zoölogie (Zoölogish Museum), Amsterdan (ZMA).

Semaprochilodus varii, new species
Figs. 1, 2, Table 1

Semaprochilodus insignis.—Mago-Leccia 1972:60.—Géry 1977:215 [Guianas].—Le Bail et al. 1984:58, Fig. 2a [French Guiana].

Holotype.—ZMA 106.222, SL 66.3 mm, Surinam, Marowijne District, Marowijne River, about 25 km south of Albina, collected by H. Nijssen, 17 Jun 1966.

Paratypes.—6, ZMA 119.877, SL 55.5–72.4 mm.—5, ZMA 106.372, SL 60.5–73.4 mm.—4, USNM 285719, SL 59.6–64.7 mm (1 specimen cleared and counterstained for cartilage and bone).—2, MZUSP 37177–78, SL 65.1–69.9 mm (all preceding paratypes with same collection data as holotype).—1, AMNH 16406, Surinam, Oelemari and Litani rivers, SL 279.6 mm, D.C. Geisjkes, 14 Mar 1939.

Diagnosis.—Distinguished from all other nominal species of *Semaprochilodus* (*S. amazonensis* (Fowler, 1906), *S. binotatus* (Schomburgk, 1841), *S. brama* (Valenciennes, 1849), *S. insignis* (Schomburgk, 1841), *S. kneri* (Pellegrin, 1909), *S. laticeps* (Steindachner, 1879), *S. squamilentus* Fowler, 1941, *S. taeniurus* (Valenciennes, 1811), and *S. teraponura* (Fowler, 1906)) by having 40 or 41 pored scales in lateral-line instead of 45 or more in those taxa. The combination of low lateral-line count and 16 horizontal scale rows around caudal peduncle, 11 to 13 scales in middorsal line between posterior termination of dorsal-fin base and adipose-fin origin, 10 to 12 median predorsal scales and 36 or 37 vertebrae, further distinguish *S. varii* within the genus.

Description.—Table 1 gives morphometrics of the holotype and paratypes. Body moderately deep, compressed, greatest depth at origin of dorsal fin. Dorsal profile of head slightly concave. Dorsal body profile slightly convex predorsally; straight and posteroventrally slanted along base of dorsal fin; straight from posterior termination of dorsal fin to adipose fin and concave on caudal peduncle. Dorsal surface of body slightly keeled predorsally and rounded transversely dorsally posterior to dorsal fin. Ventral body profile moderately convex from tip of lower jaw to termination of anal fin base, ventral profile of caudal peduncle concave. Prepelvic region flattened proximate to region of pelvic-fin insertion. A distinct midventral keel present between pelvic-fin insertion and anus.

Table 1.—Morphometrics of holotypes and paratypes of *Semaprochilodus varii*: A, range for paratypes (n = 17) collected together with the holotype, ZMA 119.877 and 106.372, USNM 285719 and MZUSP 37177–78; B, avearge for the same specimesn; C, values for the largest paratype, collected in the upper reaches of the Marowijne River system, AMNH 16406. Standard length expressed in mm; measurements 1 to 15 are percentages of standard length; 16 to 20 are percentages of bony head length.

	Holotype	A	B	C
Standard length	66.3	73.4–55.5	64.2	279.6
1. Greatest body depth	47.5	44.5–48.3	46.0	43.5
2. Snout to dorsal-fin origin	49.8	47.2–50.6	48.7	51.0
3. Snout to pelvic-fin origin	54.8	53.0–57.6	54.4	51.3
4. Snout to anus	77.8	77.7–83.4	79.3	80.9
5. Snout to anal-fin origin	81.7	81.2–85.6	82.3	84.2
6. Posterior termination of dorsal-fin base to adipose-fin origin	24.1	21.0–26.0	23.7	25.2
7. Posterior termination of dorsal-fin base to end of caudal peduncle	40.1	37.8–42.1	39.0	40.0
8. Dorsal-fin base length	19.5	17.5–21.4	19.9	17.6
9. Dorsal-fin length	34.4	33.6–43.6	40.2	29.1
10. Anal-fin base length	13.0	11.6–13.6	12.8	11.8
11. Pectoral-fin length	20.7	20.3–22.9	21.7	21.5
12. Pelvic-fin length	22.2	21.9–24.4	23.3	15.3
13. Caudal peduncle length	11.9	11.5–14.4	12.7	12.8
14. Caudal peduncle depth	12.0	11.2–12.7	11.7	12.6
15. Bony head length	31.7	29.4–33.7	31.7	31.7
16. Snout length	39.0	32.5–38.9	36.2	41.2
17. Horizontal eye diameter	30.0	29.6–33.5	31.3	22.9
18. Postorbital length	34.3	34.0–39.0	35.7	35.1
19. Least width interorbital	45.2	43.4–48.1	45.5	46.5
20. Gape width	41.9	40.4–46.2	42.5	45.8

Head acute in profile. Mouth terminal. Snout length exceeding horizontal eye diameter; with nostrils of each side close together, anterior opening circular, posterior one crescent shaped. Adipose eyelid present but scarcely developed, more pronounced on anterior border, leaving most of eye uncovered. First infraorbital greatly enlarged, its ventral border together with anterior border of anteroventrally expanded second infraorbital delimiting a triangular notch bordering posterior margin of very fleshy lips (see Roberts 1973:219, Fig. 17 for very similar situation in *Ichthyoelephas*, and Vari 1983:33, 49, for phylogenetic significance of second infraorbital form). Fleshly lips forming oral disc when protruded. Functional teeth in two rows in each jaw; internal tooth row of upper and lower jaws v-shaped. External tooth rows on both jaws follow margins of lips, with about 80 teeth in each half of upper jaw and 65 in each half of lower

Fig. 2. Map of the Guianas and neighboring region showing collecting localities of specimens reported on this paper: 1, Marowijne River, about 25 km south of Albina (holotype and all ZMA, MZUSP and USNM paratypes); 2, Approximate locality including the rivers Litani and Oelemari (AMNH 16406 paratype).

jaw in holotype. V-shaped inner tooth row on upper jaw with 11 to 15 [15] teeth on left side; v-shaped inner tooth row on lower jaw with 7 to 9 [9] teeth on left side. All teeth movably implanted in fleshly lips, of similar size, spoon-shaped in frontal view (see Mago-Leccia 1972, Fig. 4B for photograph of *Semaprochilodus* teeth). Upper and lower lips bordered by small globular fleshly papillae.

Scales cycloid. Scales in dorsal midline between posterior termination of dorsal-fin base and adipose-fin origin with tongue-shaped membraneous process on posterior border (as described by Mago-Leccia 1972: 58). Lateral-line completely pored, with 40 or 41 (2 paratypes with 40) [41] pored scales; 8 [8] transverse scale rows from origin of rayed dorsal fin to lateral-line; 8 [8] horizontal scale rows from origin of pelvic fin to lateral-line; 6 or 7 (5 paratypes with 7) [6] horizontal scale rows from origin of anal fin to lateral-line; 10 to 12 (1 paratype with 10 and 9 paratypes with 11) [10] median predorsal scales; 11 to 12 (1 paratype with 11 and 8 paratypes with 12) [12] scales in middorsal line between posterior termination of dorsal-fin base and adipose-fin origin; 16 [16] horizontal scale rows around caudal peduncle.

Dorsal fin preceded by small anteriorly bifurcated spine (see Géry 1977:367 for morphologically similar structure in *Prochilodus*) considered herein as unbranched ray in fin-ray counts. Dorsal-fin rays iii,10 [iii,10]; anal-fin rays iii,8 [iii,8]; pectoral-fin rays i,14 to i,17 (i,15 most common) [i,15]; pelvic-fin rays i,7 or i,8 (i,7 rare) [i,8]; principal caudal-fin ray count 10/9 [10/9].

Rayed dorsal-fin distally pointed; posterior unbranched and anterior branched rays longest, subequal; fin origin nearer to snout tip than to caudal-fin base. Longest length of adipose dorsal fin about two-thirds of horizontal eye diameter, its origin on vertical imaginary line crossing middle of anal-fin base. Pectoral fin distally pointed; when depressed posterior tip reaching or almost reaching pelvic-fin origin. Pelvic fin falcate, its origin slightly posterior of vertical imaginary line passing through origin of dorsal fin; when depressed posterior tip reaching approximately two-thirds of distance to anus. Axillary scale present, its length about one-third of longest pelvic-fin length. Anal fin posterior unbranched and anterior branched rays longest, subequal. Caudal fin forked. Total vertebrae 36 or 37 (3 paratypes with 36) [37].

Color in alcohol.—Background body color in holotype and in paratypes collected with it silvery to silvery-brown on dorsal half of body and head. About 13 irregular wavy dark longitudinal lines on sides of body; lines formed by chromatophore concentrations on dorsal and ventral margins of exposed fields of scales. Seven wavy lines above and 6 below lateral-line; lines less regular across caudal peduncle. Field of brown chromatophores on membranous margin of opercle and most of visible lateral surfaces of bones of pectoral girdle. Rayed dorsal fin with about 5 irregular dark lines originating at its anterior margin, roughly parallel to dorsal-fin base. Adipose dorsal fin with dusky dorsal border. Pectoral and pelvic fins hyaline. Anal fin with chromatophore fields forming 4 or fewer somewhat irregular oblique dark stripes; the three anteriormost stripes roughly parallel. Caudal fin with 10 or fewer dark stripes, one horizontal stripe extending approximately across middle fin rays; 5 or fewer oblique stripes on dorsal caudal-fin lobe and 4 or fewer oblique stripes on ventral caudal-fin lobe. Iris silvery-yellow with dusky dorsal and ventral areas.

AMNH paratype lacking guanine on scales, overall coloration tan. Number of stripes on caudal fin in this much larger specimen apparently increased. Definite statement of number of stripes not possible since fin damaged (see Mago-Leccia 1972: 58 for comments on ontogenetic change in caudal-fin color pattern in *Semaprochilodus*). Dense chromatophore field covering most of visible lateral surface of pectoral-girdle bones, creating a distinct sickle-shaped dark area immediately posterior to opercular opening; postopercular membrane dusky.

Distribution.—Marowijne River system of Surinam and French Guyana.

Etymology.—*varii*, in honor of Dr. Richard P. Vari of the National Museum of Natural History, who demonstrated the monophyly of the Prochilodontidae and also advanced a hypothesis of its phylogenetic position.

Remarks.—Mago-Leccia (1972:60), in his revision of Venezuelan prochilodontids, states that *S. insignis* (Schomburgk) occurs, among other places, in the "Guayanas." During the ongoing revisionary studies of the family Prochilodontidae no specimens of *S. insignis* were found among examined specimens from the Guianas; all Guianan specimens rather belonged to the species described herein. Mago-leccia gives no reference as the basis for his citation of *S. insignis* in the Guianas, and it is more likely his reference is to *S. varii.* Géry (1977:215) and Le Bail et al. (1984:58, Fig. 2A) reported *S. insignis* from "Guianas" and "Guyane" respectively. Géry gives a range of 38 to 41 scales in the lateral-line for the species and Le Bail et al. give as an identifying character for the species the possession of less than 42 scales in the lateral-line. Thus in both cases the cited species is *S. varii* instead of *S. insignis* (see "Diagnosis" above). In the same paper Géry states that juveniles have four oblique bars on each caudal-fin lobe and adults seven bars. In the illustration by Le Bail et al. there is a horizontal stripe on the middle caudal-fin rays and eight oblique stripes in the dorsal caudal-fin lobe and seven in the ventral one. In the same figure the anal fin has five oblique stripes and there is a sickle-shaped black mark immediately posterior of the opercular margin. These pigmentation features agree with the data obtained in this study for *S. varii* with one exception (see "Color in alcohol" for comments about possible ontogenetic increase in the number of caudal-fin stripes and development of a distinct sickle-shaped postopercular dark band). The only pigmentation difference between the figure of Le Bail et al. and the specimens examined here is the presence of five oblique dark stripes in the anal fin in their figure. None of the specimens examined in this study have more than four oblique stripes on the anal fin. This difference may be a function of an ontogenetic increase in anal-fin stripes comparable to that found for caudal-fin stripes. A definite statement in the number of stripes in very large specimens is not possible due to fin damage in the largest paratype.

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RELATIONSHIPS OF THE NEOTROPICAL CATFISH GENUS *NEMUROGLANIS,* WITH A DESCRIPTION OF A NEW SPECIES (OSTEICHTHYS: SILURIFORMES: PIMELODIDAE)

Carl J. Ferraris, Jr.

Abstract.—A new species of the Neotropical catfish genus *Nemuroglanis* is described from material from the Río Negro and Río Orinoco. Osteological characters place the genus within a large, previously recognized but unnamed clade of the Pimelodidae which contains most of the smaller sized members of the family. A more restrictive clade, which contains *Nemuroglanis* and members of several other pimelodid genera, is defined on characteristics of the fin spines and transverse processes of the anterior vertebrae.

Resumen.—Una nueva especie de pez siluriforme (bagre) perteneciente al género neotropical *Nemuroglanis* se describe del material procedente de los ríos Negro e Orinoco. Los caracteres osteológicos encontrados permiten incluir al género dentro de un clado grande, previamente reconocido, pero sin nombre, de los Pimelodidae el cual contiene la mayor parte de los miembros de tamaño pequeño de la familia. Un clado más restringido, que contiene a *Nemuroglanis* y a miembros de varios otros géneros de pimelodidos se define en base a las características de las espinas de las aletas y a los procesos tranversales de las vertebras anteriores.

The pimelodid catfish genus *Nemuroglanis* has been a taxonomic enigma since it was first described. Eigenmann & Eigenmann (1889) proposed the name for a new species, *N. lanceolatus,* based on a single specimen taken by the Thayer expedition to Brazil. While undoubtedly a new species and a member of the Pimelodidae, as currently construed, the relationships of this fish within the family remained obscure. Until quite recently, our knowledge of the species and genus was based entirely on a single, fragile, 23.5 mm standard length (SL) specimen and a brief and inaccurate original description.

Eigenmann & Eigenmann (1889) stated firmly, but incorrectly, that *Nemuroglanis* belonged to a sub-group of pimelodids with toothed vomers, a group that otherwise contained only the largest of the Pimelodidae. Gosline (1941), however, included *Nemuroglanis* in his study of those pimelodids without a free orbital rim although no other pimelodid with a toothed vomer was included, and despite his comment that it was impossible to tell from the original description whether the genus had a free orbital rim. Recent efforts to elucidate the relationships within the Pimelodidae (e.g., Hassur 1970, Stewart 1986, and Lundberg & McDade 1986) have, of necessity, had to ignore *Nemuroglanis.* Fortunately, in this time of active investigation of the relationships of Neotropical catfishes, recent collecting in the Río Negro and Río Orinoco of Venezuela has uncovered a number of specimens of a species which, while not conspecific, are closely related to *Nemuroglanis lanceolatus.* The new species is described and figured herein, and aspects of the anat-

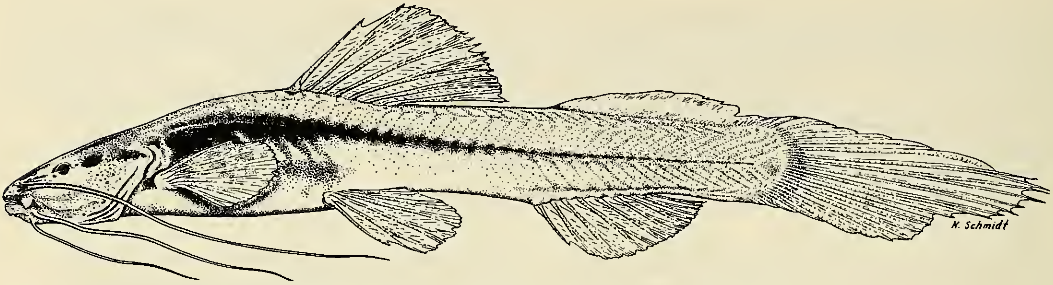

Fig. 1. *Nemuroglanis pauciradiatus,* paratype, AMNH 74410, 29.5 mm SL.

omy of this new species are discussed. This anatomical information helps shed some light on the relationship of *Nemuroglanis* within the Pimelodidae.

Materials and methods.—Measurements were made with a Helios dial caliper, to 0.5 mm, or with an ocular micrometer and a Wild M-5 dissecting microscope, to 0.1 mm. Vertebral counts were made from radiographs and cleared-and-stained specimens. Total vertebral counts include five for the Weberian complex and one for the ural complex. When meristics vary, the count for the holotype is indicated by an asterisk (*). Specimens examined during this study are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Museo de Biologia, Universidad Central de Venezuela, Caracas (MBUCV); Museum of Comparative Anatomy, Harvard University, Cambridge (MCZ); Museu Zoologia de Universidade do Sao Paulo (MZUSP); National Museum of Natural History, Washington (USNM). Anatomical illustrations were made with a camera lucida, from a single, partially disarticulated, alcian blue-alizarin stained specimen (AMNH 74410). In all anatomical drawings bone is indicated by stippling and cartilage by open circles.

The following cleared-and-stained specimens of the *Brachyrhamdia* clade of the Pimelodidae were examined in conjunction with the discussion of relationship of *Nemuroglanis*: *Leptorhamdia* sp. AMNH 74403; *Brachyglanis* sp. AMNH 74394; *B. magoi* MBUCV-V-2600; *Myoglanis* sp. AMNH 74407. Of the *Brachyrhamdia* subclade: *Pimelodella chagresi* AMNH 11406; *Goeldiella eques* AMNH 13660; *Rhamdia guatemalensis* AMNH 24871; *R. quelen* AMNH 54796. Of the *Nemuroglanis* subclade: *Nannorhamdia* sp. AMNH 74408, AMNH 77000; *Chasmocranus rosae* ANSP 137968; *Heptapterus* sp. AMNH 8668.

Genus *Nemuroglanis* Eigenmann & Eigenmann

Nemuroglanis Eigenmann & Eigenmann, 1889:29 (type species, *Nemuroglanis lanceolatus* Eigenmann & Eigenmann, 1889, by original designation).

Diagnosis.—A genus of pimelodid catfishes of the *Brachyrhamdia* clade (sensu Lundberg & McDade, 1986) characterized by a lanceolate caudal fin.

Nemuroglanis pauciradiatus, new species

Fig. 1

Diagnosis.—A species of *Nemuroglanis* with 11 or fewer anal rays. The only known congener, *N. lanceolatus,* has 14 anal fin rays.

Holotype.—MBUCV-V-16450, 27.5 mm (SL), Venezuela: Territorio Federal Amazonas; morichal 26.9 km from Puerto Aya-

Table 1.—Measurements of *Nemuroglanis lanceolatus* and *N. pauciradiatus*. All measurements, except total length and standard length, are expressed as thousandths of standard length.

	N. lanceolatus	*N. pauciradiatus*		
			Paratypes (n = 10)	
	Holotype	Holotype	Mean	Range
Total length (mm)	—	39.5		23.0–54.5
Standard length (mm)	23.5	27.5		19.5–35.5
Predorsal length	387	334	360.3	332–390
Head length	204	182	201.7	189–231
Dorsal-fin base length	98	142	143.2	123–174
Snout length	68	69	67.6	63–72
Eye diameter	26	29	30.3	23–38
Interorbital width	60	58	57.5	46–68
Snout to pelvic fin length	430	389	419.2	397–458
Snout to anal fin length	660	655	697.4	661–772
Anal-fin base length	209	146	143.3	123–164
Caudal peduncle length	115	182	152.3	127–185
Caudal pecundle depth	64	91	91.5	84–97

cucho along Puerto Ayacucho to Caicara highway; 15 Nov 1985; B. Chernoff, W. Saul, R. Royero.

Paratypes.—MBUCV-V-16451, 2, 23.0–26.0 mm SL; ANSP 159030, 12, 21.5–27.5 mm SL; MZUSP 37274 and 37275, 2, 26.0–26.5 mm SL, FMNH 97121, 2, 23.0–26.0 mm SL, taken with holotype. AMNH 74410, 3, (29.5–35.5 mm SL, one specimen cleared and alcian blue-alizarin stained), Venezuela: Territorio Federal Amazonas; Departamento Río Negro; Río Mawarinuma, 4 km downstream of Neblina base camp on left bank, in isolated pools along dried river bank, 0°55′N, 66°10′W, elevation 120 m, 7 Feb 1984, 1100–1300 hrs, C. J. Ferraris, G. Nelson, and R. Royero. AMNH 74411, 1, 28.5 mm SL. Venezuela: Territorio Federal Amazonas; Departamento Río Negro; Río Mawarinuma, at Neblina base camp, 0°55′N, 66°10′W, elevation 120 m, 11 Feb 1984, 1000–1500 hrs, C. J. Ferraris, R. Royero, and G. Nelson. USNM 268645, 1, 19.5 mm SL, Venezuela: Territorio Federal Amazonas; Departamento Río Negro, Rocky pool on island in center of Río Negro, 01°57′N, 67°03′W, 4 Dec 1984, R. P. Vari et al. USNM 268646, 1, 24.5 mm SL, Venezuela: Territorio Federal Amazonas; Departamento Ature, caño about 15 km south of El Burro, on road from Puerto Ayacucho to El Burro, 06°02′N, 67°23′W, 9 Dec 1984, R. P. Vari et al. CAS 57949, 3, 20.0–28.5 mm SL, Brazil, Amazonas, Rio Negro at São Gabriel, rock pools below rapids, Carl Ternetz, 1 Feb 1925.

Description.—A summary of the morphometric values for this species and the holotype of *Nemuroglanis lanceolatus* (MCZ 8169) is presented in Table 1.

Body cylindrical anteriorly, becoming strongly compressed caudally. Vertebral column with 38 or 39 vertebrae, 5 or 6 vertebrae bearing ribs. Head depressed, dorsal profile slightly convex. Eyes covered with skin (without free orbital margin), partially obscured ventrally by enlarged adductor mandibulae muscle mass. Mouth terminal, jaws equal. Jaw teeth fine, conical, in bands. Palate without teeth. Seven branchiostegal rays. Six short gill rakers on ceratobranchial of first arch, none on epibranchial. Three pairs of barbels. Maxillary barbels long, reaching to beneath dorsal fin. Both sets of mental barbels reaching below pectoral fin. Outer mental barbels longer.

Lateral line canal on body extending posteriorly only to below dorsal-fin origin. Ce-

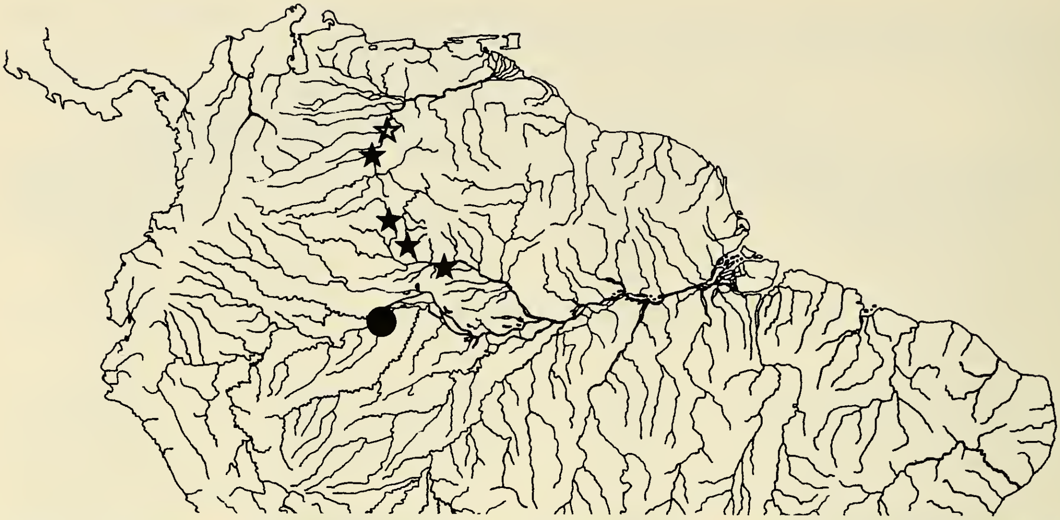

Fig. 2. Type localities of *Nemuroglanis lanceolatus* (circle) and *N. pauciradiatus* (open star). Additional collection localities of *N. pauciradiatus* (solid star).

phalic canals well developed, with an unusual connection and medial pore between nasal canals, in vicinity of posterior nostril.

Dorsal-fin origin remote from head, distance from tip of supraoccipital spine to dorsal-fin origin approximately equal to head length, origin of fin immediately behind posterior extent of appressed pectoral fin, or just anterior to vertical line at pelvic-fin origin. First dorsal "spine" absent, second "spine" filamentous. Branched dorsal-fin rays usually 6*, rarely 5; all branched rays of approximately equal length; fin margin slightly rounded. Appressed dorsal fin not reaching origin of adipose dorsal fin.

Adipose dorsal fin long, low, confluent with caudal fin. Origin of adipose along vertical running through anterior third of anal fin.

Pectoral fin margin rounded, not reaching pelvic fin base. Basal half of first ray stiffened, distal half segmented, not pungent. Rays uniformly 8 (except for single specimen from the Río Orinoco which lacks all rays but first), first and, sometimes, last, pectoral fin-ray unbranched.

Pelvic fin insertion on a vertical through middle of rayed dorsal fin. Appressed pelvic fin not reaching anal-fin base. Fin margin rounded. Rays uniformly i,5.

Anal fin short. Origin in advance of vertical through origin of adipose dorsal fin. Fin margin straight or slightly convex, all rays except first two of approximately equal size. Tip of appressed fin does not reach to caudal-fin base. Anal-fin rays 10 or 11*, anterior 3 to 5* unbranched, remaining rays branched.

Caudal fin shape unusual, called lanceolate by Eigenmann & Eigenmann (1889). Beginning at posterior margin of the adipose dorsal fin, procurrent caudal-fin rays become progressively longer. Three most dorsal branched rays of fin longest and subequal. Fin shortens abruptly between third and fifth branched ray; remaining branched rays of approximately equal length. Caudal-fin rays usually i,5,4,i*, rarely i,4,4,i. Upper procurrent rays 10–13*, lower 6–9*.

Pigmentation pattern in alcohol.—Overall body color light with scattered melanophores. Fine mid-dorsal stripe runs from nape to the adipose dorsal fin, most noticeable at dorsal fin. Midlateral stripe extends from just behind head, along the lateral line; stripe broad above pectoral-fin base, decreasing in width along abdomen, thin or absent posterior of vertical through rear of dorsal fin. Width and posterior extent of stripe varies considerably and hardly noticeable in some individuals. In individuals with dark stripes, a second oblique stripe extends from above pectoral-fin origin to just above pelvic-fin base. Eye stripe extends from snout margin through eye, after which it turns abruptly ventrally, and onto opercle. Below eye stripe, cheek remarkably light, as are undersides of the head and belly. Dorsal, adipose, and caudal fins have some scattered melanophores, but without detectable pattern. Remaining fins clear. The illustrated paratype (Fig. 1) the most darkly pigmented of the examined specimens.

Etymology.—The trivial name is derived from *paucus,* Latin for few, and *radiatus,* Latin for rayed, referring to the relatively low number of anal-fin rays in this species, relative to that of its congener.

Distribution.—*Nemuroglanis pauciradiatus* is currently known from the upper Río Negro of Brazil and Venezuela, the middle Río Orinoco, and the Río Baria system, which originates in the Cérro de la Neblina and empties into Rio Casiquiare (Fig. 2). *Nemuroglanis lanceolatus* is known at present only from the Río Amazonas, at Juthay, Brazil.

Discussion.—As stated in the diagnosis, this species can be distinguished from its congener, *N. lanceolatus* by anal-fin ray counts. Typically, *N. pauciradiatus* has 10 rays with the posterior 5 to 7 branched. The holotype of *N. lanceolatus* has 14 anal-fin rays, only three of which are branched. The difference in anal-fin ray count is reflected in relative anal-fin base length and caudal peduncle length (Table 1). *Nemuroglanis lanceolatus,* with a greater number of anal-fin rays, has a substantially longer fin base and concomitantly reduced caudal peduncle length. The caudal fin of *N. pauciradiatus* typically has 9 branched rays, whereas in the holotype of *N. lanceolatus* only the 4 longest rays are branched. *Nemuroglanis lanceolatus* has 41 vertebrae, two more than any examined specimen of *N. pauciradiatus.*

The color pattern of *Nemuroglanis lanceolatus* is described by Eigenmann & Eigenmann (1889) as uniform yellow, and reconfirmed by examination of the holotype. It appears, however, that the color is the result of loss of melanophores through bleaching and yellowing of the underlying muscle, a condition found in much of the Thayer expedition material. Thus, it is not possible at this time to determine the true pigment pattern of *N. lanceolatus.*

With the exception of fin ray counts noted above and, possibly, pigmentation, *N. pauciradiatus* is very similar in appearance to *N. lanceolatus* and is confidently placed into the same genus. In the absence of specimens of *N. lanceolatus* for anatomical examination, we are limited to data from *N. pauciradiatus* in determining relationships of *Nemuroglanis* within the Pimelodidae.

Relationships of Nemuroglanis.—*Nemuroglanis* belongs to a currently unnamed subgroup within the family Pimelodidae recently delimited by Lundberg & McDade (1986). That lineage, here termed the *Brachyrhamdia* clade, was recognized by three derived characters. The first of these is a bifurcation or even multifurcation of the posterior transverse process of the complex centrum. The second is a laterally directed, recurved process off the ventral surface of the mesethmoid (their supraethmoid). The third character is a median osseus lamina which extends between the neural spines of the complex centrum.

Nemuroglanis shows these characters quite clearly. The transverse process of the complex centrum (Fig. 3) branches twice. A basal split divides the process into a larger anterior portion and a broad posterior triangle. The anterior portion has a more lateral secondary split which is rejoined distally into a broad plate. The mesethmoid (Fig. 4) shape is identical to that of *Brachyrhamdia imitator,* as illustrated by Lund-

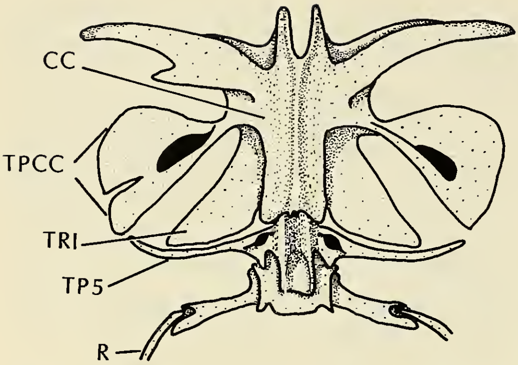

Fig. 3. Dorsal view of complex centrum and fifth vertebra of *Nemuroglanis pauciradiatus.* Abbreviations: CC—complex centrum; R—6th pleural rib; TP CC—posterior transverse process of complex centrum; TP 5—transverse process of fifth vertebra; TRI—triangular lamina of transverse process of complex centrum.

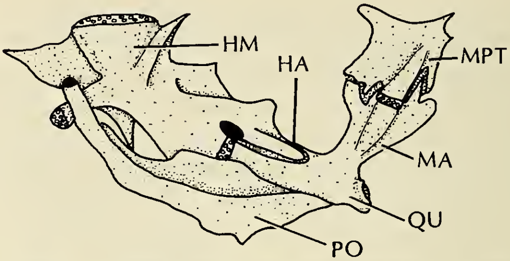

Fig. 5. Lateral view of right suspensorium of *Nemuroglanis pauciradiatus.* Abbreviations: HA—hyomandibular arm of quadrate; HM—hyomandibula; MA—metapterygoid arm of quadrate; MPT—metapterygoid; PO—preopercle; QU—quadrate.

berg & McDade (1986). A lateral, scythe-shaped osseus lamina extends from the posteroventral base of the mesethmoid. This lamina is widely separated from the lateral ethmoid, but is connected to it by a broad flattened sheet of cartilage.

In *Nemuroglanis, Brachyrhamdia,* and all other members of the *Brachyrhamdia* clade examined by me, an additional character supports the hypothesis of monophyly of the group. The quadrate (Fig. 5) has separate hyomandibular- and metapterygoid-articular surfaces, which appear as posterior and anterior projecting arms, respectively. In most catfishes, and in pimelodids outside of the *Brachyrhamdia* clade, the articular surface of the quadrate is broadly convex and it has either a single cartilagenous articular surface for the suspensorium elements or the region between the articulation of the hyomandibular and metapterygoid facets is convex. Further, the hyomandibula and metapterygoid are broadly conjoined via an interdigitating suture dorsal to the quadrate, as is shown in *Diplomystes* (Fink & Fink 1981, p. 318, Fig. 11). Although a bifid quadrate is not unique to the *Brachyrhamdia* clade, it is not found elsewhere within pimelodids and its appearance is congruent with the three characters, mentioned above, which define the *Brachyrhamdia* clade. The slender peduncle of the metapterygoid arm of the quadrate found in members of this clade is quite unlike comparable projections in other catfishes with bifid quadrates, a difference which can be taken as additional evidence of independent derivation of this structure in catfishes.

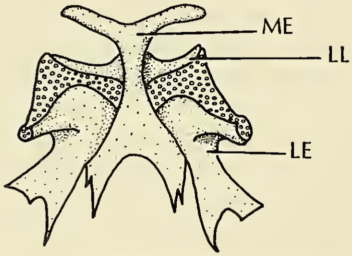

Fig. 4. Dorsal view of mesethmoid and lateral ethmoids of *Nemuroglanis pauciradiatus.* Abbreviations: ME—mesethmoid; LE—lateral ethmoid; LL—lateral lamina of mesethmoid.

Within the *Brachyrhamdia* clade, Lundberg & McDade (1986) uncovered evidence of a more restricted group, containing the genera *Cetopsorhamdia, Goeldiella, Pimelodella, Rhamdella, Rhamdia, Typhlobagrus,* "*Pimelodus*" *heteropleura,* and an undescribed species superficially similar to the poorly defined *Nannorhamdia,* which is defined by a notched and expanded transverse process of the fifth vertebra. The transverse process of *Nemuroglanis* is not of this form and, therefore, the taxon cannot be placed within that clade.

The resemblance between the shape of the transverse processes of the fifth vertebra of *Nemuroglanis* and the figured processes (Lundberg & McDade 1986) of *Nannorhamdia* lead to the discovery of yet another inclusive clade within the *Brachyrhamdia* clade. Numerous species share with *Nemuroglanis* the following suite of characters and are members of a distinct clade recognized here as the *Nemuroglanis* sub-clade:

1) 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. In other members of the *Brachyrhamdia* clade, this region does not project laterally more than one-half the distance to the tip of the transverse process of the fifth vertebra.

2) The first dorsal-fin basal pterygiophore is inserted behind Weberian complex, usually above vertebrae 7 to 10. In other members of the *Brachyrhamdia* clade and in general in catfishes, the first basal pterygiophore of the dorsal fin contacts the dorsal surface of the complex centrum and/or the fifth vertebra. In all members of the *Nemuroglanis* sub-clade, the first pterygiophore contacts the neural arches at, or posterior to, the sixth centrum.

3) The "dorsal-fin spine" is thin and flexible and the dorsal-fin lock (=first dorsal spine) is absent. Primitively, catfishes have the first two dorsal-fin rays modified into a stout, pungent spine and a more anterior, short locking element. Within the *Nemuroglanis* sub-clade, the element represented by the lock is absent and the pungent spine is, instead, a thin, segmented, unbranched ray.

4) The pectoral-fin "spine" is thin and flexible for its distal half, rather than pungent. As with the dorsal fin spine, above, the primitive condition for pimelodids is the presence of a pungent spine as the first ray of the pectoral fin. In members of the *Nemuroglanis* sub-clade, however, the first pectoral fin ray is stiffened for only the basal half. The distal half of the ray is unbranched and segmented and it is sometimes produced into a filament (e.g., *Nannorhamdia* sp. AMNH 74408).

The *Nemuroglanis* sub-clade may possibly include all members of the genera listed by Gosline (1941) as lacking a free orbital rim and having soft pectoral- and dorsal-fin spines. These include *Rhamdopsis, Acentronichthys, Heptapterus, Nemuroglanis, Cetopsorhamdia, Imparfinis, Pariolius,* and *Chasmocranus,* as well as the unlisted *Nannorhamdia.* Many of these genera are poorly diagnosed and, in all likelihood, polyphyletic, at present. Lundberg & McDade (1986) commented on this with respect to *Nannorhamdia,* placing one species within their restricted *Brachyrhamdia* clade, while illustrating a second species (their fig. 4c) which appears to belong to the clade described here. *Cetopsorhamdia* is also somewhat problematical. While the genus appears to belong to the *Nemuroglanis* sub-clade based on fin spine characteristics, Lundberg and McDade (1986) found the species examined by them to have the forked transverse process of the fifth centrum characteristic of the *Brachyrhamdia* sub-clade. While I have not had an opportunity to examine members of this genus, these examples point out the futility of trying to generalize, at this time, about the extent of these clades and emphasizes the urgent need to place members of the Pimelodidae into clades prior to attempting species level revisionary studies. Until that is done, the superficial resemblances among species, upon which the genera are currently based, will continue to confound the problem of defining genera and diminish the usefulness of resultant revisions for answering questions of evolution and biogeography of these fishes.

Acknowledgments

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A NEW CYPRINID FISH OF THE GENUS *PHOXINUS* (PISCES: CYPRINIFORMES) FROM THE TENNESSEE RIVER DRAINAGE WITH COMMENTS ON RELATIONSHIPS AND BIOGEOGRAPHY

Wayne C. Starnes and Robert E. Jenkins

Abstract.—*Phoxinus tennesseensis* is described from the upper Tennessee River drainage of Tennessee and Virginia. This sexually dimorphic and seasonally brilliantly colored new dace is rare, occurring as localized populations in a few small streams. It is distinguished from the similar *P. oreas* by differences in pigmentation, scale counts, and morphometrics. *Phoxinus tennesseensis* and *P. oreas* are hypothesized to be sister species with *P. cumberlandensis* as their next closest relative. An hypothesis of the biogeographic history of these taxa is advanced.

The small fine-scaled minnows of the genus *Phoxinus* Rafinesque, commonly called in America the redbelly daces, are among the most brilliantly colored of all fishes when spawning. Based on current understanding of cyprinid systematics (Howes 1985:66, Jenkins & Starnes, unpubl. data) *Phoxinus* is the only cyprinid genus native to both Eurasia and North Ameria. It is represented in Eurasia by *Phoxinus phoxinus* and possibly additional forms, and in North America by six species: *P. cumberlandensis, P. eos, P. erythrogaster, P. neogaeus, P. oreas,* and the species described here from the upper Tennessee River drainage in Tennessee and Virginia. All of the North American species with the exception of the relatively recently described *P. cumberlandensis* (Starnes & Starnes, 1978:509) were formerly allocated to the nominal genus *Chrosomus* Rafinesque.

The undescribed species from the Tennessee drainage has been recognized as new by ichthyologists working in the region since the 1960s. Examination of museum specimens revealed a collection made in 1867 from Virginia by Edward D. Cope and an identifiable literature record (Henshall 1889: 31) refers to specimens collected in 1888 from near Chattanooga, Tennessee by Charles Dury (see "Distribution"). These early workers and others who studied fishes from the region failed to recognize the taxon as distinct from *P. erythrogaster* until Carl L. Hubbs identified a series (UMMZ 96851) as *P. oreas.* Ross & Carico (1963:12) regarded specimens from the Pigeon River system as an undescribed subspecies of *P. oreas.* Our study indicates that these records represent an undescribed species.

Recent surveys show that the new minnow is rare, known from several localized populations in generally tiny streams. It has been listed as a species Deemed in Need of Management by the State of Tennessee, and of Special Concern by the Tennessee Heritage Program (Starnes & Etnier 1980:121). It is of Special Concern, but possibly threatened in Virginia (Jenkins & Burkhead, in press).

Methods of counts and measurements generally follow Hubbs & Lagler (1958:19–27) or are self-explanatory. In addition, "scales in longitudinal series" were counted at the level of the incomplete lateral line continuing to the caudal-fin base. "Vertical scale rows" were counted diagonally from the dorsal-fin origin to the anus. Vertebral counts were made from radiographs with the Weberian apparatus counted as four elements. Proportional measurements are expressed as thousandths of standard length. Population samples used in morphometric comparisons consisted of roughly half adult males and half adult females with gravid females excluded.

Specimens examined are deposited in the following institutions: American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Cornell University (CU), Eastern Kentucky University (EKU), North Carolina State Museum (NCSM), Northeast Louisiana University (NLU), Roanoke College (RC), Tulane University (TU), University of Alabama (UAIC), Florida State Museum, University of Florida (UF), University of Michigan Museum of Zoology (UMMZ), National Museum of Natural History, Smithsonian Institution (USNM), and University of Tennessee (UT).

Phoxinus tennesseensis, new species
Tennessee dace
Figs. 1a–c, 2b

Chrosomus erythrogaster.—(misidentifications) Cope 1868:241, 245 (Middle Fork Holston system, Va.).—Henshall 1889:31 (Whiteside, Tn.).—Evermann & Hildebrand 1916:443 (Roaring Fork, Greenville, Tn.).—Evermann 1918:339 (Clinch system, Clinton, Tn.).—Fowler 1923:9, 1924:391 (Holston system, Va.).—Fowler 1936:111 (Hiwassee system, Tn.).—Kuhne 1939:fig. 20 (female only, locality unspecified).

Chrosomus oreas subspecies.—Ross & Carico 1963:12 (Pigeon system, Tn.).—Jenkins et al. 1972:48, 98 (Tennessee drainage).

Phoxinus erythrogaster (misidentification).—Hitch & Etnier 1974:84 (Hiwassee system, Tn.).

Phoxinus sp.—Hitch & Etnier 1974:84 (Hiwassee system, Tn).

Phoxinus oreas subspecies.—Starnes & Etnier 1980:121 (range in Tn.).—Starnes & Starnes 1980a:339 (range).—Stauffer et al. 1982:35 (Tennessee drainage).—Starnes & Etnier 1986:347 (Tennessee drainage).

Holotype.—TU 97993, 52.2 mm standard length (SL) tuberculate male, Tennessee, Blount County, Little River system, spring tributary to Reed Creek by unnumbered road 8.0 km E of Walland and Tennessee Route 73, 6 Jun 1976, W. C. Starnes, L. B. Starnes, J. A. Louton.

Paratypes.—ANSP 134735, 12 specimens (21.2–48.0 mm SL), Tennessee, Roane Co., Clinch system, tributary to Bear Creek at Tn. Rt. 95 10 rd. km N Clinch River crossing, 15 Feb 1975.—TU 97994,6 (22.3–49.9), same data as holotype.—TU Osteol. 575, 4 (35.1–47.4) (cleared and stained), same data as ANSP 134735.—UAIC 5230.01, 6 (31.8–40.1), Tennessee, Hawkins Co., Holston system, Terrill Creek at county road 4.9 km SSE Surgoinsville and US Rt. 11W, 29 Apr 1976.—UF 21802, 5 (45.4–58.0), same data as UAIC 5230.01 except 15 May 1975.—UMMZ 198977, 18 (19.4–51.3), Tennessee, Hawkins Co., Holston system, Surgoinsville Creek at county road 1.9 km N US Rt. 11W at Surgoinsville, 30 Nov 1975.—USNM 216212, 15 (19.2–57.9), same data as UMMZ 198977.—USNM 288068, 3 (32.4–44.1), same data as ANSP 134735 except 22 Apr 1980.—UT 44.495, 14 (23.3–49.3), Tennessee, Polk Co., Ocoee-Hiwassee system, Indian Creek above bridge 0.2 km above Parksville Reservoir, 19 Apr 1970.—UT 44.992, 7 (29.0–41.5), same data as ANSP 134735 except 1 Dec 1974.—UT 44.1070, 1 (47.1), Tennessee, Blount Co., Little River system, Reed Creek 100 m below mouth Double Branch, 4.5 air km NE Walland, 13 Apr 1975.

Diagnosis.—*Phoxinus tennesseensis* is distinguished from its congeners except *P. oreas* by its distinctive gut morphology (Starnes & Starnes 1978:fig. 3) and the presence of an interrupted and ventrally decurved lower lateral stripe (Fig. 1a–c). In

Table 1.—Selected meristic and morphometric data (expressed in thousandths of standard length) and results of T-tests between *Phoxinus tennesseensis,* including holotype, pooled from six localities in Tennessee River drainage, and *P. oreas* pooled from New, James, Roanoke-Dan and Neuse river systems.

	P. tennesseensis n = 47 (37–58 mm SL)			*P. oreas* n = 50 (38–52 mm SL)		
	Mean	Range	Holotype	Mean	Range	T-stat.
Scales in longitudinal series	81.0	(67–95)	80	73.7	(64–81)	6.22
Vertical scale rows	31.6	(27–35)	30	30.6	(27–34)	2.49
Predorsal distance	534	(507–580)	532	558	(529–581)	8.33
Dorsal-fin origin–caudal-fin base	495	(453–544)	499	479	(434–516)	4.26
Dorsal-fin origin–occiput	331	(304–360)	334	355	(216–395)	6.65
Prepelvic distance	469	(436–507)	450	466	(444–502)	0.69
Anal-fin origin–caudal-fin base	369	(344–392)	391	360	(320–393)	2.92
Maximum body depth	218	(190–236)	213	247	(217–279)	10.57
Maximum body width	151	(116–168)	152	160	(123–196)	3.03
Least caudal peduncle depth	105	(91–118)	107	119	(98–139)	7.46
Head length	246	(220–266)	238	246	(228–261)	0.69
Head depth	158	(143–173)	156	166	(153–180)	4.81
Head width	126	(110–139)	125	125	(113–142)	0.21
Interorbital distance	086	(76–101)	080	096	(83–104)	0.23
Snout length	072	(60–81)	072	074	(60–84)	2.45
Horizontal orbit diameter	072	(60–81)	068	072	(62–88)	0.23
Upper jaw length	071	(60–81)	065	070	(62–79)	0.97
Dorsal-fin length	099	(160–234)	170	210	(156–248)	3.32
Anal-fin length	179	(153–198)	180	194	(157–228)	4.92
Pectoral-fin length	183	(146–223)	189	181	(163–207)	0.56
Pelvic-fin length	146	(104–178)	162	158	(127–187)	3.54

nuptial males, the black chin, isthmus and anterior breast, and red on the lower one-half of the opercle further distinguish these two species from congeners. *Phoxinus tennesseensis* is distinguished from the similar *P. oreas* by smaller dark dorsolateral markings, which when maximally developed, consist of specks generally smaller than pupil versus many blotches much larger than pupil in *oreas* (Fig. 1a, d); also distinguished by the typical presence of a well-developed upper black lateral stripe in adults (usually lacking in *oreas*), red immediately below lower lateral stripe on urosome of nuptial males (silver or gold stripe between lower black stripe and red venter in *oreas*), and the incomplete series of infraorbital bones in *tennesseensis* versus the complete series in *oreas* (Fig. 2). The species are further distinguished by smaller scales [mean scales in longitudinal series 81.0 (67–95) in *tennesseensis* vs. 73.7 (64–81) in *oreas*], less robust head and body [mean body depth 218 (190–236) vs. 247 (217–279)], and more anteriorly positioned dorsal fin [mean predorsal distance 534 (507–580) vs. 558 (529–581)].

Description.—Lateral profile of body evident in Fig. 1a–c. Meristic and morphometric data for holotype and paratypes summarized in Table 1. Ontogenetic variation evident in several morphometric values (see "Variation"). Maximum known standard length 60.0 mm. Body of juveniles terete to elliptical in cross-sectional profile, deeper and more parallel sided in adults. Dorsum of head nearly flat. Eye with slight curvature over top of head. Snout broadly pointed. Mouth subterminal and slightly upturned. Dorsal-fin origin above or posterior to pelvic-fin origin, its relative position sexually dimorphic, inserting more anteriorly in males (mean predorsal distance 527 vs. 540 in females). Fins with broadly

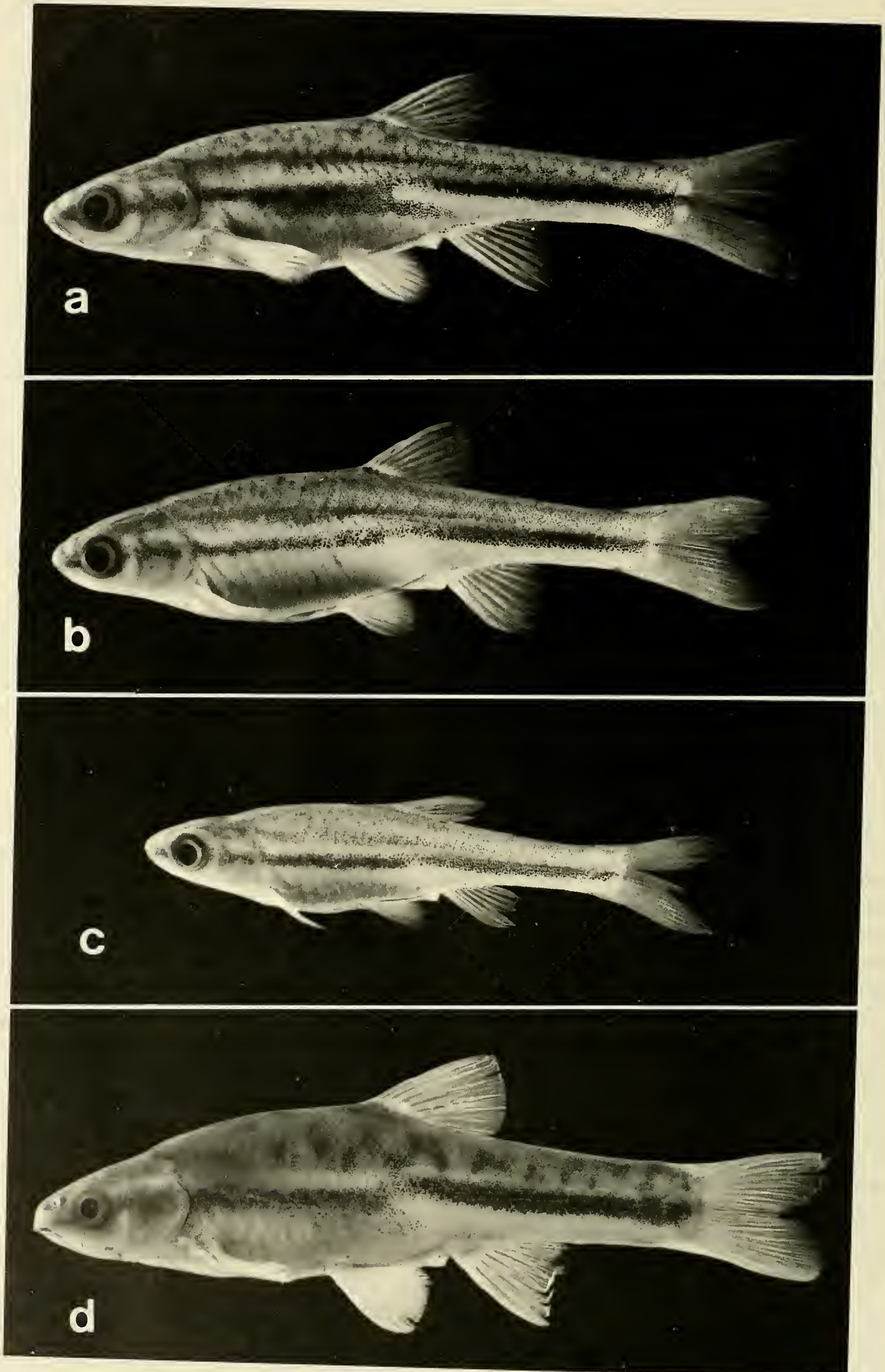

Fig. 1. a–c, *Phoxinus tennesseensis,* from top, 44.2 mm SL male, 42.0 mm SL female, 32.3 mm SL juvenile, all USNM 288068; d, *Phoxinus oreas,* 52.0 mm SL male, USNM 288066.

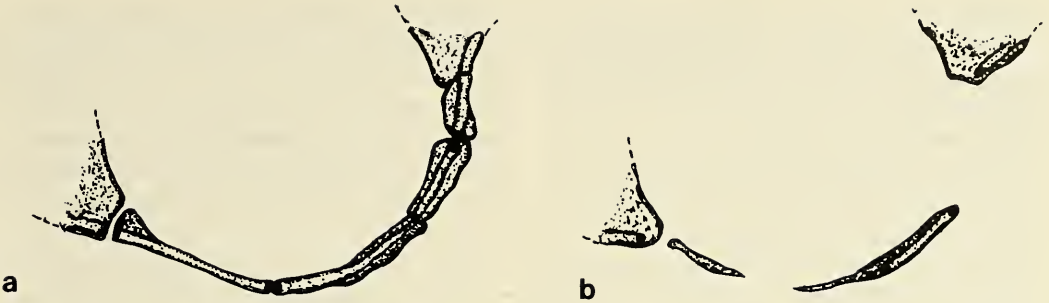

Fig. 2. Infraorbital bones of a, *Phoxinus oreas* (UT 44.1212); b, *Phoxinus tennesseensis* (TU Osteol. 575).

rounded margins. Some fins exhibiting barely significant sexual dimorphism, with dorsal, pectoral and pelvic fins averaging longer in males (mean lengths 202 vs. 195, 187 vs. 176, 150 vs. 139 respectively). No appreciable sexual dimorphism in other morphometric values.

Urogenital papilla of female with pronounced ventromedial ridge; ridge absent in males. Gut long, with about four loops lying more or less transversely (Starnes & Starnes 1978:fig. 3b).

Pharyngeal arches with lateral shelf open, well fenestrated. Each arch with single row of five long and laterally compressed teeth. Grinding surfaces of upper three teeth elongate, with lateral ridges and fine crenulations and slightly hooked at tips. Fourth tooth slightly hooked with reduced grinding surface. Fifth (ventral) tooth bluntly pointed.

Infraorbital series greatly reduced (Fig. 2b). Second and third infraorbitals reduced to narrow remnants, fourth and fifth absent. Infraorbital canal variously interrupted, with 17 to 19 external pores. Supratemporal canal broadly interrupted at midline of nape, pore formula 2-2, 2-3, or 3-3. Supratemporal canal not joined to postocular commissure and usually interrupted above orbit and posterodorsad of nares; total pores usually 8. Preoperculomandibular canal broadly interrupted at mandibular articulation, total pores usually 3 + 6.

Scales cycloid, very fine, covering entire body, absent from head. Scales of breast and belly embedded in flesh, difficult to detect. Scales of remainder of body less deeply embedded in flesh, resulting in very slippery texture and characteristic sheen. Imbrication of scales increasing anteriorly. Scale counts exhibiting geographic variation (see "Variation") and moderately variable within populations. Scales in longitudinal series 67–95 (mean 81.0). Vertical scale rows 27–35 (31.6). Lateral line poorly developed or absent, variable within populations. Pored lateral-line scales 0–33, occasionally interrupted.

Principal dorsal-fin rays 8; anal-fin rays modally 7 (6–8); pectoral-fin rays modally 15 (13–17); pelvic-fin rays modally 8 (6–8); principal caudal rays 19, rarely 18. Total vertebrae (15 specimens) 38–39, 19 precaudal + 19 caudal, or 19 + 20, or 20 + 19. Total gill rakers on first arch usually 11–13.

Breeding tubercles in both sexes on head and entire body except belly, and on rays of all fins except caudal; most prominent in males. Patterns of tuberculation and sexual dimorphism in tubercle development identical to those described in detail for *P. cumberlandensis* by Starnes & Starnes (1978: 512) and generally for *P. oreas* by Raney (1947:128). As in those species, *P. tennesseensis* has uniconic tubercles on head region. Scales on much of body with multiconic tubercles, best developed on scales of posterior portion of body, giving scales ctenoid-like texture. Males have 8 or 9 transverse rows of characteristic comb-like tubercles on each side of breast anterior to interpectoral area, and rows of strong uniserial tubercles on dorsal surfaces of second to fifth pectoral-fin rays.

Color in preservative.—Coloration variable with age, sex, and reproductive state. Darker coloration subdued in young and variable in adults, becoming boldest during spawning, maximally jet black in some males. Side with 2 parallel black stripes, lower interrupted below dorsal fin. Lower stripe relatively broad; posterior portion at mid-height of urosome straight or deflected slightly upward beneath dorsal fin; anterior portion deflected ventrally and variously developed toward anal fin base (Fig. 1a–c), at maximum development extending along base in adult males. Lower stripe continuing forward onto head, and may be well developed on opercle, preopercle, iris, and preorbital area but not on tip of snout. Upper lateral stripe narrow, about one-third width of lower, tapered posteriorly. Upper stripe usually persistent in adults anteriorly, occasionally becoming interrupted, and developed on urosome from above anal fin to hypural area, often represented by broken line posteriorly.

Portion of head and body dorsad of lower lateral stripe with moderately dense melanophore fields; belly and breast (except in nuptial males) immaculate except for few melanophores about pectoral-fin base. Scattered melanophores along anal-fin base and ventrally on caudal peduncle. Patches of melanophores forming black specks on top of head and dorsum of body in some larger individuals (Fig. 1a), particularly nuptial males, almost always smaller than pupil diameter. Middorsal streak usually well developed anterior and posterior to dorsal fin. Lips dusky in specimens of all sizes, becoming intense black in nuptial males. Lip pigmentation coincident with presence of jet black on underside of head from lips to interpectoral area. Melanophores aligned along margins of all dorsal-fin rays, anterior 4 or 5 anal-fin rays, anterior 7 or 8 pectoral-fin rays, and anterior 2 or 3 pelvic-fin rays. Males with black epibasal streak spanning anterior 4 or 5 dorsal-fin rays and membranes. Peritoneum very dusky to black, visible through body wall after preservation.

Life coloration.—In addition to dark pigmentation described above, juveniles and nonbreeding adults with head and body olive to tan dorsal to upper lateral stripe anteriorly and lower lateral stripe posteriorly. Area between lateral stripes anteriorly, and all area below lower lateral stripe on head and body silvery white. Red coloration best developed during breeding season but may be present to various degrees at any time of year and (based on aquarium observations) is rapidly changeable in response to various stimuli.

Maximum development of nuptial coloration occurs in spawning males as follows: dark markings described above jet black. Bright scarlet red covers ventral portion of body below lower lateral stripe from interpectoral area to base of caudal fin (except for black, and for silvery patches). Oblique red slash just behind upper opercle. Red laterally on snout just above upper lip, on lower half of opercle, and forming a broad stripe on upper portion of opercle just above lower black lateral stripe. Red basal band present on rays and membranes of dorsal fin below black epibasal streak. Red may be present on bases of pelvic and anal fins and is present on central caudal fin base, extending onto rays. All fins and iris bright lemon yellow. Dorsum of head and body and iris olive, tan or golden. Brilliant metallic silvery-white patches on lower portion of preopercle, suborbital area, upper one-fifth of opercle and preopercle, areas surrounding bases of pectoral and pelvic fins, and at origin of dorsal and sometimes anal fins. Two vertically aligned and vertically elongate white patches may be present at caudal fin base. Body between lateral stripes dull white or silvery, occasionally slight yellowish.

Moderately colored spawning males with less intense or diffuse red, dusky instead of black dark markings, and pale yellowish fins. Nuptial females typically lacking red and with yellow in fins and silver patches at fin bases subdued. At peak, females approximate moderately colored males.

Variation.—Phoxinus tennesseensis exhibits both ontogenetic and geographic variation. Ontogenetic analysis is based on shape changes in 52 specimens ranging 20.3–58.0 mm SL. Juveniles of *P. tennesseensis* have relatively larger heads with respect to standard length than adults. This is manifested by marked negative allometry in both head length and width and related submeasurements including interorbital distance, snout length, orbit diameter, and upper jaw length relative to standard length. The proportions of the submeasurements relative to head length or width do not change appreciably with ontogeny indicating relatively isometric growth in the head region. There is slight negative allometry in body width in concert with head width as maturing dace become less terete and more elliptical to almost parallel-sided in cross-sectional profile. Slight negative allometry occurs in caudal peduncle depth. Positive allometry is found only in prepelvic distance, indicating a relative posterior shift in the insertion of the pelvic fins with maturity. Juveniles have relatively greater dorsal-, and anal- and pectoral-fin lengths.

There is no evidence of geographic variation in morphometric proportions, pigmentation, or meristic characters other than scale counts. There is considerable clinal variation in scale counts of *P. tennesseensis,* the numbers increasing in downstream fashion from headwaters of the Tennessee drainage downstream to the Hiwassee system (Fig. 3). Specimens from the upper Holston system in Virginia (RC-REJ 667) average 75.6 (67–84) scales in longitudinal series. Proceeding downstream in the Tennessee drainage, a series from the lower Holston system (USNM 216212) averages 80.0 (75–86); lower Clinch system (ANSP 134735) 86.9 (77–95); Hiwassee system (UT 44.495) 87.0 (79–94). Numbers of vertical scale rows follow a somewhat similar trend averaging 30.6, 33.4, 32.8 and 34.0 respectively. The extent of development of pored lateral-line scales does not seem to vary in a geographic pattern but rather is highly variable within populations.

Comparisons.—Phoxinus tennesseensis is phenetically very similar to *P. oreas,* a native of several central Atlantic slope drainages and the New drainage in North Carolina, Virginia, and West Virginia. Despite this similarity (Fig. 1a, d), *P. tennesseensis* differs significantly from *P. oreas* in aspects of meristics, morphometrics, and pigmentation. Table 1 lists meristic and morphometric data for adults and the results of statistical comparisons using T-tests. *Phoxinus tennesseensis* has smaller scales on the average than *P. oreas,* having much higher average counts for scales in a longitudinal series and averaging slightly higher in vertical scale rows. Based on T-values, there are highly significant differences in predorsal, dorsal-fin origin to occiput, and dorsal-fin origin to caudal-fin base distances. These reflect more posterior insertion of the dorsal fin of *P. oreas* relative to that of *P. tennesseensis. Phoxinus tennesseensis* is distinctly less robust than *P. oreas,* with this reflected in the highly significant differences in head, body, and caudal peduncle depths, and the marginally significant difference in body width. *Phoxinus oreas* has a significantly broader interorbital distance, more dorsally flattened head, and a more declivous snout that *P. tennesseensis,* especially as adults. All fins except the pectorals are relatively shorter in *P. tennesseensis,* with significaant differences in dorsal-, anal-, and pelvic-fin lengths.

Phoxinus oreas has a complete series of infraorbital bones (Fig. 2a) and the sensory canal system in these bones is often complete with 15 external pores modally. The infraorbital series is degenerate in *P. tennesseensis* (Fig. 2b) with the fourth and fifth bones lacking and the second and third reduced. The infraorbital canal in that species is variously interrupted in the nonossified interspaces and has 17 to 19 total external pores.

When maximally developed, particularly in nuptial males, the black dorsolateral pigmentation of adult *oreas* consists of blotches usually much larger than the pupil (Fig. 1d) while that of *tennesseensis* is comprised of specks virtually always smaller than the pupil (Fig. 1a). The upper lateral stripe possessed by juveniles of both species generally persists into maturity in *tennesseensis,* though it may have minor interruptions. In *oreas* this stripe breaks up into a series of blotches or disappears altogether. The red on the ventral portion of the urosome of *tennesseensis* is essentially contiguous with the lower black lateral stripe, but in *oreas* is separated from that stripe by a silvery or golden stripe about equal in width to the black stripe.

The aforementioned clinal scale counts of *P. tennesseensis* (see "Variation"), with lower counts in headwater populations of the Tennessee River drainage (upper Holston system) approaching those of *oreas* in the adjacent New River drainage populations, raises a question of possible intergradation. However, the lack of intermediacy in morphometric attributes or coloration in the upper Holston populations is not congruent with such a possibility. *Phoxinus tennesseensis* is thus recognized as a species.

Phoxinus tennesseensis apparently has much narrower habitat tolerances than *oreas.* The latter is common in both first order and larger streams (to 10 m wide), occurs in both sheltered and more open waters, and occurs extensively in the Blue Ridge which is largely avoided by *tennesseensis.*

Young specimens of *P. tennesseensis,* lacking dorsolateral speckling and ventroflexure of the lower lateral stripe (Fig. 1c), are quite similar in appearance to and have been confused with young of the southern redbelly dace, *P. erythrogaster,* which also occurs allopatrically in the Tennessee drainage. The slight narrowing and incipient break in the lower lateral stripe beneath the dorsal fin in juvenile *tennesseensis* serves to distinguish them from *erythrogaster* which has this stripe uniformly straight throughout life.

Distribution.—*Phoxinus tennesseensis* occurs as highly localized populations in small streams of the Ridge and Valley physiographic province portion of much of the upper Tennessee River drainage in Virginia and Tennessee (Fig. 3, and Starnes & Starnes 1980a:339). While it occurs in several localities near the interface of the Ridge and Valley with the Blue Ridge and Cumberland Plateau provinces, it does not penetrate far into either of the latter two. Surveys of the Clinch-Powell system, a major headwater arm of the Tennessee drainage in the Ridge and Valley province, have failed to reveal the presence of any populations except in the lower reaches. The southwestern-most locality for *P. tennesseensis,* a small unnamed tributary at Whiteside, Marion County, Tennessee, is based on Henshall (1889:31) who clearly described nuptial coloration in this species in specimens collected in 1888 which are no longer extant. This locality has been altered by highway construction and the population is apparently extirpated. No other records are known in the Tennessee drainage downstream of the Hiwassee River system despite relatively thorough collecting.

Populations are known or were formerly known from 28 small streams, several of which, including the type locality, may now be extirpated. Such a distributional pattern may be indicative of relictual populations surviving natural processes of widespread extirpation over the millennia, but humans have had observable impacts on several populations.

Several records of *Phoxinus* from the up-

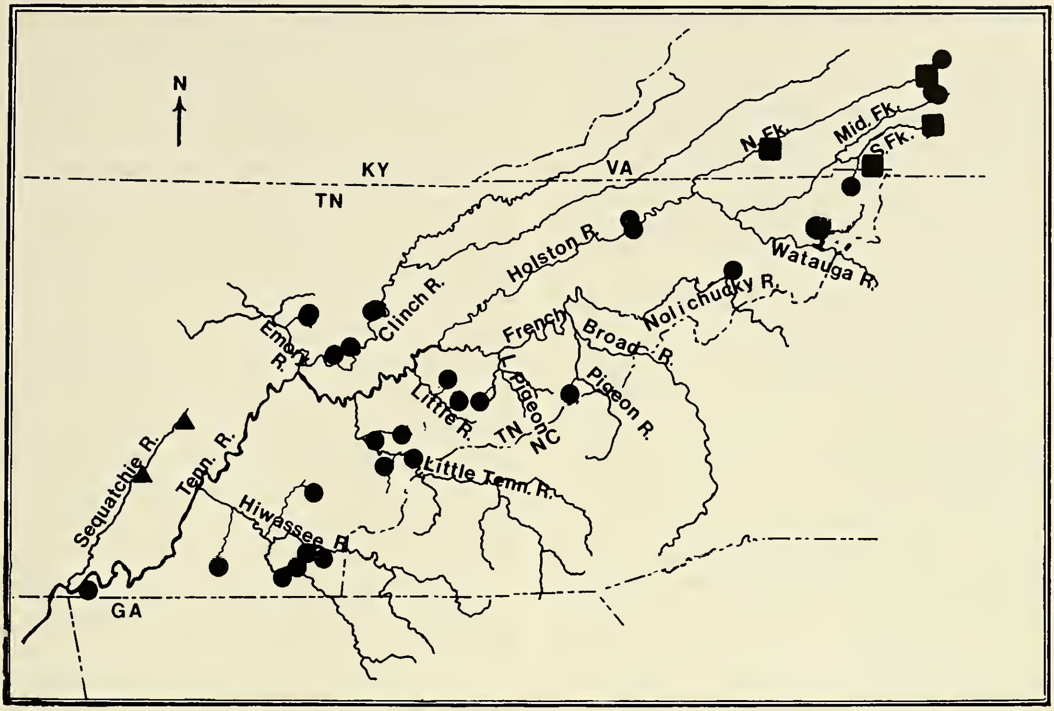

Fig. 3. Upper Tennessee River drainage showing distribution of *Phoxinus tennesseensis* (circles), putative introduced populations of *P. oreas* (squares), and proximate populations of *P. erythrogaster* (triangles).

per Tennessee drainage in Virginia (Fig. 3) do not represent *P. tennesseensis* but rather probable introductions of the similar *P. oreas* [see "Material examined" and Ross & Carico (1963:9) for localities], a species frequently seined for bait in Virginia and occasionally introduced extralimital to its native range (Jenkins & Burkhead, in press). Such introductions are noted as potential sources of confusion to future studies of distribution in these species.

Phoxinus tennesseensis has been confused in the past, particularly as juveniles, with *P. erythrogaster,* also native to the Tennessee drainage. Their distributional relationship is apparently allopatric, with *erythrogaster* occurring mainly to the west of *tennesseensis* in the Highland Rim province (Starnes & Starnes 1980b:337). Two populations of *erythrogaster* in the Sequatchie system (Fig. 3) may represent introductions from the adjacent Cumberland drainage where it is common. Two records of *erythrogaster* from within the general range of *tennesseensis* are rejected as invalild. A series of *erythrogaster* putatively taken from the Emory system in 1952 (CU 30680) is among former Tennessee Game and Fish Commission collections deposited at Cornell. A recent survey of the locality, Crab Orchard Creek, Morgan County, Tennessee, revealed no *Phoxinus* population or likely physical habitat and thus transposition of data is suspected. Equally suspect is a collection purportedly from the upper Clinch-Powell system (Indian Creek, Lee Co., Virginia) which also contains the darter *Etheostoma kennicotti* (ANSP 83177). Neither this species nor *P. erythrogaster* were found in the region in an extensive survey (Masnik 1974:126–127); they co-occur regularly only in the Cumberland and lower Tennessee drainages.

Gilbert's (1891:147) record of "*Chrosomus erythrogaster oreas*" from the Cypress Creek system in northwestern Alabama raised a question of the possible occurrence of *tennesseensis* in that region. It is puzzling to note that Gilbert's specimens (USNM 36163) are typically pigmented *P. erythrogaster,* though he described them as having an interrupted lateral stripe like that of *tennesseensis* and erroneously regarded them as intergrades between *P. erythrogaster* and *P. oreas.*

Habitat and biology.—*Phoxinus tennesseensis* occurs primarily in first order spring-fed streams of the Ridge and Valley limestone region, which range from less than a meter to two meters in width in faster flowing reaches. Specimens (UT 44.736) from lower Doe Creek, Johnson County, Tennessee, a large trout stream just above a reservoir, probably represent a bait-bucket introduction. Typical habitat streams are of relatively moderate gradient and well shaded by riparian growth or woodlands, thus remaining cool year-around with water temperatures seldom exceeding 22°C or so. Dace are not generally found in close proximity to spring sources but rather are much more common a few hundred meters downstream where they inhabit sluggish pool areas with substrates of fine gravel, sand and silt. Schools or small groups of dace congregate near cover of debris and undercut banks. Fish faunas of streams inhabited by *P. tennesseensis* are not diverse. The most common fish associates are the cyprinids *Campostoma anomalum, Notropis chrysocephalus, N. telescopus, Rhinichthys atratulus,* and *Semotilus atromaculatus* and, in the lower Clinch River system, *Notropis ardens.*

We have not observed actual spawning by Tennessee dace but an aggregation of males in spawning condition was observed in shallow water (8–10 cm depth) over clean, fine-gravel substrate at the head of a small riffle during mid-May at the type locality. This activity is similar to behavior reported for closely related congeners *Phoxinus oreas* (Raney 1947:127) and *P. cumberlandensis* (Starnes & Starnes 1981:366). Both of those species often spawn communally over the nests of gravel-nest-building cyprinids such as *Campostoma, Nocomis,* and *Semotilus.* Both *Campostoma* and *Semotilus* occur in small streams occupied by *P. tennesseensis* but mature adults of the nest-builders are more common in larger streams. Paucity of clean gravel substrates due to siltation stemming from human activities may account in part for the present extremely localized nature of Tennessee dace populations. Under such conditions it was hypothesized that the related *P. cumberlandensis* becomes dependant on nest-building cyprinids for assured purgation of spawning substrate (Starnes & Starnes 1981:367), an opportunity which may not usually be afforded to Tennessee dace.

Contents of intestinal tracts examined and similarity in gut morphology suggest that the diet of *P. tennesseensis* is similar to that of *P. oreas* and *P. cumberlandensis* (Flemer & Woolcott 1966:85, Starnes & Starnes 1978:362), consisting largely of organic detritus, algae, and diatoms. Observed size classes in collections correspond closely to those reported for *P. cumberlandensis* (Starnes & Starnes 1981:368) which has a lifespan of three years and reaches sexual maturity in one year.

Relationships.—Within the genus *Phoxinus, P. tennesseensis* shares with the phenetically very similar and geographically proximate *P. oreas* three unique and presumably derived pigmentation attributes: the interrupted and ventrally decurved lower black lateral stripe; black pigment on the chin, isthmus, and prepectoral area of nuptial males; and red pigment on the lower operculum. *Phoxinus tennesseensis* and *P. oreas* are thus hypothesized to be sister species. *Phoxinus cumberlandensis,* of the upper Cumberland River drainage in Kentucky and Tennessee, shares with these two species several conditions that are hypothesized to be shared derived features within the context of a hypothesized monophyletic grouping comprising the genus *Phoxinus,* compared to a broad selection of North American and Eurasian cyprinids. These include the configuration of the elongate, coiled gut (generalized condition shorter, fewer bends), the distinctly bilobed posterior configuration of the opercular bone (plesiomorphic condition broadly rounded) (Starnes & Starnes 1978:figs. 2, 3), the presence of random dorsolateral speckling or blotching (vs. rows of spots or plain), and the presence of two shagreen patches of breeding tubercles on the opercle (vs. single continuous patch if present). *Phoxinus cumberlandensis* is thus hypothesized to be the sister species to the phyletic line including *P. oreas* and *tennesseensis.* The results of electrophoretic studies on *Phoxinus* allozymes reported by Joswiak (1980:27) tend to support this hypothesis.

The most tenable biogeographic scenario implicit in the relationships hypothesized above, together with present-day distribution of the involved taxa, places the common ancestor to *P. cumberlandensis* and *P. oreas* + *tennesseensis* in eastern portions of the preglacial Teays River drainage [the fish fauna of the upper Cumberland River above Cumberland Falls is hypothesized to be derived largely or wholly from former Teays tributaries to the north (Starnes & Etnier 1986:339)]. Vicariance between *P. tennesseensis* and *P. oreas* was perhaps effected by capture of an upper Teays (New River) tributary by an upper Tennessee River (Holston River) tributary. A sweepstakes dispersal from the New River into the Holston through the karst region interlying the two drainages is an alternative hypothesis. *Phoxinus oreas* has subsequently dispersed into several Atlantic slope tributaries east of New River. Thus *P. cumberlandensis, P. oreas,* and *P. tennesseensis* are hypothesized to be relictual manifestations of a precursory form formerly widespread in the upper Teays region.

Etymology.—A shortened combination of "Tennessee" and the Latin suffix "-ensis," denoting place, in reference to the Tennessee River drainage to which this species is endemic.

Other material examined.—Phoxinus tennesseensis: Holston River system, Virginia: ANSP 22112-13, 2, Smyth Co., Bear Creek, trib. Mid. Fk. Holston River, 1867.—RC JRS 1, 1, Smyth Co., Bear Creek 12.1 air km NE center Marion, 1972.—RC JRS 2, 5, Smyth Co., Bear Creek 12.0 air km NE center of Marion, 1972.—RC REJ 666, 8, Smyth Co., Bear Creek at end Rt. 694, 2.7 rd. km ENE jct. rts. 622–694, 1974.—RC REJ 667, 71, Smyth Co., Bear Creek along Rt. 694, 1.5 km ENE jct. rts. 622–694, 1974.—TU 97995, 10, and TU Osteol. 576, 4 (cleared and stained), same as RC REJ 667.—RC TVA 43, 1, Middle Fork Holston River 0.3 km above Bear Creek, 1973.—RC MES 23, 12, Bland Co., Lick Creek (trib. North Fork Holston River) above uppermost Rt. 625 bridge, 3.1 air km N Ceres, 1973.—RC REJ 752, 2, Bland Co., Lick Creek off Rt. 625, 2.7 km above uppermost bridge, 2.9 air km NNW Ceres, 1976.—Tennessee: UT 44.736, 2, Johnson Co., Doe Creek, trib. to Watauga River, at Doeville, 1973.—UT 44.1700, 3, Johnson Co., Beaverdam Creek, trib. to South Fork Holston River, on US 421 7.5 air mi. NW Mountain City, 1978.—UT 44.2693, 1, same as previous except 1982. Nolichucky River system, Tennessee: UT 44.653, 1, Washington Co., tributary to Cherokee Creek at Greenwood Drive 4.7 km from jct. Brush Creek Road, 1972. Pigeon River system, Tennessee: AMNH 62947, Cocke Co., tributary to Cosby Creek 0.3 km above National Park boundary, 1960. Little River system, Tennessee: UMMZ 96851, 59, Blount Co., headwaters Reed Creek, E Walland, 1928. Little Pigeon River system, Tennessee: NLU 16066, 3, Sevier Co., Cove Creek on Covemont Church Road in Wear Cove SW Sevierville, 1967. Little Tennessee River system, Tennessee: NLU 9593, 3, Blount Co., tributary to Fourmile Creek at US Rt. 129 25.8 km S of Maryville, 1968.—TU 25660, 2, Blount Co., tributary to Fourmile Creek at jct. rts. 72–129 4.8 km NW Tallassee, 1961.—UMMZ 183714, 1, Blount Co., Tabcat Creek near Calderwood, 1957.—UT 44.98, 2, Monroe Co., Caney Branch (trib. Citico Creek), 1967. Clinch River system, Tennessee: CU 19129, 10 (combined from 3 localities), Anderson Co., Harness Creek 1.0 km W Clinton; tributary to Brushy Fork 6.9 km W Clinton; and Little Cow Creek 1.8 km N Oliver Springs, all 1950.—UT 44.765, 49, Roane Co., tributary to Bear Creek at Tn. Rt. 95 10 rd. km N Clinch River, 1971. Emory River system, Tennessee: UT 44.1098, 3, Morgan Co., Beech Fork Creek at Tn. Rt. 62 9.7 km E Wartburg, 1974. Hiwassee River system, Tennessee: ANSP 54464-67, 4, Bradley Co., Candies Creek near Cleveland, 1930.—EKU 797, 30, Polk Co., Smith Creek at Co. Rt. 4314 8.2 air km NNW Harbuck, 1976.—UT 44.496, 7, Polk Co., Indian Creek above bridge 0.2 km above Parksville Reservoir, 1970.—UT 44.575, 2, McMinn Co., Chestuee Creek at Nonaburg, 1970.—UT 44.589, 2, Polk Co., Madden Branch near Parksville Reservoir, and 12 (fin-clipped), Indian Creek near Parksville Reservoir, 1970.

Phoxinus erythrogaster: Sequatchie River system, Tennessee: UT 44.1165, 27. Tennessee River drainage, Alabama: UAIC 1965, 13; UAIC 1982, 26; UAIC 4805.03, 12; UAIC 4821.06, 2; USNM 36161, 6. Locality uncertain: ANSP 83178, 49; CU 30680, 1.

Phoxinus oreas: James River drainage, Virginia: UAIC 1048, 3; UAIC 1050, 2; UAIC 1681, 21; UAIC 2568, 1; UT 44.679, 7. Roanoke-Dan river system, Virginia: UAIC 1435, 6; UAIC 1680, 133; UAIC 3050, 26; UT 44.202, 32, UT 44.207, 26; UT 44.526, 45; UT 44.729, 7; UT 44.1212, 5 (cleared and stained). Neuse river system, North Carolina: NCSM 3775, 4; NCSM 4857, 21. New river system, Virginia: USNM 288066, 1; UT 44.239, 5; UT 44.509, 9; UT 44.730, 7; UT 44.1077, 32; UT 44.1213, 3 (cleared and stained). Tennessee River drainage, Virginia: AMNH 62748, 5, Smyth Co., Comers Creek (trib. South Fork Holston River), 1966; RC REJ 980, 1, Washington Co., Whitetop Laurel Creek (trib. South Fork Holston River), 1983; USNM 288067, 1, Bland Co., confluence Lick and Lynn Camp creeks (North Fork Holston system), 1978.

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ROTUMA LEWISI, NEW GENUS AND SPECIES OF FISH FROM THE SOUTHWEST PACIFIC (GOBIOIDEI, XENISTHMIDAE)

Victor G. Springer

Abstract.—Rotuma lewisi is described from two specimens, 18.0 and 19.3 mm SL, collected at Rotuma, about 12°30′S, 177°E. Xenisthmid and gobioid synapomorphies are discussed briefly, and some new synapomorphies are hypothesized for both groups.

The main purpose of this study is to describe a distinctive new genus and species of xenisthmid gobioid fish. The species is known from only two specimens collected during an expedition to the island of Rotuma in May, 1986.

Springer (1983) defined the gobiid subfamily Xenisthminae (accorded familial status by Hoese 1984), primarily on the basis of three synapomorphies: lower lip with an uninterrupted, free ventral margin, premaxillary ascending processes greatly reduced or absent, and the presence of a relatively large rostral bone, which replaces both ascending processes in position and, presumably, function. Homoplasies of these synapomorphies are unknown among other gobioids.

Springer (1983) proposed other osteological characters as possible synapomorphies of the Xenisthmidae, but he was uncertain of them as he lacked (still lacks) skeletal material for two of the four included genera (*Allomicrodesmus* and an undescribed genus, D. F. Hoese, in litt.): loss of basibranchials 2–4, hypobranchial 3 lost or vestigial, loss of coronomeckelian and pterosphenoid bones. The new genus and species described below exhibits all these possible synapomorphies except for two, loss of basibranchial 4 and the pterosphenoids, which, therefore, should be excluded as synapomorphies of the family.

I now hypothesize an additional xenisthmid synapormorphy: 5th ceratobranchial entirely rod-like. All other gobioids I have examined have the teeth-bearing dorsal or posterodorsal surface of the 5th ceratobranchial considerably broadened. A new gobioid synapomorphy is hypothesized in the discussion section under character 30.

Springer's (1983) Xenisthmidae included *Xenisthmus* Snyder, *Tyson* Springer, *Allomicrodesmus* Schultz, and an undescribed genus and species (D. F. Hoese, in litt.; henceforth, referred to as HUGS) different from the one herein described. Except for *Xenisthmus,* which comprises about fifteen species, all the xenisthmid genera, are monotypic, and all, with the possible exception of *Xenisthmus* and HUGS, are radically different from each other in general morphology. Hoese has informed me that HUGS appears to be similar to *Xenisthmus,* but that HUGS has vomerine and palatine teeth. Because of its striking dissimilarity to the other xenisthmid genera, I have elected to recognize a separate genus for my new species.

A cladistic analysis of the Xenisthmidae would be desirable, but is not feasible because of the lack of information on *Allomicrodesmus* and HUGS, and because a phylogenetic classification of higher level gobioid groups (families, subfamilies) has not been hypothesized (i.e., outgroup relationships are unknown).

Methods.—Methods are those described

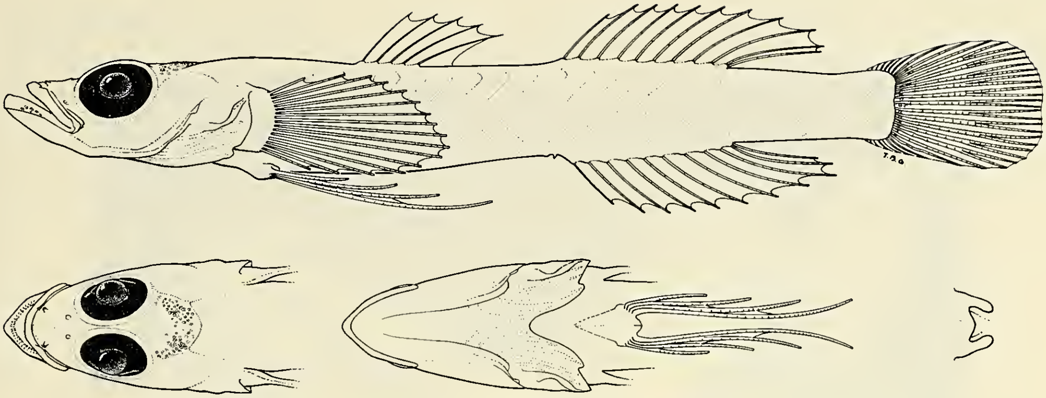

Fig. 1. *Rotuma lewisi,* USNM 280289, paratype, 18.3 mm SL, with dorsal views of head, ventral view of head and thoracic region, and urogenital papilla (much enlarged relative to other drawings).

by Springer (1983), except that I bow to convention and enumerate the last two elements as one in the dorsal and anal fins of all the genera except *Allomicrodesmus.* In all but *Allomicrodesmus,* the posteriormost pterygiophore in the dorsal and anal fins each support two rays, or in the common idiom, the last ray is split through the base. These two rays are closely applied to each other and the ray more posterior is much smaller than its mate. In *Allomicrodesmus,* the last pterygiophore in the dorsal and anal fins supports a single ray, which is similar in size and well removed posteriorly from the next ray anteriorly. To treat these last two rays as one in *Allomicrodesmus* would be misleading, although only slightly more so than the current treatment of the split-ray condition. (Hoese 1984, failed to note that the terminal dorsal- and anal-fin rays in *Allomicrodesmus* are not split through the base and, thus, counted each pair of terminal rays as two rays.)

Although among the Xenisthmidae there appears to be no intrageneric or intraspecific variation in the number of elements articulating with the terminal dorsal- and anal-fin pterygiophores, I (Springer 1967:5) have found such variation in the unrelated Blenniidae. The possibility exists, therefore, that similar variation could occur among gobioids.

I have used the convention described in Birdsong et al. (1988) in reporting the 1st dorsal-fin pterygiophore interdigitation formula in Table 1.

I rely mainly on the illustrations and Table 1 as constituting the description and comparison of *Rotuma lewisi.* The text consists mostly of a listing of available information on HUGS and *Allomicrodesmus* and general discussions and elaboration of the characters in Table 1.

Material.—The osteology of *Rotuma* (Figs. 2–8) is based on the paratype. I prepared the initial drawings, which were rendered in final form by T. B. Griswold, who also drew Fig. 1.

Information I present on HUGS was provided by D. F. Hoese. Information I present on *Allomicrodesmus* was obtained from examination and radiographs of the holotype of *A. dorotheae* (National Museum of Natural History (USNM) 113960; 20.9 mm SL) and another specimen (Australian Museum (AMS) I.18740-100; 19.8 mm SL).

Rotuma, new genus

Diagnosis (see also Table 1).—Most readily differentiated externally from other xenisthmids in having the following combination of characters: five spines in the anterior dorsal fin; four obvious, simple, seg-

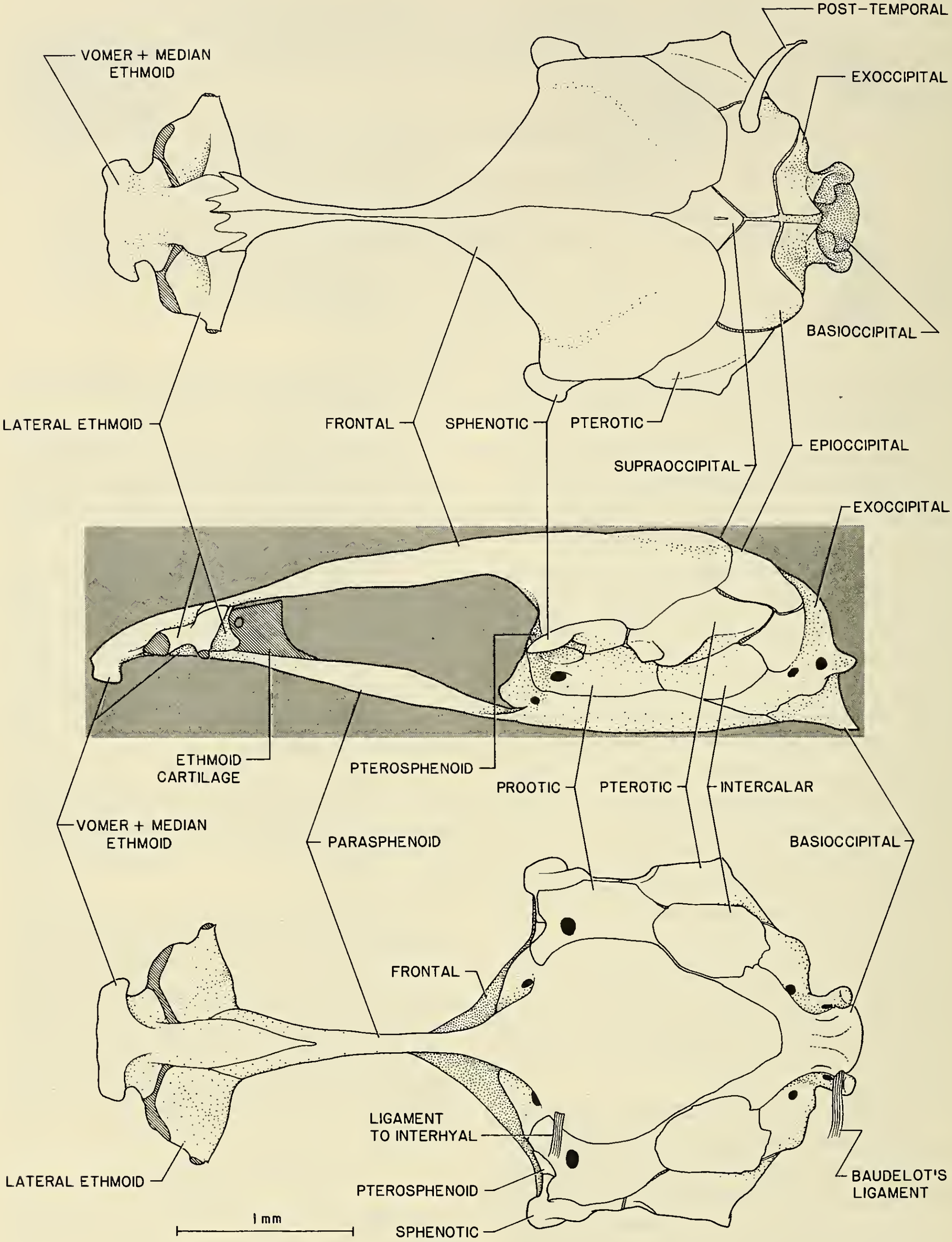

Fig. 2. *Rotuma lewisi,* USNM 280289, cranium (diagonal hatching represents cartilage anteriorly; unstained connective tissue in joints between epioccipitals, exoccipitals, and pterotics posteriorly): *top,* dorsal view; *middle,* lateral view; *bottom,* ventral view.

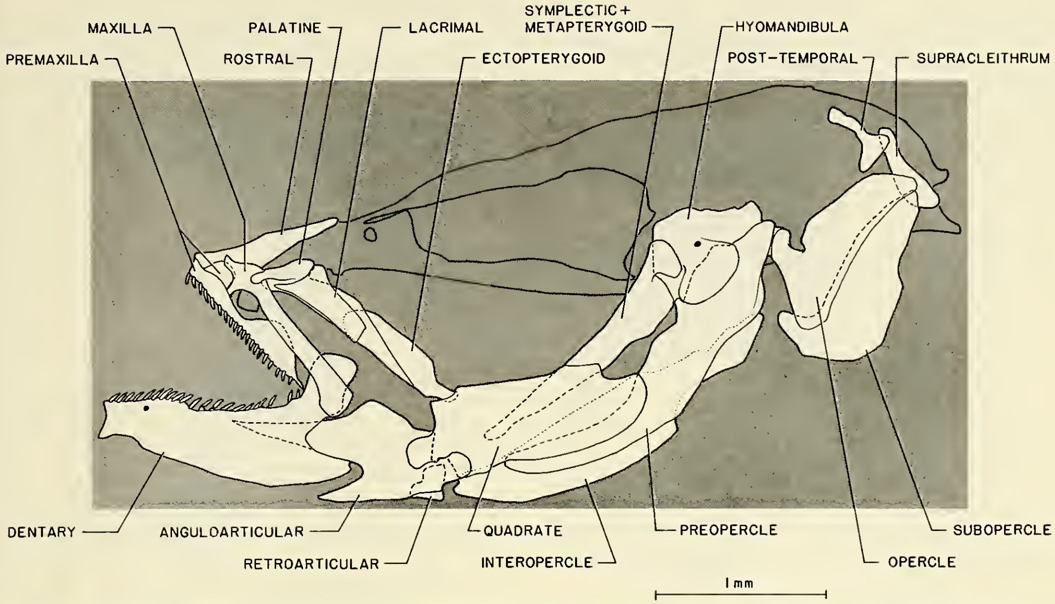

Fig. 3. *Rotuma lewisi,* USNM 280289, lateral view of superficial bones, jaws and suspensorium. (The limits of some bones obscured by others are indicated by dashed lines; see Figs. 4a and 4b for dorsoanterior view of snout and medial view of hyomandibular region.)

mented rays in each pelvic fin (a vestigial fifth ray is noticeable in the osteological preparation); scales lacking.

Remarks.—Schultz (1966) described *Kraemericus chapmani* from a single small specimen (16 mm SL), which he reported and/or illustrated as having five spines in the anterior dorsal fin, four simple, segmented pelvic-fin rays, and scales. Both I and D. F. Hoese have examined the holotype and believe it to be a young specimen of a *Xenisthmus* species. A radiograph of the holotype clearly shows that it has six spines in the first dorsal fin.

Using transmitted light and a high resolution Leitz dissecting microscope, I could

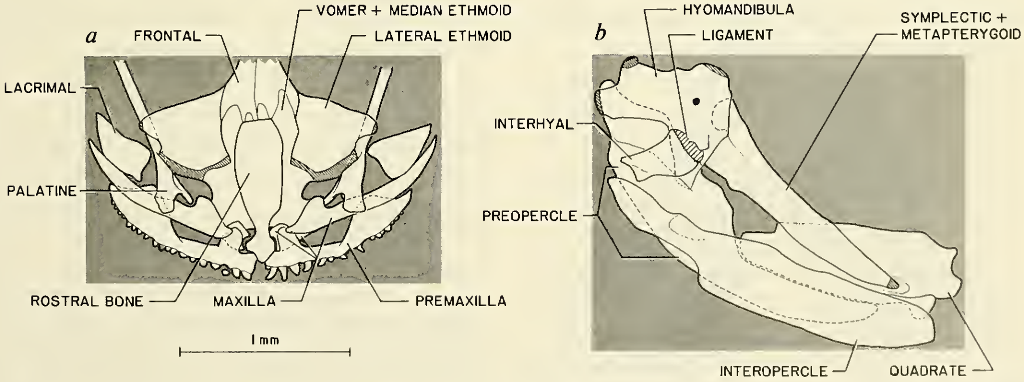

Fig. 4. *Rotuma lewisi,* USNM 280289: *a,* dorsoanterior view of snout region (frontals and palatines truncated posteriorly); *b,* medial view of hyomandibular region.

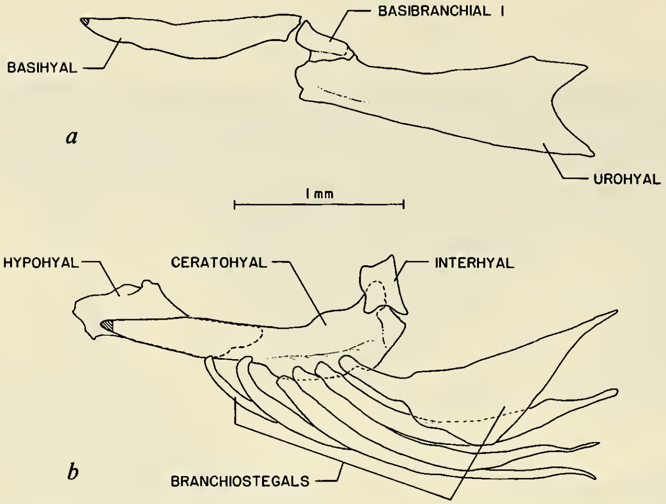

Fig. 5. *Rotuma lewisi,* USNM 280289: *a,* lateral view of urohyal, basibranchial 1, and basihyal; *b,* lateral view of left hyoid arch, rotated clockwise about long axis.

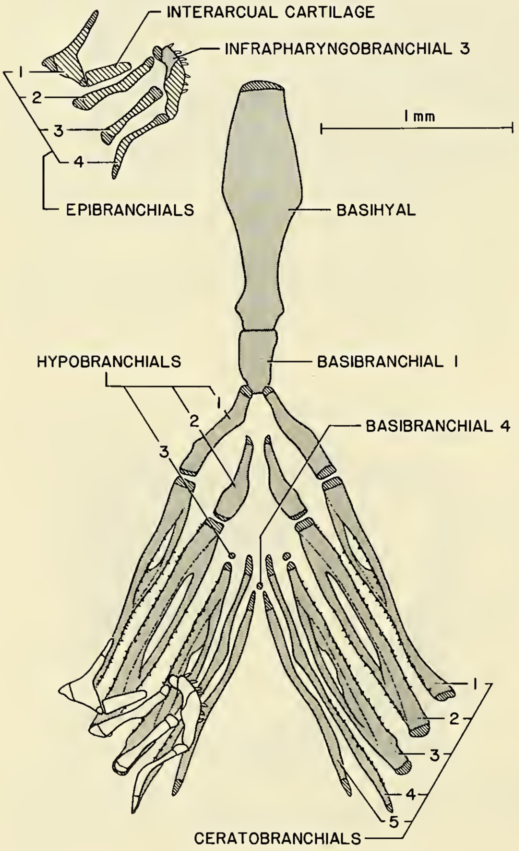

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Fig. 6. *Rotuma lewisi,* USNM 280289, dorsal view of gill arches and basihyal (right-side dorsal elements removed; left-side dorsal elements illustrated both in place and separately; except for the teeth and a small ossification of infrapharyngobranchial 3, the dorsal elements are entirely cartilaginous).

recognize a spine and four simple rays in each pelvic fin of the holotype of *Kraemericus chapmani.* Adults of *Xenisthmus* species typically have a spine and five rays, of which the posteriormost may vary from obvious, segmented, and branched to inconspicuous, unsegmented, and simple, depending on the species and size of the specimen. In small specimens of *Xenisthmus,* such as the holotype of *K. chapmani,* the posteriormost pelvic-fin ray may be indiscernible in unstained specimens.

Hoese has noticed (in litt.), and I confirm, that the presence of branched fin-rays in all the fins of *Xenisthmus* is correlated with the size of the specimen. I find that at least some of the fin-rays are branched in each fin in specimens of 18 mm SL. Hence, I believe that in the other genera (all of which are

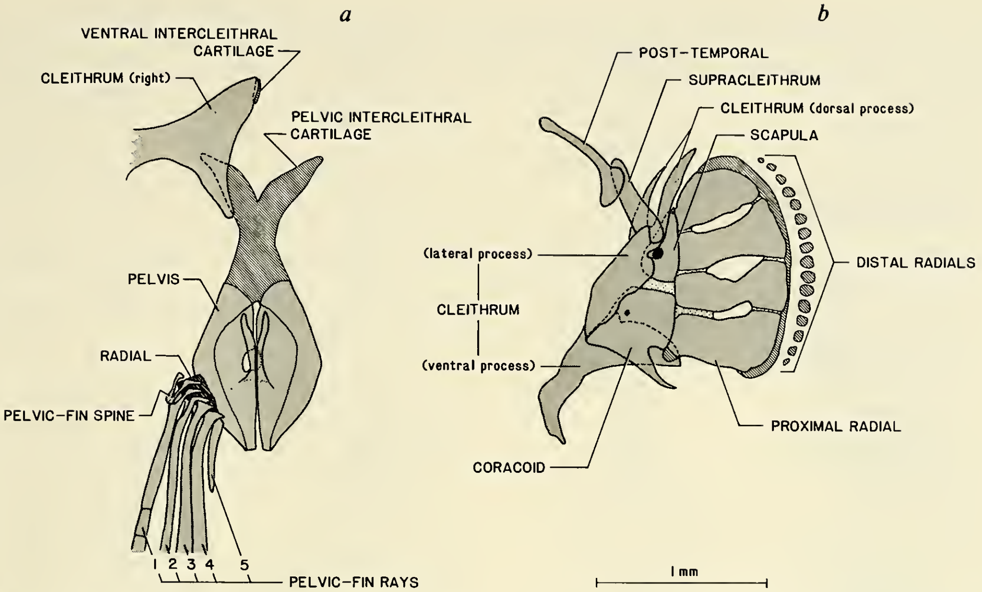

Fig. 7. *Rotuma lewisi,* USNM 280289: *a,* ventral view of pelvic-fin region (right fin-ray elements truncated; left elements and cleithrum removed; radial is cartilaginous); *b,* lateral view of pectoral fin and supports (fin-ray elements removed; unstained connective tissue present in areas between scapula and coracoid and between proximal radials proximally; distal radials and distal ends of proximal radials cartilaginous).

represented by specimens 18 mm SL or longer), those fins that I characterize as having only unbranched rays will not develop branched rays.

Etymology.—The generic name is derived from the island of Rotuma, where both known specimens were collected. Gender, masculine. The stem for formation of family-group and higher level taxa is "rotum."

Type species.—*Rotuma lewisi* Springer, by original designation and monotypy.

Rotuma lewisi, new species
Figs. 1–8

Holotype.—USNM 280290; 19.0 mm SL; immature (male?); Rotuma (ca. 12°30′S, 177°05′E), NE corner, just W of wharf, isolated patch reef in about 10.7 m; coll. 12 May 1986 by G. D. Johnson, J. D. Libbey, V. G. Springer, J. T. Williams.

Paratype.—USNM 280289; 18.3 mm SL; immature (female?); Rotuma, E side, just N of Afnaha Island, rock and coral wall, 13.7 m at base; coll. 18 May 1986, same collectors. Specimen now cleared, stained, and dissected.

Diagnosis.—See under *Rotuma.*

Etymology.—Named for Dr. Anthony D. Lewis in recognition of his support of my field work in Fiji.

Discussion

Numbered paragraphs in this section refer to numbered characters in Table 1. Information on HUGS and *Allomicrodesmus* is limited and I have not included these two genera in Table 1. Their characters, as far as known, are reported below.

1. HUGS has scales; *Allomicrodesmus* is naked.

2. HUGS has 6 spines in the first dorsal fin; *Allomicrodesmus* has 2.

3. HUGS has I,11 rays in the second dorsal fin; *Allomicrodesmus* has no spine and 30 (AMS) or 33 (holotype) segmented rays. Springer (1983) reported that the holotype of *Allomicrodesmus dorotheae* had only 32 rays, which it actually does, but there is an

Table 1.—Comparison of characters among three genera of Xenisthmidae (* in character 5 denotes pterygiophore does not support spine)

Characters \ Genera	Xenisthmus	Rotuma	Tyson
1. Scales	present	absent	absent
2. First dorsal-fin	VI	V	absent
3. Second dorsal fin	I,11 to 15	I,9	I,8 or 9
4. Branched dorsal-fin rays	present	absent	absent
5. 1st dorsal-fin pterygiophore interdigitation formula	3-2,2,1,1,0	3-1,2,2,1*,0$^{(3)}$	0$^{(12)}$
6. 2nd dorsal-fin pterygiophores	1 per interneural space	1 or 2 per interneural space	2 per interneural space
7. Anal-fin formula	I,10 to I,14	I,9	I,8 of 9
8. Anal-fin pterygiophores	1 per interneural space	1 or 2 per interneural space	1 to 3 per interneural space
9. Anal-fin pterygiophores preceding 1st hemal spine	2	1	1
10. Branched anal-fin rays	present	absent	absent
11. Pectoral-fin rays	15 to 17	16	17 to 21
12. Branched pectoral-fin rays	present	absent	absent
13. Segmented pelvic-fin rays	5	5 (5th vestigial)	1
14. Pelvic-fin spine	well developed	vestigial	absent
15. Branched pelvic-fin rays	outermost 4 in adults	absent	absent
16. Caudal procurrent rays	8 dorsal, 7 ventral^{1}	6 dorsal, 6 ventral	8 or 9 dorsal, 9 ventral
17. Caudal segmented rays	17	17	15
18. Total caudal elements	32^{1}	29	32 or 33
19. Precaudal vertebrae	10	11	13
20. Caudal vertebrae	16 or 17	15	13
21. Total vertebrae	26 or 27	26	26
22. Epipleural ribs on	vertebrae 1 to 15 or 16	vertebra 2 only	vertebra 2 only
23. Pleural ribs on	vertebrae 3 to 10	vertebrae 3 to 11	vertebrae 3 to 10
24. Hypural 5	present	present	absent
25. Epurals	2	1	1
26. Post-temporal	ventral process present	ventral process absent	ventral process absent
27. Cleithrum, dorsal process	deeply notched	deeply notched	shallowly notched
28. Cleithrum, lateral process	notched dorsally	notched dorsally	unnotched dorsally
29. Pelvis	ossified	ossified	unossified
30. Pelvic-fin radial	autogenous	autogenous	undifferentiated from pelvis
31. Scapula & coracoid	both ossified, autogenous	both ossified, autogenous	partially ossified plate
32. Proximal pectoral-fin radials	ossified, autogenous	ossified, autogenous	undifferentiated cartilaginous plate
33. Sensory canal pores on head	present	absent	absent
34. Lateral extrascapulae	present	absent	absent

aberrant, rayless gap amid the fin where a ray should be present. Springer also indicated that the two dorsal fins of *Allomicrodesmus* were continuous, but they are not.

4. HUGS has branched dorsal-fin rays; *Allomicrodesmus* has only simple rays.

5. Based on a radiograph, the first dorsal-fin pterygiophore interdigitation formula of *Allomicrodesmus* appears to be 6-1,1,0. This formula should be verified in a counterstained skeletal preparation as reduced, cartilaginous pterygiophores, which appear to be present in *Allomicrodesmus,* are often indiscernible on radiographs. I lack information on the formula for HUGS.

7. HUGS has I,10 anal-fin rays; *Allomicrodesmus* has 0,24 or 26 (latter in the holotype; Springer 1983, erred in reporting 25 rays in the holotype).

10. HUGS has branched rays in dorsal fin; *Allomicrodesmus* has only unbranched rays.

11. HUGS has 18 pectoral-fin rays; *Allomicrodesmus* has 10.

Table 1.—continued

Characters / Genera	Xenisthmus	Rotuma	Tyson
35. Rostral bone	relatively small	relatively large	relatively large
36. Nasal bone	present	absent	absent
37. Lacrimal	present	present	absent
38. Metapterygoid	autogenous	fused with symplectic	absent
39. Retroarticular	present	present	absent (fused to anguloarticular ?)
40. Vomerine teeth	absent	absent	present
41. Vomer	autogenous	fused with median ethmoid	fused with lateral and median ethmoids
42. Lateral ethmoid	autogenous	autogenous	fused with vomer and median ethmoid
43. Median ethmoid	autogenous	fused with vomer	fused with vomer and lateral ethmoids
44. Supraoccipital	autogenous	autogenous	undifferentiated
45. Pterosphenoid	undifferentiated	autogenous	undifferentiated
46. Sphenotic & pterotic	autogenous	autogenous	fused together
47. Intercalar	present	present	absent
48. Baudelot's ligament attached proximally to	basioccipital	basioccipital	basioccipital & 1st vertebra
49. Matching condyles on first vertebra and exoccipitals	present	present	absent
50. Dorsal & ventral hypohyals	autogenous or fused together	fused together	fused together
51. Anterior & posterior ceratohyals	autogenous	fused together	fused together
52. Basihyal	see Springer, 1983:fig. 11	Figure 6	see Springer, 1983:fig. 13
53. Basibranchial 1	cartilaginous	ossified	ossified
54. Basibranchial 4	absent	present (vestigial)	absent
55. Hypobranchial 3	vestigial or absent	absent	vestigial
56. Ceratobranchials 1 to 3	rod-like	double-strutted	rod-like
57. Ceratobranchial 1	with well-developed gill rakers	with fine teeth	edentate
58. Ceratobranchials 2 to 4	with well-developed tooth patches	with fine teeth	edentate
59. Ceratobranchial 5	with fine teeth	edentate	with well-developed teeth
60. Epibranchial 1	ossified	cartilaginous	cartilaginous
61. Epibranchial 1	with uncinate process	with uncinate process	lacks uncinate process
62. Epibranchial 1	with gill rakers	edentate	edentate
63. Interarcual cartilage	present	present	absent
64. Infrapharyngobranchial 1	present (vestigial)	absent	absent
65. Infrapharyngobranchial 2	present	absent	absent
66. Infrapharyngobranchial 4	present	absent	absent

[1] Incorrectly reported to comprise one less element in Springer (1983).

12. HUGS has all but the uppermost and lowermost pectoral-fin rays branched; *Allomicrodesmus* has only simple pectoral-fin rays.

13. HUGS has I,5 pelvic-fin rays. *Allomicrodesmus* has three obvious segmented pelvic-fin rays (presence of spine and vestigial rays unknown).

15. Both HUGS and *Allomicrodesmus* have only simple pelvic-fin rays.

16. HUGS has 8 dorsal and 6 or 8 ventral procurrent (unsegmented) rays. *Allomicrodesmus* has 8 dorsal and 7 ventral procurrent rays (based only on holotype).

17. HUGS has 17 and *Allomicrodesmus* has 15 segmented caudal-fin rays.

18. HUGS has 31 or 33 and *Allomicrodesmus* has 30 total caudal-fin elements (based only on holotype of *A. dorotheae*).

19–21. *Allomicrodesmus* has 18 + 25 or 27 = 43 or 45 vertebrae.

30. Springer (1983) in discussing various

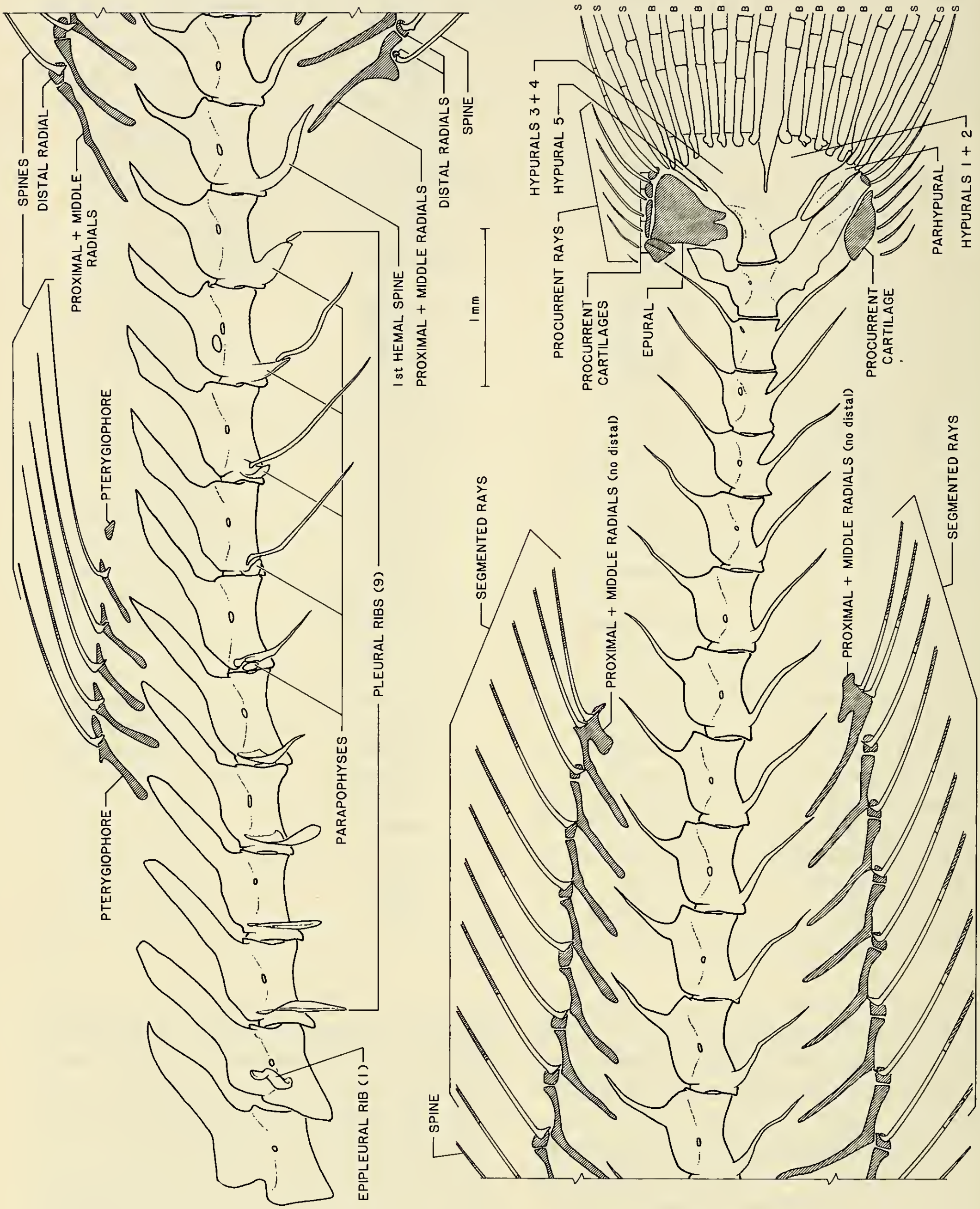

Fig. 8. *Rotuma lewisi*, USNM 280289, vertebrae and unpaired fins (segmented rays truncated; cartilaginous elements indicated by diagonal hatching).

gobioid characters, did not stress that a single, relatively large, cartilaginous radial was present in the pelvic fin of almost all gobioids. The radial (one in each fin), like the median pelvic intercleithral cartilage, is apparently an unossified portion of the initial, median cartilaginous block that gives rise to both of the ossified pelvises.

The radial supports all or most of the pelvic-fin elements, and is probably a synapomorphy of the Gobioidei, or the Gobioidei less the Rhyacichthyidae. In the Rhyacichthyidae, the homologue of the radial in the other gobioids is represented only by a thin layer of cartilage covering the lateral edge of the pelvis in the region embraced by the bases of the fin elements. In *Tyson,* the radial is autapomorphically undifferentiated (Springer 1983:fig. 16c) from the pelvis because the cartilaginous block that gives rise to the pelvises does not ossify. In the eleotridid *Butis amboinensis* (Springer 1973: listed in material), there are two radials in each fin, a block-like one anteriorly that supports all but the posteriormost ray, and a smaller ball-like one that supports the posteriormost ray.

40. HUGS has vomerine (and palatine) teeth. I was unable to determine the state of this character for *Allomicrodesmus* as I could not open the jaws of the holotype without causing damage to the specimen.

56. The double-strutted ceratobranchials 1–3 of *Rotuma* appear to be unique among all fishes. It would be desirable to verify this condition in another specimen of *Rotuma.*

65. Only the left side dorsal elements were illustrated in Fig. 6. Just anterior to infrapharyngobranchial 3 on the right side, is a tiny fragment of cartilage that possibly represents a vestigial infrapharyngobranchial 2.

Acknowledgments

I thank Dr. D. F. Hoese (AMS) for providing information on HUGS and ontogeny of fin-ray branching in gobioids, and Drs. G. D. Johnson and J. T. Williams (USNM) for discussions during the course of my work and for commenting on the manuscript. Dr. R. S. Birdsong (Old Dominion University) reviewed the manuscript and provided constructive suggestions for its improvement (he also correctly noted that Springer 1983: fig. 6, was in error in indicating that the lateral ethmoids met in the midline above the lateral ethmoid; the correct condition of the ethmoids is illustrated in fig. 3 of the same study). I am indebted to Dr. A. D. Lewis, Fisheries Officer, Government of Fiji, and Mr. R. Fonmoa, Malhaha District, Rotuma, for making arrangements and granting permission for field work in Rotuma. Financial support for field work during which the new species was collected was provided by a grant from the Max and Victoria Dreyfus Foundation.

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A REVIEW OF THE ASIAN SPECIES OF THE GENUS *LAMPROSCATELLA* HENDEL (DIPTERA: EPHYDRIDAE)

Wayne N. Mathis and Jin Zuyin

Abstract.—The Asian species of the genus *Lamproscatella* Hendel, all in the subgenus *Lamproscatella,* are reviewed, including three new species as follows: *L. sinica* (China: Sichuan and Gansu); *L. clava* (Mongolia: Bajan-Olgij aimak); *L. tibetensis* (China: Tibet). A key to these species, illustrations of structures of the male genitalia, and descriptions are provided.

While studying specimens of the subfamily Ephydrinae that were recently made available to us from Asia, we segregated three species of the genus *Lamproscatella* Hendel. Previously only two species of that genus had been reported from this area, viz., *L. coenicola* Miyagi (1977:89, Japan) and *L. sibilans* (Haliday) (Cogan 1984:172, northeastern Tibet). After comparative studies, particularly of structures of the male genitalia, we have determined that none of our newly segregated species had been described previously. The purpose of this paper is to describe and document these discoveries within the context of a review.

With description of the new species, the number of species reported from this area is five. We did not reconfirm the presence of *L. sibilans,* however, as none of the specimens we examined is a representative of that species.

We adhere generally to the methods and descriptive terminology that were used previously for this subfamily (Mathis 1979, 1982). For the convenience of the user, a more precise definition of the M vein ratio is: straight line distance along vein M between crossveins (dm-cu and rm)/distance apicad of dm-cu. Definitions of the other ratios used in the text are as published in the above-cited references.

Specimens for this study came from the collections of the Entomological Institute, Hokkaido University (HUS), Sapporo, Japan; Hungarian Natural History Museum (HNHM), Budapest, Hungary; the Northwestern Teachers College (NTC), Lanzhou, Gansu Province, China; and the Shanghai Entomological Institute (SEI), Academica Sinica, Shanghai, China, and the National Museum of Natural History (USNM), Washington, D.C.

Genus *Lamproscatella* Hendel

Lamproscatella Hendel, 1917:42. Type species: *Ephydra sibilans* Haliday, orig. des.—Cogan, 1984:172–173 [Palearctic catalog].

Diagnosis.—*Lamproscatella* is similar to several genera of the tribe Scatellini (subfamily Ephydrinae) but may be distinguished by the following combination of characters:

Head.—Lateroclinate fronto-orbital setae 2; arista bare or minutely haired, lacking long, dorsal rays; a major genal seta lacking.

Thorax. —Acrostichal setulae in 2 rows, either none well developed or only a prescutellar pair conspicuously evident; dorsocentral setae 3 (1 + 2), insertion of posteriormost pair slightly displaced laterally; wings usually hyaline to faintly infumate, lacking white spots or a pattern; costal vein extended to vein M.

Discussion.—Within the tribe Scatellini, *Lamproscatella* is very similar and probably closely related to the genus *Amalopteryx* Eaton. Both genera are unique within the tribe in lacking a genal seta, although the loss of this seta could have happened independently and is not conclusive evidence for a close relationship. A more definitive study is needed, especially of structures of the male genitalia, to determine if there is a sister-group relationship between these genera.

Lamproscatella presently includes three subgenera (*Haloscatella* Mathis, *Thinoscatella* Mathis, and the nominate subgenus), but only the nominate subgenus is known to be represented in Asia.

Subgenus *Lamproscatella* Hendel

See generic synonymy.

Diagnosis.—This subgenus is distinguished from *Haloscatella* and *Thinoscatella* by the following combination of characters: general coloration brown.

Head.—Mesofrons with dense to sparse microtomentum, at most subshining; posterior fronto-orbital seta inserted closer to anterior fronto-orbital seta than to inner vertical seta; eye nearly round; eye-to-cheek ratio 0.25 or less.

Thorax.—Posterior notopleural seta inserted closer to posterior angle than to dorsal angle and at approximately the same level as anterior seta; length of basal scutellar setae ½ or less that of apical setae; wing macropterous.

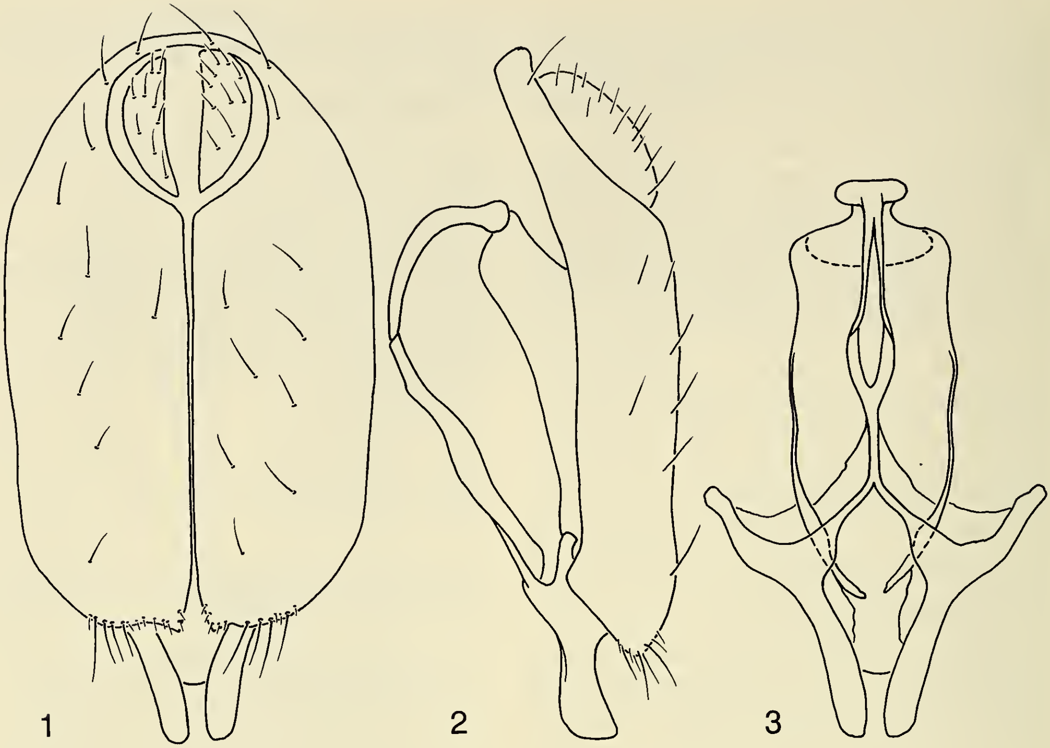
Abdomen.—Structures of the male genitalia as follows: surstylus either lacking or fused indistinguishably to ventral margin of epandrium; cercal cavity generally small, usually not longer than combined length of epandrium plus surstylus; aedeagal apodeme generally slender, curved, C- to J-shaped; gonite in lateral view projected ventrally, shape variable but usually broadly V-shaped in anterior view. Female ventral receptable as follows: operculum flat, extended process much wider near operculum, becoming considerably narrower and more abruptly curved away from operculum.

Distribution.—Subgenus *Lamproscatella* is the most widespread of the genus, occurring in all faunal realms except the neotropics and Australia.

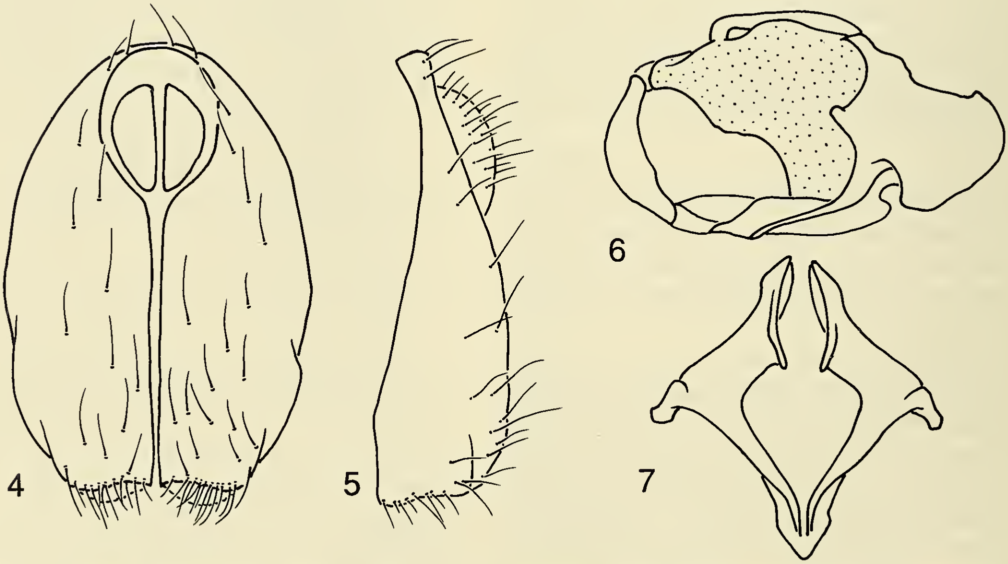
Discussion.—Because the external features of species of this subgenus are very similar, we have provided an extensive description only for *L. sinica*; for the other descriptions, we have only given additions or differences from it. For the most part, we have relied on characters of the male genitalia to distinguish between species, especially in the key to follow.

Key to Asian Species of *Lamproscatella* Hendel

1. Aedeagus slender, length 4× width, tapered gradually to a point (Figs. 12, 15); ventral extension of gonite pointed in lateral view (Figs. 12, 15) 2
– Aedeagus broad and/or short, length at most slightly more than 2× width (Figs. 2, 6, 9); ventral extension of gonite broadly rounded or truncate in lateral view (Figs. 2, 6, 9) 3
2. Ventral margin of epandium bearing long setae, length subequal to width of epandrium at apex (Fig. 14); cercal cavity subequal to ½ total length of epandrium (Fig. 14); 5th sternum broadly U-shaped (Fig. 16); gonite with feather-like fringe (Fig. 15); median part of aedeagal apodeme with lateral triangular flanges (Fig. 16) .... *L. tibetensis,* new species
– Ventral margin of epandrium bearing short setae, each much shorter than width of epandrium at apex (Fig. 11); cercal cavity slightly more than ⅓ total length of epandrium (Fig. 11); 5th sternum subrectangular, with short anteroventral processes (Fig. 13); 5th sternum subrectangular, with short anteroventral



Figs. 1–3. Male genitalia of *Lamproscatella clava*. 1, Epandrium and cerci, posterior view. 2, Genitalia, lateral view. 3, Gonites and aedeagus, anterior view.



Figs. 4–7. Male genitalia of *Lamproscatella coenicola*. 4, Epandrium and cerci, posterior view. 5, Epandrium and cercus, lateral view. 6, Internal genitalia, lateral view. 7, Gonites, anterior view.

processes (Fig. 13); gonite lacking feather-like fringe (Fig. 12); median part of aedeagal apodeme with a slightly rounded lateral extension (Fig. 13) .... *L. sinica,* new species

3. Gonite long, moderately narrow, and subtruncate apically, width about ½ length (Figs. 2–3) .... *L. clava,* new species

– Gonite short, wide, and broadly rounded apically, width about equal to length (Figs. 6, 9) 4

4. Aedeagus broadly elliptical in anterior or posterior views, strongly constricted medially, apex acutely pointed (Fig. 10) .. *L. sibilans* (Haliday)

– Aedeagus moderately narrow in anterior or posterior views, lateral margins sinuate, but not strongly constricted medially (Fig. 6) .... *L. coenicola* Miyagi

Lamproscatella (*Lamproscatella*) *clava,* new species

Figs. 1–3

Description.—As in *L. sinica* except as follows: small shore flies, length 1.65 to 1.90 mm.

Head.—Head ratio 0.51; eye ratio 1.09; eye-to-cheek ratio 0.23.

Thorax.—Costal vein ratio 0.13; M vein ratio 1.70.

Abdomen.—Fifth tergum of male subtrapezoidal in dorsal view, posterior margin truncate or very shallowly rounded. Male genitalia (Figs. 1–3) as follows: epandrium parallel sided, dorsal margin rounded, ventral edge sinuate and terminated medially as 2 broadly based points, median epandrial fissure weak but continued to cercal cavity; aedeagal apodeme slender, allantoid, enlarged dorsally; aedeagus moderately wide in posterior view, narrower apically, terminated as a spatulate process with a rough margin; gonites broadly V-shaped, each arm slightly recurved distally and produced ventrally into a long extension, which, in lateral view, is a wide, apically enlarged flange that is somewhat pointed posteriorly.

Type material.—The holotype male (HNHM) is labeled "Mongolia: Bajan-Olgij aimak, am Fluss Chovd gol bei der Stadt Olgij, 1750 m Exp. Dr. Z. KASZAB, 1968/ Nr. 1046 30. VI. 1968 [30 Jun 1968]." The allotype female and two paratypes (1 ♂, 1 ♀; HNHM) bear the same label data as the holotype. The holotype is double mounted (minute nadel in foam block) and is in good condition (the abdomen has been removed and dissected; the structures are in an attached microvial).

Distribution.—Palearctic. Mongolia: Bajan-Olgij.

Etymology.—The species epithet, *clava,* is a Latin noun referring to the club-shaped gonite of the male genitalia.

Remarks.—This species may be distinguished from its congeners in the subgenus *Lamproscatella* principally by structures of the male genitalia, especially the club-like gonite and moderately wide aedeagus (see figures and description above).

Lamproscatella (*Lamproscatella*) *coenicola* Miyagi

Figs. 4–7

Lamproscatella coenicola Miyagi, 1977:89.
Lamproscatella (*Lamproscatella*) *coenicola.*—Cogan, 1984:172 [Palearctic catalog].

Description.—As in *L. sinica* except as follows: small to moderately small shore flies, length 1.85 to 2.15 mm.

Head.—Head ratio 0.67; eye ratio 0.86; eye-to-cheek ratio 0.22. Face unicolorous, brownish gray.

Thorax.—Costal vein ratio 0.16; M vein ratio 0.76.

Abdomen.—Fifth tergum of male subtriangular, posterior margin acutely rounded. Male genitalia (Figs. 4–7) as follows: epandrium more or less parallel sided, subrectangular to elliptical, dorsal margin rounded, ventral margin truncated posteriorly, becoming rounded anteriorly, median epandrial fissure conspicuous and continued to cercal cavity; aedeagal apodeme lunate, swollen in middle, comparatively robust, symmetrical; aedeagus relatively narrow in anterior view, lateral margins sinuate; both gonites together in anterior view roughly diamond shaped, each arm projected posterolaterally and distinctly angled posteromedially, apex, in lateral view, very broadly produced, as high as wide, rounded apically.

Type material.—The holotype male (HUS) is labeled "Utonai-ko Iburi 5-0VII-1961 [5 Jul 1961]/Japonia Hokkaido I. Miyagii." The holotype and two male paratypes (HUS) (listed as a male and a "female" in the original publication) are double mounted (minute nadel in a cardboard rectangle) and are in good condition (the abdomens of the male paratypes have been removed and dissected; for one specimen, the structures had been slide mounted, for the other, these structures are in an attached microvial).

Distribution.—Palearctic. Japan: Hokkaido (Utonai-ko Iburi).

Remarks.—Miyagi (1977) noted the similarity between this species and *L. sibilans* but stated that the former could be distinguished by having four large scutellar setae. We have not been able to separate the two species by this character. In the specimens we examined, the scutellar setae are nearly the same size, with only minor variation in length. Thus, for the present, we have had to use characters from the male genitalia to distinguish between them.

?*Lamproscatella* (*Lamproscatella*) *sibilans* (Haliday)

Figs. 8–10

Ephydra sibilans Haliday, 1833:175.

Lamproscatella (*Lamproscatella*) *sibilans.*—Andersson, 1975:166 [figures of male genitalia].—Cogan, 1984:172 [Palearctic catalog].

Remarks.—Cogan (1984:172) listed northeastern Tibet in the distribution for this species in his recent catalog of palearctic species. We have not examined the specimen(s) upon which this record is based but we have studied a teneral specimen recently collected from Tibet that represents a new species (see below). Because the species of the subgenus *Lamproscatella* are very similar externally, there is a possibility that the record of *L. sibilans* from Tibet is based on a misidentification and also represents the new species we have identified.

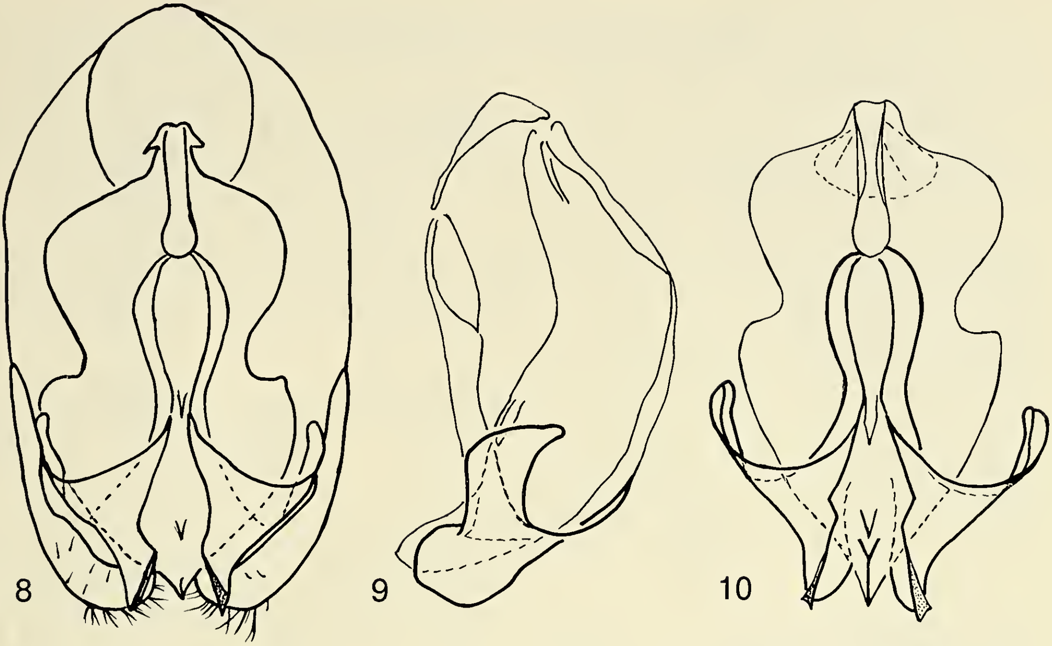
Lamproscatella (*Lamproscatella*) *sinica*, new species

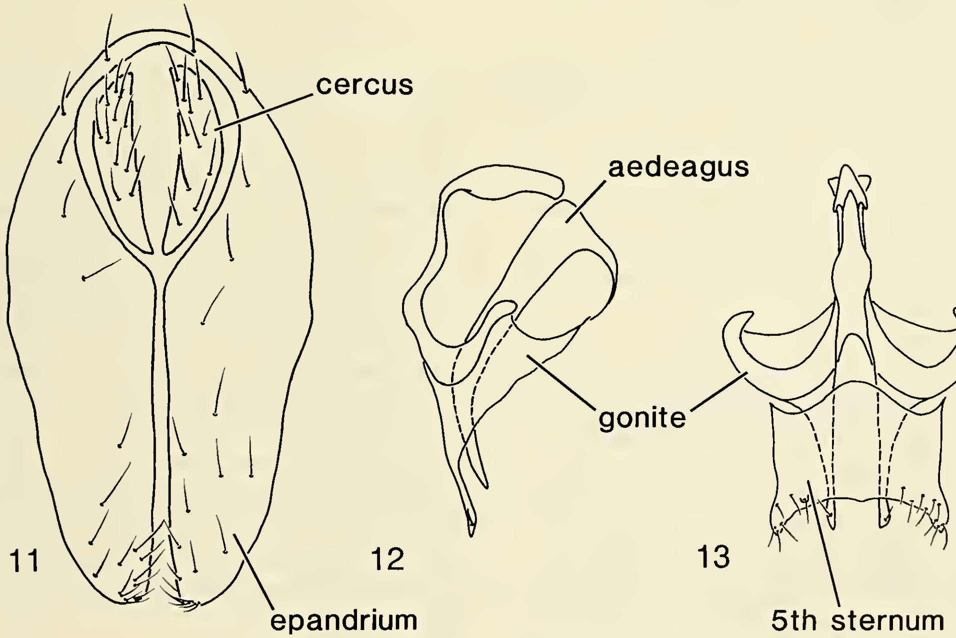
Figs. 11–13

Description.—Small to moderately small shore flies, length averaging 2.0 mm (1.70–2.40 mm); body mostly brown.

Head.—Head width-to-height ratio averaging 0.67; frontal triangle and fronto-orbits subshining, brown, contrasted with microtomentose, blackish remainder of frons; frontal triangle bearing several setulae along anterolateral margins; ocellar triangle concolorous with frontal triangle or a little more reddish; 2 large, lateroclinate, fronto-orbital setae and 2–3 setulae in front of and between these; 1 pair of strong ocellar setae, these longer than distance between anterior ocellus and ptilinal suture. Antenna black, microtomentose; arista micropubescent, length longer than combined length of 2nd segment and 1st flagellomere. Face brown to golden, with very sparse, light grayish microtomentum; face wider than high, not greatly protrudent; usually only 3 lateral facial setae; 5–7 parafacial/genal setae. Eye oval; eye ratio averaging 0.81. Genal coloration lighter than face, brownish; eye-to-cheek ratio averaging 0.22. Palpus blackish.

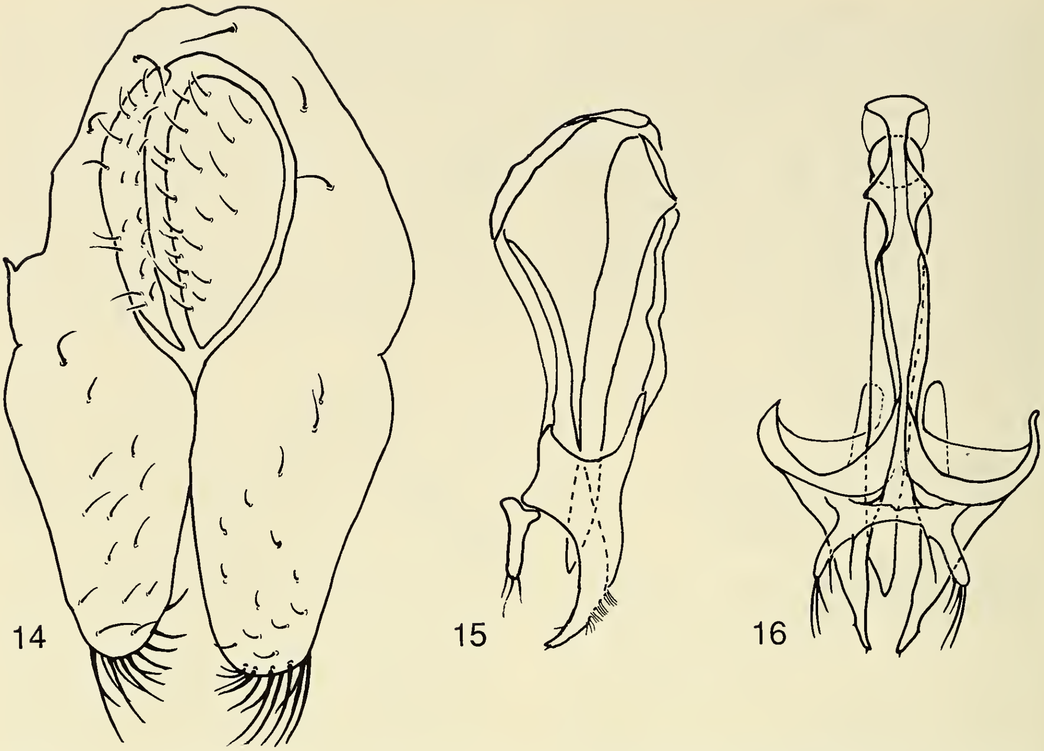
Thorax.—Mesonotum mostly brown but with some bluish coloration anteriorly; scutellum concolorous with scutum; pleural area brown, becoming bluish gray along anterior part of anepisternum and ventral part





Figs. 8–10. Male genitalia of *Lamproscatella sibilans.* 8, Male genitalia, anterior view. 9, Genitalia, lateral view. 10, Gonites and aedeagus, anterior view.

Figs. 11–13. Male genitalia of *Lamproscatella sinica.* 11, Epandrium and cerci, posterior view. 12, Internal genitalia, lateral view. 13, 5th sternum and gonites, anterior view.



Figs. 14–16. Male genitalia of *Lamproscatella tibetensis.* 14, Epandrium and cerci, posterior view. 15, Internal genitalia, lateral view. 16, Gonites and aedeagus, anterior view.

of katepisternum. Legs black; femora with some metallic green luster. Wing hyaline; costal vein ratio averaging 0.147; M vein ratio averaging 0.67.

Abdomen.—Dorsum concolorous with mesonotum, becoming darker ventrally. Structures of male genitalia (Figs. 11–13) as follows: ventral margin of each side of epandrium acutely rounded, bearing a few small setulae; median epandrial fissure very evident, extended to cercal cavity; 5th sternum generally subrectangular, lateroventral corners produced into processes, median dorsal margin broadly produced into large rounded extension; aedeagal apodeme short, sublinear, with small anterolateral flange; gonite from anterior view shaped like 2 J's that are fused along longer arms but with long, acutely pointed extension medioventrally; aedeagus very slender, broader basally, tapered to acutely pointed apex.

Type material.—The holotype male (USNM) is labeled "Beh Luh Din 30 mi N Chengtu iv 1–15 1935 [1–15 Apr 1935, date handwritten] China D C Graham." The allotype female and five paratypes (1 ♂, 4 ♀; USNM) bear the same locality label data as the holotype. Five additional paratypes are as follows: China: Gansu; Wudu (grass near wheat field), 9 Apr 1979, Jin Zuyin (1 ♂, 4 ♀; NTC). The holotype is double mounted (glued to a paper point) and is in poor condition.

Distribution.—Presently known only from two sites in China as follows: Chengtu (the type locality), in the province of Sichuan, and Wudu, in the province of Gansu.

Etymology.—The species epithet, *sinica,* is a Latinized adjective for China, the country from which all known specimens of this species were collected.

Remarks.—This species is very similar, especially externally, to *L. sibilans,* and can be distinguished from it and other congeners of the subgenus *Lamproscatella* only by reference to the shape of the male genitalia, which are figured (Figs. 12–14) and described above. The shape of the aedeagus and gonite is of particular importance.

Lamproscatella (*Lamproscatella*) *tibetensis,* new species

Figs. 14–16

Description.—As in *L. sinica* except as follows: small shore fly, length about 2.0 mm (estimate, abdomen removed for dissection before measurement made).

Head.—Head ratio 0.64; eye ratio 1.14; eye-to-cheek ratio 0.23.

Thorax.—Costal vein ratio 0.64; M vein ratio 1.38.

Abdomen.—Fifth tergum of male subtrapezoidal in dorsal view. Male genitalia (Figs. 14–16) as follows: epandrium subovate, ventral margin of each side slightly curved, bearing several moderately long setae that are nearly as long as width of apex of epandrium; cercal cavity large, subequal to one-half length of combined epandrium and fused surstyli; 5th sternum band-like, lateroventral corners produced into longer processes, apex of process bearing 3 setae, 2 on ventral margin; aedeagal apodeme short, median part with lateral triangular flanges; gonite similar to *L. sinica,* but with feather-like fringe on the subapex of medioventral pointer extension; aedeagus very slender, broader basally, tapered to pointed apex.

Type material.—The holotype male (SEI) is labeled "Tibet: Lhasa, 12085 feet, 5–6 June 1980[,] Mary L. Ripley." The holotype is double mounted and is in poor condition (somewhat teneral; abdomen removed for dissection, the structures are stored in an attached microvial).

Distribution.—Palearctic. China: Tibet (Lhasa).

Etymology.—The species epithet, *tibetensis,* refers to the geographic region where this species was collected.

Remarks.—This species is represented only by the holotype, which is in rather poor condition. We are describing the species now, however, because the male genitalia are well sclerotized, and species discrimination in this subgenus is primarily based on these structures. Furthermore, it is unlikely that we or another dipterist will be able to collect additional specimens in the near future, and we would like to make this review as complete as possible.

Acknowledgments

For reviewing a draft of this paper, we thank T. Pape and Curtis W. Sabrosky. We also acknowledge with grateful thanks the following curators for lending specimens for this study: Dr. H. Takagi (HUS), Dr. L. Papp (HNHM). We extend special thanks to Mrs. Mary L. Ripley, who took the time and effort to collect the only known specimen of *L. tibetensis* while she was conducting field work there with her husband.

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MYODOCOPINE OSTRACODA OF THE ALASKAN CONTINENTAL SHELF

Louis S. Kornicker

Abstract.—Myodocopina in the voucher collection of the California Academy of Sciences obtained by the NOAA-BLM Alaskan Outer Continental Shelf Environment Assessment Survey during 1976–1978 comprise four species: Beaufort Sea: *Philomedes brenda* (Baird, 1850); Bering Sea: *Bathyleberis beringensis,* n. sp.; Gulf of Alaska: *Scleroconcha diplax,* n. sp.; Chukchi Sea: *Bathyleberis* species A. The last three species are described and illustrated. A supplementary description is presented of the holotype of *Bathyleberis thrix* Kornicker, 1988, from the Beaufort Sea.

This study was initiated by a request from Barbara Hudler, Senior Curatorial Assistant, NOAA/BLM Project, Icthyology Department, California Academy of Sciences, to assist in further identification of Ostracoda in a voucher collection of specimens from the NOAA-BLM Alaskan Outer Continental Shelf Environment Assessment Survey during 1976–1978. Of the 17 samples examined only five contained Myodocopina: two samples from the Beaufort Sea contained *Philomedes brenda* (Baird, 1850); one sample from the Bering Sea contained *Bathyleberis beringensis,* n. sp.; a sample from the Gulf of Alaska contained *Scleroconcha diplax,* n. sp., and a sample from the Chukchi Sea contained a juvenile left in open nomenclature as *Bathyleberis* species A.

Cylindroleberididae

The Cylindroleberididae comprise three subfamilies: Cylindroleberidinae, Cyclasteropinae, and Asteropteroninae. Only the first subfamily is present in the collection. One species of Cyclasteropinae (*C. sharpei* Kornicker, 1981) may occur off the Alaskan coast (Kornicker 1981:2, 99); no members of the Asteropteroninae have been reported in the vicinity of Alaska.

Cylindroleberidinae

One genus, *Bathyleberis* Kornicker, 1975, is represented in the collection. That genus as well as the genus *Empoulsenia* Kornicker, 1975, have previously been reported from Arctic seas (Chavtur 1978, 1983; Kornicker 1988).

Bathyleberis Kornicker, 1975

Type species.—*Bathyleberis grossmani* Kornicker, 1975.

Composition.—Five species have been reported from northern seas and three from southern oceans (Kornicker 1988). The new species, *B. beringensis,* from the Bering Sea brings to nine the number of species referred to the genus. The specimen from the Chukchi Sea designated *Bathyleberis* species A may be an additional new species. A supplementary description of the holotype of *B. thrix* Kornicker, 1988, from the Beaufort Sea is presented here.

Bathyleberis beringensis, new species
Figs. 1, 2

Etymology.—Named for type locality.

Material.—Ovigerous female (holotype), California Academy of Sciences #023999, on slide and in alcohol; collected 12 May 1976, by personnel of the University of Alaska (Dr. Howard Feder, Principal Investigator).

Distribution.—Bering Sea, Alaska, 56°31′12″N, 167°55′54″W, 119 m (type locality).

Description of adult female (Figs. 1, 2).—Carapace elongate with subparallel dorsal and ventral margins (Fig. 1a); posterior evenly rounded in lateral view; incisur well developed and at about valve midheight.

Infold (Fig. 1b, c): Rostral infold dorsal to list with about 40 long bristles (10 along list, remainder forming 2 irregular rows parallel to anterodorsal shell margin); and additional short bristles (not all bristles shown on illustration) (Fig. 1b); about 10 bristles forming irregular row between list and dorsal edge of incisur. Anteroventral infold with 5 small bristles near inner end of incisur, about 17 long bristles and 12 minute bristles ventral to list, and about 10 minute bristles dorsal to list. Narrow list (with anterior end just ventral to incisur) paralleling and close to inner margin of anteroventral and ventral infold, then broadening along posteroventral and posterior infold. Ventral infold ventral to narrow list with about 25 fairly long bristles forming row about midway between list and valve edge (posterior 7 bristles more closely spaced). Infold between valve edge and broad posteroventral and posterior list with 45–48 bristles forming row near valve edge (22–25 long bristles in anterior part of row followed by about 23 small bristles; 1–4 minute pustules between several pairs of the small bristles), and 4 fairly stout processes about midway between list and valve edge (Fig. 1c). Broad posteroventral and posterior list with 15 flap-like bristles (about 8 tubules observed at base of some flap-like bristles) and 165 bristles along proximal edge of list; many bristles along ventral half of list longer than those along dorsal half (Fig. 1c; all bristles not shown on illustration).

Vestment (Fig. 1b): Numerous slender spines present posterior to inner margin of anterodorsal infold.

Size: Length 2.13 mm, height 1.09 mm.

First antenna (Fig. 1d): 1st joint with medial and lateral spines forming short rows. 2nd joint spinous, with 2 spinous bristles (1 lateral, 1 dorsal). 3rd joint separated from 4th joint by fairly distinct lateral and medial sutures, combined 3rd and 4th joints forming square; 3rd joint with 7 bristles (1 small ventral, 6 spinous, dorsal, and arranged as 2 single and 2 paired sets). 4th joint with slightly concave distal margin, with 3 bristles (2 ventral, 1 dorsal). Sensory bristle of 5th joint with 1 short proximal filament and 6 long terminal filaments. Medial bristle of 6th joint long, with base near ventral edge of joint. 7th joint: a-bristle claw-like, shorter than bristle of 6th joint; b-bristle with 4 marginal filaments (1 short proximal, 3 longer distal); c-bristle reaching slightly past tip of sensory bristle of 5th joint, with 6 short marginal filaments. 8th joint: d-bristle longer than a-bristle, bristle-like with pointed tip; e-bristle filament-like, distal part broken off on both limbs of holotype; f-bristle bent dorsally, with 5 or 6 marginal filaments; g-bristle about same length as c-bristle, with 5 or 6 marginal filaments (distal filament minute).

Second antenna: Protopodite with hairs along distal dorsal margin and on anterodorsal part of medial surface, none along ventral margin, and with small distal medial bristle (Fig. 1e). Endopodite with 3 well defined joints (Fig. 1f); terminal filament about ⅓ longer than stem. Exopodite: bristle of 2nd joint reaching 9th joint, with slender ventral spines; bristles of joints 3 and 4 with slender ventral spines proximal to midlength, and natatory hairs; bristles of joints 5–8 with few indistinct slender ventral spines proximal to midlength, and natatory hairs; 9th joint with 3 bristles (2 long with natatory hairs, 1 small with few minute spines); 1st joint with long distal hairs on concave margin; joints 2–8 with minute indistinct spines forming distal row; basal spines absent; 9th joint with small lateral spine about ½ length of joint.

Mandible (Fig. 2a, b): Coxale with medial spines. Coxale endite (Fig. 2a): ventral branch with spines forming 4–5 oblique rows and elongate club-like tip (aberrant?); small bristle near base of branch; ventral margin of dorsal branch with single pair of teeth followed by 7 single rounded teeth and short main spine; tip of branch protracted to fine point; dorsal bristle extending well past tip of branch and with slender spines at base. Basale (Fig. 2b): endite with 4 end bristles, 2 triaenid bristles with 11 pairs of spines proximal to terminal pair, 2 dwarf bristles and glandular peg; U-shaped depression present near ventral margin of basale at about midlength; proximal and dorsal margin of basale with dense spines; dorsal margin distal to midbristle with spines forming 2 rows extending onto lateral surface; dorsal margin with backward oriented spinous midbristle and 2 spinous terminal bristles (proximal less than half length of other). Exopodite tapering distally, about ¾ length of dorsal margin of 1st endopodial joint, hirsute, with 2 short terminal hirsute bristles (Fig. 2b). Endopodite (Fig. 2b): 1st joint: ventral margin with 3 stout bristles (medial with short spines, others with long spines except near tip). 2nd joint: dorsal margin with 2 proximal bristles and stout a-, b-, c-, and d-bristles; lateral side near dorsal margin with long bristle between b- and c-bristles and c- and d-bristles; medial side with short spines forming rows, 2 cleaning bristles between a- and b-bristles, 4 cleaning bristles forming oblique row between b- and c-bristles, 6 cleaning bristles forming oblique row between c- and d-bristles, and 1 long spinous bristle just distal to base of d-bristle; ventral margin with 3 long spinous terminal bristles. End joint with straight bare dorsal claw and 5 spinous bristles (4 long stout, 1 short slender). (All marginal spines on bristles not shown on illustrated limb.)

Maxilla (Fig. 1g): Epipodial appendage reaching to about midlength of dorsal margin of basale, hirsute distally, with pointed tip. Endite I with 4 bristles (3 long stout spinous and 1 short slender); endite II with 3 long spinous bristles. Basale: medial surface spinous (not all spines shown on illustration), with 3 bristles near dorsal margin (proximal shorter than others); lateral surface near midheight with short proximal bristle; ventral margin with 1 proximal, backward oriented bristle, 1 minute, indistinct distal bristle, and 1 long spinous terminal bristle. Endopodite: 1st joint with short alpha-bristle and long spinous beta-bristle; end joint with spinous terminal bristle longer than beta-bristle.

Fifth limb (Fig. 2c): Lateral side of comb with stout spinous expodial bristle, 1 slender bristle just ventral to base of exopodial bristle, 2 pairs of bristles closer to ventral margin, and 4 additional bristles almost on ventral margin (1 proximal, 1 medial near proximal paired bristles, and 2 distal); ventral margin with long and short bristles forming single row (not all shown on illustration; distal 4–5 bristles longer than others).

Sixth limb (Fig. 2d, e): Small medial proximal bristle set farther back from anterior margin than usual (Fig. 2d); anterior margin with upper and lower bristles on well defined endite sutures; anteroventral corner of skirt with 3 small hirsute bristles; lateral flap with 2 slender recurved hirsute bristles (Fig. 3d); anterior tip with 5 anterior bristles curving in same direction when viewed ventrally with limb not compressed under cover slip (Fig. 2e); posteroventral margin of skirt with 14–16 spinous bristles (those at posterior corner longer) (Fig. 2d).

Seventh limb (Fig. 2f); 6–7 bristles in proximal group, 3 or 4 on each side (one bristle on each side longer and with 4 bells, others with 2–3 bells); 2 short bristles on subterminal segment, 1 on each side, each with 3 bells); 4 bristles on terminal segment,

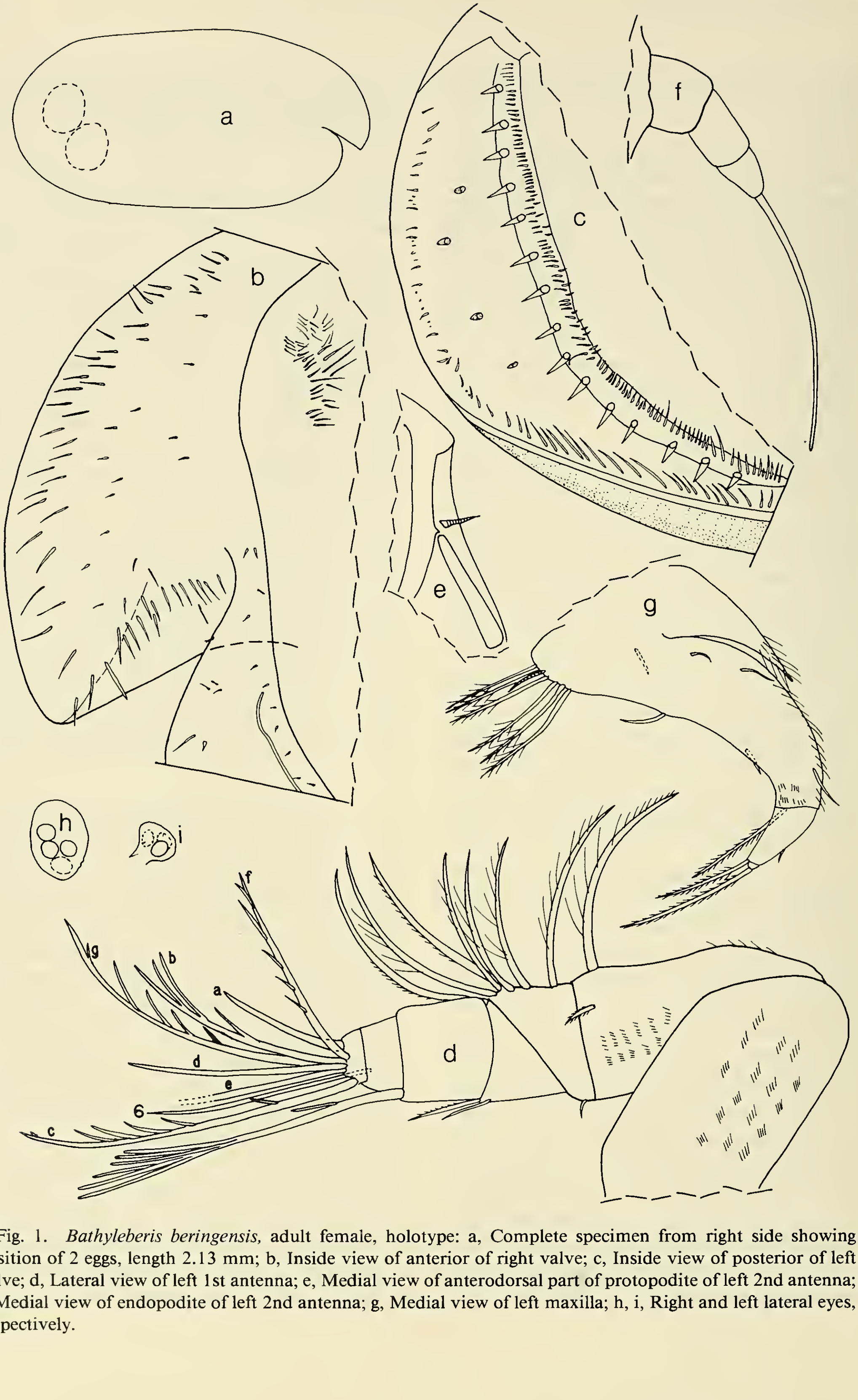

Fig. 1. *Bathyleberis beringensis,* adult female, holotype: a, Complete specimen from right side showing position of 2 eggs, length 2.13 mm; b, Inside view of anterior of right valve; c, Inside view of posterior of left valve; d, Lateral view of left 1st antenna; e, Medial view of anterodorsal part of protopodite of left 2nd antenna; f, Medial view of endopodite of left 2nd antenna; g, Medial view of left maxilla; h, i, Right and left lateral eyes, respectively.

2 on each side (distal with 2 bells, proximal with 4–5). Terminus with opposing combs, each with 12–13 spinous teeth (spines not shown on illustrated limb).

Furca (Fig. 2g): Each lamella with 9 claws; claws 1–8 claw-like, with posterior marginal spines; claw 9 bristle-like, bare; claws 1–6 with hairs along anterior margin; claws of right lamella anterior to like-numbered claws of left lamella; edge of lamellae following claws with minute spines.

Bellonci organ (Fig. 2h): Elongate, slightly broader at midlength and with rounded tip.

Eyes: Medial eye unpigmented, bare (Fig. 2h); lateral eye indistinct with 3–4 ommatidia (Fig. 1h, i).

Upper lip (Fig. 2i): With hirsute lobe on each side of saddle; each lobe with 2 minute anterior spines, saddle with minute anterior spine. Lower lip with lateral hirsute flap on each side of mouth.

Posterior of body (Fig. 2j): Hirsute and with small thumb-like spinous process.

Y-sclerite (Fig. 2k): Typical for subfamily.

Comparisons.—The only species of the genus reported previously from the Bering Sea is *B. kurilensis* (Chavtur, 1978). The species was described by Chavtur (1978:154) from the Kuril Islands. In a later publication (Chavtur 1983:81) the range of the species was expanded to the Northwest Pacific from Hokkaido Island to the Chukchi Sea, including the far eastern seas of Russia and in the northeast area at Unimak Island (Aleutian Is.), and Vancouver Island. The length of the carapace of the female *kurilensis* is 2.9–3.6 mm (longest in the Bering and Chukchi seas). The length of the female *beringensis* from the Bering Sea is 2.13 mm, considerably smaller than that of *kurilensis*. The carapace of *beringensis* also differs from that of *kurilensis* in other characters: the posterior infold of *beringensis* bears 15 flap-like bristles on the list and four processes between the list and the posterior edge of the valve; whereas, on *kurilensis* the list bears at least 35 flap-like bristles and has no processes between the list and posterior edge of valve (based on Chavtur 1978:fig. 4); also, in lateral view the dorsal and ventral margins of the carapace of *kurilensis* are more convex than those of *beringensis* (compare Chavtur 1978:fig. 4, and Fig. 1a, herein). The appendages of *beringensis* and *kurilensis* are quite similar, with perhaps a difference in the number of posteroventral bristles on the skirt of the 6th limb (14–16 for *beringensis*, 21 for *kurilensis*), and the beta-bristle of the maxilla is shorter than the terminal bristle of the end joint on *beringensis* and the reverse on *kurilensis*. *B. beringensis* has small lateral eyes, whereas *kurilensis* has none. *Bathyleberis beringensis* differs from *B. thrix* from the Beaufort Sea in having a short proximal filament on the sensory bristle of the 5th joint of the 1st antenna, and in having 12–13 bristles compared to 29–31 bristles on the 7th limb. *Bathyleberis beringensis* is closely related to *B. hancocki* Baker, 1979, reported from off Southern California and Oregon. The shell of that species differs from that of *beringensis* in having no processes between the posterior infold and posterior edge of the shell. *Bathyleberis hancocki* is without lateral eyes and has 11 rather than 6–7 proximal bristles on the 7th limb. Also, the medial eye of *hancocki* is hirsute, whereas that of *beringensis* is bare. The tip of the ventral branch of the coxale endite of the left mandible of *beringensis* differs from that of other members of the genus on which it is known in being club-like and without terminal teeth; however, the endite on the right limb of the single specimen in the collection was not observed, and that of the left limb could be aberrant.

Bathyleberis thrix Kornicker, 1988
Fig. 3a

Material.—Holotype (USNM 193381), female (adult or late instar).

Distribution.—Beaufort Sea.

Supplementary description of holotype.—

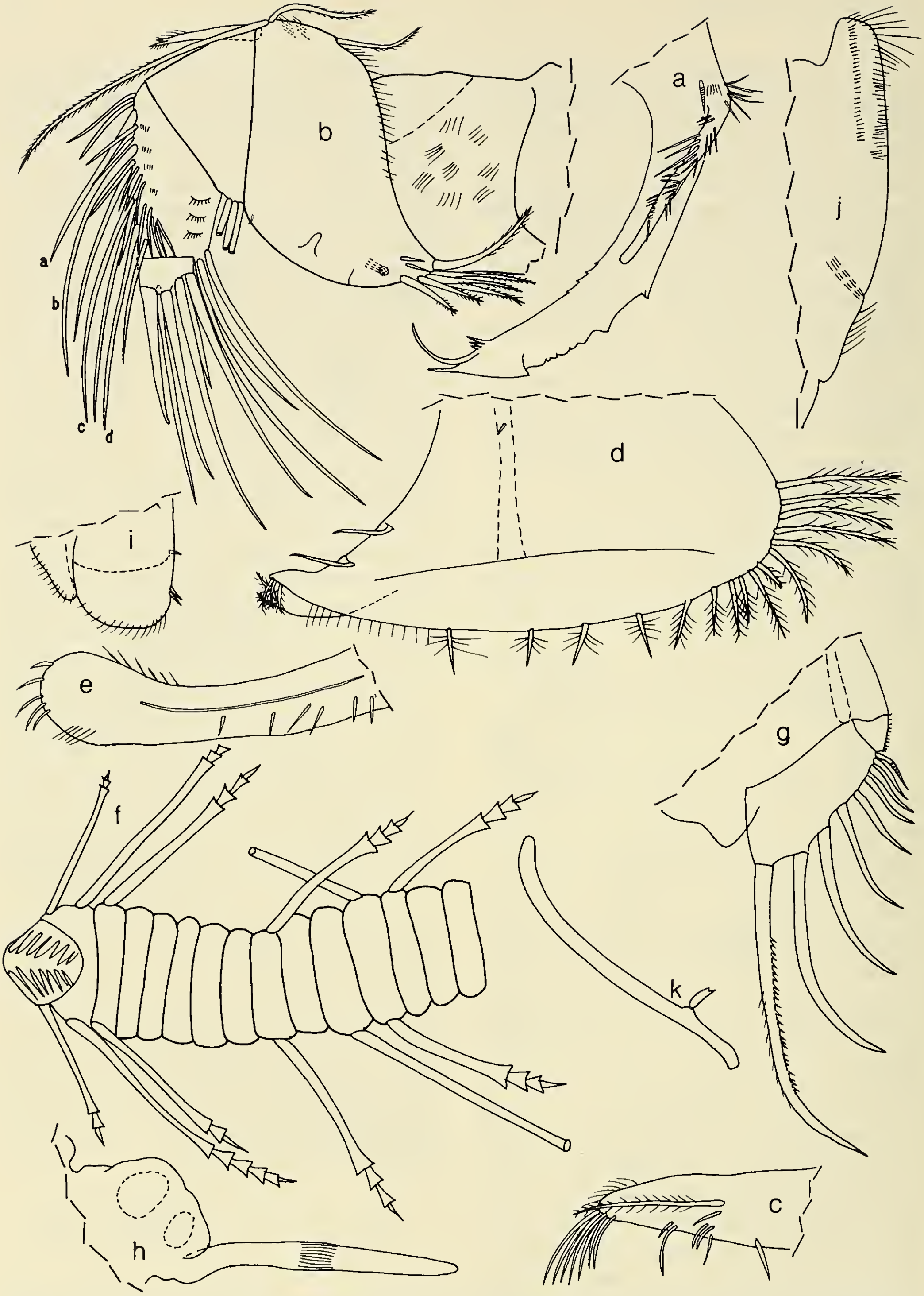

Fig. 2. *Bathyleberis beringensis,* adult female, holotype: a, Medial view of coxale endite of left mandible; b, Medial view of right mandible; c, Lateral view of comb of left 5th limb; d, Medial view of right 6th limb; e, Ventral view of anterior tip of left 6th limb (limb not under cover slip); f, 7th limb; g, Left lamella of furca; h, Medial eye and Bellonci organ; i, upper lip, anterior to right; j, Posterior of body; k, Y-sclerite, anterior to left.

In the description of the protopodite of the 2nd antenna (Kornicker 1988), the small medial bristle was not mentioned, and therefore, is illustrated herein (Fig. 3a).

Bathyleberis sp. A
Figs. 3b–l, 4

Material.—1 A-1 male, California Academy of Sciences #023476, on slide and in alcohol, collected 17 Aug 1976 in ring net of 308 μm mesh, USCGC *Glacier.*

Distribution.—Chukchi Sea, W of Pt. Barrow, Alaska, 71°31′30″N, 159°09′00″W, 0–160 m.

Description of A-1 male (Figs. 3b–l, 4).—Carapace elongate with convex dorsal and ventral margins in lateral view (Fig. 3b); posterior with posterodorsal corner angular and posteroventral corner evenly rounded; incisur well developed and just ventral to valve midheight.

Infold (Fig. 3c, d): Rostral infold dorsal to list with about 90 long bristles (about 12 along list, remainder forming 2 irregular rows along anterodorsal margin), and additional shorter bristles (not all shown on illustration) (Fig. 3c); about 10 bristles forming row between list and dorsal edge of incisur. Anteroventral infold with several small bristles near inner end of incisur, about 45 long bristles and 7 or more minute bristles ventral to list, and no bristles dorsal to list. Narrow list (with anterior end just ventral to incisur) paralleling and close to inner margin of anteroventral and ventral infold, then broadening along posteroventral and posterior infold. Ventral infold ventral to narrow list with about 40 bristles forming row about midway between list and valve edge. Infold between valve edge and broad posteroventral and posterior list with about 60 bristles forming row near valve edge and about 7–8 small processes about midway between list and valve edge (only ventral 6 of processes shown in Fig. 3d). Broad posteroventral and posterior list with 38 flap-like bristles (5–10 tubules at base of flap-like bristles) and 85 mostly small bristles forming row along proximal edge of list (generally 1–3 bristles just anterior to space between flap-like bristles; all bristles not shown in Fig. 3d).

Vestment (Fig. 3c): Numerous spines arranged in clusters posterior to inner margin of anterodorsal infold.

Central adductor muscle attachments (Fig. 3e): Comprising many individual scars.

Size: Length 2.90 mm, height 1.69 mm.

First antenna (Fig. 3h, i): 1st joint with medial and lateral spines forming rows. 2nd joint spinous, with 2 bristles (1 lateral, 1 dorsal). 3rd joint separated from 4th joint by well defined medial suture and ill defined lateral suture except near dorsal margin; combined 3rd and 4th joints forming square; 3rd joint with 7 bristles (1 small ventral, 6 spinous, dorsal, arranged as 2 single and 2 paired sets (proximal 3 bristles with long spines, distal 3 bristles with short marginal spines); 4th joint with concave distal margin well defined on medial side only, and 3 bristles (2 ventral, 1 dorsal). Sensory bristle of 6th joint with 1 short proximal filament and 6 long terminal filaments. Medial bristle of 6th joint long, spinous, with base near ventral edge of joint. 7th joint: a-bristle claw-like, shorter than bristle of 6th joint (Fig. 3h), a-bristle aberrant on left limb of holotype (Fig. 3i); b-bristle with 4 marginal filaments (1 short proximal, 3 long distal); c-bristle reaching slightly past tip of sensory bristle of 5th joint, with about 18 filaments (proximal 5–6 filaments minute; 3rd from last filament fairly long). 8th joint: d-bristle about same length as a-bristle, bristle-like with pointed tip; e-bristle longer than d-bristle, filament-like with blunt tip; f-bristle bent dorsally with about 20 filaments (bristles of proximal half very small); g-bristle about same length as c-bristle, with 7 marginal filaments.

Second antenna: Protopodite with hairs along distal dorsal margin and on anterodorsal part of medial surface, and along posteroventral corner, and with small distal medial bristle (Fig. 3f). Endopodite with 3 well defined joints (Fig. 3g): 1st joint short bare; 2nd joint elongate, with 2 slender distal spines or bristles; 3rd joint shorter than 2nd, with proximal filament almost reaching pointed tip of joint. Exopodite: bristle of 2nd joint reaching just past 9th joint, with long slender ventral and dorsal spines; bristles of joints 3–5 with long slender proximal spines and distal natatory hairs; bristles of joints 6–8 with natatory hairs; 9th joint with 4 bristles (2 long, with natatory hairs, 1 medium with natatory hairs, 1 small, dorsal, with small marginal spines); joints 4–8 with minute basal spines; 9th joint with minute lateral spine, length of spine not more than ¼ length of joint; joint 1 with long spines along concave margin; joints 2–8 with indistinct minute spines along distal margin.

Mandible (Fig. 4a, b): Coxale with medial spines. Coxale endite (Fig. 4a): ventral branch with spines forming 5–6 oblique rows and tip with 2 small teeth (ventral tooth with tip curving dorsally); small bristle near base of branch; ventral margin of dorsal branch with 3–4 nodular teeth followed by several smaller nodes and small main spine; tip of branch with 2 small spines; dorsal bristle extending well past tip of branch and with indistinct marginal hairs. Basale (Fig. 4b): endite with 4 end bristles, 3 triaenid bristles with 7–13 pairs of spines proximal to terminal pair, 2 dwarf bristles and glandular peg; U-shaped depression present near ventral margin of basale at about midlength; proximal and dorsal margin of basale with dense spines; dorsal margin distal to midbristle with spines forming rows extending onto lateral surface; ventral margin distal to U-shaped depression with spines forming rows extending onto lateral surface; dorsal margin with backward oriented spinous midbristle and 2 spinous terminal bristles (proximal less than half length of other). Exopodite tapering distally, about ⅔ length of dorsal margin of 1st endopodial joint, hirsute with 2 short terminal bristles. Endopodite (Fig. 4b): 1st joint: ventral margin with 3 stout bristles (medial with short spines, others with long spines except near tip). 2nd joint: dorsal margin with 3 proximal bristles and stout a-, b-, c-, and d-bristles; lateral side near dorsal margin with long bristle between b- and c-bristles and c- and d-bristles; medial side with short spines forming rows, 1 cleaning bristle just proximal to base of a-bristle, 2 cleaning bristles between b- and c-bristles, 3 cleaning bristles forming oblique row near b-bristle, 4 cleaning bristles forming oblique row near base of c-bristle, 2 cleaning bristles near base of c-bristle, 7 cleaning bristles forming oblique row near c- and d-bristles, and 1 long spinous bristle just distal to base of d-bristle; ventral margin with 3 long spinous terminal bristles. End joint with straight dorsal claw and 5 spinous bristles (4 long stout, 1 short slender). (All marginal spines on bristles not shown on illustrated limb.)

Maxilla (Fig. 4c): Epipodite short, triangular, hirsute distally with pointed tip. Endite I with 4 bristles (3 long stout spinous and 1 short slender); endite II with 3 long spinous bristles. Basale: medial surface spinous (not all spines shown on illustration), with 3 bristles near dorsal margin (proximal shorter than others); lateral surface near midheight with short proximal bristle; ven-

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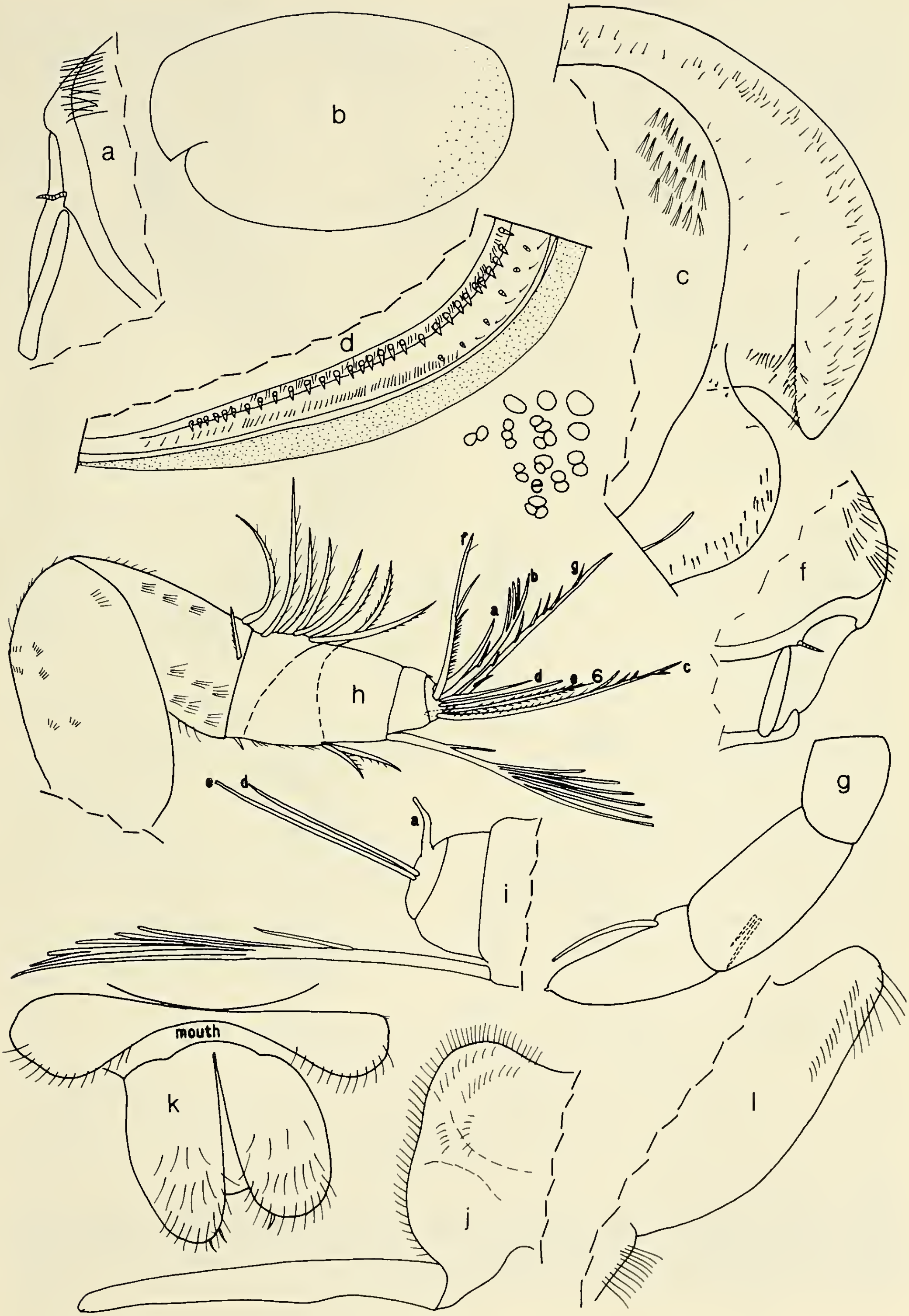
Fig. 3. *Bathyleberis thrix* Kornicker, holotype: a, Medial view of anterodorsal part of protopodite of right 2nd antenna. *Bathyleberis* species A, A-1 male: b, Complete specimen from left side, length 2.90 mm; c, Inside view of anterior of left valve, d, Inside view of posteroventral corner of right valve; e, Lateral view of central adductor muscle ends where attached to left valve, anterior to left; f, Medial view of anterodorsal part of protopodite of left 2nd antenna; g, Medial view of endopodite of left 2nd antenna; h, Lateral view of right 1st antenna; i, Lateral view of tip of right 1st antenna (not all bristles shown); j, Medial eye and Bellonci organ; k, Ventral view of upper and lower lips and mouth area, anterior to bottom; l, Posterior of body.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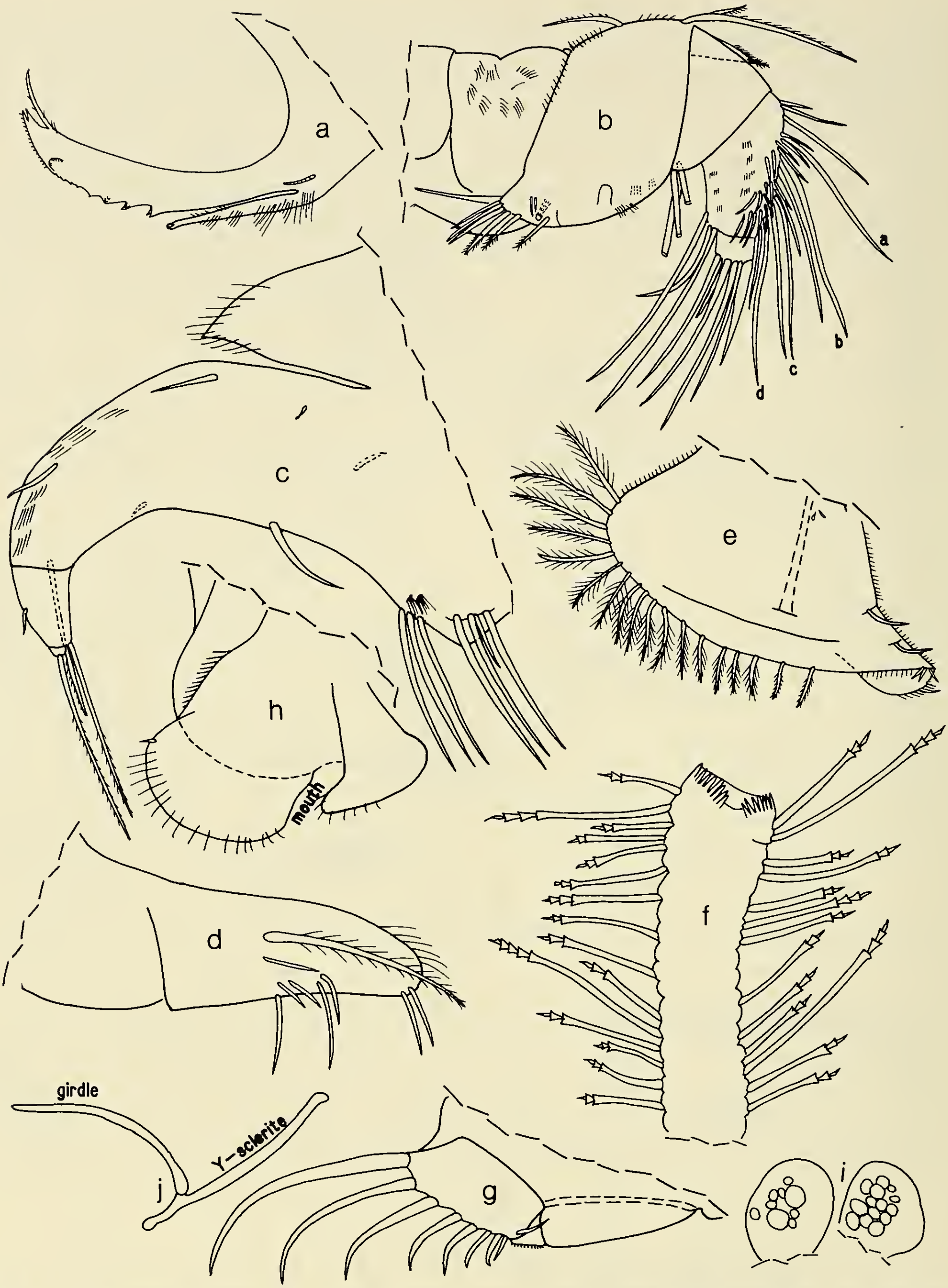

Fig. 4. *Bathyleberis* species A, A-1 male: a, medial view of coxale endite of left mandible; b, Medial view of left mandible; c, medial view of right maxilla; d, Lateral view of comb of right 5th limb; e, Medial view of left 6th limb; f, 7th limb; g, Left lamella of furca; h, Upper and lower lips and mouth area, anterior to left; i, Right and left lateral eyes; j, Y-sclerite and girdle, anterior to right.

tral margin with 1 proximal, backward oriented bristle, 1 minute distal bristle, and 1 long spinous terminal bristle. Endopodite: 1st joint with short alpha-bristle and long spinous beta-bristle; end joint with spinous terminal bristle slightly longer than beta-bristle.

Fifth limb (Fig. 4d): Lateral side of comb with stout spinous exopodial bristle, 1 slender bristle just ventral to base of exopodial bristle, 2 pairs of bristles closer to ventral margin, and 3 additional bristles almost on ventral margin (1 near proximal paired bristles and 2 distal).

Sixth limb (Fig. 4e): 2 small medial proximal bristles set back from ventral margin on both limbs; anterior margin with upper and lower bristles on well defined endite sutures; anteroventral corner of skirt with 3 small bristles; lateral flap with slender recurved bristle; posteroventral margin of skirt with 18–19 spinous bristles (those at posterior corner longer).

Seventh limb (Fig. 4f): Bristles fairly evenly distributed, not divided into proximal and distal groupings; left limb with 28 bristles (13 on one side, 15 on other; right limb missing from specimen); most bristles short with 2 bells, but 4 longer with 3–4 bells; bristles present on most distal 16 segments (including terminal segment bearing comb teeth), some segments with 2 bristles (1 on each side); terminal segment with 4 bristles (2 on each side). Terminus with opposing combs, each with 15 spinous teeth (spines not shown on teeth of illustrated limb).

Furca (Fig. 4g): Each lamella with 9 claws and bristles; claws 1–7 recurved claw-like; claw 8 straight bristle-like; claw 9 bristle-like oriented dorsally; claws 1–7 with teeth along posterior margins and slender hairs along anterior margins; claws of right lamella slightly anterior to like claws of left lamella; edge of lamellae following claws with minute spines.

Bellonci organ (Fig. 3j): Elongate, broadening slightly at midlength, and with rounded tip.

Eyes: Medial eye extremely hirsute but unpigmented (Fig. 3j). Lateral eyes small, unpigmented, each with many poorly defined and indistinct ommatidia (Fig. 4i).

Lip (Figs. 3k, 4h): With hirsute lobe on each side of saddle, each lobe with 1–2 slender anterior spines. Lower lip with hirsute flap on each side of mouth.

Posterior of body (Fig. 3l): Hirsute, with short spinous thumb-like dorsal process.

Genitalia: Small lobe anterior to furca on each side of body (not identified with certainty as copulatory organs).

Y-sclerite (Fig. 4j): Typical for subfamily.

Gills: 7 well-developed gills with broadly rounded tips on each side of posterior of body.

Comparisons.—The carapace length of *B.* sp. A is similar to that of *B. kurilensis,* but species A has more bristles on the 7th limb (28 compared to 13–26) and the angle between the toothed combs of the 7th limb is acute on *B. kurilensis* and obtuse on *B.* sp. A. The 7th limb of *B.* sp. A strongly resembles that of *B. thrix,* which was described from three specimens from the Beaufort Sea (Kornicker 1988). The length of the carapace of the A-1 male of *B.* sp. A is 2.90 mm, whereas the length of the largest known specimen of *B. thrix* (a female adult or late instar) is only 2.14 mm, but the difference could be negated if the largest specimen of *B. thrix* should prove to be one or more stages younger than *B.* sp. A, or if the size difference is sex-related; however, I think this unlikely. The sensory bristle of the 1st antenna of *B. thrix* does not have the short proximal filament that is on the sensory bristle of *B.* sp. A, but it has been shown previously that the sensory bristle of the A-1 male of some species in the Cylindroleberidinae have a proximal bristle that is absent on females (Bowman & Kornicker 1967:16); whether this relationship holds for *B. thrix* is unknown. An unusual character of the 6th limbs of *B.* sp. A is the presence of two proximal medial bristles. Other species have only one bristle, but because only a single specimen of *B.* sp. A is on hand the variability of this character could not be ascertained. It is quite possible that the specimen referred to *B.* sp. A is a juvenile of *B. thrix,* but I find it expedient to keep them separate until the ontogeny of *thrix* or *B.* sp. A is known better.

Philomedidae

The Philomedidae comprise two subfamilies, Philomedinae and Pseudophilomedinae. Only the former is represented in the study area.

Philomedinae

This subfamily is represented on the Alaskan continental shelf by two genera, *Philomedes* Liljeborg, 1853, and *Scleroconcha* Skogsberg, 1920.

Philomedes Liljeborg, 1853

Type species.—*Philomedes longicornis* Liljeborg, 1853:176 [=*Cypridina Brenda* Baird, 1850].

Composition.—This genus has numerous species. *Philomedes brenda* has been reported previously from the Beaufort Sea (MacGinitie 1955:147; Kornicker 1988). A juvenile collected from the vicinity of Kodiak Island (Aleutian Islands) and referred to a new species *P. kadjakensis* by Chavtur (1983:56) was referred by Kornicker (1988) to *Philomedes* species indeterminate.

Philomedes brenda (Baird, 1850)

Philomedes brenda (Baird, 1850).—See Kornicker (1982:3; 1988) for comprehensive synonymy.

Lectotype.—British Museum (Natural History), B.M. 1945.9.26 91, dried and broken carapace, by subsequent designation (Sylvester-Bradley 1950:777).

Material.—Beaufort Sea: 1 juvenile, sta 23, haul 2, cross reference number K28, 30 Aug 1976, California Academy of Sciences #011460, 71°22′N, 152°20′W, 20–0 m, collected in ring net of 308 μm mesh; 1 juvenile, sta 10, haul 1, 10 Aug 1977, California Academy of Sciences #011461, 71°35′N, 153°29′W, 41–0 m, collected in bongo net of 505 μm mesh.

Distribution.—Widespread in the Arctic Ocean and in the North Atlantic (to 54°N in east Atlantic, and 44°N in west Atlantic). Generally collected at shelf and upper slope depths.

Discussion.—Both specimens in the collection are juveniles incapable of swimming. Therefore, although the samples were collected with plankton nets, the specimens were probably collected at the bottom. Kornicker (1988) reported the minimum depth at which the species was collected in the Beaufort Sea to be 27 m. The minimum depth for the species in the vicinity of Alaska is here reduced to 20 m.

Scleroconcha Skogsberg, 1920

Type species.—*Philomedes* (*Scleroconcha*) *appelloefi* Skogsberg, 1920.

Composition.—This genus has 15 species including a new species described here. Only one species has been reported previously from the continental shelf of Alaska, *S. ruffi* Kornicker, 1988. Another species has been reported from the Vancouver Island area of Canada, *S. trituberculatus* (Lucas, 1931). Six species have been reported from the northwestern Pacific: *S. ochotensis* Chavtur, 1978, *S. kubotai* Hiruta, 1981, *S. pavljuchkovi* Chavtur, 1983, *S. lucasae* Chavtur, 1983, *S. rectangularis* Chavtur, 1983, and *S. nanocristata* Chavtur, 1983. The remaining seven species have been reported from distant seas.

Scleroconcha diplax, new species

Figs. 5–7

Etymology.—From the Greek *diplax* (=double) in reference to the two proximal

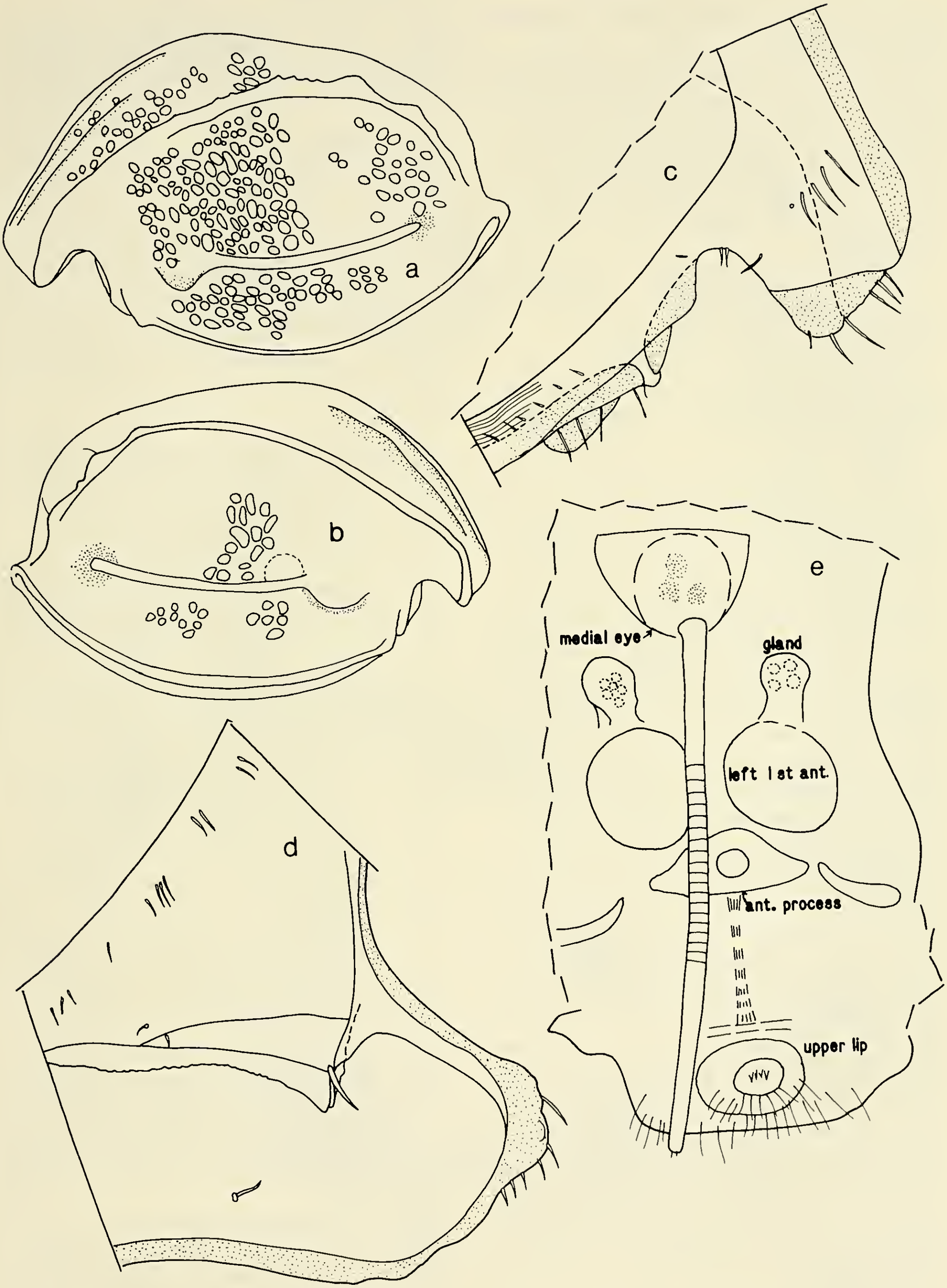

Fig. 5. *Scleroconcha diplax,* adult female, holotype: a, b, Left and right views of whole specimen, respectively, not all reticulations shown, length 2.79 mm; c, Inside view of anterior of left valve; d, Inside view of posterior of right valve; e, Anterior view of body.

anterior bristles on the 3rd and 4th endites of the 6th limb.

Material.—1 ovigerous female (holotype), California Academy of Sciences # 010852, on slide and in alcohol, collected on 25 Aug 1978 by personnel of the University of Washington on the R/V *Yankee Clipper* (Dr. Mark Wangerin, Principal Investigator).

Distribution.—Gulf of Alaska, S coast of Kodiak Is., Kaiugnak, Alaska, 57°03′55″N, 153°40′05″W, 18 m (type locality).

Descripton of adult female (Figs. 5–7).—Carapace oval in lateral view, with prominent rostrum and small rounded caudal process (Fig. 5a–d).

Ornamentation (Fig. 5a, b): Lateral surface with subdued rib just within ventral margin terminating anteriorly in small anteroventral process, and terminating posteriorly on caudal process; very small process present on anteroventral margin of valve anterior to end of ventral rib. 2nd rib just ventral to central adductor muscle attachments with anterior end bending ventrally to form arc and terminating posteriorly in small bulge anterior to caudal process. 3rd rib dorsal to central adductor muscle attachments terminating anteriorly as process extending very slightly past anterior edge of rostrum, and terminating posteriorly on or near caudal process; 2 small processes present on rib near posterodorsal corner of valve. 4th rib just within anterodorsal margin of valve. 5th anterodorsal subdued rib between 3rd and 4th ribs terminating anteriorly on rostrum, and posteriorly not reaching valve midlength. Surface of valve with abundant, weakly developed, round fossae, appearing darker in transmitted light (Fig. 5a, b) (not all fossae shown in illustrations). Undivided bristles, some with broad bases, sparsely distributed over valve surface but not shown in illustrations.

Infold (Fig. 5c, d): Rostral infold with 6–7 bristles (1 bristle represented by socket on Fig. 5c); 2 bristles present on valve edge close to selvage at inner end of incisur (could not be ascertained whether bristles medial or lateral to selvage) (Fig. 5c); 1 small bristle present ventral to inner edge of incisur; anteroventral infold with about 9 ridges and, also, 11–14 bristles forming row parallel to valve edge; infold along middle of ventral margin bare; posterior end of ventral infold in vicinity of caudal process with numerous slender bristles forming groups of 1–4 bristles; infold of caudal process with narrow flap with stout bristle at posterior tip and 2–3 smaller anterior bristles (Fig. 5d); 1 small bristle between flap and ventral valve edge.

Selvage: Broad lamellar prolongation with marginal fringe present along anterodorsal, anterior, and ventral margins of valve. Selvage divided at inner edge of incisur.

Size: Length 2.79 mm, height 1.93 mm.

First antenna (Figs. 5e, 6a, 7f): 1st joint with minute lateral spines forming rows near dorsal margin. 2nd joint spinous with 3 bristles (1 ventral, 1 dorsal, 1 lateral). Short 3rd joint with few spines and 3 bristles (1 ventral, 2 dorsal). 4th joint spinous, with 6 bristles (4 ventral, 2 dorsal). 5th joint with sensory bristle with about 7 small marginal filaments and tip with several filaments (filaments not shown in Fig. 6a). 6th joint minute, fused to 5th joint; medial bristle with long proximal and short distal spines. 7th joint: a-bristle similar to that of bristle of 6th joint; b-bristle broken on left limb (Fig. 6a) and obscure on right limb, with several short marginal filaments; c-bristle about same length as sensory bristle of 5th joint, with short marginal filaments. 8th joint: d- and e-bristles about same length as c-bristle, bare with blunt tips; f- and g-bristles about same length as c-bristle, with short marginal filaments.

Second antenna: Protopodite bare. Endopodite 2-jointed (Fig. 6b): 1st joint short, with 5 proximal bristles (1 slightly longer than others) and 1 distal bristle about same length as proximal bristles; 2nd joint with 1 very long spinous proximal bristle, and 1

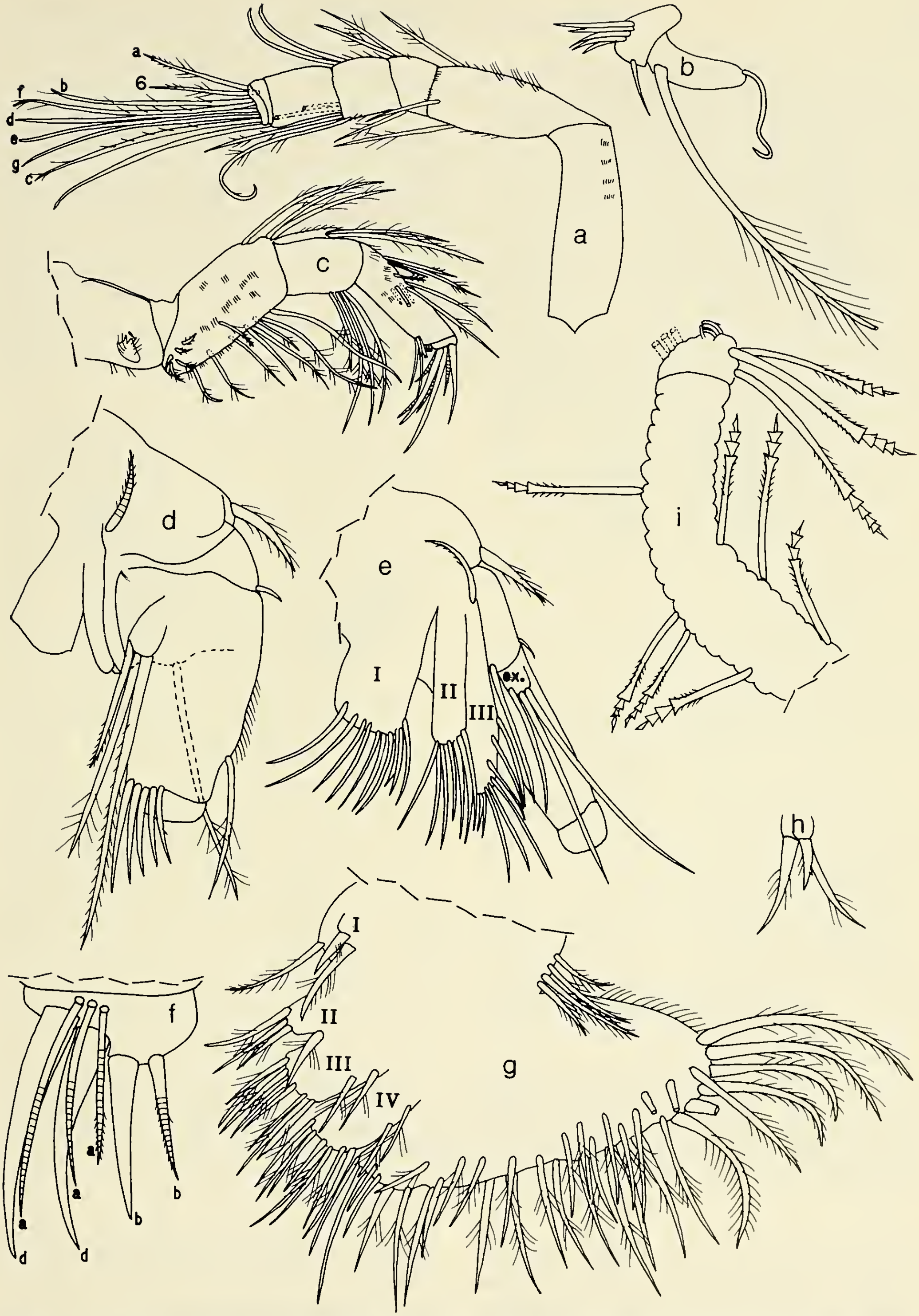

Fig. 6. *Scleroconcha diplax,* adult female, holotype: a, Lateral view of left 1st antenna; b, Medial view of endopodite of right 2nd antenna; c, Medial view of left mandible; d, e, Lateral views of right maxilla ("e" drawn while appendage not under cover slip); f, Lateral view of end joint of right maxilla (not all c- and d-bristles shown); g, Medial view of right 6th limb; h, Medial view of endite I of left 6th limb; i, 7th limb.

Fig. 7. *Scleroconcha diplax,* adult female, holotype: a, Posterior view of left 5th limb (not all spines on bristles shown); b, Detail of largest constituent tooth of 1st exopodial joint, from "a"; c, Anterior view of right 5th limb (drawn while not under cover slip); d, Mounted right 5th limb showing posterior view of 2nd exopodial joint and anterior view of 1st joint and endites; e, Right lamella of furca; f, Anterior of body showing medial eye and Bellonci organ, anterior process, upper lip, and 1st joint of right 1st antenna.

shorter terminal bristle. Exopodite: 1st joint with minute medial bristle on distal margin; bristles of joint 2–4 bare, fairly short but all reaching well past 9th joint; bristles of joints 5–8 broken; 9th joint with 7 bristles (3 long stout broken, 1 medium broken, 3 short, slender); joints 2–8 with slender spines forming row along distal margin, and with minute basal spine or spines.

Mandible (Fig. 6c): Coxale with spines along ventral margin; endite bifurcate, hirsute spinous, bifurcate tips pectinate; minute bristle dorsal to base of endite. Basale: dorsal margin with 3 spinous bristles (1 distal to midlength, 2 subterminal); medial surface hirsute, with 5 proximal bristles (3 pectinate unringed, 2 ringed with long proximal and short distal spines), and 1 bristle (with long proximal and short distal spines) at midlength; ventral margin with 8 spinous bristles (5 shorter bristles with bases on lateral surface). Exopodite about ¾ length of dorsal margin of 1st endopodial joint, hirsute with 2 minute spines at tip, and with 2 subterminal bristles bearing wreaths of long spines (distal outer bristle shorter). 1st endopodial joint with 4 ventral bristles bearing wreaths of long spines. 2nd endopodial joint: ventral margin with bristles forming 2 distal groups (3 bristles in each group); dorsal margin with 9 bristles near middle, some with bases on medial and lateral sides of joint; medial surface and proximal dorsal margin spinous. End joint with 3 bare claws (dorsal claw about ¾ length of ventral medial claw; ventral medial claw shorter than ventral lateral claw), and 4 bristles.

Maxilla (Fig. 6d–f): Coxale with hirsute dorsal bristle. Endite I with 10 spinous and pectinate bristles; endites II and III narrow, each with about 8 distal bristles; endite III also with proximal bristle (Fig. 6d, e). Basale with 3 bristles along distal margin (dorsal of these small; medial and ventral long). Exopodite with 3 spinous bristles. 1st endopodial joint spinous, with 1 spinous alpha-bristle and 5 beta-bristles (bare or with few spines) (Fig. 6d) End joint with 3 a-bristles (bare or with few spines) (Fig. 6f), 2 b-bristles (1 ringed and bearing small spines, 1 stout, unringed, claw-like, bare); 2 d-bristles stout, unringed, claw-like, bare; remaining c- and d-bristles slender, ringed, bristle-like, but not counted (these not shown in Fig. 6f).

Fifth limb (Fig. 7a–d): Epipodite with 54 hirsute bristles. Endite I with 5–6 spinous bristles; endite II with 7 spinous bristles; endite III with about 9 bristles (not all endite bristles shown in Fig. 7a, c). 1st exopodial joint: anterior side with 2 spinous bristles at midwidth (Fig. 7c), and 1 short bristle on lobe near outer edge (Fig. 7c, d); main tooth with 4 constituent teeth, each with 3–5 small marginal teeth (Fig. 7a); distal constituent tooth with proximal tooth-like process (Fig. 7b); 1 spinous bristle proximal to 4 constituent teeth (Fig. 7a). 2nd exopodial joint: large tooth with 1 small pointed tooth along inner margin (arrow on Fig. 7a, d); distal outer corner of large tooth with minute posterior d-bristle (Fig. 7d); long proximal posterior c-bristle bare; outer bristle farthest from main tooth of 3 posterior a, b-bristles short, other outer bristle about ⅔ length of middle bristle, all bare (Fig. 7a). 3rd endopodial joint (Fig. 7a): inner lobe with 3 bristles (2 shorter bristles bare or with few spines, longest bristle with long proximal and short distal spines); outer lobe with 2 bristles (short bristle with long proximal hairs and short distal spines; long bristle with wreaths of long spines). 4th and 5th joints fused, hirsute, with total of 6 spinous bristles (Fig. 7a).

Sixth limb (Fig. 6g, h): Endite I with 3 spinous bristles; endite II with 1 proximal and 3 terminal spinous bristles; endite III with 1 or 2 proximal and 8 terminal spinous bristles; endite IV with 2 proximal and 7–8 terminal bristles. End joint with 33–35 hirsute and spinous bristles. Four epipodial bristles with long proximal hairs.

Seventh limb (Fig. 6i): Terminus consisting of comb with 4 small teeth opposite single peg. Each limb with 13 bristles, 6 in terminal group (3 on each side) and 7 in proximal group (3–4 on each side); proximal bristles with 3–4 bells, terminal bristles with 3–6 bells; all bristles with distal marginal spines.

Furca (Fig. 7e): Each lamella with 15 claws with small teeth along posterior margins; hairs present along lamellae following claws; right lamella slightly anterior to left.

Bellonci organ (Figs. 5e, 7f): With about 12 well defined and 3 poorly defined sutures

(sutures not shown in Fig. 7f); proximal and distal ⅓ without sutures; tip broadly rounded and with terminal spine.

Eyes: Medial eye with dark brown pigment, bare (Figs. 5e, 7f). Lateral eyes not observed.

Upper lip (Figs. 5e, 7f): Normal for genus, with about 4 small anterior processes.

Anterior of body (Figs. 5e, 7f): Single rounded process between upper lip and medial eye.

Posterior of body: A few minute spines in vicinity of posterodorsal corner.

Y-sclerite: Normal for genus.

Eggs: Holotype with 6 eggs in marsupium.

Comparisons.—The new species *S. diplax* differs from *S. ruffi* in having two proximal bristles along the anterior margin of the 4th endite of the 6th limb; the variability of this character for *diplax* is not known, but all other species of *Scleroconcha* on which the 6th limb has been described have only one proximal bristle on the endite. The two species also appear to differ slightly in the morphology of the lower lateral rib (rib just ventral to central adductor muscle attachments): on *ruffi* the anterior end of the rib forms a low mound, whereas, on *diplax* the anterior end bends ventrally to form an arc. In addition to *ruffi* and *diplax, S. rectangularis* and *S. pavluchkovi* have Bellonci organs with rounded tips, all other species on which the character is known have pointed tips. *Scleroconcha diplax* differs from *rectangularis* in having fewer bristles on the rostral infold (6–7 compared to 16–18), and in not having the lower lateral midrib bending ventrally to meet the ventral rib. The carapace of *diplax* differs from that of *pavluchkovi* in not having a process at the anterior end of the lower lateral midrib. *Scleroconcha trituberculatus* differs from *diplax* in having 16 claws instead of 15 on the furca, and in having a much shorter distal bristle on the 1st endopodial joint of the 2nd antenna.

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BYTHOCHERES PROMINULUS, A NEW GENUS AND SPECIES (COPEPODA: SIPHONOSTOMATOIDA) FROM DEEP-WATER COLD SEEPS AT THE WEST FLORIDA ESCARPMENT

Arthur G. Humes

Abstract.—A siphonostomatoid copepod, *Bythocheres prominulus,* new genus, new species, is described from a depth of 3260 m at cold seeps near the base of the West Florida Escarpment. Among its distinctive features are: the first antenna 15-segmented with an aesthete on the penultimate segment, the second antenna without an exopod, an elongate siphon, both second maxilla and maxilliped with their tips finely spinulose, legs 1–4 biramous with 3-segmented rami, and leg 5 with the free segment having 3 setae. The new copepod cannot be placed satisfactorily in any of the currently recognized families of Siphonostomatoida. Males are unknown and the family position is not designated.

Nearly 30 species of copepods, both Poecilostomatoida and Siphonostomatoida, have been described from deep-sea hydrothermal vents (Humes & Dojiri 1980, Humes 1984, Humes, 1987). However, copepods from cold seeps in the deep sea have not been reported until now. It is the object of this paper to describe a new siphonostomatoid copepod recently collected at cold seeps in deep water off the west coast of Florida.

The new copepod was found at a depth of 3260 m (a little more than 2 miles), near the base of the West Florida Escarpment, "a gigantic limestone cliff that rises some 2000 meters above the 3280-meter-deep floor of the Gulf" (Florida Escarpment Cruise Participants, C. K. Paull, Chief Scientist, 1984:32). Hypersaline water of Lower Cretaceous fresh-water origin seeps into the sea water from strata in the interior of the Florida Platform (Paull et al. 1984).

The cold seeps where the copepods were collected have very different characteristics from those of hydrothermal vents, although both environments are aphotic and under great hydrostatic pressure. At Galapagos-type hydrothermal vents, the water temperature may reach 15°C or higher (Grassle 1985), or as high as 350°C at black smoker vents at 21°N on the East Pacific Rise (Grassle 1986). However, "Despite the elevated temperatures in the immediate vicinity of the vents, most vent animals live at close to the ambient (2°C) temperature." (Grassle 1986:302–303). Sulfide of geothermal origin is present in discharged vent water at high concentrations. On soft sediments in the Guaymas Basin, Gulf of California, the flux of hydrothermal fluid may lead to growth of extensive mats of the bacterium *Beggiatoa.* In cold seeps, on the other hand, where the bottom water temperature averages 4.39°C (Paull et al. 1984), no primary sulfide discharge is found but is secondarily produced in the sediments by bacterial sulfate reduction. Consequently, at these cold seeps the mats that exist are composed primarily of inorganic materials, largely sulfur, and only to a small extent of sulfide-oxidizing bacteria (H. Jannasch, pers. comm.).

The Poecilostomatoida and Siphonostomatoida known from hydrothermal vents (Humes & Dojiri 1980, Humes 1984, Humes, 1987) belong to genera not found in other areas. Siphonostomatoida are particularly abundant both in numbers and diversity. The record of *Bythocheres* demonstrates that copepods occur in the deep sea at cold seeps as well as at hydrothermal vents.

The slurp gun, a device by means of which the copepods were collected from the base of the escarpment wall, was operated from the Deep Submergence Research Vehicle *Alvin.* It consists of a large container in the opening of which are fitted a tube whose external inlet can be directed to chosen collecting spots by *Alvin,* a filter, and a pump that draws sea water into the container (see Editor, National Geographic Magazine, 1979:684). In operation, organisms are filtered out and collect at the bottom of the container. Excess water is ejected by the pump.

The copepods were studied and measured in lactic acid, using the wooden slide technique described by Humes & Gooding (1964). The letter after the explanation of each figure refers to the scale at which the figure was drawn.

Bythocheres, new genus

Diagnosis.—Siphonostomatoida. Female: Body unmodified. Segment bearing leg 1 fused with cephalosome. Urosome 5-segmented. Caudal ramus with 6 setae.

Rostrum weakly developed. First antenna 15-segmented with aesthete on penultimate segment. Second antenna lacking exopod; endopod with second segment bearing 4 setae, 3 terminal and 1 surficial. Siphon elongate, prominent. Mandible without palp, blade long and slender. First maxilla with outer lobe having 2 setae, inner lobe bearing 3 setae and 2 small spines. Second maxilla with second segment having 2 setae on proximal part, distal part clawlike and finely spinulose. Maxilliped 5-segmented, recurved claw finely spinulose.

Legs 1–4 biramous with 3-segmented rami. Leg 1 with inner seta on basis; third segment of exopod with III,5 and that of endopod with 1,2,3. Third segment of exopod of legs 2–4 with III,I,5. Third segment of endopod of leg 2 with 1,2,3, that of leg 3 with 1,1,I,3, and that of leg 4 with 1,1,I,2.

Leg 5, carried ventrally, with first segment fused with body and bearing 1 seta. Free segment short, broad, with 3 setae.

Leg 6 represented by 1 seta and 2 very small spines.

Egg sac unknown.

Male.—Unknown.

Type species.—*Bythocheres prominulus,* new species.

Gender.—Masculine.

Etymology.—The generic name is a combination of the Greek word *bythos,* meaning the depths of the sea, and *cheres,* a combining form often used for siphonostomatoids.

Bythocheres prominulus, new species
Figs. 1–19

Type material.—10 ♀♀ in 3243 m, in slurp gun sample, 26°01′N, 84°55′W, DSRV *Alvin* dive no. 1756, 17 Oct 1986, C. Van Dover collector; 2 ♀♀, in 3266 m, in slurp gun sample from small patches of whitish mats at edge of dark or black areas of reduced sediments, West Florida Escarpment cold seeps, 26°01.8′N, 84°54.9′W, *Atlantis II/Alvin* Cruise 118-2, DSRV *Alvin* dive no. 1758, 20 Oct 1986, H. Jannasch collector.

Female.—Body (Figs. 1, 2) with moderately broad prosome slightly pointed anteriorly and forming lateral shieldlike extensions. Length (not including setae on caudal rami) 1.96 mm (1.95–2.19 mm) and greatest width 0.77 mm (0.75–0.84 mm), based on 10 specimens in lactic acid. Greatest dorsoventral thickness at level of siphon 0.50 mm, at maxillipeds 0.39 mm. Segment bearing leg 1 fused with cephalosome. Epimeral areas of segments bearing legs 1–4 rounded. Ratio of length to width of prosome 1.43:1. Ratio of length of prosome to that of urosome 1.43:1.

Segment bearing leg 5 (Fig. 3) 117 × 203 μm, in dorsal view concealing fifth pair of legs. Genital segment 265 μm long, laterally expanded in anterior half, width 234 μm, narrowed in posterior half, width 174 μm. Genital areas located dorsolaterally in posterior part of anterior half of segment. Each area (Figs. 4, 5) with small seta 34 μm and 2 minute spines 5 μm and 3 μm. Three postgenital segments from anterior to posterior 122 × 146, 91 × 135, and 185 × 169 μm, last segment much longer than either of preceding two.

Caudal ramus (Fig. 6) elongate, 187 × 78 μm, ratio 2.40:1. Outer lateral seta 40 μm and displaced a little dorsally, dorsal seta 52 μm, both smooth. Outermost terminal seta 154 μm and subterminal in position, innermost terminal seta 198 μm, and 2 median terminal setae 275 μm (outer) and 335 μm (inner); all 4 terminal setae with long setules.

Sclerotization of body weak. Body surface with refractile points (sensilla?) on dorsal surface of urosome as in Fig. 3.

Egg sac unknown.

Rostral area (Fig. 7) weakly developed. First antenna (Fig. 8) 15-segmented, 495 μm long (not including terminal setae), with aesthete on penultimate segment. Armature: 1,1,2,1,2,2,2,1,6,2,2,2,2,1 + 1 aesthete, and 11. All setae smooth. Aesthete 253 μm.

Second antenna (Fig. 9) less than half length of first antenna, 234 μm (excluding terminal setae). Longest terminal seta 78 μm. Coxa and basis unarmed. Exopod absent. Endopod 2-segmented. First and second segment with small spinules along outer surface. Second segment with 1 surficial barbed seta near midregion and 1 subterminal and 2 terminal setae.

Siphon (Fig. 7) elongate, pyriform, 380 μm in length, projecting at nearly right angle with prosome (Fig. 2) and enclosing mandibles.

Mandible (Fig. 10) lacking palp. Blade extremely long and slender, 363 μm, with several minute terminal teeth. First maxilla (Fig. 11) with slender exopod and endopod, endopod twice length of exopod. Exopod with 2 terminal long barbed setae and having few outer marginal setules. Endopod terminally with 3 long barbed setae and 2 short smooth spines. Second maxilla (Fig. 12) with long unornamented first segment; elongate second segment with proximal part having 2 small distal inner setae, subterminal seta weakly barbed, smaller terminal seta smooth, distal part forming short stout claw 80 μm (Fig. 13) with many minute spinules on concave surface. Maxilliped (Fig. 14) 5-segmented. First segment with small distal inner barbed seta. Second segment with small inner smooth seta. Third segment with small delicately barbed distal outer seta. Fourth segment with distal barbed inner seta. Fifth segment with inner terminal unilaterally barbed seta and outer recurved claw 99 μm long and densely covered with minute spinules.

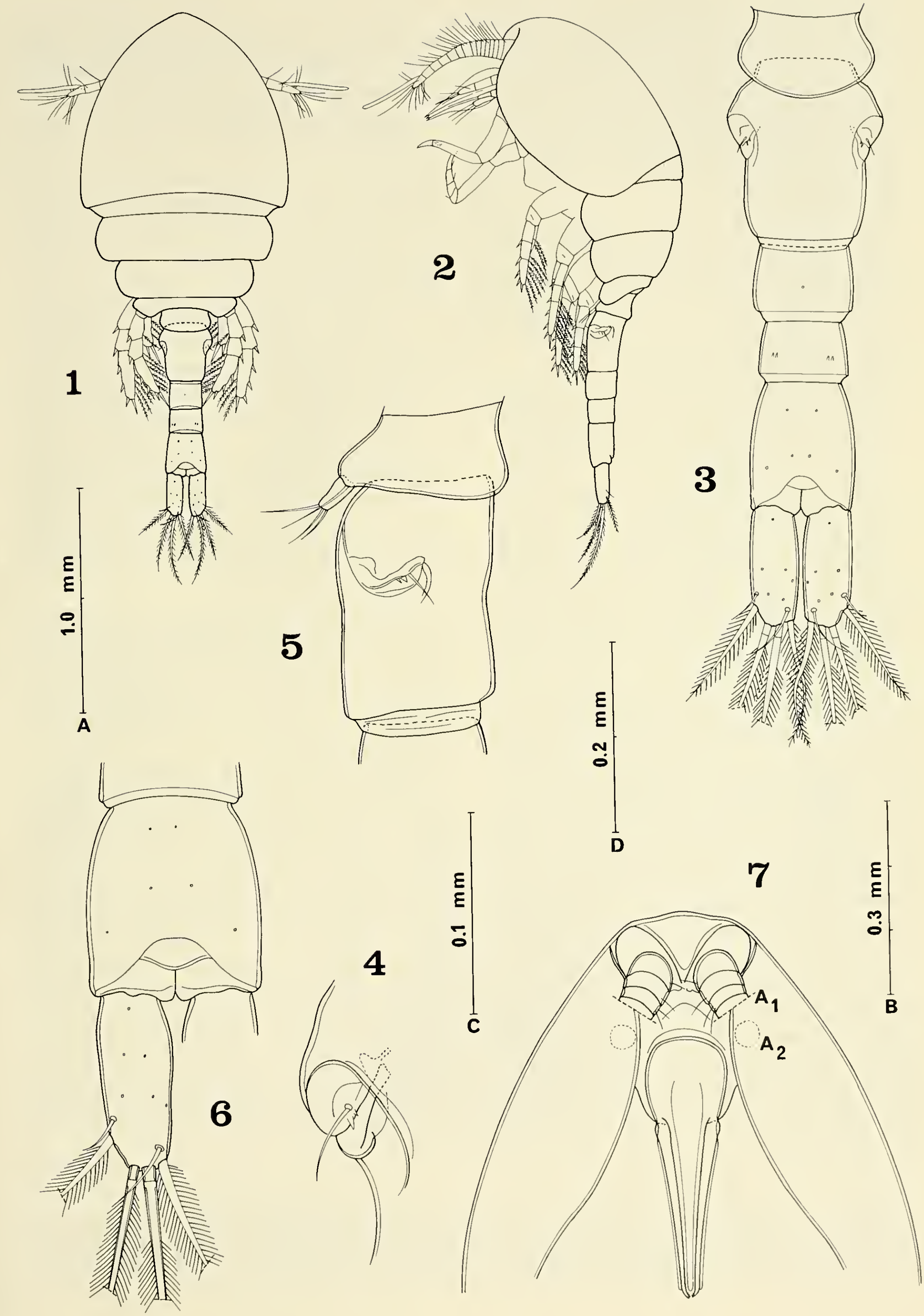
Ventral area between maxillipeds and first pair of legs protuberant as in Fig. 2.

Legs 1–4 (Figs. 15, 16, 17, 18) biramous, with 3-segmented rami. Spine and setal formula as follows (Roman numerals representing spines, Arabic numerals indicating setae)

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

→

Figs. 1–7. *Bythocheres prominulus,* female. 1, Dorsal (scale A); 2, Lateral (A); 3, Urosome, dorsal (B); 4, Genital area, dorsal (C); 5, Segment bearing leg 5 and genital segment, lateral (D); 6, Anal segment and caudal ramus, dorsal (D); 7, Rostrum and siphon, ventral (B). A_1 = first antenna, A_2 = second antenna.


1
2
3
4
5
6
7
1.0 mm
A
0.2 mm
D
0.1 mm
C
0.3 mm
B
A1
A2

Leg 1 lacking inner seta on coxa and with basis bearing inner barbed seta 26 μm long; third segment of exopod with III,5. Legs 2–4 with long pinnate inner coxal seta and third segment of exopod with III,I,5. Third segment of endopod of legs 1 and 2 with 1,2,3, that of leg 3 with 1,1,I,3, and that of leg 4 with 1,1,I,2.

Leg 5 (Fig. 19) with first segment fused with body and bearing outer seta 78 μm. Free segment short and broad, 44 × 37 μm, with 3 setae from outer to inner 31, 39, and 65 μm. All setae smooth. Minute spinules near insertion of longest seta.

Leg 6 probably represented by seta and 2 minute spines on genital area (Figs. 4, 5).

Color of living specimens unknown.

Male.—Unknown.

Etymology.—The specific name alludes to the prominent siphon.

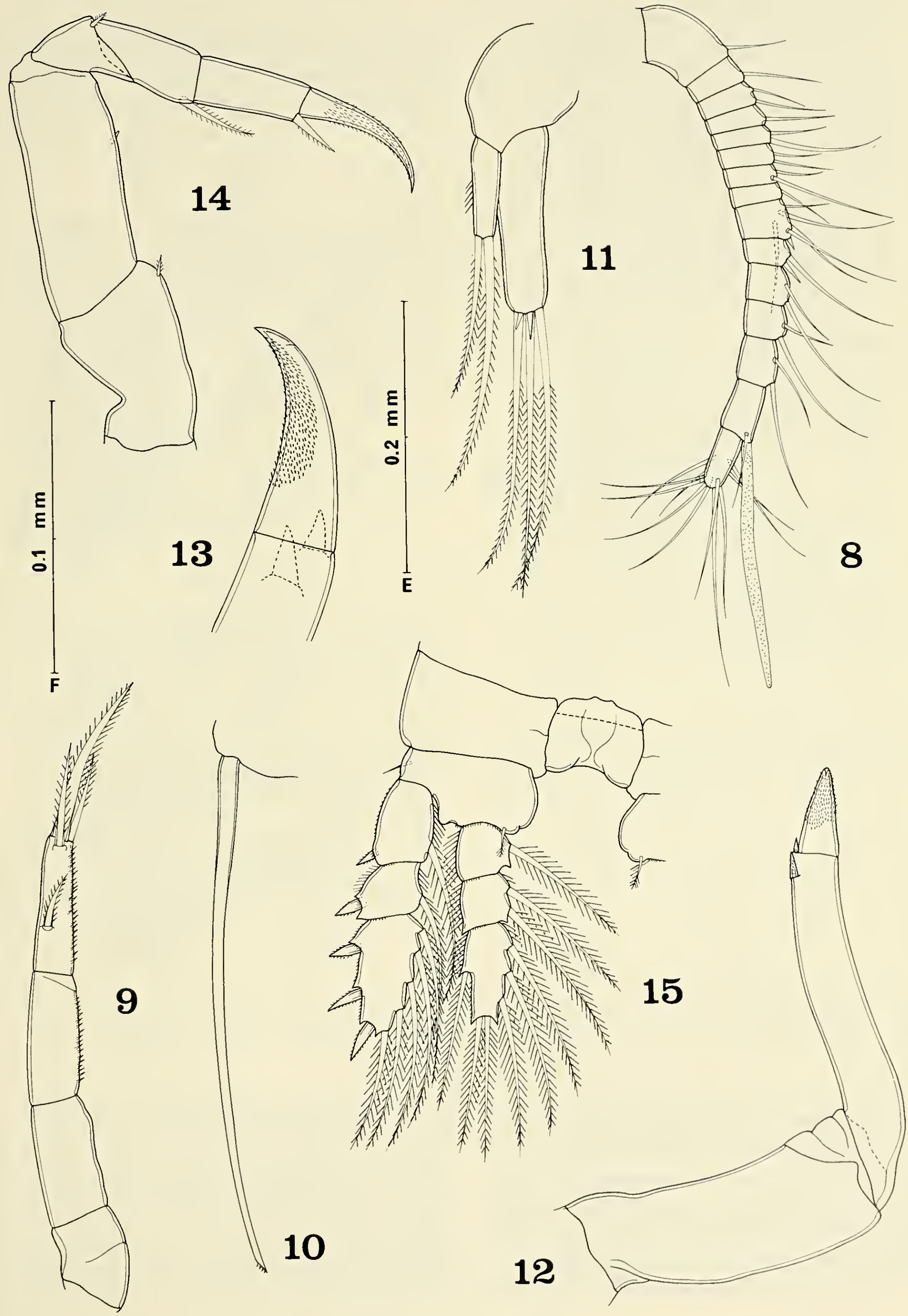
Remarks.—The new genus *Bythocheres* does not fit comfortably in any of the currently recognized families of Siphonostomatoida whose members are free-living or associated with invertebrate hosts (excluding those parasitic on fishes). In many families the body is strongly modified or transformed and quite unlike that in *Bythocheres* (Artotrogidae, Calvocheridae, Cancerillidae, Entomolepidae, Herpyllobiidae, Micropontiidae, Nanaspididae, Nicothoidae, Saccopsidae, Spongiocnizontidae, Stellicomitidae, and Xenocoelomatidae). In the remaining nine families, all with unmodified bodies, four have an exopod on the second antenna and less than 15 segments in the first antenna which has an aesthete on the last segment (Dyspontiidae, Megapontiidae, Myzopontiidae, and Pontoeciellidae), thus differing from *Bythocheres.* In most Asterocheridae a mandibular palp is present, the number of segments in the first antenna may be 15 or more, and the second antenna generally has an exopod (though this is vestigial or absent in some). The other four families may be distinguished from *Bythocheres* on the basis of other characters. In the Dirivultidae the endopod of leg 4 is 2-segmented. In the Brychiopontiidae leg 5 is a lobe with four setae and the first antenna of the female is 18-segmented with an aesthete on segments 15 and 18. In the Rataniidae the basis of leg 1 does not have an inner seta or spine and the free segment of leg 5 has five setae. Finally, in the Dinopontiidae the first antenna of the female is 8- or 9-segmented and the third segment of the endopod of leg 4 has the formula 0,I,2. Casual inspection of the undissected body of *Bythocheres* might suggest a similarity with such copepods as *Ratania* (see Boxshall 1979, fig. 17A), but a detailed study of the external anatomy reveals differences as outlined above.

We are left with a genus of Siphonostomatoida for which the family position seems unclear. Until males of *Bythocheres* are found and described, it is considered preferable to leave the new genus without familial assignment.

While a number of copepods from hydrothermal vents are believed to be associated with various invertebrates (for example, vestimentiferans, bivalve mollusks, polychaetes, and shrimps), no information on a possible association of *Bythocheres* with a host is available. The large prominent siphon, however, suggests that *B. prominulus* may be associated with a host. Various invertebrates eligible as hosts occur in the vicinity of cold seeps, among them anemones, gastropods, clams, mussels, vestimentiferans, holothurians, ophiuroids, shrimps, and galatheid crabs (Paull et al. 1984). Since *By-*

→

Figs. 8–15. *Bythocheres prominulus,* female. 8, First antenna, anteroventral (scale D); 9, Second antenna, anterior (C); 10, Mandible, posterior (B); 11, First maxilla, anterior (E); 12, Second maxilla, postero-inner (E); 13, Distal part of second maxilla, antero-outer (F); 14, Maxilliped, posterior (E); 15, Leg 1 and intercoxal plate, anterior (D).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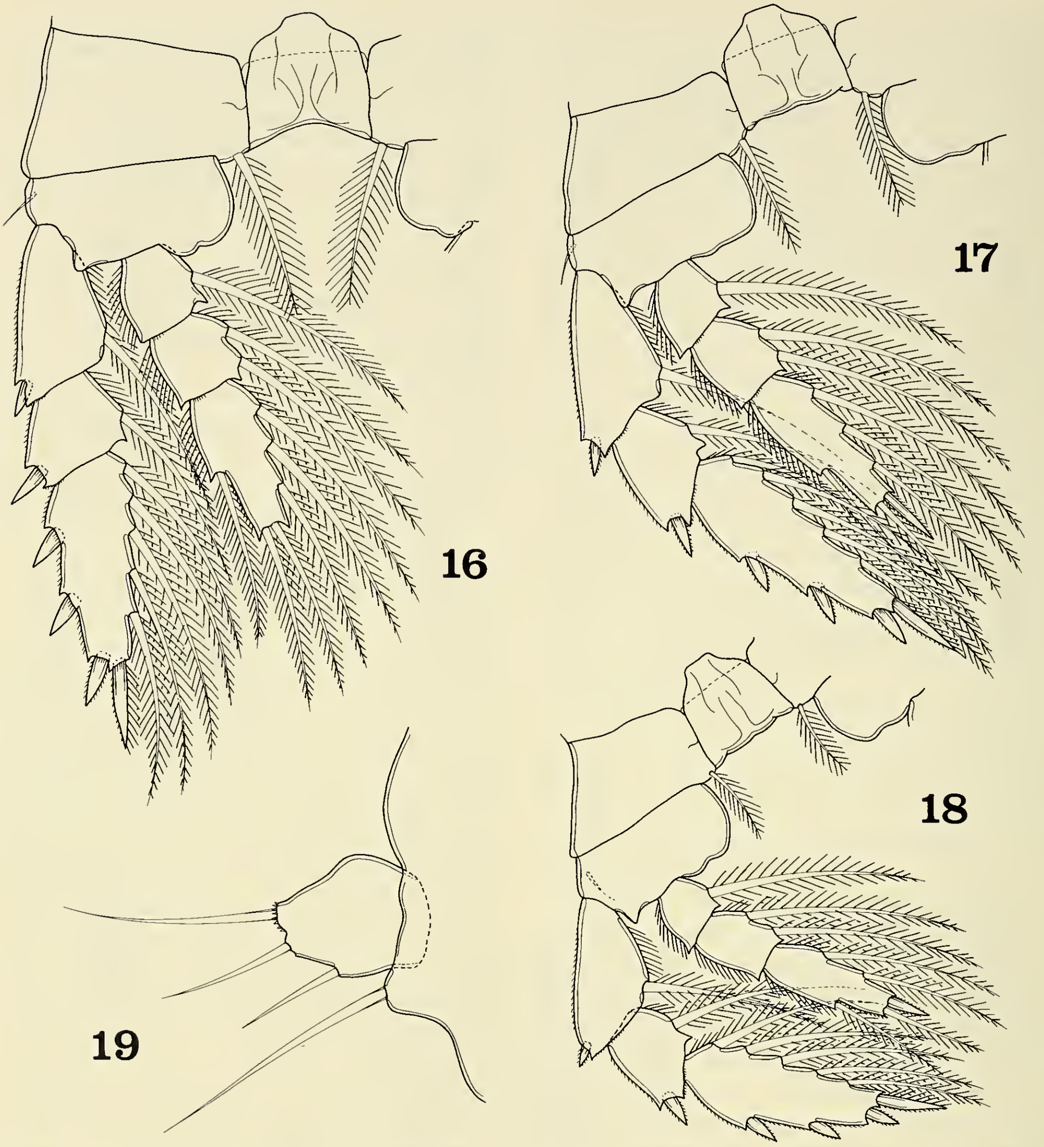

Figs. 16–19. *Bythocheres prominulus,* female. 16, Leg 2 and intercoxal plate, anterior (scale D); 17, Leg 3 and intercoxal plate, anterior (D); 18, Leg 4 and intercoxal plate, anterior (D); 19, Leg 5, ventral (F).

thocheres prominulus was found only in slurp gun samples and was absent from six box core samples from the same general area, the copepod appears to be epibenthic, living perhaps only on mats of inorganic material and sulfide-ozidizing bacteria present at the seeps, and is not part of the infauna.

The diversity of poecilostomatoid and siphonostomatoid copepods at vents and cold seeps in the deep sea is becoming apparent with the introduction of new techniques of collection by means of submersibles such as *Alvin.* Humes (1987, table 1) listed six poecilostomatoids and 10 siphonostomatoids then known, and in the same work described three new poecilostomatoids and

24 new siphonostomatoids. With the addition of *Bythocheres prominulus* to the list the number of species of copepods known from deep-sea vents or cold seeps is now 44.

Acknowledgments

I thank Dr. Holger Jannasch and Cindy Van Dover, Woods Hole Oceanographic Institution, both of whom collected specimens of the new copepod, for providing material of this deep-sea form. I am particularly indebted to Dr. Jannasch for information on the cold seeps and to Dr. F. Frederick Grassle and Dr. Carl O. Wirsen, Jr., for comments on the manuscript.

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PSEUDIONE PARVIRAMUS AND *APOROBOPYRUS COLLARDI,* TWO NEW SPECIES OF BOPYRIDAE (ISOPODA: EPICARIDEA) FROM THE GULF OF MEXICO

Daniel L. Adkison

Abstract.—*Pseudione parviramus,* n. sp. is described from the pandalid shrimp, *Parapandalus longicauda* Rathbun. *Aporobopyrus collardi,* n. sp. is described from the porcellanid crab, *Pachycheles rugimanus* A. Milne Edwards. Three bopyrid species are transferred to *Aporobopyrus* from *Pseudione*: *Pseudione lenticeps* Shiino, 1958; *P. orientalis* Shiino, 1933; *P. trilobata* Nierstrasz and Brender à Brandis, 1925. *Pleurocryptosa* Nierstrasz and Brender à Brandis, 1929, is considered a junior synonym of *Aporobopyrus* Nobili, 1906.

A review of the bopyrid literature shows an immense diversity of forms included in *Pseudione* Kossmann, 1881, a large, poorly defined genus that would greatly benefit from a world-wide review. *Aporobopyrus* is one of several Pseudioninae genera that are synonymous with *Pseudione* as historically defined. The distinction of *Aporobopyrus* from *Pseudione* is clarified by an amended generic diagnosis of *Aporobopyrus* and transferal of three species from *Pseudione* to *Aporobopyrus.*

Pseudione parviramus, new species
Figs. 1, 2

Material examined.—Investing *Parapandalus longicauda* Rathbun, 1902. Northern Gulf of Mexico, *Oregon II* sta 14003; 28°44′N, 89°38′W, trawl, 133 m, 29 Nov 1973, D. L. Adkison coll., M. R. Dardeau det. host, 1 ♀ (gravid), 1 ♂ USNM 172443.—Sta BLM I-C-c-7, 26°26′N, 84°19′W, trawl, 200 m, 28 Jan 1976, T. S. Hopkins coll., M. R. Dardeau det. host, 1 ♀ (gravid, holotype) USNM 172441, 1 ♂ USNM 172442.

Description.—Female (Figs. 1, 2a, b): Length 9.0 to 11.0 mm; width across pereomere 3, 6.0 mm; distortion 18 to 22°.

Head: Eyes present. Frontal lamina longer laterally than medially. First antenna of 3 articles. Second antenna of 6 articles. Maxilliped subquadrate; palp articulated, setose and medially directed. Posterior lamina with 2 pairs of lanceolate projections.

Pereon broadest across pereomere 3. Coxal plates prominent on pereomeres 1–4, larger on expanded side. Dorsolateral bosses present on pereomeres 1–4, larger on concave side. Tergal area not greatly developed; lateral plates on pereomeres 5–7 arising from coxal area, lateral plates larger on expanded side. Oostegite 1 with posterolateral point blunt and internal ridge ornamented laterally with low rounded projections. Pereopods without carinae.

Pleon of 6 segments; lateral plates on pleomeres 1–5, decreasing in length posteriorly. Pleopods, 5 biramous pairs; each exopod larger than endopod; exopods of anterior pleopods longer than lateral plates, posterior exopods and lateral plates nearly equal; endopods of pleopods 1 and 2 ovate; posteriorly, endopods becoming progressively longer. Uniramous uropods similar in shape to and smaller than exopod of pleopod 5.

Male (Fig. 2c–h): Length 3.7 mm; width across pereomere 3, 1.2 mm.

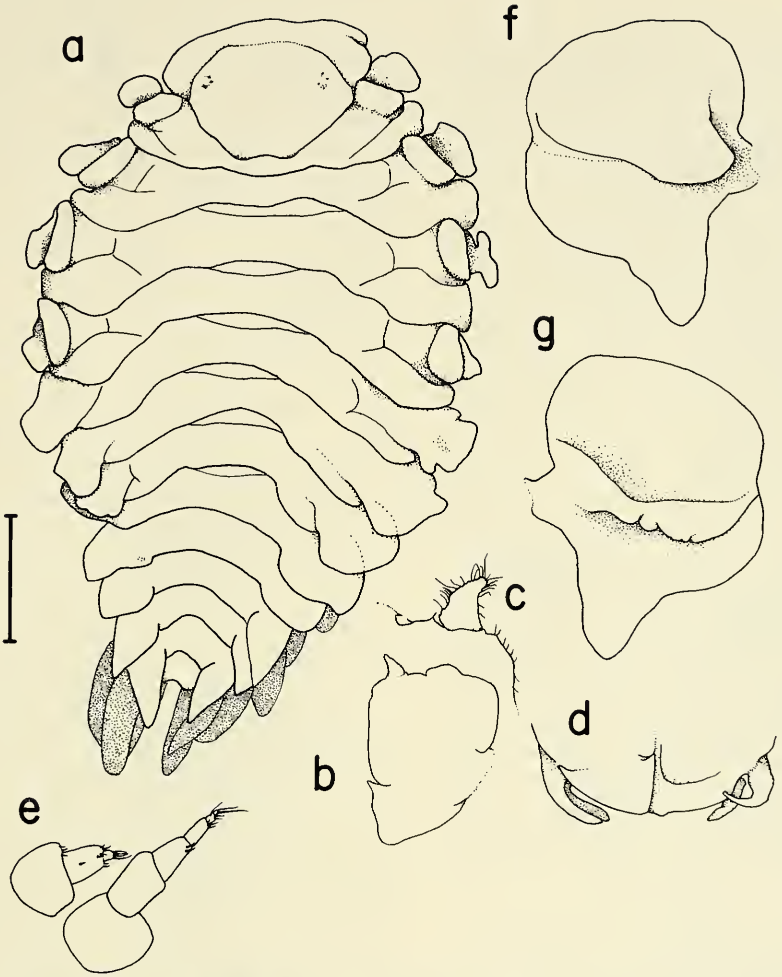

Fig. 1. *Pseudione parviramus,* female holotype: a, Dorsal view; b, Maxilliped, external view; c, Palp, internal view; d, Posterior lamina, right maxilliped present; e, Antennae; f, Oostegite 1, external view; g, Same, internal view. Scale = 2.0 mm (Fig. a).

Head trapezoidal, eyes present. First antenna of 3 articles. Second antenna of 7 articles. Maxillipeds present.

Pereon with pereopods of similar size, dactyls of pereopods 1 and 2 longer than others. Midventral tubercles on pereomeres 6 and 7.

Pleon of 6 pereomeres; 5 pairs of uniramous pleopods, smaller posteriorly, not visible in lateral view. Midventral tubercles on pleomeres 1 and 2. Pleomere 6 broadly Y-shaped, anal cone indistinct.

Etymology.—The specific name alludes to the short pleopodal endopods of the female.

Distribution.—*Pseudione parviramus* is only known from the type series from the coastal waters of the Gulf of Mexico.

Discussion.—*Pseudione parviramus* is similar to *P. affinis* (Sars, 1882) and *P. tattersalli* Nierstrasz & Brender à Brandis, 1923. All three species infest pandalid shrimps: *P. affinis* on *Dichelopandalus bonnieri* (Kinahan), *Pandalus montagui* Leach, *Plesionika antiquai* Zariquiey Alvarez, *P. heterocarpus* (Costa) and *P. martia* (Milne

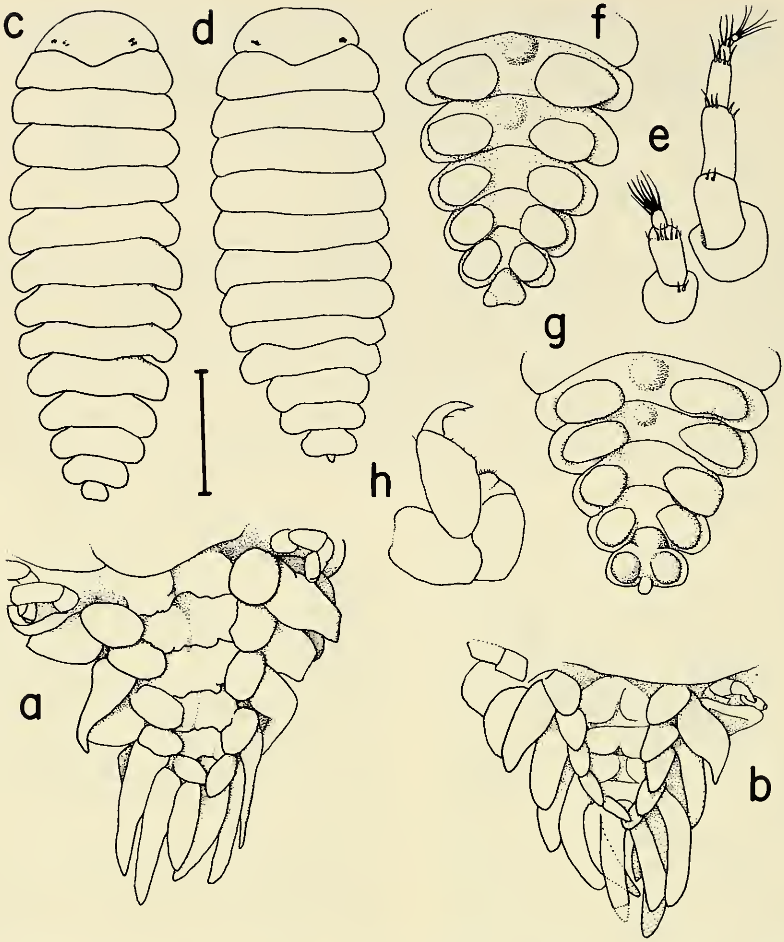

Fig. 2. *Pseudione parviramus,* a, b female; c–h male: a, Pleon of holotype, ventral view; b, Pleon of paratype, ventral view; c, d, Dorsal view; e, Antennae; f, g, Pleon, ventral view; h, Pereopod 1. Figure c, f from USNM 172443. Figure d, e, g, h from USNM 172442. Scale = 1.0 mm (Fig. c, d).

Edwards) as reported by Bourdon (1968); *Pseudione tattersalli* on *Plesionika ensis* (Milne Edwards) as reported by Bourdon (1972); and *Pseudione parviramus* on *Parapandalus longicauda.*

Pseudione parviramus females differ from females of *P. affinis* and *P. tattersalli* by enlarged lateral areas of pereomeres 5–7 and shorter endopods of anterior pleopods. Both *P. tattersalli* and *P. parviramus* have articulated maxilliped palps, while *P. affinis* has a non-articulated maxilliped palp. Males of *P. parviramus* have eyes and reduced pleopods not visible in lateral view of the pleon.

The only abnormality noted was that the sixth pleomere of one male apparently failed to develop normally and is indicated by the small projection posterior to fifth pereomere.

Aporobopyrus Nobili, 1906

Diagnosis.—Female: Body only slightly distorted, all regions and segments distinct. Head large; anterior lamina narrow medially, laterally developed into distinct lobes with acute points; maxilliped with palp reduced, palp location indicated; posterior ventral lamina with 2 pairs of reduced projections. Pereon with small coxal plates on pereomeres 1–4; small dorsolateral bosses on pereomeres 1–4; lateral plates reduced. Pleon with lateral plates reduced or absent; 5 pairs of biramous pleopods, near lateral margins of pleomeres, visible in dorsal view; uropods uniramous.

Male: All segments distinct. Pleon of 6 pleomeres, decreasing in width posteriorly; pleopods reduced or absent; uropods absent.

Type-species.—*Aporobopyrus aduliticus* Nobili, 1906.

Discussion.—As diagnosed above, the females of *Aporobopyrus* differ from those of *Pseudione* thus: dorsolateral bosses are small, pleon lateral plates are reduced or absent, and pleopods are visible in dorsal view. The head of the female *Aporobopyrus* is also relatively large and its posterior ventral lamina projections small.

In light of the amended diagnosis of *Aporobopyrus,* four species previously assigned to *Pseudione* are here reassigned to *Aporobopyrus*: *Pseudione lenticeps* Shiino, 1958; *P. petrolistheae* Shiino, 1933; *P. orientalis* Shiino, 1933; and *P. trilobotata* Nierstrasz & Brender à Brandis, 1925. *Aporobopyrus lenticeps* (Shiino, 1958) is known from Japan on *Munida japonica heteracantha* Ortmann; *A. petrolistheae* (Shiino, 1933) is known from Japan on *Petrolisthes japonicus* (de Haan) and from Amboine on *P. militaris* (Heller) as *A. petrolistheae palpifera* (Bourdon, 1976); *A. orientalis* (Shiino, 1933) is known from Japan on *Galathea orientalis* Stimpson; and *A. trilobotata* (Nierstrasz & Brender à Brandis, 1925) is known from Curaçao on *Neopisoma angustifrons* (Benedict) and from the Pacific coast of Mexico on *Petrolisthes hians* Nobili. With the transference of these species, *Aporobopyrus* differs from *Pseudione* in the development of the anterior lamina into long lateral projections as pointed out by Markham (1975).

With the improved diagnosis of *Aporobopyrus* and more distinct separation from *Pseudione,* it became apparent that *Pleurocryptosa* Nierstrasz & Brender à Brandis, 1929, falls within the diagnosis of *Aporobopyrus.* The development of the frontal lamina of the female distinguishes *Aporobopyrus* and *Pleurocryptosa* but is too variable (Bourdon 1976, 1983). Therefore, *Pleurocryptosa* is considered a junior synonym of *Aporobopyrus* and its five species: *P. calypso* Bourdon, 1976; *P. enosteoides* Markham, 1982; *P. megacephalon* Nierstrasz & Brender à Brandis, 1929; *P. parvula* Bourdon, 1983; and *P. pleopodata* Bourdon, 1983, are here assigned to *Aporobopyrus* accordingly. *Aporobopyrus calypso* (Bourdon, 1976) is known from Brazil on *Pachycheles ackleianus* (A. Milne Edwards); *P. enosteoides* (Markham, 1982) is known from Hong Kong on *Enosteoides ornatus* (Stimpson); *P. megacephalon* (Nierstrasz & Brender à Brandis, 1929) is known from Thailand on an undetermined porcellanid crab; *P. parvula* (Bourdon, 1983) n. comb. is known from Seram Island on *Lissoporcellana spinuligera* (Dana); and *P. pleopodata* (Bourdon, 1983) is known from Marsegu Island on *Polyonyx obesulus* Miers.

Aporobopyrus collardi, new species

Figs. 3–5

Material examined.—Infesting *Pachycheles rugimanus* A. Milne Edwards, 1880, coll. by T. S. Hopkins, except as noted; all hosts det. by D. L. Adkison. Eastern Gulf of Mexico: sta MAFLA III-E(39), 29°45′N, 86°00′W, Capetown dredge, 45 m, 5 Jun 1974, 1 ♀, 1 ♂ USNM 173443.—Sta MAFLA II-D(246), 28°38′06″N, 84°19′06″W, diver collected, 41 m, 11 Jun 1974, 1 ♀ (gravid), 1 ♂ ZMC.—Sta MAFLA III-G(141), 30°01′03″N, 85°54′54″W, diver collected, 30 m, 6 Jun 1974, 2 ♀ (gravid), 2 ♂ MNHN Ep. 110 and 111 (host present).—Sta MAFLA III-F(41), 29°47′30″N, 85°54′30″W, diver collected, 41 m, 11 Jun 1974, 3 ♀ (gravid), 3 ♂ RMNHL I-5910.—Sta BLM 13 V-A-2, 29°55′N, 86°06′W, Capetown dredge, 20 Jul 1975, 2 ♀ (gravid), 2 ♂ USNM 173444.—Sta BLM 19-151; 28°32′15″N, 84°18′45″W, diver collected, 28–38 m, 27 Oct to 2 Nov 1975, 1 ♀ (gravid), 1 ♂ USNM 173450.—Sta 33 I-A-a-3, 26°24′N, 82°58′W, Capetown dredge, 37 m, 29 Feb 1976, 1 ♀, 1 ♂ USNM 173445.—Sta BLM 37 247, 28°36′16″N, 84°15′51″W, diver collected, 28–38 m, 3 Jun 1976, 1 ♀, 1 ♂ USNM 173446.—Sta BLM 37 151, 28°32′15″N, 84°18′45″W, diver collected, 28–38 m, 7 Jul 1976, 1 ♀ (gravid), 1 ♂ USNM 173447.—Sta 2315-401870830, 28°58′N, 85°23′W, trawl, 38 m, 30 Jul 1977, 1 ♀ (gravid), 1 ♂ MNHN Ep. 85.—Sta 2426-181870901, 28°58′N, 85°23′W, Capetown dredge, 82 m, 1 Oct 1977, 1 ♀, 1 ♂ USNM 173448.—Sta 2103-191871023, 26°24′N, 82°58′W, Capetown dredge, 38 m, 23 Oct 1977, 1 ♀, 1 ♂ USNM 173449.—Sta 2103-171880201, 26°24′N, 82°58′W, trawl, 37 m, 1 Feb 1978, 1 ♀ (gravid, holotype) USNM 173441, 1 ♂ USNM 173442.

Description.—Female (Figs. 3, 4): Length 1.5 to 3.6 mm; width across pereomere 3, 1.6 to 2.4 mm; distortion 10 to 35°.

Head, large, length and width approximately equal; anterior lamina distinct, medially narrow, broadening into lobes laterally. Eyes present, often visible only in ventral view. First antenna of 3 articles. Second antenna of 5 articles, basal segment enlarged. Second antenna nearly twice as long as length of first antenna. Maxilliped with distinct non-articulated palp to sharp anteromedial corner lacking palp. Posterior lamina with 2 pairs of small projections, lateral pair often with lateral tubercle; medial pair of projections with 1–3 tubercles.

Pereon with coxal plates on pereomeres 1–4, larger on expanded side and posteriorly; on expanded side, pereomere 5 rarely with coxal plate distinct. Dorsal bosses on pereomeres 1–4; on expanded side, tergal area reduced. Pereopods longer posteriorly; on expanded side, pereopods 3–7 with basal carinae, carinae larger posteriorly; on reduced side, pereopods without carinae. First oostegite with short posterolateral projection and internal ridge ornamented with few small tubercles laterally.

Pleon with short lateral plates, those on expanded side larger, all shorter posteriorly. Five pairs of biramous pleopods; rami of pleopods 1–2 oval, others elongate; all pleopods with endopods larger than exopods. Uniramous uropods, length often unequal.

Male (Fig. 5): Length 1.5 to 2.4 mm; width across pereomere 4, 0.5 to 0.8 mm.

Head broadly rounded anteriorly. First antenna of 3 articles. Second antenna of 5 articles. Second antenna less than twice length of first antenna. Maxillipeds present.

Pereon widest across pereomere 4, tapering both anteriorly and posteriorly; pigment spots dorsally on some pereomeres. Midventral tubercles absent. Pereopod 1 larger than others.

Pleon of 6 pleomeres, narrower posteriorly. Pleopods absent, indicated only by shallow depressions. Pleomere 6 with posterior margin produced into 2 lateral lobes and central anal cone.

Etymology.—This species is named for Dr. Sneed B. Collard, who started me on the study of the Epicaridea.

Distribution.—*Aporobopyrus collardi* is only known from the type series collected in the eastern Gulf of Mexico.

Discussion.—*Aporobopyrus collardi* is most similar to *A. trilobata* and *A. calypso.* The female of *A. collardi* differs from *A. trilobata* thus: its second antenna has five articles, coxal plates are larger on expanded side, dorsal bosses on reduced side are not bilobed, and endopod of pleopod 1 is folded onto itself. The female of *A. collardi* differs from *A. calypso* thus: its first oostegite has a tuberculate internal ridge, coxal plates are larger, lateral area of pereomeres 5–7 has a defined tergal area, first pleomere on expanded side has larger lateral plate and endopod of first pleopod is not greatly larger than exopod. The male of *Aporobopyrus col-*

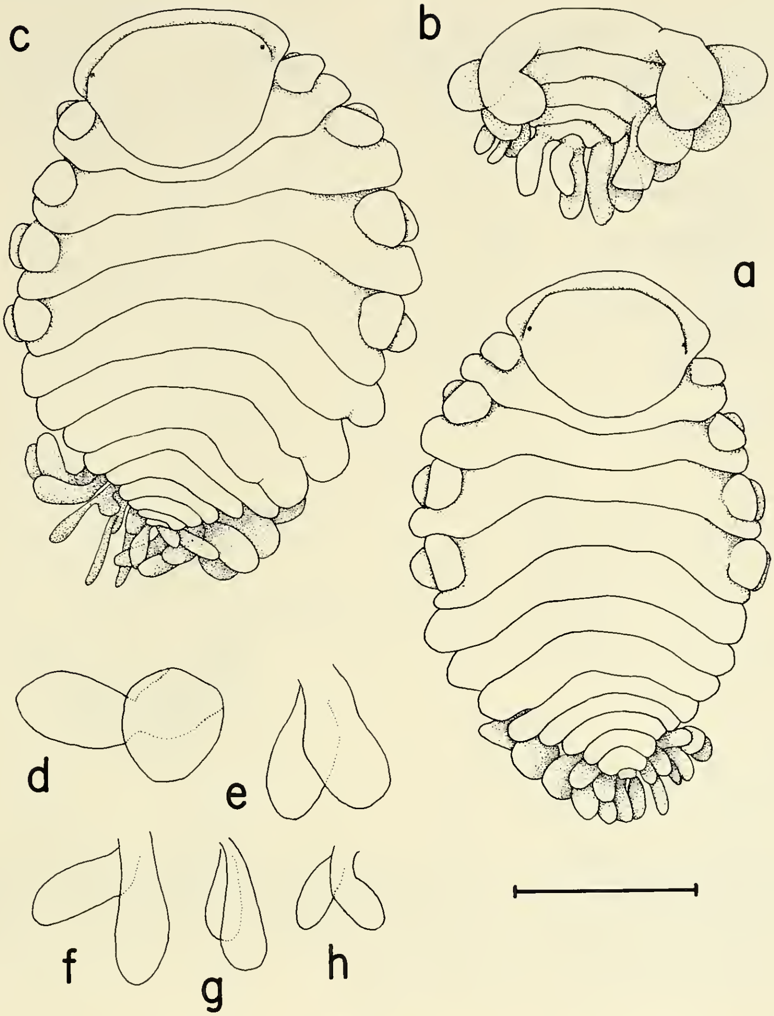

Fig. 3. *Aporobopyrus collardi,* female: a, Dorsal view; b, Pleon, ventral view of a; c, Dorsal view; d–h, Pleopods from expanded side; d, Pleopod 1; e, Pleopod 2; f, Pleopod 3; g, Pleopod 4; h, Pleopod 5. Figure c–h from USNM 173444. Scale = 1.0 mm (Fig. a, b).

lardi lacks pleopods and therefore differs from the males of both other species. The pleopods of male *A. collardi* are indicated by oval concave areas visible only after staining.

Aporobopyrus collardi is the second species of *Aporobopyrus* reported from the western North Atlantic and differs from *A. curtatus* (Richardson) for the female thus: first antenna of 5 articles; posterior ventral lamina of head with 2 pair of projections; on expanded side, pereopods 3–7 with basal carinae; pleopods non-tuberculate; and for the male pleopods are absent.

Differences in the relative size of the rami of the posterior pleopods for female *A. collardi* were seen. Less mature females differ from mature females by a much larger endopod relative to the exopod for immature females. The lack of a full maturation series

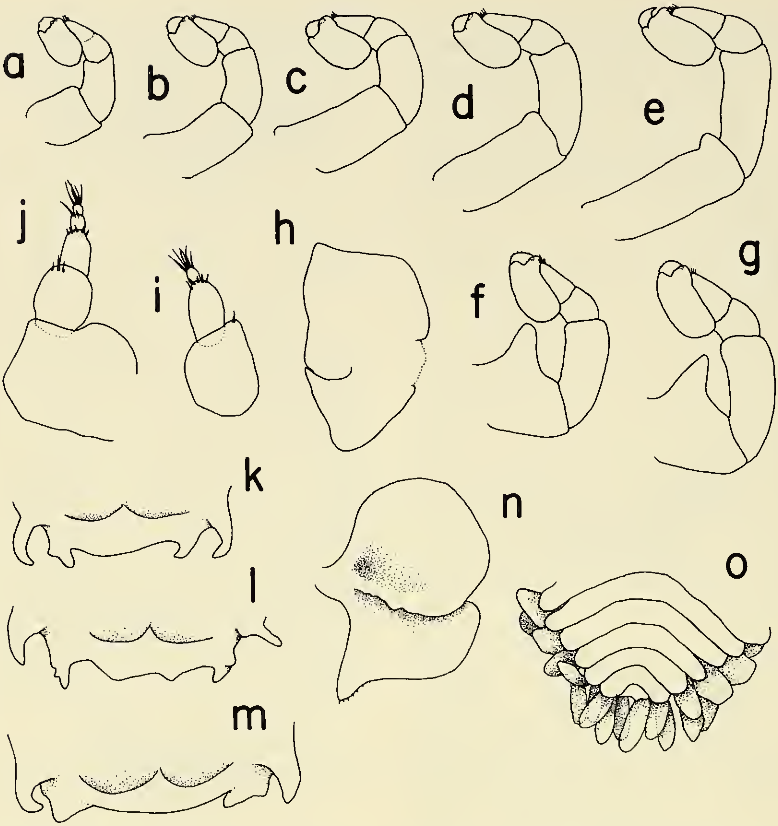

Fig. 4. *Aporobopyrus collardi,* female: a–e, pereopods, reduced side; a, Pereopd 1; b, Pereopod 4; c, Pereopod 5; d, Pereopod 6; e, Pereopod 7; f–g, Pereopods, expanded side; f, Pereopod 6; e, Pereopod 7; f–g, Pereopods, expanded side; f, Pereopod 6; g, Pereopod 7; h, Maxilliped; i, Antenna 1; j, Antenna 2; k–m, Posterior lamina; n, Oostegite 1, internal view; o, Pleon, dorsal view. Figure a–k, o from USNM 173444. Figure l, m from RMNHL I-5910. Figure n from holotype. Scale = 1.0 mm (Fig. a, b).

precludes definitive demonstration of proportional changes in the pleopodal rami proportions with maturation.

Two male forms were found differing in the degree of separation of the pereomeres. The forms differed in no other characteristics noted.

Two abnormal male specimens of *A. collardi* were found. One specimen appeared damaged and had only four pleomeres. The fourth pleomere was wider than normal and had an irregular posteromedial margin with two small projections, possibly indicating pleomeres 5–6 had been removed in the past. The other specimen had six pleomeres on the left side but only five pleomeres on the right side with pleomeres 3–4 fused.

Of the 14 female specimens that were with their hosts, seven were in the right branchial chamber (4 ♀ host, 3 ♂ host) and seven in the left (3 ♀ host, 4 ♂ host). Three female hosts were gravid. Unlike their effects on most host families, bopyrids often do not castrate female porcellanids. Gravid host are common though onset of reproduction is delayed and the number of eggs carried is reduced (see Van Wyk 1982 for discussion).

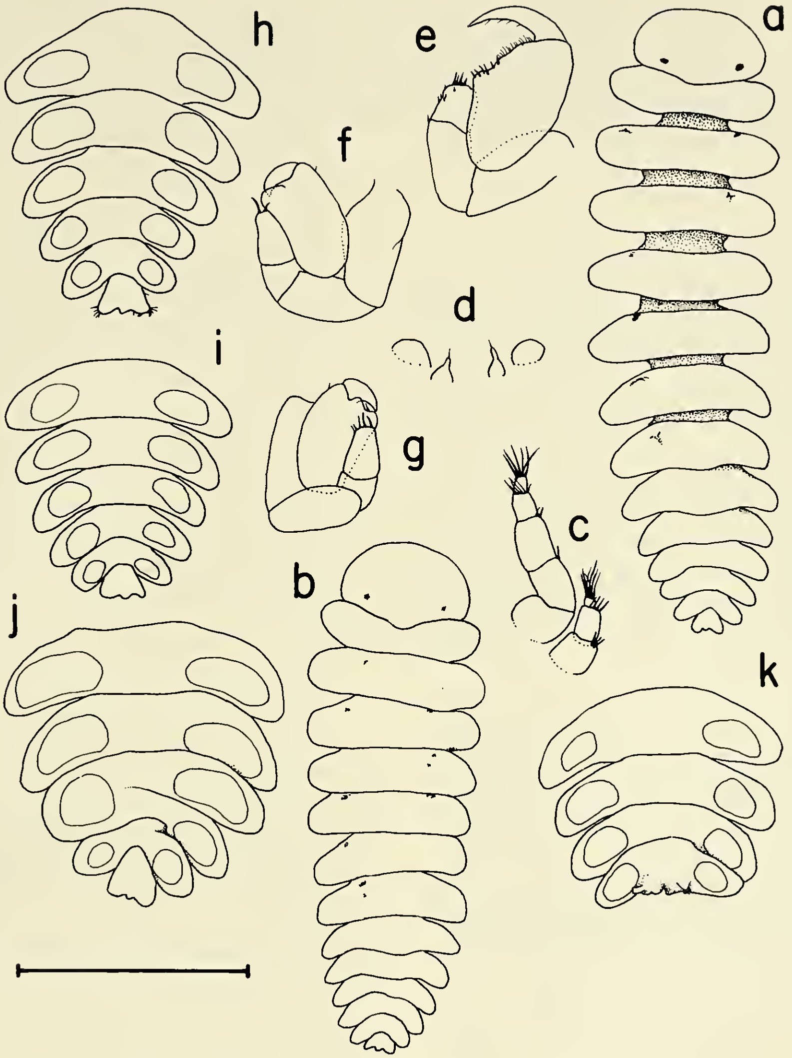

Fig. 5. *Aporobopyrus collardi,* male: a, Dorsal view, chain form; b, Dorsal view, compact form; c, Antennae; d, Maxillipeds; e, Pereopod 1; f, Pereopod 7, anterior view; g, Pereopod 7, posterior view; h–k, Pleon ventral view. Figure a, h, k from RMNHL I-5910. Figure b, d, i from ZMC. Figure c, e–g from USNM 173444. Figure j from USNM 173450. Scale = 1.0 mm (Fig. a, b).

Acknowledgments

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Smithsonian Institution, Washington, D.C. (USNM); Universitetets Zoologiske Museum, Copenhagen (ZMC); Rijksmuseum van Natuurlijke Historie, Leiden (RMNHL); and Muséum National d'Histoire Naturelle, Paris (MNHN).

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NEW RECORDS OF FISH PARASITIC MARINE ISOPOD CRUSTACEANS (CYMOTHOIDAE, SUBFAMILY ANILOCRINAE) FROM THE INDO-WEST PACIFIC

Niel L. Bruce and Elizabeth B. Harrison-Nelson

Abstract.—New records of Indo-Pacific Anilocrinae are reported on, principally from the collections of the Smithsonian Institution, British Museum (Natural History), and the Zoologisch Museum, Amsterdam.Twenty-nine species from the genera *Anilocra, Creniola, Nerocila, Pleopodias* and *Renocila* are recorded or reported on, with remarks given for all species, and figures for those species that are poorly known. The hosts of three isopod species are recorded for the first time, and new host records are given for a further six species.

New figures are given for *Anilocra marginata* (Bleeker), *Anilocra rhodotaenia* Bleeker is relegated to *species inquirenda.* The following new synonyms are recorded: *Nerocila arres* Bowman & Tareen with *N. sigani* Bowman & Tareen; *Anilocra acuminata* Haller with *A. capensis* Leach; and *Pleopodias superatus* Williams & Williams with *P. diaphus* Avdeev.

Bruce (1987a, b, c) recently revised the Australian genera and species of the subfamily Anilocrinae. In the course of that work the type material of most species of *Anilocra, Nerocila, Renocila* and *Pleopodias* was examined and drawn. In 1986 the senior author visited the Smithsonian Institution, the British Museum (Natural History), and other museums in Europe. Using the new taxonomy (Bruce 1987a, b, c) and unpublished drawings of the types, it was possible to identify nearly all anilocrine species encountered. Many species here have had their reported distribution greatly expanded. Figures are given for the less well known species.

A total of 29 species is reported on. Of all the specimens examined only five apparently undescribed species were encountered. All these are in the collection of the Smithsonian Institution. These were a large species of *Renocila* from the Philippines (identified by Richardson 1910, as *R. ovata*), *Anilocra* sp. of Monod (1976) (6 specimens from Ambon, two from Madang, Papua New Guinea, all of which show they are distinct from *Anilocra apogonae* Bruce), another *Anilocra* from Madang, and a number of specimens belonging to the *Anilocra dimidiata-leptosoma* complex of species. The low number of unnamed taxa encountered suggests the probability that most of the Indo-Pacific Anilocrinae have now been described. Notwithstanding Williams & Williams (1986, 1987) have recently described several new taxa from Japanese waters.

The synonymization of a recently described species of *Nerocila* merits some discussion. *Nerocila sigani* was described from the holotype only. Since then, Bruce (1987a) has shown species of *Nerocila* to be far more variable in morphology than related genera. It would seem therefore that while describing other distinctive species of cymothoids from single adult specimens is potentially acceptable, it is not advisable to do so for *Nerocila* species. The synonymization here of *Pleopodias superatus* Williams & Williams, 1987 with *Pleopodias diaphus* Avdeev, 1975 highlights the need for thorough literature coverage when dealing with the Cymothoidae. Poorly described species are still a problem in the family. There are still several such species of Indo-Pacific Anilocrinae (listed by Bruce 1987a, b, c) to which can be added *Anilocra huacho* Rokitsky, 1984 from the East Pacific.

This work therefore has two aims: to record the new data and synonymies for those species treated herein, and to provide additional figures and data for several of the poorly known Indo-Pacific species.

All measurements are in millimeters.

Abbreviations.—BMNH—British Museum of Natural History, London; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; MHNG—Museum d'Histoire Naturelle, Geneva; NRS—Naturhistoriska Riksmuseet, Stockholm; NTM—Northern Territory Museum, Australia; QM—Queensland Museum, Australia; RMNH—Rijksmuseum van Naturlijke Historie, Leiden, The Netherlands; ZMA—Zoologisch Museum, Amsterdam, The Netherlands.

Genus *Anilocra* Leach, 1818

Anilocra alloceraea Koelbel

Restricted synonymy.—*Anilocra alloceraea.*—Bruce, 1987a:93, figs. 4, 5.

Material examined.—2 ♀♀ (ovig 17.5, nonovig 24.5), Singapore, 26 Aug 1967, coll. Chun (USNM 233273). ♀, Sero, near Karang, Indonesia, 23 Mar 1908, on *Stolopherus* (ZMA).

Remarks.—Distribution here extended westwards to Singapore.

Anilocra amboinensis Schiödte & Meinert

Fig. 1

Anilocra amboinensis.—Schiödte & Meinert, 1881:116, pl. 8, fig. 9.

Anilocra amboinensis.—Nierstrasz, 1915:87; 1931:129.—Monod, 1976:856, figs. 5–7.—Trilles, 1979:247.

Material examined.—Holotype, ♀ (30.0 mm), Amboina, Moukkon, coll. E. W. Ludeking (RMNH 17). 2 ♀♀ (ovig 29.0, 27.5), Gane (Gillola) Island, 1 Dec 1909 (USNM 233274); ♀ (ovig 27.0), Dowarra Island, 2 Dec 1909 (USNM 233275); ♀ (ovig 31.5), Uki, Bouri Island, N.I., Indonesia, 9 Dec 1909 (USNM 233276); ♀ (ovig 29.0), Limbe Strait, Celebes, Indonesia, 11 Nov 1909 (USNM 233277); all coll. U.S. Bureau of Fisheries *Albatross* Expedition 1907–9. ♀ (ovig 28.5), Saparna Island, SE tip of Haria Bay, Indonesia, 03°35'S, 128°36'E, 5 Mar 1974, 1.5–5.0 m depth (USNM 231186). 2 ♀♀ (ovig 25.5, 22.5), Tandjung, Honimau, northeast of Ambon Island, Indonesia, 03°30.5'S, 128°20.0'E, 16 Mar 1974 (USNM 231185). ♀, west coast of Binongha, Indonesia, 1–3 Nov 1899, Siboga Expedition Sta 220, on *Ballistes* sp. (ZMA).

Remarks.—Widely distributed in Indonesia and the Philippines. This large species is easily recognized by its wide body, broadly rounded pleotelson, and uropods that are usually concealed in dorsal view.

The similarity between this species and the holotype of *Anilocra marginata* Miers suggests that further study and redescription may show them to be synonymous.

Hosts.—Monod (1976) recorded *Naso thynnoides* (F. Acanthuridae) as host; also recorded from *Ballistes* sp. (F. Balistidae).

Anilocra apogonae Bruce

Anilocra apogonae Bruce, 1987a:112, figs. 22, 23.

Material.—♀ (ovig 13.0), off Port Moresby, Papua New Guinea, 20 Jun 1970, coll. B. B. Collette (Sta 1527) (USNM 233272).

Remarks.—The range is here extended to southern Papua New Guinea. Examination of material in the USNM shows that *Anilocra* sp. recorded by Monod (1976) is not

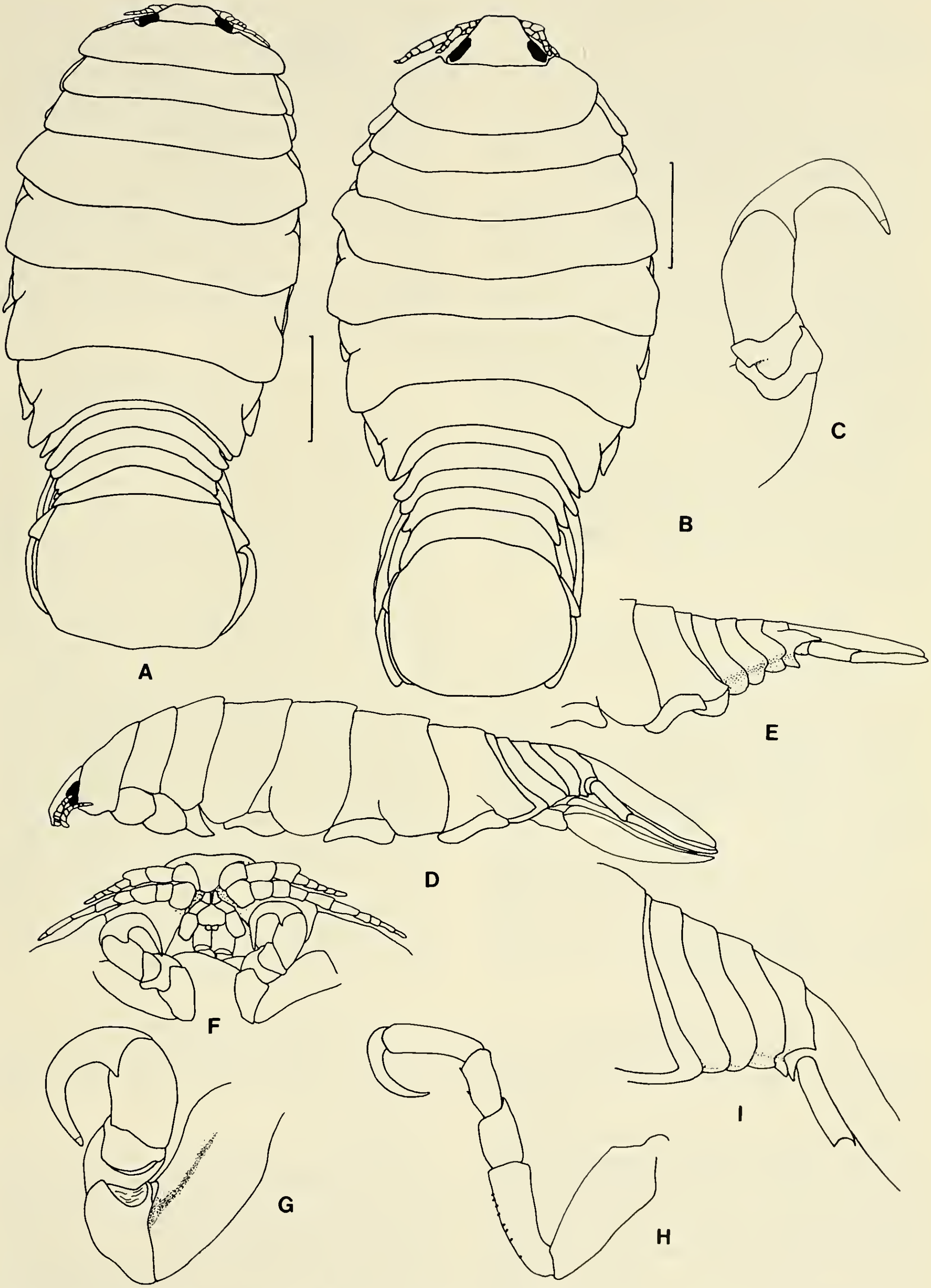

Fig. 1. *Anilocra amboinensis,* A, D, F–I, holotype, remainder Celebes, USNM 233277. A, Dorsal view; B, Dorsal view; C, Pereopod 1; D, Lateral view; E, Pleon, lateral view; F, Frons; G, Pereopod 1; H, Pereopod 7; I, Pleon, lateral view. Scale lines represent 5.0 mm.

conspecific, contrary to the synonymy given by Bruce (1987a).

Anilocra capensis Leach

Restricted synonymy.—*Anilocra capensis.*—Trilles, 1975:304, pl. 1, fig. 1.

Anilocra acuminata.—Haller, 1880:389, 393, pl. 18, figs. 18, 19 (new synonymy).

Remarks.—Examination of the two syntypes of *A. acuminata* from Mauritius (MHNG 13) reveals no difference from the type material of *Anilocra capensis,* and the species is here placed in synonymy with *Anilocra capensis.*

Trilles (1975) cites records from Indonesia, but the majority of records are from southern Europe, West Africa and southern Africa. Mauritius falls well within the distribution of this species.

Anilocra cavicauda Richardson

Restricted synonymy.—*Anilocra cavicauda.*—Bruce, 1987a:95, fig. 6.

Material examined.—2 ♀♀ (ovig 36.0, 32.0), Cataingua Bay, Philippines, 17 Apr 1908, coll. U.S. Bureau of Fisheries *Albatross* Philippine Expedition, 1907–9 (USNM 233271).

Remarks.—The specimens recorded here were not reported on by Richardson (1910), but agree well with the figures of the holotype given by Bruce (1987a). There exist no host records for this species.

Anilocra dimidiata Bleeker

Restricted synonymy.—*Anilocra dimidiata.*—Bruce, 1987a:99, figs. 9–11; 1988.

Material examined.—2 ♀♀ (non-ovig 19.0, 19.5), Tsiuipaika Bay, Madagascar, ca. 1959, coll. A. Crosnier (USNM 109233). 4 ♀♀ (ovig 23.5, 21.5, 20.5, 19.5), Galle Harbour, Sri Lanka, 06°01.0′N, 80°14.2′E, 26 May 1970, 2–5 m depth, coll. T. Iwamotu (USNM 233278). ♀ (ovig 22.0), Palk Bay, 6 Feb 1902, coll. Herdman (BMNH 1928.12.1:893–894). 2 ♀♀ (ovig 25.5, 26.5), Tana Keke Island, Philippines, 21 Dec 1909, coll. U.S. Bureau of Fisheries *Albatross* Philippines Expedition, 1907–9 (USNM 233279). ♀ (ovig 19.0), Salayer, 26 Oct 1899, Siboga Expedition Sta 213 (ZMA).

Remarks.—Previously recorded from the Indo-Malaysian area, Australia (Bruce 1987a) and Hong Kong (Bruce 1988), the range is here extended, and now includes the tropical western Indian Ocean, Sri Lanka and Philippines.

Anilocra gigantea (Herklots)

Restricted synonymy.—*Anilocra gigantea.*—Trilles, 1972:9, figs. 1, 2, photos. 7, 8.

Material examined.—♀ (ovig 72.0), ♂ (37.0), off Suva reefs, Suva, Fiji, 30 Aug 1980, off gills of *Epinephelus* sp., depth 240 m (QM W13118); ♀ (non-ovig 59.0), ♂ (30.0), off Suva reefs, Suva, Fiji, 17 Sep 1980, off gills of *Pristipomoides flavipinnis* (QM W14305); both coll. Institute of Marine Resources, University of the South Pacific.

Remarks.—This is the second record from the Pacific, having been previously recorded from New Caledonia (Trilles 1972). *Epinephelus* (F. Serranidae) and *Pristipomoides flavipinnis* (F. Lutjanidae) are new host records for *Anilocra gigantea.* Trilles (1972) recorded the species from another deep water lutjanid *Etelis carbunculus.* All records of position on the host are from the gills, a position unique in the genus.

Anilocra koolanae Bruce
Fig. 2H

Anilocra koolanae Bruce, 1987a:112, figs. 20, 22.

Material examined.—2 ♀♀ (ovig 32.0, 25.0), Pulan Tikos Pulau Pari Group, Pulau Seribu, Indonesia, 05°51.0′S, 100°34.0′E, 6 Apr 1974, (USNM 231182).

Remarks.—Known previously from the holotype, this specimen extends the distribution to southern Indonesia.

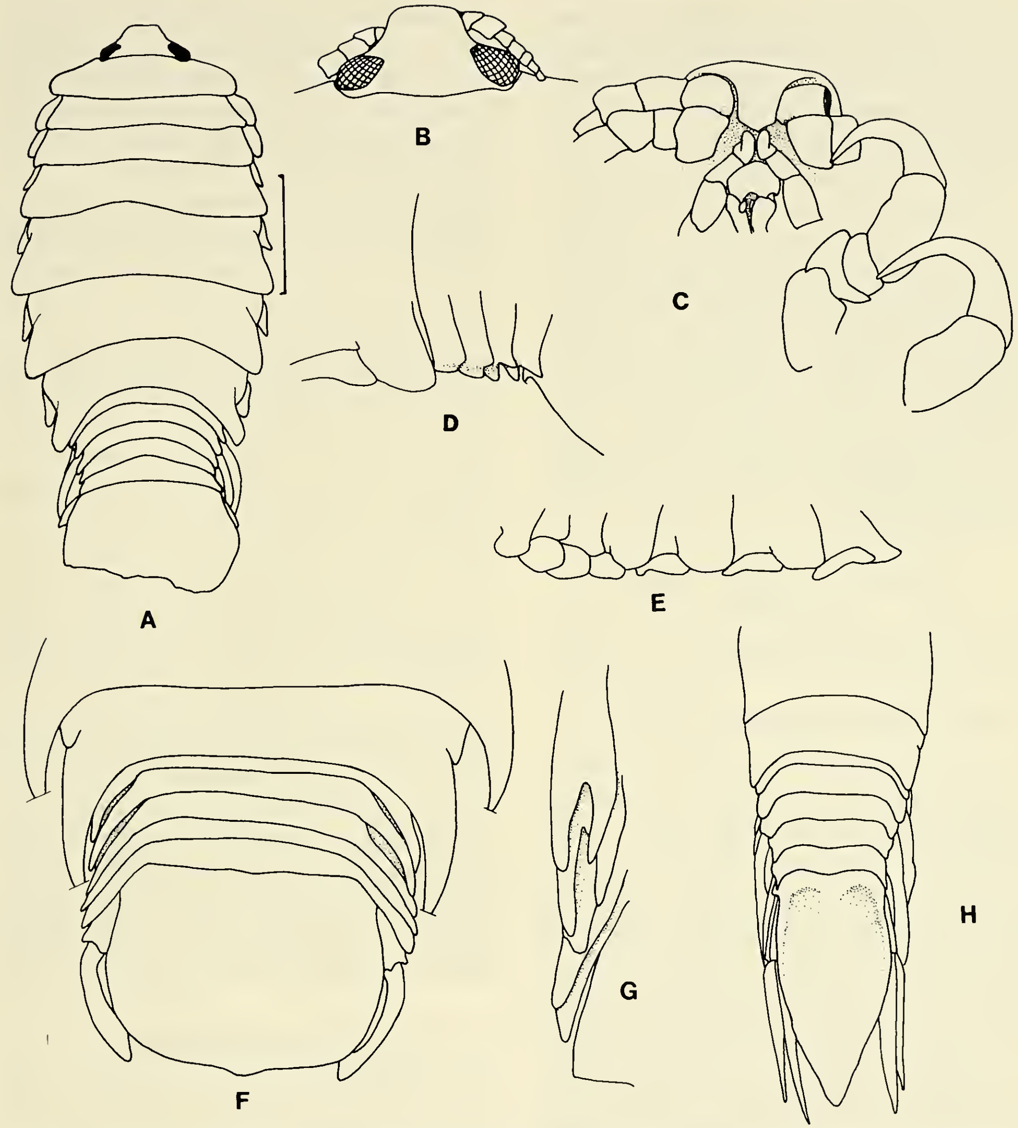

Fig. 2. *Anilocra marginata,* ? Syntype 23.0 mm. A, Dorsal view; B, Cephalon; C, Frons, and pereopods 1, 2; D, Pleonites, detail; E, Pereon lateral view. *Creniola breviceps*: F, Pleon, dorsal view, USNM 231178; G, Pleonites, ventral view, USNM 231177. *Anilocra koolane,* USNM 231182: H, Pleon. Scale line represents 5.0 mm.

Anilocra longicauda Schiödte & Meinert

Restricted synonymy.—*Anilocra longicauda.*—Bruce, 1987a:117, figs. 24, 25.

Material examined.—♀ (ovig 39.0), Ragay Gulf, Pasacao, Philippines, 9 Mar 1909, coll. U.S. Bureau of Fisheries *Albatross* Expedition 1907–9 (USNM 40999). ♀ (non-ovig 27.0), Maribuyoc Bay, Bohol Island, Philippines, 26 Mar 1909, coll. U.S. Bureau of Fisheries *Albatross* Expedition 1907–9 (USNM 40997).

Remarks.—Recently redescribed by Bruce (1987a), the present material falls within the known distribution of the species. The specimens differ from the lectotype and Australian material described by Bruce (1987a) in having the antennae extending to the posterior of pereonite 1.

Anilocra prionuri Williams & Williams, 1981, is very similar to this species, and can best be separated by having a distinctly shorter pleotelson which is exceeded by the uropod rami, and a bulbous rather than triangular-digitiform rostral fold. Japanese material has longer antennae (Williams & Williams 1986) than Australian (Bruce 1987a), but antennal length varies, and in view of Philippine specimens with longer antennae, this difference cannot be regarded as species specific.

Anilocra marginata (Bleeker)
Fig. 2A–E

Cymothoa marginata Bleeker, 1857:21, 36, pl. 2, fig. 14.
Anilocra marginata Miers, 1880:462.

Material examined.—♀♀ (23.0, 14.5), Malaysia, presumed syntypes of *Cymothoa marginata* Bleeker (BMNH 80.6).

Remarks.—This specimen has a label "*Cymothoa marginata* Blekr." Most of Bleeker's (1857) type specimens are held by the Rijksmuseum van Natuurlijke Historie in Leiden, but a search of the collections there did not locate material of *Cymothoa marginata.* Miers (1880) remarked that he was examining Bleeker's material. In view of the label identifying it as *Cymothoa marginata* and the correspondence of Bleeker's figure to the present material, it seems probable that these are the syntypes of that species.

The exact distribution of this species is unknown, but it is likely to be Indonesia, where all of Bleeker's material came from.

Anilocra morsicata Bruce

Anilocra morsicata Bruce, 1987a:122, figs. 29, 30.

Material examined.—3 ♀♀ (non-ovig 16.8, 22.1, 23.4), 1 immature (13.3), 20 km east of Cape Moreton, southeastern Queensland, 16 Aug 1987, from *Astronesthes lucifer* in stomach of yellowfin tuna, coll. N. L. Bruce and D. Parsons (QM W14305).

Remarks.—The specimens agree with the description given by Bruce (1987a). *Astronesthes lucifer* is a deepwater bentho-pelagic fish (H. Masuda et al. 1984) and as well as being the first host record for *A. morsicata,* it is the first time a mesopelagic host has been recorded for *Anilocra.* The position on the host was dorsal, anterior to the dorsal fin.

Hosts.—*Astronesthes lucifer* (F. Astronesthidae).

Anilocra pomacentri Bruce

Anilocra pomacentri Bruce, 1987a:124, figs. 31, 32.

Material examined.—♀ (ovig 10.6), Ashmore Reef, Western Australia, 12°15.0′S, 122°59.0′E, 22 Jul 1986, 10–12 m depth, coll. L. Vail (NTM Cr 004512).

Remarks.—The specimen was collected at a fish poison station and was not in association with its host. The range is here extended from the Great Barrier Reef, Queensland, to Western Australia.

Anilocra rhodotaenia Bleeker

Restricted synonymy.—*Anilocra rhodotaenia.*—Trilles, 1979:249, pl. 7, fig. 1.

Remarks.—The status of this species is uncertain. Bleeker (1857) examined five specimens, but I have not been able to locate that material. Bleeker's description does not allow the identity of his species to be established although it does appear to belong to the *A. leptosoma-A. dimidiata* group of species. Trilles (1979) gave a figure of *A. rhodotaenia,* and although his photograph does not allow for specific assessment, the animal figured appears similar to *A. nemip-*

teri Bruce (Trilles' (1979) material was not available for examination).

All museum material identified as *A. rhodotaenia* that I have examined has proved to be conspecific with *A. amboinensis.*

Without recourse to type material the identity of *Anilocra rhodotaenia* cannot be established, and the species should be regarded as *species inquirenda.*

Genus *Creniola* Bruce, 1987

Creniola breviceps (Schiödte & Meinert)

Fig. 2F–G

Restricted synonymy.—Creniola breviceps.—Bruce, 1987c:391, 401, fig. 32.

Material examined.—All Oahu, Hawaii. ♀ (ovig 20.0), Honauma Bay, 14 Apr 1961, on caudal fin of *Priacanthus* sp., coll. Nick Ferris (USNM 231178). ♀ (ovig 21.5), off Diamond Head, 5 Sep 1959, on pectoral fin of *Acanthurus dussumieri,* coll. A. Lewis and Sam Kaolulu (USNM 231177). ♀ (ovig 19.5), Pupukea, 14 May 1961, coll. E. and L. B. Trott (USNM 232014). ♀ (ovig 19.0), ♂ (8.0) between Diamond Head and Koko Head, 7 Nov 1959, on *Ctenochus otrigosus,* 19–25 m, coll. Sam Kaolulu and A. Lewis (USNM 232013). ♀ (ovig 19.0), Cocoanut Island, Kaneohe Bay, 13 Aug 1959, on caudal fin of *Acanthurus dussumieri,* coll. A. Lewis (USNM 232011).

Remarks.—Apparently a Hawaiian endemic, all specimens having been collected from Oahu. Host identity has not been recorded previously for this species.

Hosts.—*Priacanthus* sp. (F. Priacanthidae), *Acanthurus dussumieri,* and *Ctenochaetus otrigosus* (F. Acanthuridae).

Genus *Nerocila* Leach, 1818

Nerocila congener Miers

Restricted synonymy.—Nerocila congener.—Bruce, 1987c:366, figs. 8, 9.

Material examined.—♀ (ovig 33.5), Cebu market, Cebu, Indonesia, 3 Sep 1909, U.S. Bureau of Fisheries *Albatross* Expedition 1907–9 (USNM 232073).

Remarks.—Widely distributed, recorded from Indonesia, Philippines and Australia. No host has been recorded for this species.

Nerocila depressa Milne Edwards

Fig. 3

Nerocila depressa Milne Edwards, 1840:254, pl. 31, fig. 17–21.—White, 1847:108.—Schiödte & Meinert, 1881:15, pl. 1, figs. 10–11.—Stebbing, 1893:351.—Lanchester, 1900:265, pl. XII, fig. 5.—Thielemann, 1910:33.—Nierstrasz, 1931:124.—Trilles, 1975:318, pl. II, fig. 13; 1979: 251.—Bruce, 1987c:404; 1988: in press.

Nerocila dolichostylis Koelbel, 1879:411, pl. II, fig. 3a–b.—Bruce, 1987c:404.

Nerocila pigmentata Bal and Joshi, 1959: 565, pl. 2, figs. 6–10.—Bruce, 1987c:406.

Nerocila pigmenta.—Joshi and Bal, 1960: 446 (? lapsus).

Not *Nerocila pigmentata.*—Parimala, 1984: 180–181, fig. 1 (=*Nerocila* sp.?).

Material examined.—♀ (ovig 11.5), Gulf of Siam, 3 Jul 1923, H.S. 32, fish host, Pla Sai Tan (=*Cyclocheilichthys apogon* Cuvier & Valenciennes) coll. H. Smith (USNM 232075). ♀ (ovig 12.0), Chao Phya River, Thailand, 21 May 1925, side of *Engraulis* sp., 8.5 cm long, (USNM 232074). ♀ (ovig 11.0), Bagan api api, Sumatra, 1912, on *Coilia dussumieri,* coll. Herbst (ZMA).

Remarks.—Two characters readily distinguish this species from the similar *N. loveni*: the coxae and posterolateral corners of the pleonites are posteriorly directed and are not bent dorsally. The species has been recorded from the northern Indian and Pacific oceans with a probable range from India eastwards to Hong Kong.

Parimala (1984) gives a photograph of a species that is of uncertain identity, but clearly not *N. depressa.*

Hosts.—*Coila dussumieri, Engraulis* sp., both Engraulididae; *Cyclocheilichthyes apo-*

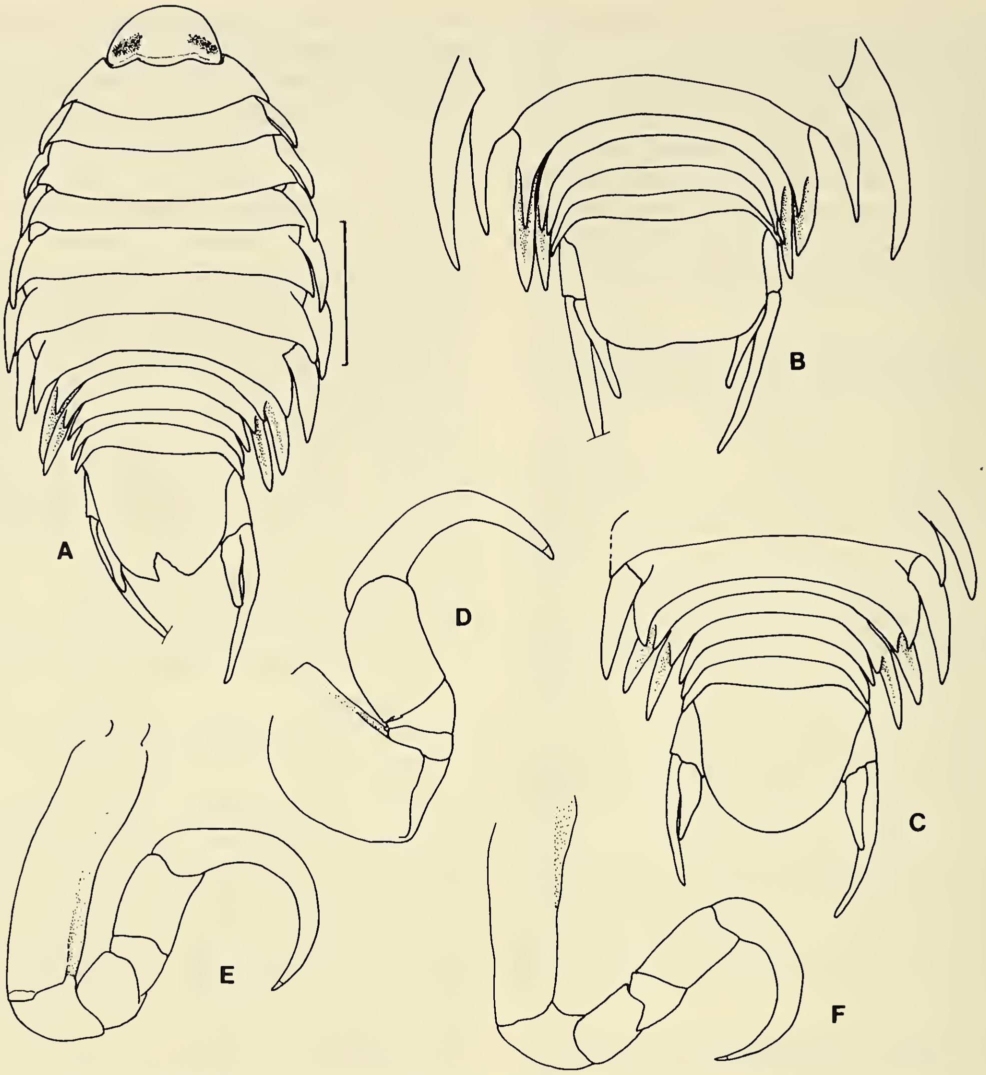

Fig. 3. *Nerocila depressa,* A, D–F, female, Gulf of Siam, USNM 232075. A, Dorsal view; B, Pleon, female, Thailand, USNM 107850; C, Pleon, female, Paknam, USNM 232074; D, Pereopod 1; E, Perepod 6; F, Perepod 7. Scale line represents 3.0 mm.

gon (Cyprinidae). Bal & Joshi (1959) recorded the host *Opisthopterus turtoor* (=*O. tardoore*); Bruce (1988) recorded *Sardinella fimbriata* (F. Clupeidae).

Nerocila exocoeti Pillai
Fig. 4

Nerocila exocoeti Pillai, 1954:12.—Kurochkin, 1980:289.—Bruce, 1987c:404.

Material examined.—♀ (ovig 24.0), Keelung, Taiwan, 6 Jun 1957, on *Parexocoetus brachypterus,* coll. H. Teng (USNM 227097). ♀ (ovig 20.0), Papua New Guinea, 08°00′S, 144°32′E, 27 Sep 1976, from *Scomberomorus multiradiatus* gut contents (USNM 233280). ♀ (ovig 22.5), Poeloe Nako, ? Indonesia, no date, coll. Kleiveg de Zwaan (ZMA).

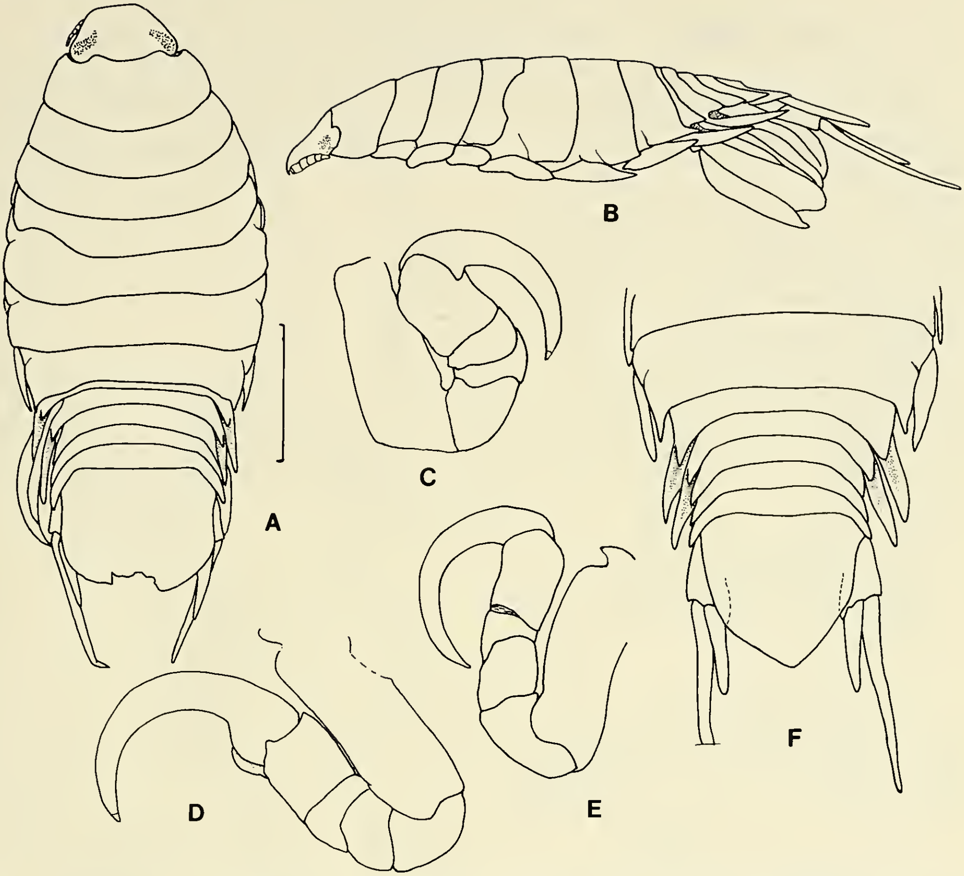

Fig. 4. *Nerocila exocoeti,* A–E, female, Taiwan, USNM 227079. A, Dorsal view; B, Lateral view; C, Pereopod 1; D, Pereopod 6; E, Pereopod 7; F, Pleon, female, Papua New Guinea, USNM 233280. Scale line represents 3.0 mm.

Remarks.—No figures have been published for this inadequately described and poorly known species, but as the host has been identified as *Parexocoetus brachypterus,* the assumption is made here that these specimens are *N. exocoeti. Nerocila exocoeti* belongs to a group of species characterized by short coxae and lack of, or reduced posterolateral pereonite extensions. *Nerocila trichiura,* parasitic on flying fishes of the genera *Exocoetus* and *Cypselurus,* has the coxae and pereonite posterolateral extensions bluntly rounded.

Distribution is here extended from southern India to Papua New Guinea, Indonesia, and Taiwan.

Nerocila kisra Bowman & Tareen

Nerocila kisra Bowman & Tareen, 1983:8, figs. 6–8.—Bruce, 1987c:404.

Material examined.—6 ♀♀, Kuwait, on *Helotes* and *Therapon* (BMNH 1982:84–86).

Remarks.—This material agrees well with the original description.

Nerocila loveni Bovallius
Fig. 5

Nerocila lovéni Bovallius, 1887:6, pl. 1, figs. 13–17, pl. 2, figs. 18–21.—Stebbing, 1893: 352, pl. 15.

Nerocila loveni.—Nierstrasz, 1915:73; 1931:

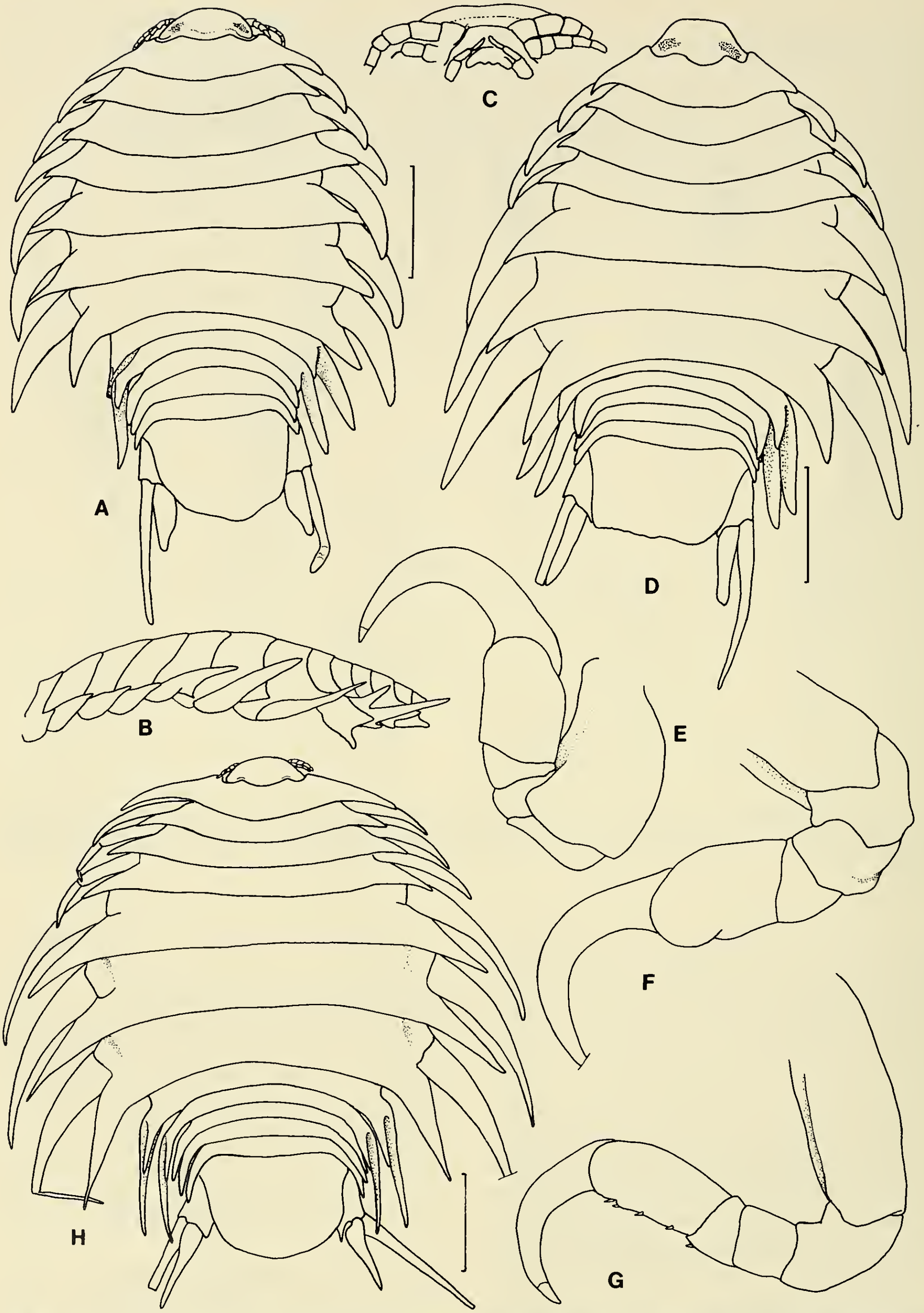

Fig. 5. *Nerocila loveni,* C–G, female, Gulf of Siam, USNM 232077. A, Female, Singapore, USNM 232077; B, Lateral view of pereon and pleon, USNM 232076; C, Frons; D, Dorsal view; E, Perepod 1; F, Pereopod 6; G, Pereopod 7; H, Female, Sarawak, BMNH 1986: 421. Scale lines repreent 3.0 mm.

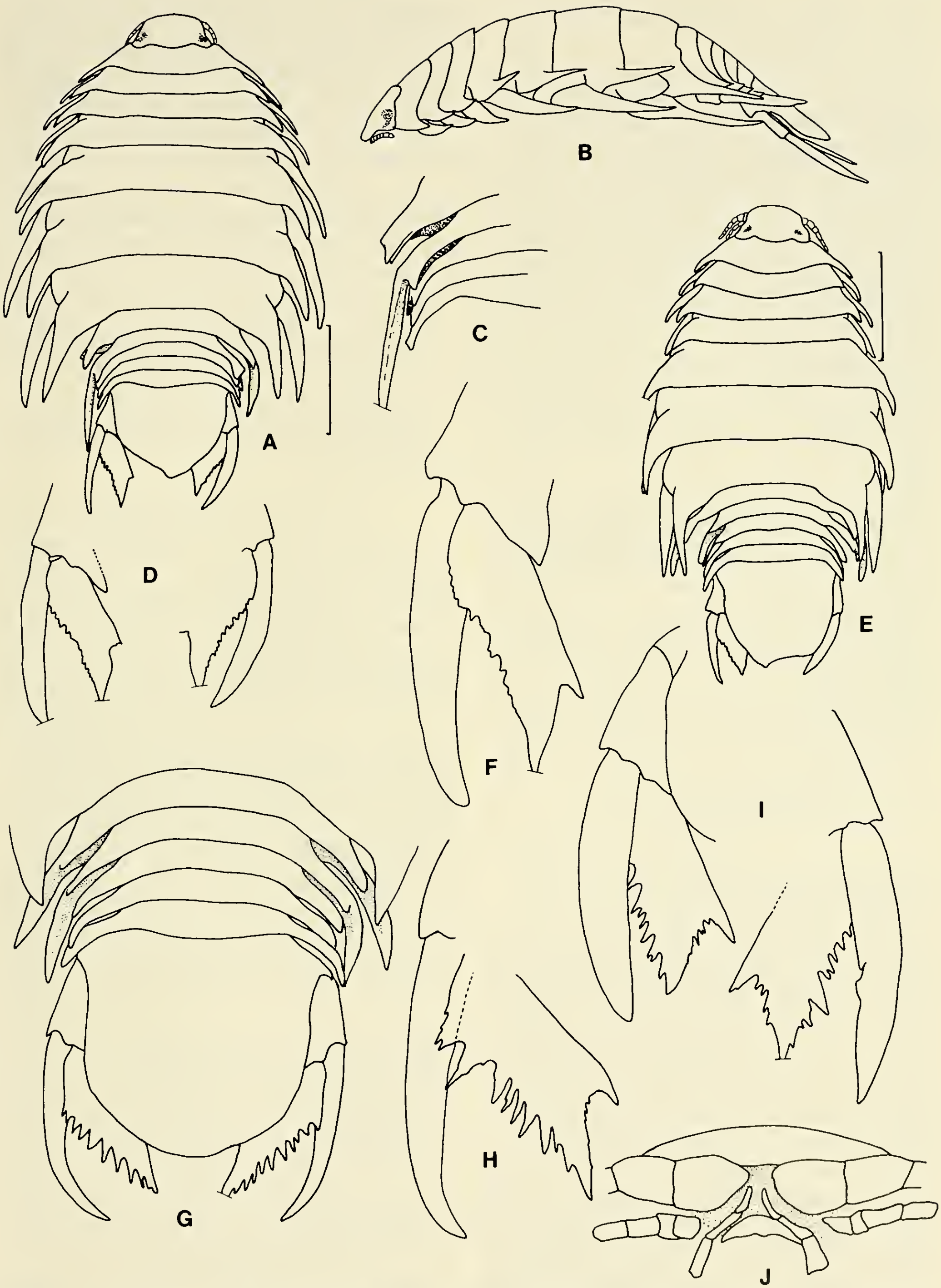

Fig. 6. *Nerocila serra,* A–F, female syntype, NRS Is. 4974. A, Dorsal view; B, Lateral view; C, Left pleonites; D, Left and right uropods; E, female, Jaffna Lagoon, BMNH 1980: 141.1; F, Uropod, female, Jaffna Lagoon. *Nerocila sigani*: G, Pleon, female, Taiwan, USNM 232017; H, Uropod, female, Penang, USNM 232015; J, Frons, USNM 232017. *Nerocila monodi*: I, Left and right uropods, female, Trobriand Islands, USNM 232071. Scale lines represent 5.0 mm.

124.—Trilles, 1979:251, pl. 7, fig. 2.—Bruce, 1987c:404.

Material examined.—♀ (non-ovig 13.5), Singapore, 20 Feb 1908, no host, coll. Chun (USNM 232076). ♀ (ovig 13.5), off Tachalom, Gulf of Siam, 20 Jul 1923, from pla pan pak moo (host presumably), coll. H. Smith (USNM 232077). ♀ (ovig 9.5), Lem Nam Point, southeast Lem Nam Peninsula, Gulf of Siam, 12°02.9′N, 102°35.6′E, 29 Oct 1957, GVF Sta 29 (USNM 107850). 13 ♀♀ (8 ovig, 5 non-ovig, 11–17.5), Borneo, coll. Hose (BMNH 1895:7:2:1–10). ♀ (ovig 15.0), Sarawak, pre-1895, on caudal peduncle of *Leiognathus* sp., coll. Hose (BMNH 1986:421).

Remarks.—This species can be distinguished from *N. depressa* by having the coxae and pereonite posterolateral extensions bent dorsally, and expressed laterally rather than posteriorly.

Distributed in the northern central Indo-Pacific region: Singapore, Thailand, Borneo and Sarawak.

Hosts.—*Leiognathus* sp. (Leiognathidae).

Nerocila monodi Hale
Fig. 6I

Restricted synonymy.—*Nerocila monodi.*—Bruce, 1987c:384, figs. 20–22.

Material examined.—♀ (ovig 22.0), Tana Keke, 21 Dec 1909, dynamite station (100% linen tag 13592), U.S. Bureau of Fisheries *Albatross* Philippines Expedition, 1907–9 (USNM 232072). ♀ (ovig 24.0), Labuandata Bay, Gulf of Bori, Philippine Islands, 18 Dec 1909, dynamite station, coll. U.S. Bureau of Fisheries *Albatross* Philippines Expedition, 1907–9 (USNM 232070). ♀ (ovig 18.5), Babelthvap Island, Karamado Bay, Palau, 7°30.01′N, 134°31.03′E, 7 Sep 1955, coll. H. A. Fehlmann, S. Pierce and R. Harry, George Vanderbilt Foundation (USNM 233291). ♀ (ovig 14.0), Kiriwina Inlet, Trobriand Islands, Papua New Guinea, 6 Jun 1970, BBC Sta 1506, coll. B. B. Collette (USNM 232071). ♀ (ovig 17.5), as previous, and beach seine (USNM 232069). ♀ (25.0), ♂ (15.0), Port Moresby, Papua New Guinea, no date or host, coll. N. T. Talbot (BMNH).

Remarks.—A common species in northern and eastern Australia (Bruce 1987c), material recorded here shows the species to be widespread in the tropical western Pacific extending northwards to the Philippines.

Nerocila orbignyi (Guérin-Menèville)

Restricted synonymy.—*Nerocila orbignyi.*—Bruce, 1987c:374, figs. 12–17.

Remarks.—One specimen of this species was recorded from Eilat, Red Sea, Israel, by Bruce (1987c).

Nerocila phaiopleura Bleeker

Restricted synonymy.—*Nerocila phaiopleura.*—Bruce, 1987c:384, figs. 18, 19.

Material examined.—4 ♀♀ (ovig 21.0, 19.5, 19.0, 18.5), Kaneda Bay, Tokyo Bay, Japan, 3 Feb 1978, on *Sardinops melanosticta,* coll. I. Mitani (USNM 184998). 12 aegathoids (18.0–19.5), as previous, but on *Engraulis japonica* (USNM 184999). 4 ♀♀ (ovig 18.5, 18.5, 13.5, non-ovig 15.0), Chantabru River, Thailand, 7 Aug 1927, coll. H. M. Smith (USNM 232068). 2 ♀♀ (ovig 22.0, 20.5), Lem Sing, Thailand, 18 Nov 1933, sides of *Chirocentrus,* coll. H. M. Smith (USNM 232067). ♀ (ovig 21.5), Pak Poon, Thailand, 20 Oct 1923, on clupeid, HS35 (USNM 233282). 2 ♀♀ (ovig 22.0, 18.5), Pak Nakara, 20 Oct 1923, side of *Engraulis,* H. S. '34 (USNM 233284). 3 ♀♀ (ovig 20.0, 19.0, 18.5), Paknam Chao Phya, Thailand, 17 Feb 1928, on *Sardinella fimbriata* (label reports 100% infestation on pectoral fin or caudal peduncle), coll. H. Smith (USNM 233283). ♀ (ovig 18.0), Gulf of Siam, on *Clupea,* coll. H. Smith (USNM 233285). ♀ (ovig 19.5), off Paknam, Gulf of Siam, 11 Aug 1923, on side of *Harengula* (H.S. 30) coll. H. Smith (USNM 233281). 1 ♀ (ovig 17.0), Singapore, 20 Feb 1968, coll. Elwin (USNM 232066). 2 ♀♀ (ovig 19.0, 17.0), Kakinada, India, 29 Apr 1977, on *Illisha melastoma* (BMNH). ♀ (ovig 26.0), Tamil Nadu, Bay of Bengal, circa 1982, on *Formio niger* (BMNH 1983:54:1).

Remarks.—A common Indo-Pacific species, not previously recorded from Japan. All host species recorded here are new records.

Hosts.—*Sardinops melanosticta, Sardinella fimbriata, Illisha melastoma* (F. Clupeidae), *Engraulis japonica* (F. Engraulididae), *Parastromateus niger* (F. Carangidae). Previous host records given by Bowman & Tareen (1983) and Bruce (1987c).

Nerocila serra Schiödte & Meinert
Fig. 6A–F

Restricted synonymy.—*Nerocila serra.*—Bruce, 1987c:390.

Material examined.—♀ syntype (21.0), Bangka Str. Salmin (NHR Is. 4974). 2 ♀♀ (ovig 19.0, 23.5), Chantabun River, Thailand, 7 Aug 1927, coll. H. M. Smith (USNM 232020). ♀ (non-ovig 20.5), Jaffna Lagoon, Sri Lanka, circa 1979, coll. D. Thiagarajah (BMNH 1980:145:1).

Remarks.—This species is poorly known, and has been considered a junior synonym of *N. trivittata* Milne Edwards by Trilles (1979). This view has not been supported by Bowman & Tareen (1983) or Bruce (1987c). Bowman & Tareen (1983) described three new species of *Nerocila* with serrate uropods, and prior records of *N. serra* and *N. trivittata* can no longer be accepted as accurate.

The exact distribution of this species is uncertain. Reliable records are one from Australia (Bruce 1987c), the original record by Schiödte & Meinert (1881), and the material recorded here; the distribution appears to be Indo-Malaysian.

Nerocila sigani Bowman & Tareen
Fig. 6G, H, J

Nerocila (*Nerocila*) *sigani* Bowman & Tareen, 1983:12, fig. 9.
Nerocila (*Nerocila*) *arres* Bowman & Tareen, 1983:12, figs. 10–12 (new synonymy).
Nerocila sigani.—Bruce, 1987c:406.

Material examined.—2 ♀♀ (non-ovig), Eilat, Israel, 585, Paperna (USNM 232019). ♀ (ovig 14.5), Maintirano, west coast of Madagascar, no date, on *Sciaenia dussumieri*, coll. A. Crosnier (USNM 109239). ♀ (ca. 22.0), ♂ (15.0), Richards Bay, South Africa, date?, on *Argyrosomus hololepidotus* (BMNH 1979:285:2). 6 ♀♀ (ovig and non-ovig 19.5–24.0), 4 ♂♂, Durban Bay, South Africa, date?, on *Pomadasys* sp. (BMNH 1979:224:10). 1 ♀ (14.0), Hikkaduwa, Sri Lanka, 13 Feb 1970, 15 m depth, poison station, coll. C. Koenig (USNM 232010). ♀ (ovig 18.0), Tamil Nadu, India, Bay of Bengal, circa 1980, on *Formio niger,* coll. S. K. Baru (BMNH 1983:51:1). 1 ♀ (ovig 17.0), southeast of Pu Kendi Island, southwest Penang, Malaysia, 05°12′N, 100°11′E, 6 May 1969, (Sta 6975, 3818), coll. Schwartz (USNM 232015). ♀ (ovig 23.0), Keelung, Taiwan, 4 Aug 1957, on *Argyrosoma macrocephalus* (Tang), coll. H. T. Teng (USNM 232016). ♀ (ovig 25.5), Keelung, Taiwan, 1 Nov 1956, on *Argyrosoma nibe* (Jordan & Thompson), base of caudal fin, coll. H. C. Yang (USNM 232017).

Remarks.—Bowman & Tareen (1983) described three species of *Nerocila,* all with serrate uropodal endopods. One, *N. kisra,* they placed in the subgenus *Emphylia,* the remaining two in *Nerocila* (*Nerocila*). Bruce (1987c) placed all three species in a redefined "*Emphylia* group."

Nerocila sigani, described from a single specimen, and *N. arres* were separated by: 1, presence or absence of a caudomedial lobe; 2, presence or absence of dactylus nodules; 3, antennule articles 1 and 2 being distinct or partially fused; 4, uropod exopod linear or curved; 5, deeper uropod serrations in *N. arres* than in *N. sigani.*

Of these character states, antennule articles often show varying degrees of fusion (as in *Nerocila monodi*), and uropod serration is similarly variable. The presence or absence of a caudomedial lobe on the pleotelson is a similarly unreliable character, and is frequently found to be absent from species such as *N. orbignyi* and *N. monodi* that "normally" have it. This leaves only the presence or absence of dactylus nodules, which can also vary in prominence, to separate the two species.

In the material examined here there is a specimen with a rounded pleotelson (Taiwan, USNM 232017 on *A. nibe*) but with uropods the same as those of *N. arres*: a specimen from Eilat with linear uropodal exopods (=*N. sigani*),but with a distinct caudomedial lobe (=*N. arres*). In view of the variable morphology of many *Nerocila* species, and the specimens examined here that are intermediate between the two species, it is concluded that *Nerocila sigani,* which has page precedence, is the senior synonym to *Nerocila arres.*

Nerocila sigani is now known from the western Indian Ocean: Arabian Gulf, Red Sea, Madagascar, and South Africa. Other records are from the northern Indo-Pacific: Sri Lanka, Bay of Bengal, Penang, and Taiwan. It is probable that records of *N. serra* from South Africa (Barnard 1925, Kensley 1978) are actually *N. sigani.*

Hosts.—New records: *Sciaenia dussumieri, Argyrosoma hololepidotus, A. macrocephalus, A. nibe* (F. Sciaenidae); *Parastromateus niger* (F. Carangidae); *Pomadasys* sp. (F. Pomadasydae). Bowman & Tareen (1983) recorded: *Siganus orami* (F. Siganidae); *Epinephilus tauvina* (F. Epinephilidae); *Acanthopagrus latus* (F. Sparidae); *Nemipterus japonicus, N. tolu* (F. Nemipteridae).

Nerocila sundaica Bleeker

Restricted synonymy.—Nerocila sundaica.—Bowman, 1978:35, figs. 1–7.—Trilles, 1979:252.

Material examined.—♀ (ovig 16.5), Paknam Chao, Thailand, Phya, pong pang net, 16 Aug 1924 (H.S. 27) (USNM 233286). ♀ (ovig 23.5), Lem Sing, Thailand, 12 Jan 1924 (H.S. 26) on throat of *Sciaena* (USNM 233287). ♀ (ovig 22.5), off Menam, Gulf of Siam, 12 Jul 1923, on *Eleutheronema* (H.S. 36), coll. H. M. Smith (USNM 233288). ♀ (ovig 18.5), as previous, but 12 Jan 1924 (H.S. 29) (USNM 233289). ♀ (ovig 23.0), Tachalon, Thailand, 26 Jul 1923, on *Mugil* sp. (H. S. 28) (USNM 233290).

Remarks.—Redescribed in great detail by Bowman (1978), this is one of the most common Indo-Pacific species of *Nerocila,* but has only been recorded from the northern Indian and Pacific oceans.

Hosts.—There exist few records of the hosts used by *N. sundaica.* Here recorded from *Sciaena* sp. (F. Sciaenidae), *Eleutheronema* sp. (F. Polynemidae) and *Mugil* sp. (F. Mugilidae).

Nerocila trichiura (Miers)
Fig. 7

Restricted synonymy.—Nerocila trichiura.—Trilles, 1979, pl. 2, fig. 10; 1976; 621.—Kurochkin, 1980:289.—Bruce, 1987c:406.

Material.—Holotype, ♀ (27.0), Mauritius, pres. R. Templeton, BMNH 186:104. ♀ (22.0), south of India, 10°20′S, 70°00′E, 7 Jun 1963, on *Exocoetus volitans,* base of pectoral fin, coll. A. Brown (USNM 128555). (Also examined, ♀ (27.0 mm), Dakar Harbour, Senegal, 1 Sep 1964, coll. Geronimo, USNM 119490.)

Remarks.—A widespread species occurring in the Atlantic, Pacific and Indian oceans. At present it does not seem possible to separate *N. excisa* Richardson, 1901, from *N. trichiura,* both having similar coxae, pereonal and pleonal morphology. Unfortunately the holotype of *Nerocila excisa* is in poor condition with the pleotelson torn and the uropods missing (Bruce 1987c, fig. 34F). It seems probable that the two species are conspecific, there being no discernable differences between the holotype of *N. excisa* and specimens of *N. trichiura.*

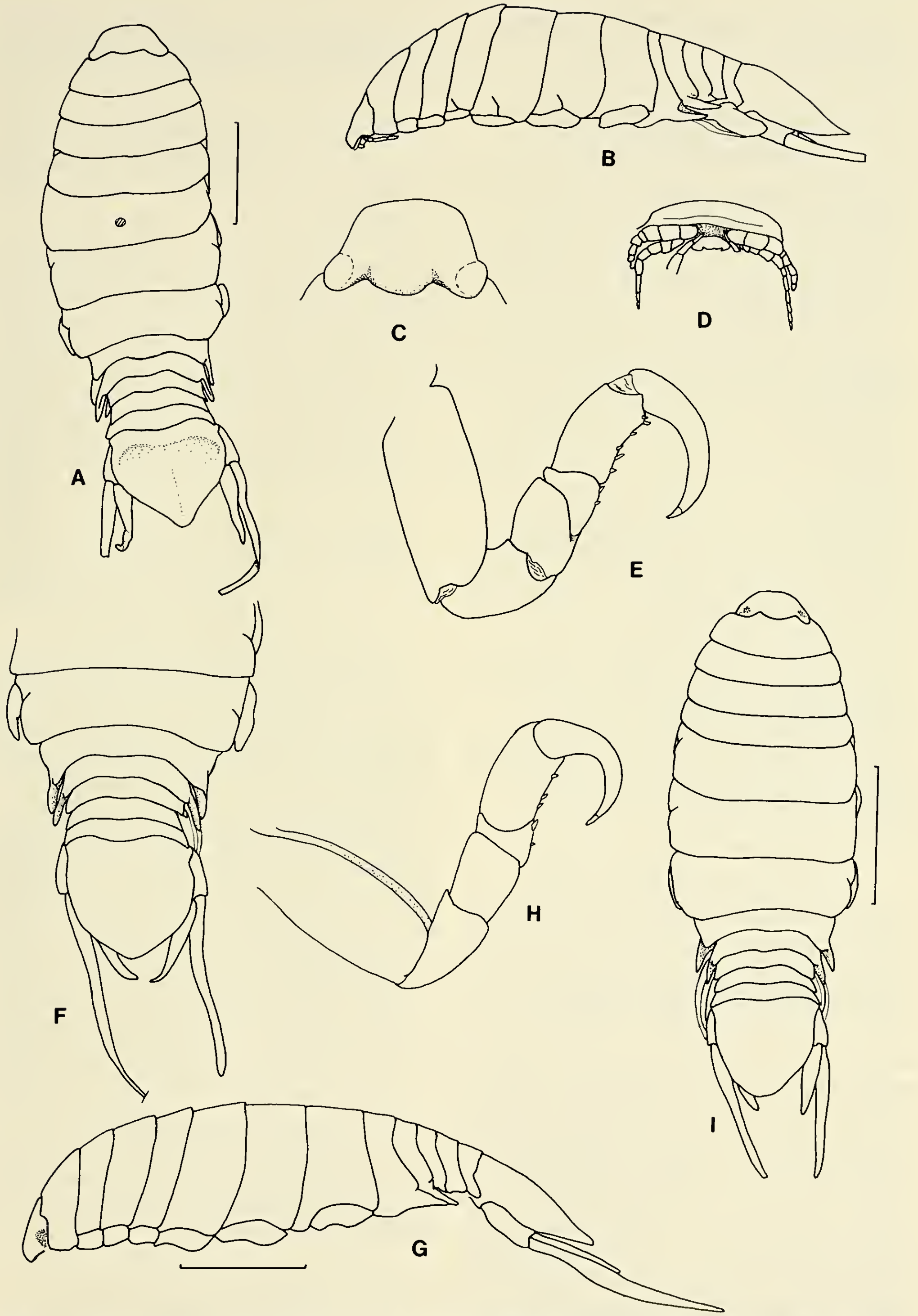

Fig. 7. *Nerocila trichiuri,* A–E, holotype; F–H, female, Senegal, USNM 119490. A, Dorsal view; B, Lateral view; C, Cephalon; D, Frons; E, Pereopod 7; F, Pleon and pleotelson; G, Lateral view; H, Pereopod 7; I, Female, South of India, USNM 128555. Scale lines represent 6.0 mm.

Hosts.—*Exocoetus volitans,* as are all previous records.

Genus *Pleopodias,* 1910
Pleopodias diaphus Avdeev

Pleopodias diaphus Avdeev, 1975:254, figs. 1–11.
Pleopodias superatus Williams & Williams, 1986:656, figs. 62–68 new synonymy).

Remarks.—Williams & Williams (1986) were clearly unaware of *Pleopodias diaphus* recorded from the East China Sea by Avdeev (1975), nor was the species mentioned by Bruce (1987a) in the remarks for that genus. Although Avdeev's figures are not as detailed as those of Williams & Williams, the correspondence of the pleotelsonic notch, somatic morphology and antennule and antennal morphology of the two species clearly indicates that *Pleopodias superatus* is a junior synonym of *P. diaphus.*

Distribution.—East China Sea (=Sea of Japan) (Avdeev 1975) and off Honshu, Japan (Williams & Williams 1986).

Hosts.—Avdeev (1975) recorded the host *Diaphus coeruleus* (F. Myctophidae), a species of deep water lantern fish.

Genus *Renocila* Miers, 1880

Remarks.—Two recent papers (Bruce 1987b; Williams & Williams 1987) described new taxa within *Renocila.* Bruce (1987b) offered a revised diagnosis of the genus, while Williams & Williams (1987) gave a key to the world species. This key does not include the new data given by Bruce (1987b). That is two new species and two new combinations, the synonymization of *R. dubia* with *R. ovata,* and furthermore that *R. periopthalma* Stebbing, *R. recta* (Nierstrasz) and *R. limbata* (Schiödte & Meinert) are juveniles or males and are unrecognizable. Identification of Indo-Pacific *Renocila* is best achieved by using the species descriptions given in both papers rather than the key of Williams & Williams (1987). New World *Renocila* can be identified from the descriptions of Williams & Williams (1980).

Renocila indica Schiödte & Meinert

Renocila indica Schiödte & Meinert, 1884: 417, pl. 18, figs. 14–16.—Bruce, 1987b: 170, fig. 1.

Material examined.—Saint Brandon's Shoals (=Cargados Carajos) Mauritius, Indian Ocean: ♀ (ovig 19.0), lagoon south of Saint Brandon's Shoals, 16°28′S, 59°37′E, 8 Apr 1976, 4 m (USNM 231191); 2 ♀♀ (ovig 19.5, 15.5), 16°32′S, 59°41′E, 30 Mar 1976, 2 m (USNM 231189); 2 ♀♀ (ovig 18.0, non-ovig 12.5), SE side of Grande Passe, 16°28′S, 59°40′E, 5 Apr 1976 (USNM 231194); ♀ (ovig 17.5), Tortue Island, 16°29′S, 59°41′E, 7 Apr 1976 (USNM 231184); 2 ♀♀ (ovig 18.5, 16.5), northwest shoal, Albatross Island, 16°15′S, 59°35′E, 25 m (USNM 231193); all coll. V. G. Springer et al.

Remarks.—This species has been little recorded since first described. Bruce (1987b) gave new figures of the type specimen. Present material is the first record with precise locality data. There are no host records for this species.

Williams & Williams (1987) described *Renocila kohnoi* from Japan. The characters which they used to discriminate *R. kohnoi* from all other species in the genus, in fact fail to distinguish *R. kohnoi* from *R. indica.*

Comparison of the type material of *R. kohnoi* to the specimens of *R. indica* reported on here, and drawings of the holotype of *R. indica* given by Bruce (1987b) revealed but a single difference: the nodules on the anterior margin of pereopods 1–4 of *R. indica* are distinct, while those of *R. kohnoi* are subtle. Unless these characters are shown to intergrade the two species should be regarded as distinct.

Renocila ovata Miers

Restricted synonymy.—*Renocila ovata.*—Bruce, 1987b:172, figs. 2–3.

Material examined.—♀ (non-ovig 17.5), Gomono Island, Philippines, 3 Dec 1909, on *Chaetodon pleini,* coll. U.S. Bureau of Fisheries (Linen tag #9642) (USNM 233270). ♀ (non-ovig 9.5), south of Param, Indonesia, 06°59.5'N, 158°15.7'E, 6 Sep 1980, coll. V. G. Springer et al. (USNM 231190). ♀ (ovig 19.5), ♂ (10.0), Talabassi Bay, Big Damalawa Islet, Kabaeng Island, Celebes, Indonesia, 05°17.3'S, 122°04'E, 25 Feb 1974, 2–15 m depth (USNM 231188).

Remarks.—Renocila ovata has been recorded from Australia and Indonesia (Bruce 1987b); the range is here extended to the Philippines, the first Pacific record. The precise habitat of this species has not been recorded, but recorded hosts are coral reef fishes.

Hosts.—Chaetodon pleini (F. Chaetodontidae), the only previous host record is *Eupomacentrus fasciolatus.*

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BOORALANA TRICARINATA, A NEW SPECIES OF ISOPOD FROM THE WESTERN ATLANTIC OCEAN (CRUSTACEA: ISOPODA: CIROLANIDAE)

David K. Camp and Richard W. Heard

Abstract.—Booralana tricarinata is described from deep-shelf and upper-slope waters off the Bahamas and the Antilles. It is the third species to be assigned to the recently erected cirolanid genus *Booralana* Bruce, 1986, and the first record of the genus beyond Australian waters. The large species, reaching 54 mm in length, can be distinguished from the other two species by the presence of a median and a pair of submedian carinae on the dorsal surface of the pleotelson.

Bruce (1985:714) discussed 15 genera in a synopsis of the Cirolanidae of the Caribbean Sea and Gulf of Mexico and presented a key to the 12 nontroglobitic genera known from that area. Kensley (1987) added a new genus, *Xylolana,* to the Caribbean cirolanid genera. The new species described below represents another cirolanid genus now known to occur in that region: *Booralana* Bruce, 1986. The genus previously comprised only two other species, *B. bathynella* (Bruce, 1981) and *B. wundurra* Bruce, 1986, from the Indo-West Pacific Region at Australia (Bruce 1986).

All measurements are in millimeters (mm). Specimens are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; the Florida Department of Natural Resources Marine Invertebrate Collection (FSBC I), St. Petersburg; the Gulf Coast Research Laboratory Invertebrate Collection (GCRL-I), Ocean Springs, Mississippi; and personal collections.

Cirolanidae
Genus *Booralana* Bruce, 1986
Booralana tricarinata, new species
Figs. 1–5

Holotype.—1 male, 53 mm; Atlantic Ocean, Northwest Providence Channel, about 3 km southeast of Lucaya, Grand Bahama Island, 200–250 m, baited mollusk trap; coll. J. Worsfold, Mar 1984; USNM 229974.

Paratypes.—1 non-incubatory female, 47 mm; Atlantic Ocean, Straits of Florida, west of Little Bahama Bank, 27°04.0′N, 79°18.8′W, ALVIN dive 77-761, no. F-1, 610 m, from fish trap; May–Jun 1977; USNM 229969.—1 male, 51 mm, 66 juveniles, 10–26 mm, 8 fragments; Atlantic Ocean, Northwest Providence Channel, off Lucaya, Grand Bahama Island, 180–220 m, from baited mollusk trap; coll. W. Lyons, J. Worsfold, and R. Quigley, 24 May 1981; FSBC I 32700.—6 males, 34–47 mm, 1 incubatory female, 49 mm, 1 non-incubatory female, 35 mm, 8 subadults 21–29 mm; same data as for holotype; USNM 229975 (2 males, 1 female), FSBC I 32701 (4 males, 1 female, 8 subadults).—4 males, 37–47 mm, 2 incubatory females, 47 and 48 mm, 8 non-incubatory and subadult females, 30–54 mm; Atlantic Ocean, off north coast of Puerto Rico, 18°30′N, 65°42′W, 435 m, R/V *Oregon II* Station 31794, from baited fish trap; coll. S. Candileri, 10 Jul 1980; FSBC I 32347 (2 females), GCRL-I-87-1129 (3 males, 5 females), collection of N. Bruce (1 female), collection of R. Heard (1 male, 2 females).—1 male, fragment; Caribbean Sea, due east of Vieques Island, Puerto Rico, 110 m, from stomach of *Lutjanus vivanus* (male, fork length 44 cm); coll. E. Rainey, 21 Apr 1971; USNM 229967.—2 adult (?) males (damaged), about 35 and 45 mm, plus several fragments and mancas; Caribbean Sea, Anegada, British Virgin Islands, 65–95 fathoms (118–173 m), from combined stomachs of 5 *Lutjanus buccanella* (fork lengths 26–33 cm); 1 Jun 1971; USNM 229968.—1 female, 31 mm; Caribbean Sea, Redonda Island, West Indies, Smithsonian-Bredin Station 74-A-58, night-light at anchorage (dip net); 17 Apr 1958; USNM 229965.—1 female, 42 mm; Caribbean Sea, west of Portsmouth, Dominica, 274 m, Station 72-59; Finlay mollusk trap; 19 Apr 1959; USNM 229966.

Diagnosis.—Dorsal surface of pleotelson with median carina and one pair of submedian carinae.

Description of holotype male.—Cephalon slightly more than twice as wide as long, rounded anteriorly, lacking rostrum (Fig. 1); medial part of posterior margin concave in dorsal view, only slightly embedded in pereonite 1. Eyes ventrolateral (Fig. 1C), almost completely obscured by cephalon in dorsal view, elongate, more than 3 times longer than deep, extending to posterolateral corners of cephalon; each eye approximately ⅓ length of anterior margin of cephalon. Anterior margin of cephalon with 4 narrow, sinuous carinae; dorsalmost carina extending uninterrupted around margin of cephalon just above eyes; second carina similar and parallel to first one, running along dorsal margin in contact laterally with dorsal margins of eyes; third carina confined to interocular region; fourth carina in contact laterally with ventral margins of eyes, curving dorsally around antennae, extending posteriorly only to midpoint of eyes. Two short, curved grooves on dorsal posterior surface of cephalon lateral to medial concavity of margin.

Pereonite 1 medial length about 1.3 times length of cephalon; lengths of remaining pereonites subequal, less than that of first. Anteroventral margin of pereonite 1 subacute, produced anteriorly beyond posterolateral margin of eye; lateral margin with marginal carina. Pereonites 2 and 3 coxal plates subrectangular. Pereonites 4–7 coxal plates well developed, produced posteriorly into strong, acute lobes. Pereonite 7 posterior margin usually with single row of small tubercles or granules.

Pleonites all free, all visible dorsally. Pleonite 1 partially covered by pereonite 7. Pleonite 3 ventrolateral margin strongly produced, with deep posterior notch; posterolateral margin above notch produced posteriorly beyond those of pleonites 4 and 5. Pleonites 2–5 posterior margins each with single row of small tubercles.

Pleotelson subtrapezoidal, wider than long, widest anteriorly; anterolateral margin concave at junction with uropod; lateral margins slightly raised, convex, converging toward truncate posterior margin; posterior margin straight or sinuous, sometimes appearing bilobed, armed with numerous blunt denticles. Dorsal surface with 3 carinae; one pair of long submedian carinae extending entire length of pleotelson, posteriorly narrow, widening anteriorly and becoming less distinct; one median carina originating at anterior fourth of pleotelson, extending to posterior margin. Pair of pores present anteriorly on dorsal surface of pleotelson lateral to anterior ends of submedian carinae.

Antenna 1 extending posteriorly slightly beyond lateral margin of cephalon. Peduncle not reaching beyond distal half of peduncle segment 4 of antenna 2; bases set slightly apart; segments 1 and 2 subequal in length; segment 3 approximately equal to combined lengths of segments 1 and 2. Flagellum with 23–28 articles. Antenna 2 extending posteriorly as far as pereonite 5. Peduncle segments 1–3 with combined lengths less than that of segment 4; length of segment 5 subequal to that of segment 4; flagellum with 53–58 articles.

Frontal lamina subtriangular, with 2 parts; anterior half subpentagonal, widest posteriorly, with median carina and raised lateral margins; posterior half subcircular, produced anteriorly, highly punctate, with well-rounded posterior margin. Clypeus slightly concave posteromedially, forming 2 pronounced anterior lobes enclosing posterior basis of frontal lamina.

Mandibles asymmetrical; left incisor overlapping right (Fig. 2). Posterior cusp of incisor process of left mandible enlarged, with posterior margin folded ventrally, forming receptacle for posterior cusp of incisor process of right mandible. Lacinia mobilis present on both mandibles, left bearing about 18 slightly curved, corneous marginal spines, right bearing about 15 spines; spines irregular in size and shape. Palp with 3 segments; segment 2 approximately twice length of segment 1, length approximately 2.5 times greatest width; inner face of distal half with dense cluster of simple setae; distal segment weakly falcate, with concave margin bearing dense row of simple setae, distalmost seta longest.

Maxilla 1 exopod with 12 dark, corneous spines; distal portion of exopod broadened, with 3 lateral spines, distalmost strongly developed, robust; row of lateral spines curving to join row of 8 medial spines; single smaller spine present between medial and lateral rows. Endopod hatchet-shaped; outer distal angle almost square; inner margin with 3 plumose spines.

Maxilla 2 and maxilliped as illustrated, typical for family. Maxilliped endite with 2 coupling hooks.

Pereopods 1–3 anteriorly directed, subequal in length; pereopods 4–7 posteriorly directed, increasing in length posteriorly.

Pereopod 1 stouter than remainder (Fig. 3); dactylus with dark, corneous unguis; propodus flexor margin with 5–6 blunt tubercles, distal margin of each tubercle armed with secondary, short, corneous spine; carpus short, inserted into merus; merus deeply notched laterally, with well developed, anteriorly directed pad on flexor margin extending almost to distal margin of carpus, pad armed with 6–7 short, corneous spines laterally and 4–5 blunt tubercles medially, tubercles similar to those on propodus, dorsal extensor margin lacking spines; ischium dorsal extensor margin with 2–3 setae, lacking spines.

Pereopods 2–3 similar; dactylus and propodus similar to those of pereopod 1 but more slender; carpus inserted into shallow notch of merus, distal flexor margin armed with 3–5 short, corneous spines; merus with pad on flexor margin not extending to distal margin of carpus, pad armed with 9–12 short, corneous spines laterally, lacking medial tubercles, dorsal flexor margin armed distolaterally with 3 prominent, corneous-tipped spines and 3–4 smaller spines; extensor margin of ischium with single, strong distal spine and 3–4 setae.

Pereopods 4–5 similar; propodus with 3 acute spines, often paired, along distal half of flexor margin; carpus well developed, length subequal to merus, distolateral margin with 10–12 stout spines, ventromedial margin with row of 4–6 spines; merus with about 15 strong spines along distal margin, irregular row of 4–5 corneous spines on flexor margin; ischium with 3–4 corneous spines on distal extensor margin and 6–7 corneous spines on distal flexor margin, ventral margin with 2 clusters of short, corneous spines at approximately ⅓ and ⅔ length of margin.

Pereopods 6–7 similar to pereopods 4–5, but much longer and with more spines.

Penes short, subrectangular.

All pleopods laminar (Fig. 4); bases with reniform lobe on lateral margin; lobes more strongly developed on posterior pleopods.

Pleopod 1 exopod with inner margin rounded, tapering to narrow, rounded distal end; lateral margin straight; plumose setae on entire margin of exopod except proximal half of inner margin. Endopod with lateral and medial margins subparallel, distal end broadly rounded; setae present only on margin of distal third of ramus.

Pleopod 2 endopod and exopod subequal in length, broadly rounded distally. Exopod with plumose setae on entire margin except proximal ⅗ of medial margin. Endopod with row of small, plumose setae on distal half of medial margin, continuing to midpoint of distal tip of ramus; margin of proximal half of ramus with very fine pubescence. Appendix masculina originating at base of endopod, styliform, unornamented, not extending beyond tip of endopod.

Pleopods 3 and 4 similar. Exopod broadly rounded distally, with very weak indication of suture; plumose setae on distal half of margin. Endopod with lateral margin evenly rounded; medial margin straight proximally, with prominent angle at midpoint of ramus; distal margin sinuous, tapering to narrow tip.

Pleopod 5 endopod and exopod subequal in length. Exopod broadly rounded distally, with very weak indication of suture; plumose setae on entire margin except proximal ⅗ of medial margin; proximal part of lateral margin ending in posteriorly curved lobe.

Uropod basis with acute posteromedial process extending over half length of endopod, bearing short plumose setae distally, and with dorsal transverse carina ending laterally at junction of rami. Exopod lanceolate, narrow, 3 times longer than wide, approximately ⅘ length of endopod, tapering distally to subacute tip. Endopod narrow proximally, broadest distally; posterior margin truncate, slightly sinuous, almost straight, reaching posterior margin of pleotelson. Lateral margins of both rami fringed with dense cluster of plumose setae; distal margins and distal half of inner margins of both rami fringed with single row of plumose setae.

Females.—Other than the usual sexual characters, females differ from mature males by lacking the dense setation on lateral margins of both uropodal rami and having 3–5 movable spines distally on the inner margin of the uropodal exopod (Fig. 5G). Females also differ from males by having plumose setae on the exopod of pleopod 1 confined to the distal half of both the medial and lateral margins, whereas on males the setae are confined to the distal half of the medial margin but continue more densely along the entire length of the lateral margin. There is a possibility that spination on the dorsal extensor margin of the ischium of pereopod 1 differs between mature males and females. In males the dorsal surface of that article has setae and no spine, but on most females there is a single strong spine similar to that on the same article of other pereopods. However, one smaller female (35 mm total length) has a pair of setae there and lacks the spine seen on larger females. Finally, medial margins of endopods of pleopods 3 and 4 on females are straight, lacking the prominent angle at midlength evident in males.

Young.—Specimens range in size from 10 to 54 mm total length, and ontogenetic change in some morphological features is great. Manca stages differ from larger specimens in several respects. The median carina on the anterior part of the frontal lamina is obscure in the manca stage but prominent in adults. Pereopod 7 is absent from 40 specimens with total lengths of 10–12 mm and present but not fully developed in 9 specimens with lengths of 14–16 mm; all intact post-manca specimens longer than 17 mm have pereopod 7 fully developed. Relative lengths of pereonal coxae 6 and 7 change with increasing size of the specimens. In specimens shorter than 14 mm, the coxa of pereopod 6 extends posteriorly far beyond the tip of the coxa of pereopod 7, but in longer specimens the coxa of pereopod 7 extends beyond that of pereopod 6.

Setation of the pleopods and uropods also differs between young and adults. In the young, setae on pleopods are relatively longer than in adults, and the distal tip of the endopod of pleopod 4 has 8–9 fine setae, lacking in adults. Setation of the uropods of juveniles is much less dense than that of adults, and an extremely dense cluster of setae occurs along lateral margins of the uropodal rami in adult males. Function of the

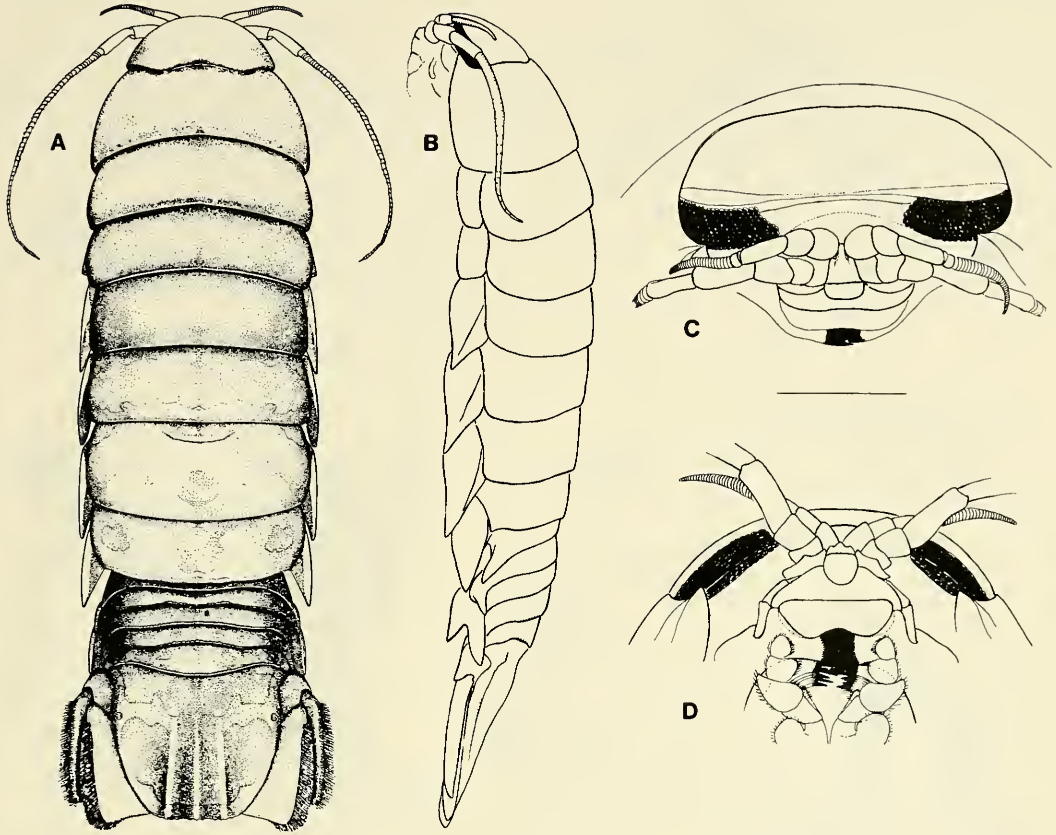

Fig. 1. *Booralana tricarinata,* holotype male: A, Dorsal aspect; B, Lateral aspect (pereopods and pleopods omitted). Adult 42 mm female from Grand Bahama Island: C, Cephalon, onface view; D, Cephalon, ventral view. Scale = 4 mm for C, D.

dense setal cluster in males is unknown, but its presence may indicate sexual maturity. Young males and all females have 3–5 spines on the inner margin of the uropodal exopod, lacking in mature males.

Geographic variation.—There are usually marked differences between males and minor differences between females from the western Bahamas and those from Antillean localities represented by our material. However, the sample size is too small to draw firm conclusions about the significance of differences noted, and there are exceptions in each case. The Bahamian material consists of eight males, three females, and many mancas. The only two intact males from the Antilles and most (12 of 14) of the Antillean females are from a single locality off the north coast of Puerto Rico; the remaining Antillean males are represented only by fragments from fish stomachs.

One difference noted between the two populations is the relative width of the body with respect to its length. Bahamian specimens, for the most part, appear to be relatively narrower than most Antillean specimens, but there are exceptions. The mean body width to length ratio of Bahamian specimens is 1:3.1 ± 0.252 ($n = 9$), whereas the mean ratio for Antillean specimens is 1:2.9 ± 0.183 ($n = 14$). The difference is caused by the relatively longer individual pereonal

Fig. 2. *Booralana tricarinata,* holotype male: A, Right mandible, ventrolateral aspect; B, Right mandible, dorsomedial aspect; C, Incisor and lacinia mobilis of left mandible, medial aspect; D, Maxilla 1; E, Maxilla 1, onface view of exopodal spines; F, Maxilla 2; G, Maxilliped, ventral aspect; H, Inner plate of maxilliped, dorsomedial aspect. Adult 42 mm female from Grand Bahama Island: I, Left maxilliped. Upper scale = 1 mm for A, B, D, F, G; 0.5 mm for C, E, H. Lower scale = 2 mm for I.

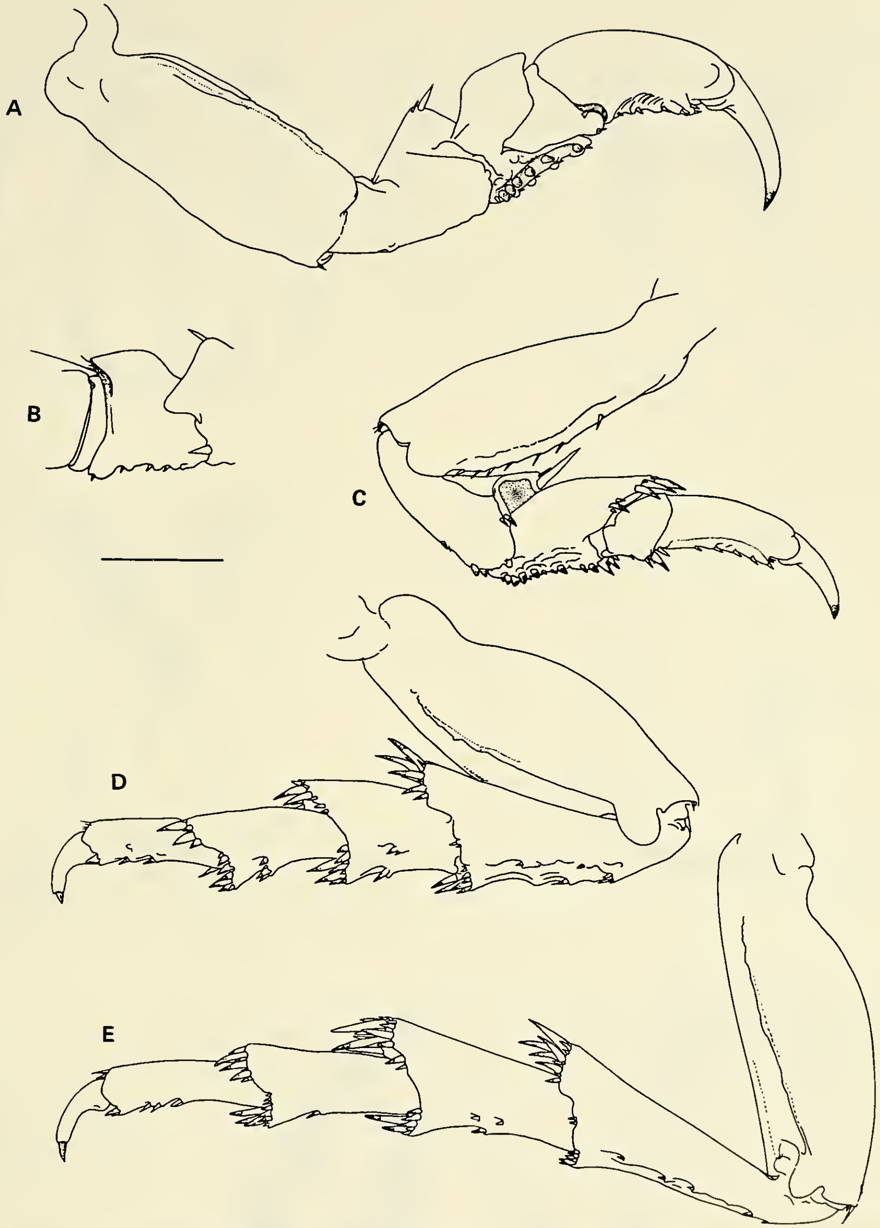

Fig. 3. *Booralana tricarinata,* holotype male: A, Pereopod 1, lateral aspect; B, Pereopod 1, medial aspect, ventral and distal spination of merus and ischium, respectively; C–E, Pereopods 2, 5, and 7, lateral aspects. Scale = 1 mm.

somites of Bahamian specimens when compared to those of Antillean specimens of the same width. Ranges of the overall width to length ratios of the two populations overlap, however. The range for Bahamian specimens is 1:2.8 to 1:3.3, and the range for Antillean specimens is 1:2.6 to 1:3.2.

Another difference involves dentition and setation of the endopod of the uropod (compare Fig. 1B and Fig. 5A–F). In mature Ba-

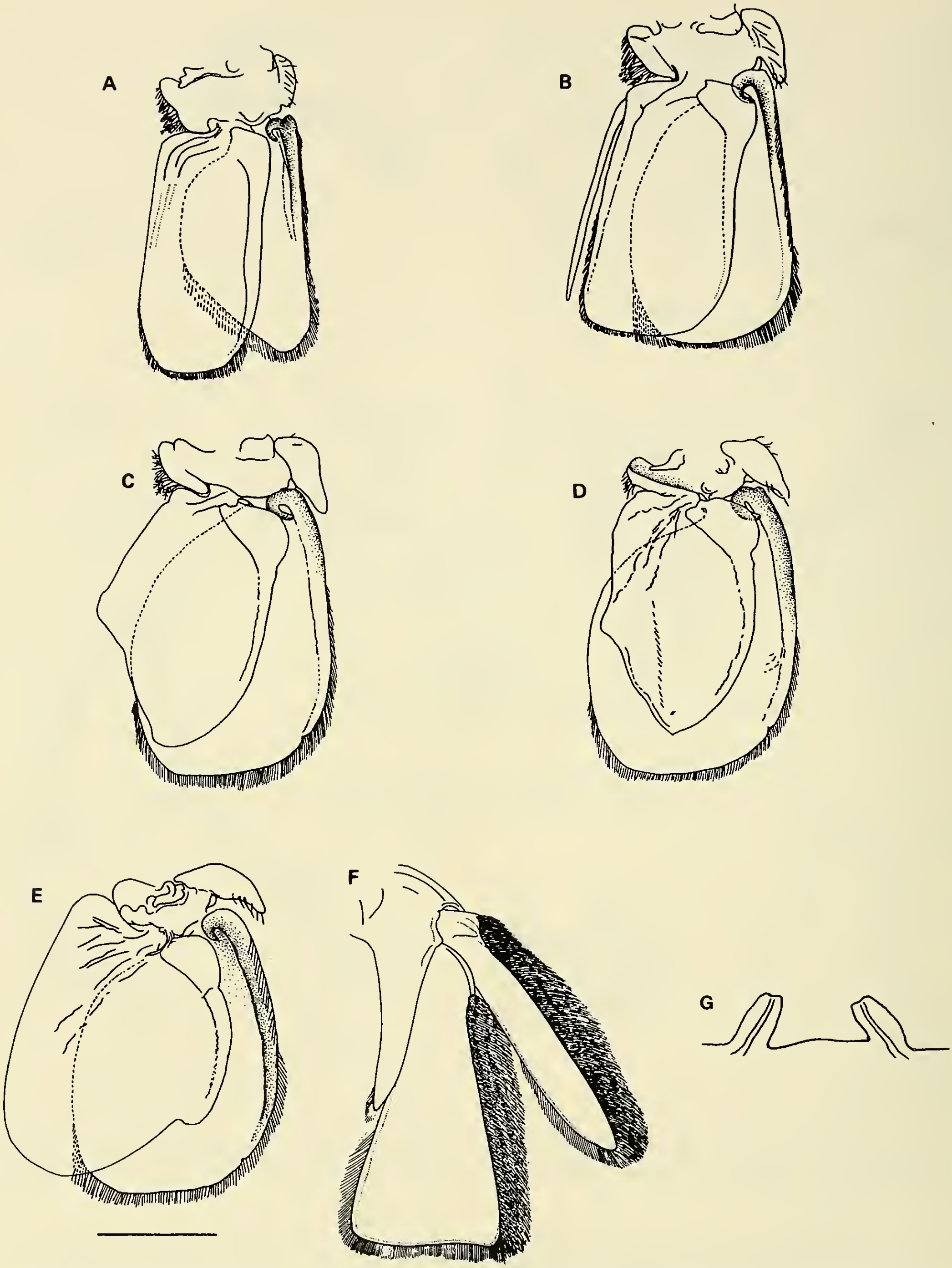

Fig. 4. *Booralana tricarinata,* holotype male: A–E, Pleopods 1–5; F, Right uropod; G, Penes. Scale = 1 mm for A–F, 3 mm for G.

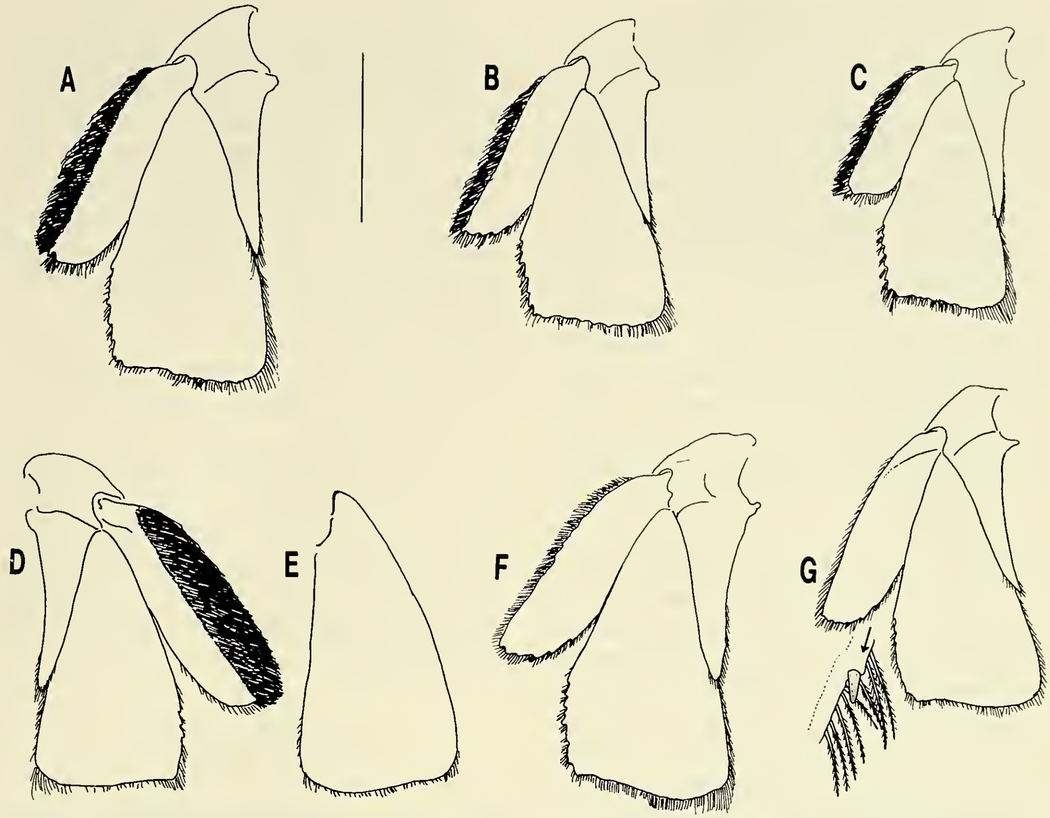

Fig. 5. *Booralana tricarinata:* A–C, Left uropods of 47, 41, and 37 mm males, respectively, from Puerto Rico; D, Right uropod, adult (?) male from British Virgin Islands (fish stomach); E, Endopod, right uropod, adult (?) male from Puerto Rico (fish stomach); F, Left uropod, adult 47 mm female from Puerto Rico; G, Left uropod, adult 42 mm female from Grand Bahama Island. Scale = 2 mm.

hamian males, including the holotype, the distolateral margin of the endopod is entire and has a dense fringe of setae; whereas Antillean males have several sharp tubercles along the distolateral margin and a thin fringe of setae, similar to the condition seen on females from both areas and on smaller subadult males from the Bahamas. Moreover, the tubercles on the distolateral margin are more strongly developed on females from Puerto Rico than on females of similar size from the Bahamas.

The appendix masculina on Bahamian males is relatively shorter than that of males from the Antilles, although there is an exception in this case, too. The appendix masculina on each Bahamian male does not reach the distal end of the inner ramus of the second pleopod, whereas it does reach the distal end of the ramus on each of the two intact males from off the north coast of Puerto Rico and on two of the three fragmented males from elsewhere in the Antilles. However, on one of the fragmented males from Anegada, British Virgin Islands, the appendix masculina is short, not reaching the end of the ramus.

The populations from the Bahamas and the Antillean Islands may be diverging, or the species may be quite variable. We may be seeing in our limited material phenotypic effects of great water depth or temperature differences between the localities represented. Nevertheless, the absence of a dense setal fringe on the endopods of uropods of apparently adult males from the Antilles is worrisome. For now, we have chosen to conservatively consider the populations as one variable species. When more material becomes available, a further investigation can be made of their differences.

Affinities.—Booralana tricarinata can be distinguished immediately from *B. bathynella* and *B. wundurra* by the presence and configuration of carinae on the dorsal surface of the pleotelson. *Booralana tricarinata* has one longitudinal carina on the midline of the pleotelson and a pair of submedian carinae. *Booralana bathynella* lacks carinae on the pleotelson; *B. wundurra* has a pair of submedial carinae but lacks one on the midline. The shape of the pleotelson of *B. tricarinata* is most similar to that of *B. bathynella*; in both species the lateral margins of the pleotelson are convex, sloping evenly to a broad, truncate posterior margin. In *B. wundurra* the posterior margin is relatively much narrower than in the other two species, and it is upturned in males. Finally, the eyes of preserved specimens of *B. tricarinata* are brown or black, but the eyes of *B. wundurra* are red (Bruce 1986:136).

The posterolateral notch in the enlarged lateral margin of the third pleonite may be a reliable generic character, although the notch is more weakly developed in *B. wundurra* than in the other two species (N. Bruce, pers. comm.). In specimens of *B. tricarinata* the basal segment of the uropod becomes inserted in the notch when the pleotelson is flexed ventrally. Functionally, this meshing of the pleotelson and pleonite appears to be a locking mechanism used for leverage when the isopod is clinging to a fish carcass.

Etymology.—The specific name, *tricarinata,* refers to the three prominent carinae on the dorsal surface of the pleotelson.

Type locality.—Atlantic Ocean, Northwest Providence Channel, about 3 km southeast of Lucaya, Grand Bahama Island (approximately 26°32′N, 78°33′W), 200–250 m depth.

Distribution and ecology.—Booralana tricarinata is known from outer-shelf and upper-slope depths off the Little Bahama Bank and the Antilles Islands; 110–610 m depths.

There was no depth recorded with the sample from Smithsonian-Bredin Station 74-A-58 at Redonda Island, but the female was taken at the anchorage there. The collection data includes the entry "(dip net?)." We have found that the collection was made in depths shallower than those at the collection sites of other material examined, at the surface, with light and dip net.

The limited data indicate that *B. tricarinata* is an epibenthic scavenger, because most of the specimens came from baited mollusk or fish traps. Another isopod captured with *B. tricarinata* in baited mollusk traps off Grand Bahama Island is *Cirolana minuta* Hansen, 1890 (see Kensley & Schotte 1987:233–236).

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IPANEMIDAE, NEW FAMILY, *IPANEMA TALPA*, NEW GENUS AND SPECIES, FROM THE SURF ZONE OF BRAZIL (CRUSTACEA: AMPHIPODA: HAUSTORIOIDEA)

J. L. Barnard and James Darwin Thomas

Abstract.—A new family of haustorioid Amphipoda resembling the Phoxocephalopsidae and Urothoidae has been discovered in sands of the surf zone off Rio de Janeiro, Brazil. Like the recently described Cheidae, the new species-genus-family combines various characters of haustorioids in a unique manner and bears one unprecedented apomorphic character: an alate, uncleft telson.

The new taxon has the following characters of Urothoidae: antenna 2, head, and distal parts of pereopods but has a distinctive antenna 1, coxae 1–2, mandibular palp, telson and epimera 1–2. *Ipanema* has the following characters of Phoxocephalopsidae: coxae, mandibles, and uropod 1 but has distinctive antennae 1–2, epimera 2–3, pereopods 5–7 and telson. The taxon has some characters found mostly or only in Urohaustoriidae, such as epimera 2–3, but differs in many ways from that family, such as: head, antennae 1–2, parts of mandibles and maxillipeds, maxilla 1, parts of pereopods 3–7, epimeron 1, and especially uropods 1–2.

The Ipanemidae are created for *Ipanema talpa.* The unusual combination of antennae 1–2 with mouthparts, uropods 1–2, head shape and pereopods precludes its assignment to any existing family group. It bears an apomorphic telson not heretofore described from the superfamily Haustorioidea except in the otherwise remote Urohaustoriidae. *Ipanema* combines characters of Phoxocephalopsidae, Urothoidae and Urohaustoriidae. For example, antenna 2 and to a certain extent antenna 1 have characters of Urothoidae, whereas coxae 1–4 and uropod 1 are like Phoxocephalopsidae while the epimera have some characters of Urohaustoriidae.

Corrections to literature.—We have reevaluated the cephalic cheek of Phoxocephalopsidae to be well developed in contrast to the opinion of Barnard & Drummond (1982).

Ipanemidae, new family

Type genus.—*Ipanema,* new genus. Gender feminine.

Etymology.—A beach of Rio de Janeiro, Praia de Ipanema.

Diagnosis.—Rostrum weak, broad; cheek strong. Antenna 1 of neither haustoriid nor urothoid form, peduncle short, no articles elongate, each thick, article 1 with weak setation, article 2 furnished with dense row of spines, article 3 about 0.67 as long as article 1, poorly armed; no geniculations present; flagellum longer than peduncle and heavily armed with aesthetascs; accessory flagellum 2-articulate. Antenna 2 of urothoid form, articles 4 and 5 slender, with long lines of spines not organized into ranks, posterior margins lacking glass-spines (typical of Urohaustoriidae), ordinary setae and bulbar setae extremely sparse, flagellum very short, 3-articulate. Epistome and upper lip fused together, lower margin rounded. Right and left mandibles alike, with narrow but stubby and simple incisors lacking teeth laciniae mobiles alike, rakers absent, molar of medium size (compared to Urothoidae), weakly triturative, choppers weak to absent; palp 3-articulate, article 3 with urohaustoriid setal-spine distribution (versus urothoid setal distribution), spines hooked but unawned. Lower lip with mandibular lobes well developed. Maxilla 1 with biarticulate palp, inner plate small and spout-like, with 1 large seta. Inner plate of maxilla 2 without oblique facial seta row, with one medial seta. Maxillipeds with unexpanded bases and no baler lobes, with rather small inner plate but normally enlarged and spinose outer plate; palp 4-articulate, article 2 expanded, article 4 rectangular, with 2 thin nail-setae.

Coxae 1–2 minute and hidden by coxa 3, coxa 4 dominant, weakly excavate behind, coxa 3 adz-shaped; coxae 5–6 with comma-shaped posterior lobe. Gnathopods feeble, subsimilar, simple (gnathopod 2 with minute palm), article 3 short. Article 5 of pereopods 3–4 slender, not lobate; dactyls of pereopods 3–7 well developed; pereopod 5 of weakly haustorious form, article 2 expanded, articles 4–5 weakly expanded and with few facial spines; article 2 of pereopods 5 and 7 diverse, with that of pereopod 6 intermediate in form; no pereopod with underslung articulation. Gills on coxae 2–5 only, 6–7 apparently without gills because of long forward reach of beating pleopods, gill 2 (on coxa 2) spear-shaped, others decreasing in size, subrectangular sacs.

Pleopods like urohaustoriids, thus peduncles wider than long, pleopod 3 inferior; peduncles as long as wide. Epimeron 1 fully developed, small, with 1 seta, epimera 2–3 equally dominant, all epimera with posterodorsal "hip." Urosomites ordinary. Rami of uropod 1 styliform, naked; of uropod 2 rod-like and spinose; uropod 3 of ordinary haustorioid-phoxocephalid kind, neither ramus dominant, article 2 on outer ramus small and poorly setose.

Telson very short, much wider than long, essentially entire, each side with alate lobe projecting upward.

Relationship.—Differing from the Phoxocephalopsidae in the completely distinctive antennae 1–2, of which antenna 1 has a heavily spinose (versus setose) article 2 and the accessory flagellum is poorly developed; of which antenna 2 has slender articles 4–5 bearing large facial spines in lines rather than small spines in ranks and on which the posterior margins have almost no long setae, almost no bulbar setae and no glass spines. Also differing from Phoxocephalopsidae in the thin article 5 of pereopods 3–4; the diversity of article 2 on pereopods 5–7, with article 2 on pereopod 5 constricted apically; thin apical articles of pereopods 5–7; the presence of a long comma-shaped posterior lobe on coxae 5–6; the equal size of epimera 2–3 and the hips on epimera 1–3; the strange telson (versus ordinary and cleft); and the reduced inner plate of maxilla 1 bearing a single seta.

Differing from Urothoidae in the short articles of the peduncle on antenna 1, with article 2 heavily spinose, the long primary flagellum of antenna 1; the kind and distribution of setal-spines on article 3 of the mandibular palp (versus regular setae and presence of an A-seta in Urothoidae); the tiny coxae 1–2; the hipped shapes of epimera 1–3; and the more delicate mandible.

Phoxocephalopsidae and Urothoidae appear to be more closely related than previously perceived: both have a well developed lateral cephalic cheek, styliform rami on uropods 1–2 and many similarities in mandibles, maxillae, and maxillipeds. Phoxocephalopsids differ from urothoids principally in the antennae, in which articles 1–3 of antenna 1 are short, not geniculate, with huge setal patch on article 2; article 4 of antenna 2 is widely expanded and bears 3 kinds of posterior armaments, including glass spines; article 5 also is expanded and bears 2 kinds of armaments posteriorly; the mandibular palp bears hooked setal-spines


Hd
6
G2
Ht
B
A1

and the dactyl of the maxilliped is less elongate and less unguiform.

Differing from the Cheidae in the large molar and lack of significant rostrum, normal uropod 2, untoothed incisors and simple gnathopods.

Differing from the complex Pontoporeiidae in the shortened peduncles of the pleopods, the short article 1 of antenna 1 and the lack of long setae (distinct from spines) on pereopods 5–7; also differing from all pontoporeiids except *Priscillina* in the spinose antenna 2.

Differing from the Haustoriidae in the 4-articulate (versus 3-) palp of the maxilliped, the presence of only spines (no flexible setae) on pereopods 5–7, the hidden coxae 1–2, large mandibular lobes of the lower lip, the presence of only a few stiff spines (no long flexible setae) on mandibular palp article 3, the unexpanded article 4 of antenna 2, the poor setation on the inner plates of maxillae 1–2 and the ordinary, non-enlarged outer plate of maxilla 2.

Ipanema, new genus

Type species.—*Ipanema talpa,* n. sp.

Diagnosis.—With the characters of the family.

Ipanema talpa, new species
Figs. 1–4

Etymology.—L., talpa, mole.

Description (of holotype male "s" 2.57 mm).—Rostrum obsolescent; eyes medium, ommatidia few, interspersed in alcohol with faint purplish pigment, each with anteromedial ovate ganglion. Antenna 1 article 1 with sparse penicillate setules, article 3 almost naked, accessory flagellum 3-articulate, primary flagellum long, with 8 articles, formula of aesthetascs on articles 1–8 = 2-6-5-4-4-1-1-x (vestigial). Article 4 of antenna 2 with anterolateral line of 14 spines mostly alternating long and short spines pointing in alternate directions, with 3 anterodistal spines; posterior margin and face with 3–4 bulbar setules, posterodistal corner with line of 4 spines and seta and 2 marginal setae; article 5 with anterolateral line of 8 spines mixed long and short, posterior margin mostly naked, posterodistal corner and apex with 5 long setae, 2 bulbar setae; flagellum with 2 articles.

Upper lip and epistome forming large subcircle from anterior view. Right and left mandibles identical, incisor extended, moderately narrow, simple; lacinia mobilis linguiform; rakers absent; molar large, weakly triturative, with weak chopper region, no seta; mandible organized so that when pressed into flat plane palp extending in odd direction (see illustration of labral-mandibular complex), article 1 short, article 2 with 1–2 small midlateral setae, article 3 with 5 mixed-size apical spines in haustoriid formula of 2-2-1. Lower lip without cones. Maxilla 1 with small spout-like inner plate bearing one long seta, outer plate with 9 simple spines, palp feeble, 2-articulate, slender, reaching less than two-third along outer plate, with 2 huge apical setae. Inner plate of maxilla 2 narrower and shorter than outer plate, without oblique facial seta row, with one medial seta, outer plate with 2 apicolateral setae. Inner plate of maxilliped rather small and very broad (relative to other haustorioids), with one medial seta, one apical seta and 2 penicillate spines; outer plate spinose medially, naked apically; palp huge, article 2 expanded and medially setose, ar-

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Fig. 1. *Ipanema talpa,* holotype male "s" 2.57 mm. Capital letters in figures refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as described below: A, antenna; B, body; C, coxa; E, epimeron; G, gnathopod; H, head; J, prebuccal; L, labium; M, mandible; P, pereopod; Q, spine; R, uropod; S, maxilliped; T, telson; U, upper lip; V, palp; W, pleon; a, anterior; d, dorsal, t, left.

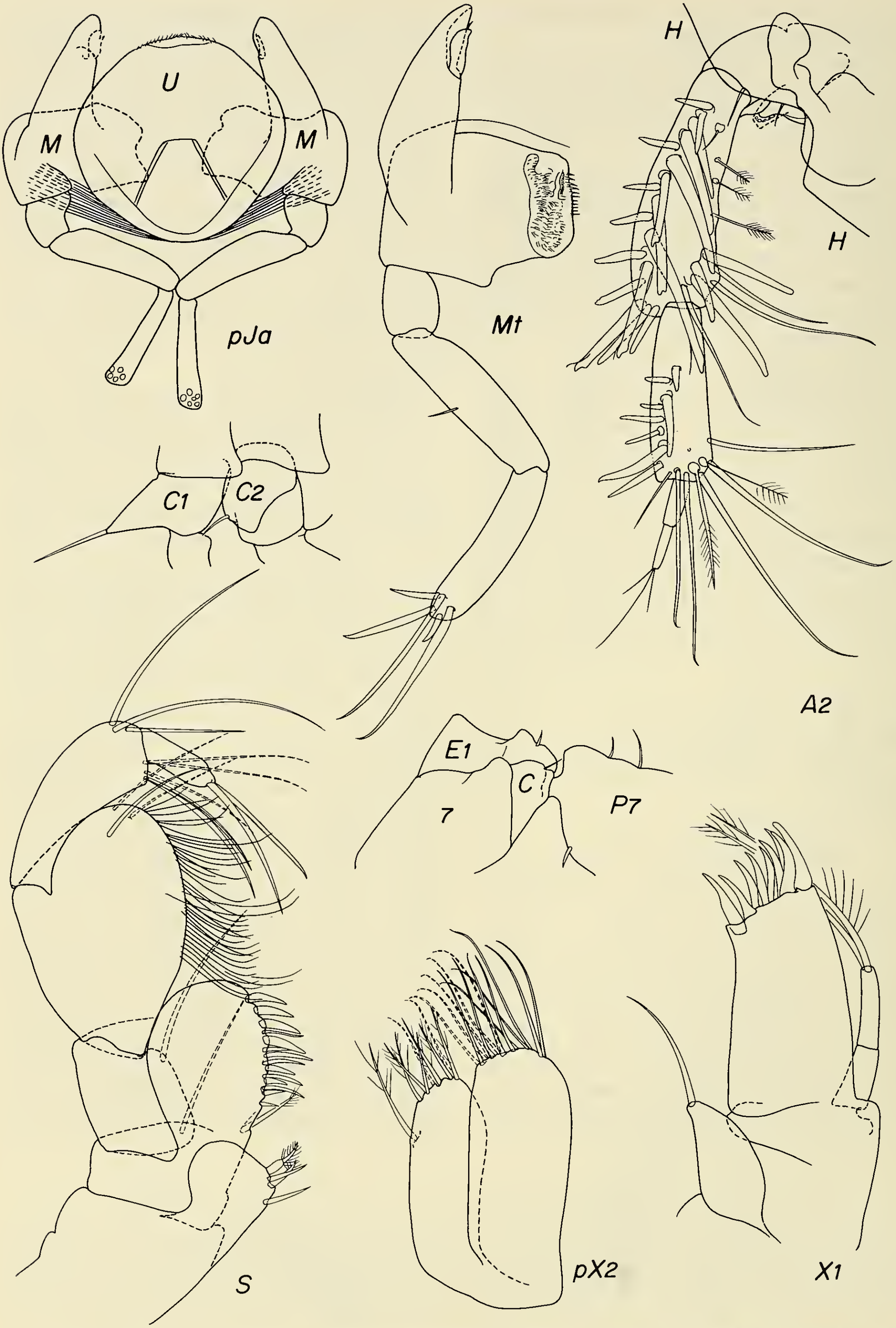

Fig. 2. *Ipanema talpa,* unattributed figures = holotype male "s" 2.57 mm; p = male "p" 2.98 mm. Letter codes, see Fig. 1.

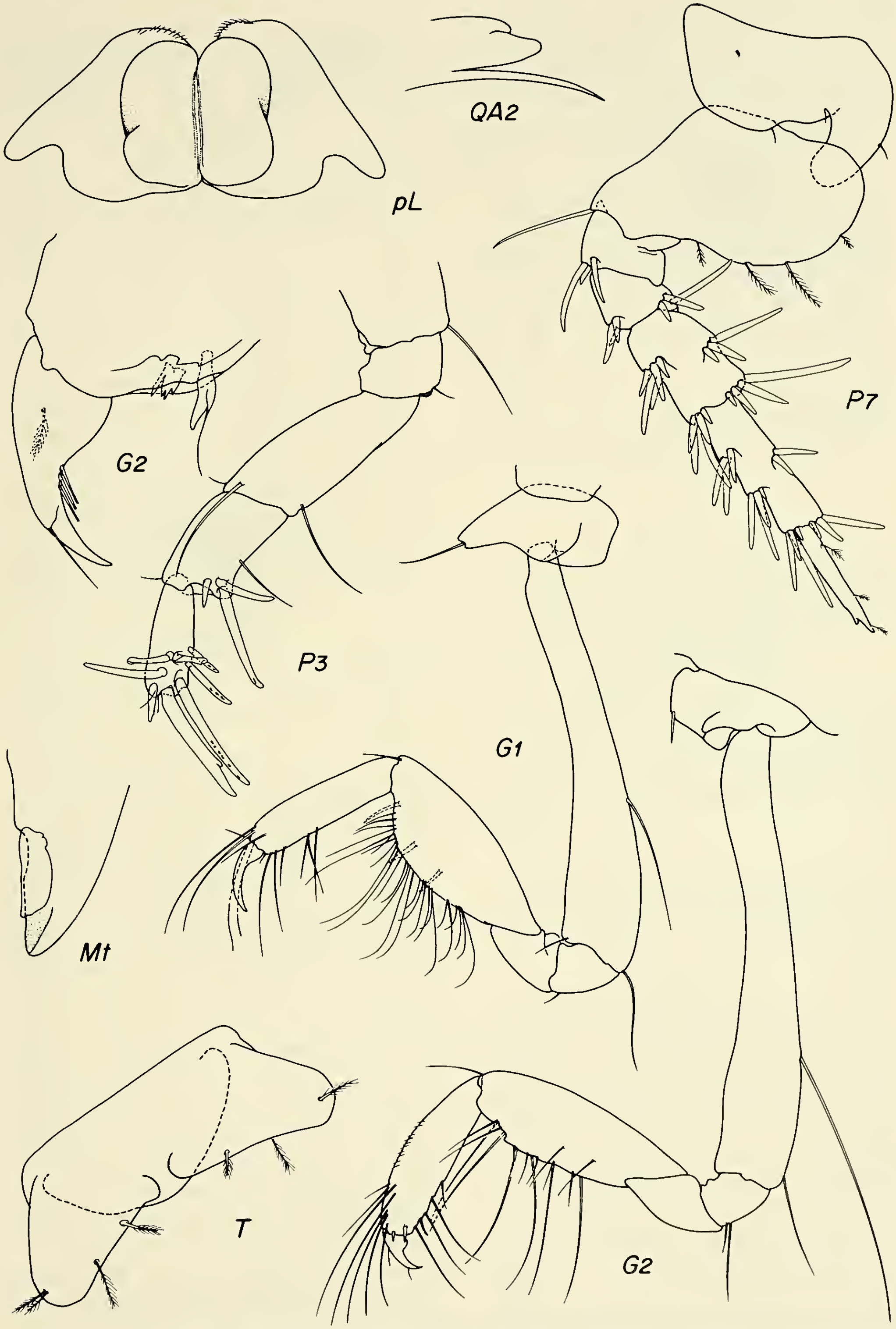

Fig. 3. *Ipanema talpa,* unattributed figures = holotype male "s" 2.57 mm; p = male "p" 2.98 mm. Letter codes, see Fig. 1.

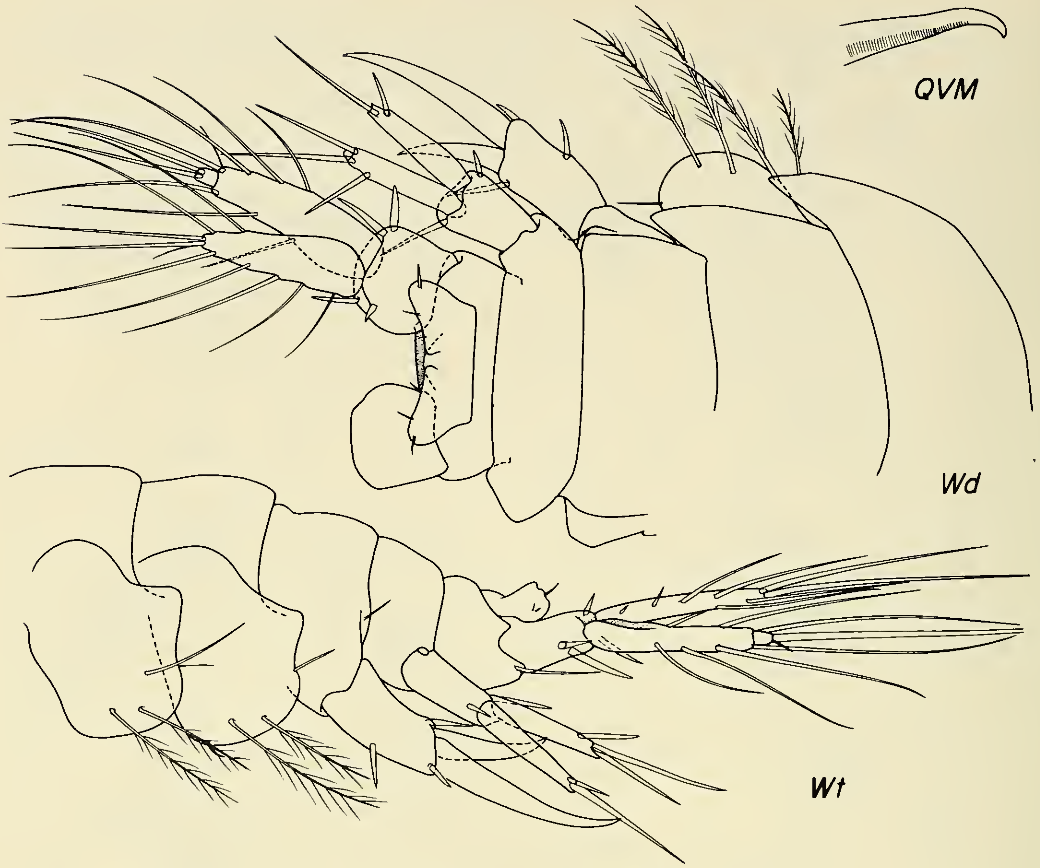

Fig. 4. *Ipanema talpa,* holotype male "s" 2.57 mm. Letter codes, see Fig. 1.

ticle 3 curved and fitting hump of article 2, dactyl not unguiform but not stubby, rectangular, armed with 2 huge apical setal-spines.

Coxae 1–2 very small, hidden by coxa 3, coxa 1 extended forward into point armed with stiff setal-spine. Article 2 of gnathopods 1–2 and pereopods 3–4 poorly setose; article 5 of gnathopod 1 broader and more strongly setose than on gnathopod 2, gnathopod 1 simple, gnathopod 2 scarcely subchelate, with shorter dactyl than gnathopod 1, with minute non-skid scales on propodus (see enlarged illustration, Fig. 1).

Pereopods 3–4 alike, article 4 with naked margins, one long seta at each apex, article 5 narrow but with weak posterodistal lobe armed with 3 spines; many spines of all pereopods with lines of bosses and apical bifidation formed by enlarged boss, some multibossed at apex; article 6 slender, spine formula = 3-3-1; dactyl long and straight, with inner boss near apex. Article 2 of pereopod 5 grotesque, expanded and lobate proximally, tapering sharply at apex, of pereopod 7 almost evenly ovatorectangular and bearing about 7 long posterior setae, of pereopod 6 intermediate between 5 and 7; dactyls elongate, like those of pereopods 3–4. Pereonites 6–7 and pleonites 1–3 with lateral ridge. Epimera 1–3 similar, with hipped posterodistal corner, weakly excavate posterior margin bearing setule, rounded ventral margin with 2 long facial setae on epimera 2–3, epimeron 2 also with mid-posterior facial seta. Pleopods with 2 coupling hooks, outer rami about 1.5 times as long as inner, articles on outer rami = 9-8-7, on inner rami = 6-6-5.

Urosome ordinary. Uropod 1 with short peduncle bearing ventrolateral spine, ventrodistal spine, distomedial spine, rami styliform and naked, outer very long and exceeding apex of uropod 2, inner much shortened. Uropod 2 with short peduncle and apical spine on each side; rami rod-like, outer with one apical and one apicolateral spine, inner with 2 apical and one apicomedial spine. Uropod 3 with short peduncle bearing 2 apical spines on each side, rami elongate, inner almost as long as outer, well setose, outer with small second article bearing 2 long setae. Telson 2.4 times as wide as long, with lateral wings bearing 3 setules each.

Female.—None. All specimens are males, with large penial processes.

Illustrations.—Mandible and maxilla 1 enlarged equally.

Holotype.—USNM 195181, male "s" 2.57 mm.

Type locality.—Brazil, Rio de Janeiro, Praia Vermelha, Rio Orca Beach, 7 May 1985, coarse sand, 4 m, with numerous small echinoids and platyischnopid amphipods, coll. J. D. Thomas.

Material.—From type locality, USNM 196184, male "p" 2.98 mm, male "q" 2.95 mm, male "r" 2.10 mm and 4 other males.

Distribution.—Brazil, Rio de Janeiro, outer surf zone, 4 m.

Acknowledgments

We thank Dr. David Challinor, Assistant Secretary for Science of the Smithsonian Institution, for providing funds to travel to Brazil. The second author also was supported by NSF Grant BSR-8515168. We thank Linda B. Lutz of Vicksburg, Mississippi for inking our illustrations. Janice Clark assisted us in the laboratory. Dr. Gloria Alonso kindly offered us valuable suggestions for improvements.

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NEW RECORDS FOR *OGYRIDES ALPHAEROSTRIS* AND A NEW SPECIES, *OGYRIDES TARAZONAI* (CRUSTACEA: OGYRIDIDAE), FROM THE EASTERN PACIFIC OCEAN

Mary K. Wicksten and Matilde Mendez G.

Abstract.—A new species, *Ogyrides tarazonai,* related to *O. hayi,* is described from Nicaragua and Peru. This shallow-water species has only one spine on the dorsal midline of the carapace. Specimens of *O. alphaerostris* (Kingsley) have been found off southern California and western Mexico.

Species of *Ogyrides* (Caridea: Ogyrididae) are burrowing shrimps of warm-temperate and tropical waters. In the eastern Pacific, the genus is reported from specimens taken off western Mexico (Wicksten 1983, Carvacho & Olson 1984). Examination of material from California, Mexico, Nicaragua, and Peru led to the determination that two species are present in the eastern Pacific. The specimens discussed herein are deposited in the collections of the Allan Hancock Foundation, University of Southern California (AHF), the California Academy of Sciences (CAS), the Instituto del Mar del Peru (IMARPE), and the Estación Mazatlán (EMU). We thank Michel Hendrickx, Estación Mazatlán, for allowing us to examine specimens from off Sinaloa. The illustrations are by Debbie Meier, Texas A&M University.

Ogyrides tarazonai, new species
Fig. 1

Description.—Rostrum triangular, acute, setose; slightly longer than width at base and longer than extracorneal teeth. Extracorneal teeth rounded, infracorneal teeth shorter than extracorneal but rectangular. Pterygostomial angle projected but rounded. Carapace carinate along midline posterior to rostrum, setose, bearing 1 strong movable spine directed forward.

Eyestalks reaching beyond end of antennular peduncles, thickened at base, curving slightly mesad toward narrowed midlength, then broadening distally toward slightly expanded but small terminal cornea. First antennular article about equal to second when measured from base, second article 2× as long as broad, third 0.5× second. Stylocerite with 2 strong spines, superior spine almost reaching end of first segment of antennular peduncle, inferior spine surpassing it. Squamous part of scaphocerite broad, lanceolate, with tiny lateral spine, exceeding second segment of antennular peduncle. Carpocerite as long as or slightly surpassing antennular peduncle. Distoinferior margin of basicerite bearing 2 small acute spines.

Third maxilliped exceeding antennules. Ratio of article lengths 10:6:2.

First chelipeds 0.4× length of third maxillipeds, symmetrical. Ischium 0.6× merus, bearing rounded protrusion on inferior margin. Merus 3× long as broad. Carpus 4× long as broad distally, with distal end 1.8× as broad as proximal and bearing 1 stout spine or knob on lateral margin. Chela about as broad as carpus, but not as long, with fingers 0.7× length of palm.

Carpal articles of second legs 4, with length ratio of 10:4:3:4 progressing distally.

Third legs with ischium unarmed, shorter than merus. Merus 3× as long as broad, bearing large spine subterminally on inferior margin. Carpus 0.7× merus, broadened

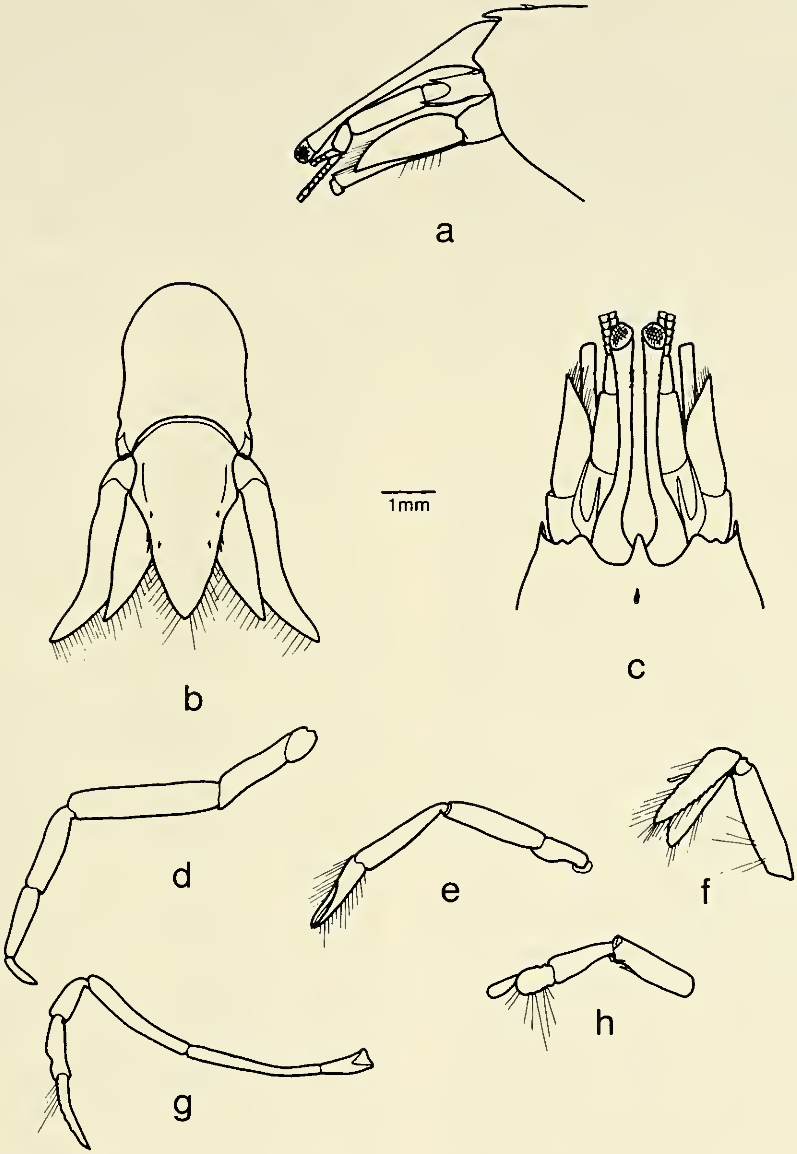

Fig. 1. *Ogyrides tarazonai,* paratype, female: A, Lateral view of front; b, Telson and uropods; c, Frontal region in dorsal view; d, Fourth pereopod; e, First pereopod; f, Second pleopod; g, Fifth pereopod; h, Third pereopod. Third maxillipeds, second pereopods and thelycum-like structure broken or missing in this specimen.

distally and bearing many long setiferous bristles. Propodus stout, 1.7× long as broad, with setose margin, bases of setae forming serrate edge. Dactyl spatulate, shorter than propodus. Fourth legs slender, ischium 0.6× merus. Merus 5× as long as broad, bearing long setae. Carpus 0.6× merus. Propodus shorter than carpus, tapered distally. Both carpus and propodus bearing long setae. Dactyl curved, spatulate, 0.5× propodus. Fifth legs very slender, ischium about equal to merus, merus 6× as long as broad, carpus shorter than propodus, propodus and dactyl of approximately equal length. Propodus and dactyl setose, dactyl spatulate.

Thelycum-like structure of female narrow and elongate, lying between coxae of fourth legs and ventral to sternal plates, anteriorly reaching bases of third legs, anterior margin with V-shaped cleft, lateral margins nearly straight, posterior margins apparently attached to coxae of legs and to sternum. Coxae of fifth legs bearing lobes joining as low, continuous process reaching from leg to leg.

Second pleopod with appendix interna on endopod.

Telson 1.8× as long as broad, tip subacute, part distal to posterolateral spines representing 0.4 of total telson length. Lateral margins bearing broad, low rounded projection just anterior to middle. Outer spines of posterolateral pair short, inner spines longer. Low ridges on dorsal surface of telson. Two pairs of dorsal spines, difficult to see, well separated. Both uropod rami exceeding telson.

Type material.—Holotype: female, total length in millimeters 19.4; Ventanilla (11°50′S), Peru, shallow water, 40 m from high tide line, 18 Mar 1984, Juan Tarazona, IMARPE.—Paratype: female, ovigerous, total length 27.7; about 15 km S of San Juan del Sur, Pacific coast of Nicaragua, 27 Jan 1974, A. J. Ferreira, CAS 044016.

Remarks.—Only one other species of *Ogyrides* has only a single dorsal spine on the carapace. *Ogyrides hayi* Williams, from the western Atlantic, shares this feature with *O. tarazonai,* as well as also having four segments in the carpus of the second pereopod. However, *O. hayi* has a spine on the ischium of the third leg. The spines on its stylocerite do not reach or surpass the first segment of the antennular peduncle.

Of the two specimens of the new species, the holotype is more intact. We deposited the holotype at the Instituto del Mar del Peru, hoping to illustrate it later. Unfortunately, neither of us was able to return to Callao to draw this specimen, nor did we trust the postal service to send the holotype to us safely. We therefore illustrated what we could from the paratype, which is broken and damaged on the ventral surface. The description in the text is of the holotype.

Etymology.—The specific epithet honors Juan Tarazona, collector of the new species and dedicated benthic ecologist.

Ogyrides alphaerostris (Kingsley)

Ogyris alphaerostris Kingsley, 1880:420, pl. 14, fig. 7.

Ogyrides alphaerostris.—Williams, 1981: 144; 1984:107, fig. 74.—Carvacho & Olson, 1984:66, figs. 3–4. (See Williams, 1981, for a fuller synonymy.)

Material.—Off Huntington Beach, California (33°38′30″N, 118°03′00″W), 26–28 m, sand, 20 Apr 1940, *Velero III* sta 1127–40, 1 specimen, AHF.

Remarks.—The specimen from off Huntington Beach agrees with the description of *O. alphaerostris* as given by Williams (1984). The number of dorsal spines on the carapace of this species is variable, ranging from three to 14. The specimen from California bears nine carapace spines.

We have been unable to reexamine the specimens of *Ogyrides* mentioned in the monograph by Wicksten (1983). These probably belong to *O. alphaerostris,* which we have identified in grab samples from off the coast of Sinaloa, Mexico. The latter records will be published elsewhere in a report on benthic decapod crustaceans of Sinaloa (M. E. Hendrickx, pers. comm.).

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NOTES ON ALBUNEID CRABS (CRUSTACEA: DECAPODA: ALBUNEIDAE) FROM THE CENTRAL EAST COAST OF FLORIDA

Raymond B. Manning

Abstract.—Three species are reported: *Albunea paretii* Guérin-Méneville, 1853, *Lepidopa benedicti* Schmitt, 1935, and *L. websteri* Benedict, 1903. The latter species is recorded from southeast Florida for the first time. Study material includes rare males of both species of *Lepidopa.* A key to western Atlantic albuneids is presented.

Until now, one species of the albuneid genus *Lepidopa* Stimpson, 1858, *L. benedicti* Schmitt, 1935, had been reported from the southeast coast of Florida (Holthuis 1960, Efford 1971). Of the six Atlantic species of the genus, only two, *L. benedicti* and *L. websteri* Benedict, 1903, had been reported from localities in Florida (Efford 1971, Gore et al. 1978, Abele & Kim 1986), although a larva, tentatively identified with a third species, *L. richmondi* Benedict, 1903, was taken in the plankton east of Jupiter Inlet, Martin County, on the Atlantic coast of Florida (Gore & Van Dover 1981).

In 1982 and 1983, collections made with a yabby pump in the vicinity of Fort Pierce, Florida, yielded material of both *L. benedicti* and *L. websteri* at one locality on the Atlantic coast just north of the St. Lucie Inlet (St. Lucie site of Gore et al. 1978).

There are few records for members of *Albunea* from the central east coast of Florida, although this is well within the known range of the two western Atlantic species. Material available for study included a specimen from the Indian River at Fort Pierce.

East American Species of Albuneidae

The east American albuneids comprise ten species in four genera: *Albunea* Weber, 1795 (two species), *Blepharipoda* Randall, 1840 (one species), *Lepidopa* Stimpson, 1858 (six species), and *Zygopa* Holthuis, 1960 (one species). In all, the family now includes seven genera; Efford & Haig (1968) provided a key to the genera.

The two species of *Albunea* Weber (1795:94), *A. gibbesii* Stimpson (1859:78) and *A. paretii* Guérin-Méneville (1853:48), were treated by Williams (1984) and Abele & Kim (1986). Both have wide ranges in the Americas, from the Carolinas to Brazil, and *A. paretii* also occurs off West Africa.

The single east American species of *Blepharipoda* Randall (1840:130), *B. doelloi* Schmitt (1942:2), is known only from Argentina.

Efford (1971) reviewed the American species of *Lepidopa* Stimpson (1858:230), and recorded five species from the Atlantic coast of the Americas. Since then a sixth east American species, *L. dexterae* Abele & Efford, 1972, has been described from Panama. Efford (1971:99) recognized four species groups in the genus: *Myops, benedicti, venusta,* and *californica.* The first three of these are represented in the western Atlantic.

The following species of *Lepidopa* are known from the western Atlantic:

L. benedicti Schmitt (1935:210); southeastern and northwestern Florida to southeast of Veracruz, Mexico, in the Gulf of Mexico.

L. dexterae Abele & Efford (1972:502); Panama.

L. distincta Corrêa (1968:77); Dominican Republic and Brazil.

L. richmondi Benedict (1903:895); West Indies and Caribbean Sea to Brazil.

L. venusta Stimpson (1859:79); West Indies to Brazil.

L. websteri Benedict (1903:892); Atlantic coast of southeastern United States.

The genus *Zygopa* was established by Holthuis (1960:21) for *Z. michaelis* Holthuis (1960:22), from Curaçao. Since its original description, *Z. michaelis* has been recorded from off Palm Beach and Miami on the east coast of Florida (Gore & Becker 1977), and from the Florida west coast (Reames et al. 1982).

The east American albuneids can be distinguished by means of the following key.

1. Carapace with 4 lateral spines [*Blepharipoda*] .... *B. doelloi* Schmitt
– Carapace with 1 lateral spine 2
2. Carapace lacking median spine or angled projection on anterior margin. Eyes very small, fused together [*Zygopa*] ...... *Z. michaelis* Holthuis
– Carapace with median spine or angled projection on anterior margin. Eyes separate 3
3. Eyes narrow, elongate, with distinct cornea. Lateral spine of carapace below linea anomurica [*Albunea*] ... 4
– Eyes (eye plates) broad, oval or squarish, lacking distinct cornea. Lateral spine of carapace above linea anomurica [*Lepidopa*] 5
4. Dactyli of second and third pereopods with blunt lobe basally on anterior border .... *A. gibbesii* Stimpson
– Dactylus of second pereopod with broad spur, of third pereopod with acute, slender spur at base of anterior border .... *A. paretii* Guérin-Méneville
5. Eye plates distinctly squarish, flattened anteriorly, anterior edge with teeth or denticles [*benedicti* Group] 6
– Eye plates round or oval, anterior edge smooth 8
6. Groove along posterior edge of carapace continuous, not interrupted in middle of posterior margin [subrostral spine present] .... *L. richmondi* Benedict
– Groove along posterior edge of carapace interrupted medially 7
7. Subrostral spine present .... *L. dexterae* Abele & Efford
– Subrostral spine absent .... *L. benedicti* Schmitt
8. Antennal flagellum with 7 articles. Carpus of third maxilliped extending over propodus, overlapping dactylus. Subrostral spine absent [*myops* Group] ....*L. distincta* Corrêa
– Antennal flagellum with 8 articles. Carpus of third maxilliped not extending to dactylus. Subrostral spine present [*venusta* Group] 9
9. Width of emargination in edge of second abdominal somite no greater than length of this somite along midline. Anterior margin of carapace extending in almost straight line between base of orbit and anterolateral projection ... *L. websteri* Benedict
– Width of emargination in anterior edge of second abdominal somite greater than length of this somite along midline. Anterior margin of carapace with distinct anterior bulge between base of orbit and anterolateral projection ... *L. venusta* Stimpson

Almost all of the material reported here was taken at the same site (St. Lucie, Atlantic, of Manning collections; see Manning & Felder, in press). Locality data are as follows: Atlantic Ocean, Florida, Martin County, about 1 mile north of St. Lucie Inlet, 27°10.9′N, 80°09.5′W, shallow sand flat between emergent sabellariid reef and sand beach. Most of the specimens were taken with a yabby pump, a suction device used to sample infaunal organisms; some were

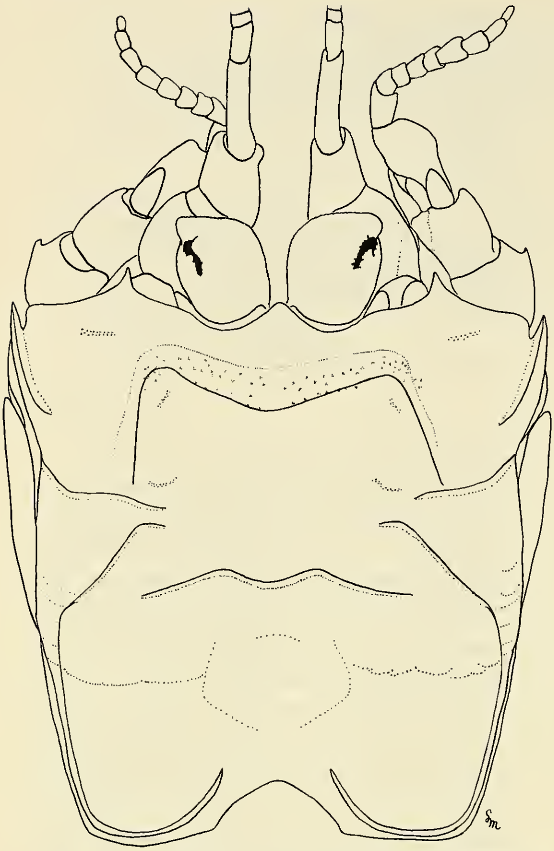

Fig. 1. *Lepidopa benedicti* Schmitt, female, cl 5.0 mm, sta FP-82-2: Carapace.

taken with a garden rake, used on sand at the edge of the wave line. The lepidopas were disturbed by the rake and could be seen re-burying themselves.

Specimens have been deposited in the Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, Fort Pierce, Florida (IRCZM), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Albunea paretii Guérin-Méneville, 1853

Albunea paretii.—Gore & Becker, 1977:220 [no material].—Young, 1978:177 [South Carolina].—Williams, 1984:249, fig. 183 [original citation and other references given here].—Fox & Ruppert, 1985:52, 122, 128, 259, 286 [South Carolina].—Abele & Kim, 1986:x, 38, 427, 428, 748, figs. d–g on p. 429 [Florida].—Chace et al., 1986:338, fig. on pl. 112 [Bermuda].

Albunea paretti.—Pequegnat, 1975:45 [no localities].

Material.—Florida, St. Lucie County, Indian River, island west of Coon Island, Fort Pierce Inlet; intertidal, with yabby pump; 6 Mar 1985; W. D. Lee and S. Petry; 1 male (USNM).

Size.—Carapace length of male 10.9 mm.

Remarks.—There are other representatives of this species from off Jacksonville Beach, off Daytona Beach, and off Cape Canaveral in the collections of the National Museum of Natural History. The species has a wide range in the Atlantic, from North Carolina to Texas, the West Indies to Brazil, and off West Africa (Holthuis & Manning 1970, Williams 1984).

Lepidopa benedicti Schmitt, 1935
Fig. 1

Lepidopa scutellata.—Benedict, 1903:891, 894, fig. 6 [Pensacola and Morris Cut, Miami; not *L. scutellata* Fabricius, 1793].

Lepidopa benedicti Schmitt, 1935:210 [Replacement name for *L. scutellata* sensu Benedict, 1903].—Holthuis, 1960:31, 32, 33, 34, 35, fig. 5 [several records, from east coast of Florida to southwest coast of Texas; lectotype selected].—Efford, 1971:76, figs. 1a, 2e, 3a, 4e, p, q, 5a, 6e, n, 7a [Florida to Mexico].—Gore & Becker, 1977:220 [no material].—Gore et al.,1978:231, 247 [central east Florida].—Gore & Van Dover, 1981:1016, 1030, 1033 [southeastern and central eastern Florida; no material].—Abele & Kim, 1986:x, 38, 427, 428, 752, fig. h on p. 429 [Florida].

Material.—RBM stations: FP-82-2, 13 Jul 1982, R. B Manning and C. W. Hart, Jr., yabby pump, 1 female. FP-82-7, 16 Jul 1982, R. B. Manning, yabby pump, 1 male [taken together with *L. websteri*]. FP-83-6, 13 Jul 1983, R. B. and L. K. Manning, W. D. Lee, rake, 1 male, 2 females [taken together with *L. websteri*]. All specimens USNM.

Vero Beach, 100 meters south of South Beach Park, along shore, in colony of *Emerita,* 4 Mar 1973, 1 female (IRCZM 89:514).—Fort Pierce Inlet, St. Lucie County, worm reef, 6 Feb 1974, 1 female (IRCZM 89:2558).—Walton Rocks, St. Lucie County, worm reef, LES, LB, MGR leg., 19 Jul 1974, 1 female (IRCZM 89:2604).

Size.—Carapace lengths of 2 males, 3 mm and 3.5 mm, of 6 females, 4.5 to 17 mm. Efford (1971) reported that the largest specimen known was a female 22 mm long; he studied only 2 males, the largest measuring 4 mm.

Remarks.—Eye pigment is present in all of these specimens, two lots of which were taken together with *L. websteri.*

Apparently these specimens are from the northernmost locality known for this species on the east coast of Florida, and they demonstrate that the species is fairly common off the Florida east coast.

The specimens in the collections of the Indian River Coastal Zone Museum may have been the basis for the comment by Gore & Van Dover (1981:1016), "The second continental species, *L. benedicti* Schmitt, 1935, occurs in the Gulf of Mexico and along the southeastern and central eastern Florida coastline (. . . Gore, unpublished)."

Lepidopa websteri Benedict, 1903
Figs. 2, 3

Lepidopa websteri Benedict, 1903:891, 892, fig. 3 [Fort Macon, North Carolina].—Efford, 1971:91, figs. 1b, k, 2j, 3r, 4h, m, 5g, i, 6o [North Carolina, South Carolina, west Florida, Mississippi].—Gore & Becker, 1977:220 [no material].—Young, 1978:177 [South Carolina].—Williams, 1984:250, fig. 184 [additional records from Sapelo Island, Georgia, and Petit Bois Island, Mississippi].—Fox & Ruppert, 1985:39, 114, 122, 129, 187, 196, 259, 286 [South Carolina].—Abele & Kim, 1986: x, 38, 427, 428, 752, fig. i on p. 429 [Florida].

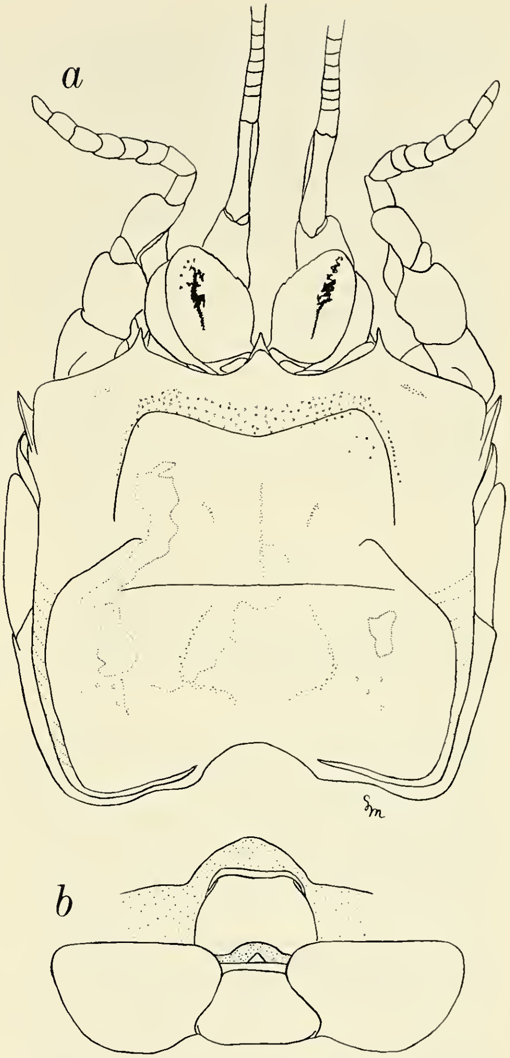

Fig. 2. *Lepidopa websteri* Benedict, female, cl 5.0 mm, sta FP-83-3: a, Carapace; b, Second abdominal somite.

Material.—RBM stations: FP-82-7, 16 Jul 1982, R. B. Manning, yabby pump, 1 female [taken with *L. benedicti*]. FP-83-3, 8 Jul 1983, R. B. and L. K. Manning, yabby pump,

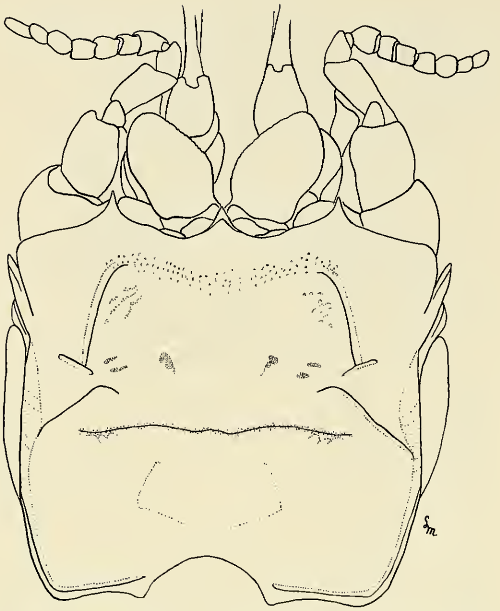

Fig. 3. *Lepidopa websteri* Benedict, female, cl 9.0 mm, sta FP-84-4: Carapace.

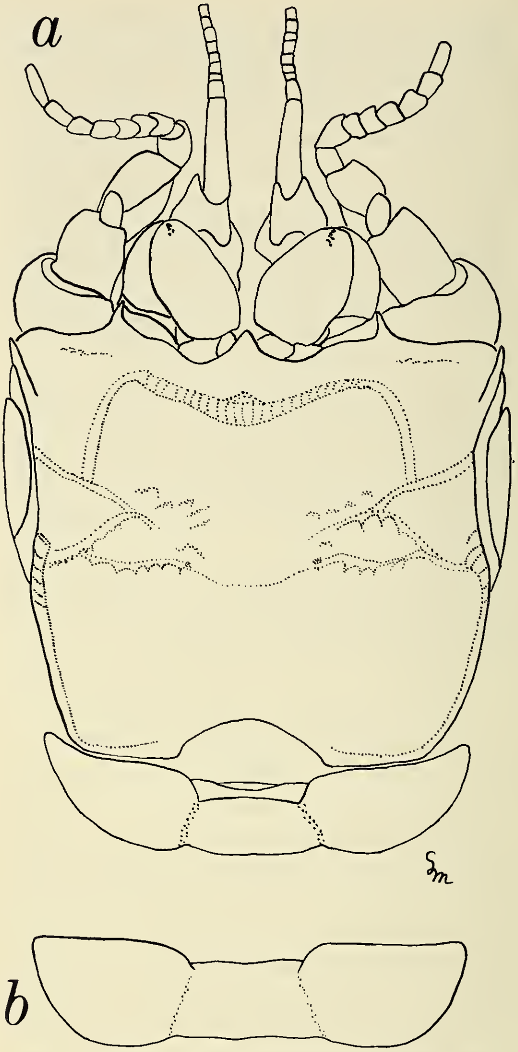

Fig. 4. *Lepidopa venusta* Stimpson, female, cl 6.5 mm, Trinidad (USNM 141353): Carapace.

1 female. FP-83-6, 13 Jul 1983, R. B. and L. K. Manning, W. D. Lee, rake, 1 male [taken with *L. benedicti*]. FP-84-4, 10 Jul 1984, R. B. and L. K. Manning, D. L. Felder, and W. D. Lee, yabby pump, 1 female.

Specimen from FP-82-7 deposited in IRCZM, remainder deposited in USNM.

Size.—Carapace length of male, 4 mm, of 3 females, 5 to 9 mm. Williams (1984) reported a specimen 19 mm long, and Efford (1971) reported a male 6 mm long.

Remarks.—The male and the smallest female (Fig. 2) differ from the two larger specimens (Fig. 3) in having a distinct elongate patch of dark pigment in each eye; this pigment is completely absent in larger specimens of this species. Efford (1971:61) noted that eye pigment was always present in juveniles.

Until now this species was not known south of Sapelo Island, Georgia, on the Atlantic coast of the United States (Williams 1984). Like some other Carolinian species generally considered to be restricted to the Carolinas and Georgia on the Atlantic coast, e.g., *Callichirus major* (Say, 1818) (see Manning & Felder 1986) and *Pinnixa cristata* Rathbun, 1900 (see Manning & Felder, in press), this species appears to be not uncommon in the central Florida east coast.

Efford (1971:91) noted that "the easiest character separating *venusta* from *websteri*" is the presence in *L. venusta* of a bulge or obtuse projection on the anterior margin of the carapace, between the ocular sinus and the anterolateral spine. This is a subtle but distinctive character, and as I can find no published figure of the carapace of *L. venusta* in which this feature is well illustrated, I provide here a figure of *L. venusta* (Fig. 4). Curiously, Efford (1971), in his revision of *Lepidopa,* gave no figure of the carapace of *L. venusta.* The only recent figure of the carapace of this species was given by Gomes (1965); in it the bulges are not well marked.

Acknowledgments

This study was carried out at the Smithsonian Marine Station at Link Port, Fort Pierce, Florida, and is contribution number 199 from that laboratory. The help of W. D. Lee in the field is gratefully acknowledged. I thank Paula Mikkelsen for allowing me to study material of *Lepidopa* in the collection of the Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, and Richard Heard, Gulf Coast Research Laboratory, for reading a draft of the manuscript. The figures were prepared by my wife Lilly.

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HETEROCARPUS CUTRESSI, NEW SPECIES, AND *PLESIONIKA MACROPODA* CHACE, 1939: TWO CARIDEAN SHRIMPS OF THE FAMILY PANDALIDAE (CRUSTACEA: DECAPODA) FROM PUERTO RICO AND THE U.S. VIRGIN ISLANDS

Oscar E. Monterrosa

Abstract.—Two species of deep-water (320–777 m) pandalid shrimps (Crustacea: Decapoda: Caridea) are reported. Previously undescribed, *Heterocarpus cutressi,* n. sp., has two longitudinal lateral carinae with the dorsalmost originating anteriorly at the antennal spine; the abdomen has a blunt median ridge on the third, fourth, and fifth somites. *Plesionika macropoda* Chace, 1939 has the dorsal surface of the rostrum smooth except for eight to 10 teeth on the basal crest; the dactyls of the walking legs are armed with five teeth along the posterior margin. Specimens of both species were collected in baited, wire-mesh traps.

In this paper, a prelude to a more complete report on deep-water shrimps collected in the waters around Puerto Rico and the U.S. Virgin Islands, I describe one species of pandalid and redescribe another. The former is in the genus *Heterocarpus* A. Milne-Edwards, 1881, consisting of over 20 species and subspecies and characterized by a dorsal and at least one longitudinal lateral carinae (one exception) and with the second pair of pereopods unequal and dissimilar. The other belongs to the genus *Plesionika* Bate, 1888, with over 60 species, and characterized by a carapace without lateral carinae and an abdomen that is unarmed dorsally. A redescription of *Plesionika macropoda* Chace, 1939 was decided upon due to the lack of figures in the original description. For a thorough report on the Pandalidae, the reader is referred to Chace (1985).

Holotype and paratypes of *Heterocarpus cutressi* are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); paratypes are also deposited in the Museum of Natural History, Paris, France (MNHP); and in the Marine Invertebrate Museum of the University of Puerto Rico at the Department of Marine Sciences Field Station, Mayaguez, Puerto Rico (UPR).

Heterocarpus cutressi, new species
Figs. 1–3

Material.—Holotype: USNM 234162, 1 ♂, southwest of Puerto Rico, 17°51.7′N, 67°15.4′W, 777 m, 22 Dec 1983, coll. D. Hensley, 37.4 mm carapace length.

Paratypes: USNM 234163, 1 ♂, 1 ♀ (ovig.), south of Puerto Rico, 17°54.3′N, 66°51.0′W, 500 m, 28 Mar 1985, coll. O. Monterrosa; UPR, 2 ♂, St. Thomas, U.S. Virgin Islands, May 1983, coll. M. Brandon; UPR, 1 ♀, north-northwest of Buck Island, St. Croix, U.S. Virgin Islands, 550–650 m, Jun–Jul 1985, coll. I. Clavijo.

Size of paratypes (carapace length): male, 23.8–37.3 mm ($n = 3$); female, 36.1 mm; ovigerous female, 34.2 mm.

All specimens were captured in baited wire-mesh fish traps.

Description.—Rostrum somewhat longer than carapace in smaller specimens, slightly shorter than carapace in larger ones, di-

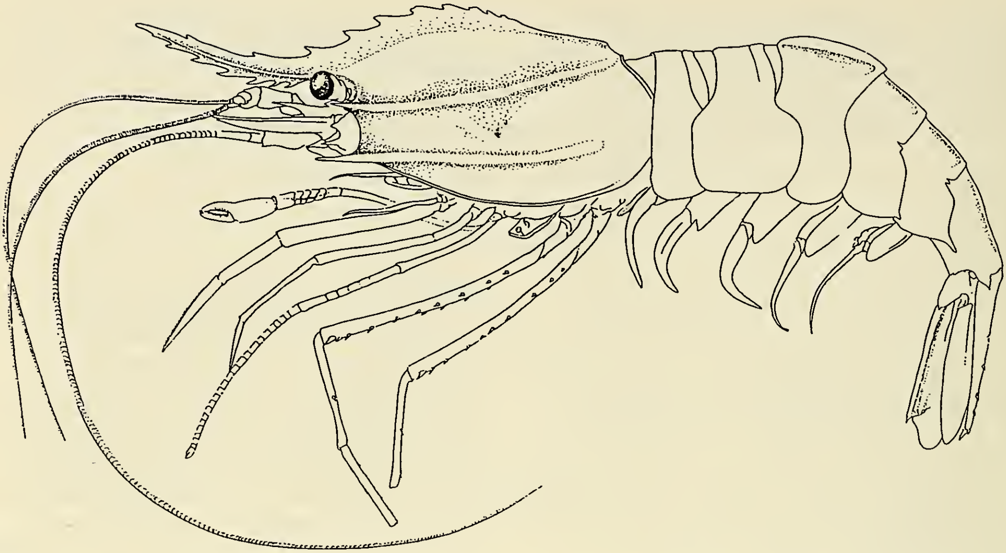


Fig. 1. *Heterocarpus cutressi,* male holotype from South Puerto Rico, carapace length 37.4 mm (Magnification: ×1.8).

rected slightly dorsad, with lateral carina extending over posterior ⅔–⅞ of length; armed with 10 or 11 dorsal teeth extending to anterior end, including 5–7 postorbital teeth, armed ventrally with 6–10 teeth. Carapace with median postrostral ridge nearly complete; with 2 lateral carinae, dorsalmost directly in line with antennal spine and extending to posterior margin, lateral carina reaching ⅔ to ¾ carapace length; with slight depression found at midlength, between carinae; branchiostegal spine slightly overreaching antennal spine (Fig. 1).

Abdomen (Fig. 2A) with 1st and 2nd somites rounded dorsally, 3rd somite with distinct middorsal carinae, somites 4 and 5 slightly carinate middorsally, somite 6 with subparallel ridges partially subdivided by a middorsal sulcus. Pleuron 4 with small posteroventral tooth, pleuron 5 posteroventrally produced into elongate spine. Telson 1⅜ length of 6th somite, with shallow middorsal concavity reaching almost to posterior tip; 5 pairs of dorsolateral spinules, posteriormost pair situated dorsolateral to base of long, lateral spine of 2 apical pairs.

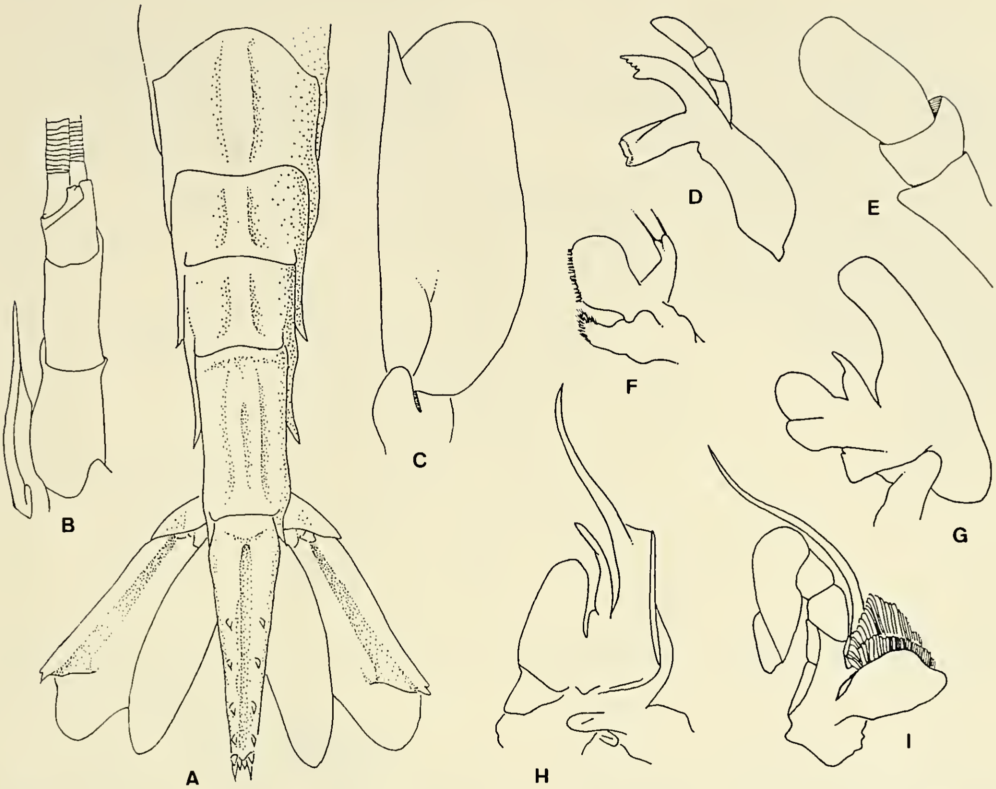
Eye subpyriform, maximum diameter about ⅑ of carapace length; ocellus lacking.

Antennular peduncle (Fig. 2B) with stylocerite acute, reaching at least to midlength of external margin of 2nd segment of peduncle.

Antennal scale (Fig. 2C) with blade slightly overreaching distolateral spine, distal margin broadly rounded.

Mouthparts (Fig. 2D–I) as illustrated. Mandibular palp (Fig. 2D) with basal article lobate at inner distal angle, 2nd article (Fig. 2E) broad, about ½ length of terminal article. Third maxilliped overreaching antennal scale by ⅔ length of terminal article, armed terminally with small corneous spine, penultimate segment about ⅔ length terminal segment.

Pereopods with well-formed epipods on 4 anterior pairs. First pereopod slightly overreaching antennal scale; fingers small (Fig. 3D), less than 1 mm in length, with single apical spine on each finger. Second pair of pereopods with shorter one (Fig. 3C) reaching distal ⅘–⅞ of antennal scale, chela subequal to carpus in length, fingers with



Figs. 2. *Heterocarpus cutressi,* male holotype from South Puerto Rico: A, Posterior part of abdomen, dorsal aspect including telson and uropods; B, Left antennule, dorsal aspect; C, Left antennal scale, dorsal aspect; D, Right mandible; E, Right mandibular palp, reverse aspect; F, Left 1st maxilla; G, Left 2nd maxilla; H, Left 1st maxilliped; I, Left 2nd maxilliped (Magnifications: A, ×3.2; B, C, D, F, G, H, I, ×65.; E, ×13.5).

entire cutting edges, subequal to palm in length, carpus comprising 6 articles, ischium carinate along posterior margin; longer 2nd pereopod (Fig. 3E) overreaching antennal scale by lengths of chela and distal ½ of carpus, latter with 22–25 articles. Third pereopod (Fig. 3D) extending beyond antennal scale by lengths of dactyl, propodus and distal ¼ to ⅜ of carpus; dactyl (Fig. 3E) ⅙ length of propodus, with 5 spines on posterior margin; carpus, in addition to row of spines along posterior margin, with 1 or 2 spines on lateral margin at ⅓–⅔ its length; 3 distal segments, combined, slightly longer than carapace. Fourth pereopod overreaching antennal scale by lengths of dactyl and propodus; dactyl as in 3rd pereopod; 1 or 2 spines projecting posterolaterally from carpus; 3 distal segments, combined, slightly longer than carapace. Fifth pereopod overreaching antennal scale by length of dactyl and ⅔–¾ of propodus; dactyl as in 3rd and 4th pereopods; carpus with accessory spine projecting midlaterally; 3 distal segments, combined, 1⅒–1⅖ as long as carapace.

Endopod of first pleopod of male (Fig. 3F) nearly ½ length of exopod, distally broadened with mesial margin strongly sinuous, bearing minute hooks, without obvious notch or sinus. Appendix masculina of 2nd pleopod (Fig. 3G) armed with over 20 spines of varying lengths on anteromesial and distal margins (Fig. 3H). Exopod of 3rd pleopod about ⅖ as long as carapace. Mesial

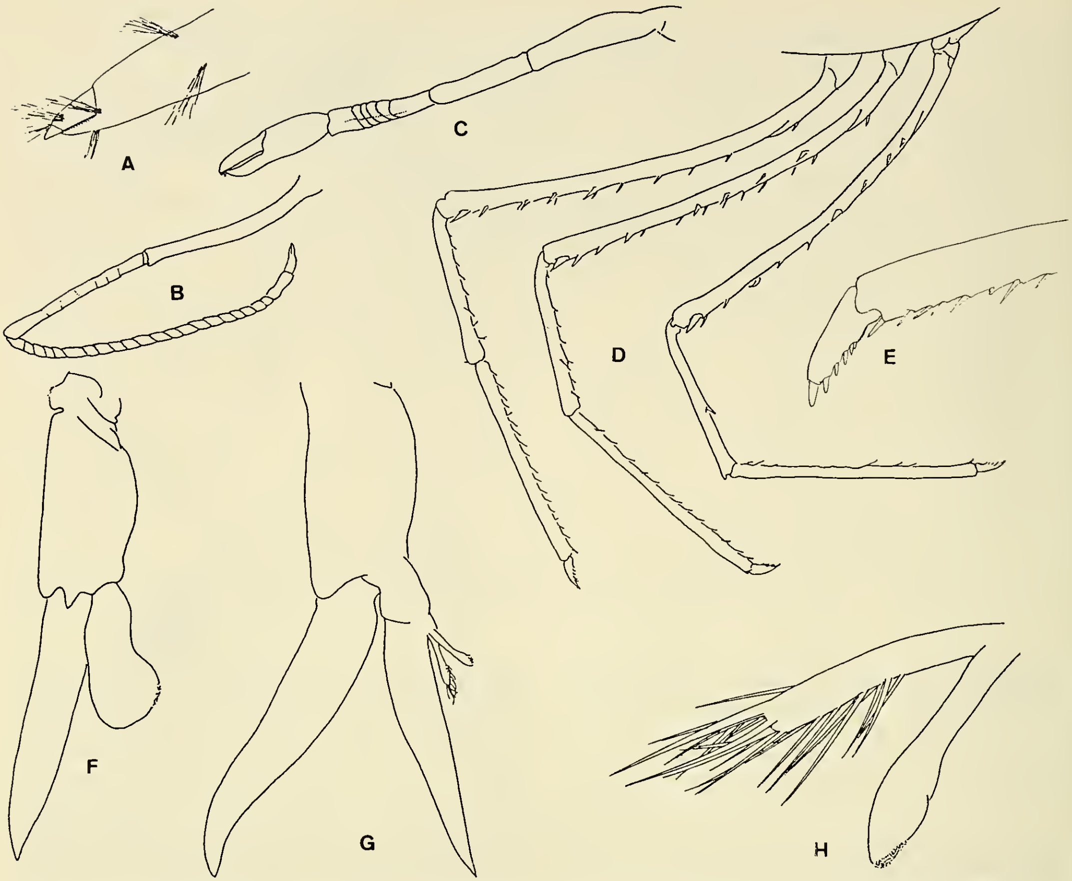


Fig. 3. *Heterocarpus cutressi,* A–C, F–H, male holotype from South Puerto Rico; D, E, male paratype from southwest Puerto Rico: A, Chela left 1st pereopod; B, Left 2nd pereopod; C, Right, same; D, Left 3rd, 4th, 5th pereopod; E, Dactyl left 3rd pereopod; F, Right 1st pleopod; G, Right 2nd pleopod showing appendices masculinae and internae; H, Right appendices masculinae and internae, mesial aspect (Magnifications: D, ×3.2; B, C, F, G, ×6.7; E, ×12.4; A, ×25; H, ×37.5).

branch of uropod slightly overreaching telson proper; lateral branch slightly longer.

Coloration.—Integument orange-red except for white areas on midlateral surface and dorsal posterior margin of carapace, lateral surface of each abdominal somite, base of uropods, telson, antennal scale and basicerite. Ova red-brown.

Habitat.—A sediment sample for one of the trapping stations indicated a mud bottom.

Remarks.—Of the 21 species and subspecies within *Heterocarpus,* only *H. cutressi* and the Indo-Pacific *H. woodmasoni* Alcock, 1901 have a carapace with the dorsalmost of two lateral carinae originating anteriorly at the antennal spine (i.e., directly in line). The West Indian species is easily distinguished from *H. woodmasoni* by the absence of the median tooth near the midlength of the 3rd abdominal somite of the latter species (Chace 1985).

Etymology.—It is a pleasure to name this species for Prof. Charles E. Cutress who inspired this investigation. His experience includes 22 years of dedicated teaching of ma-

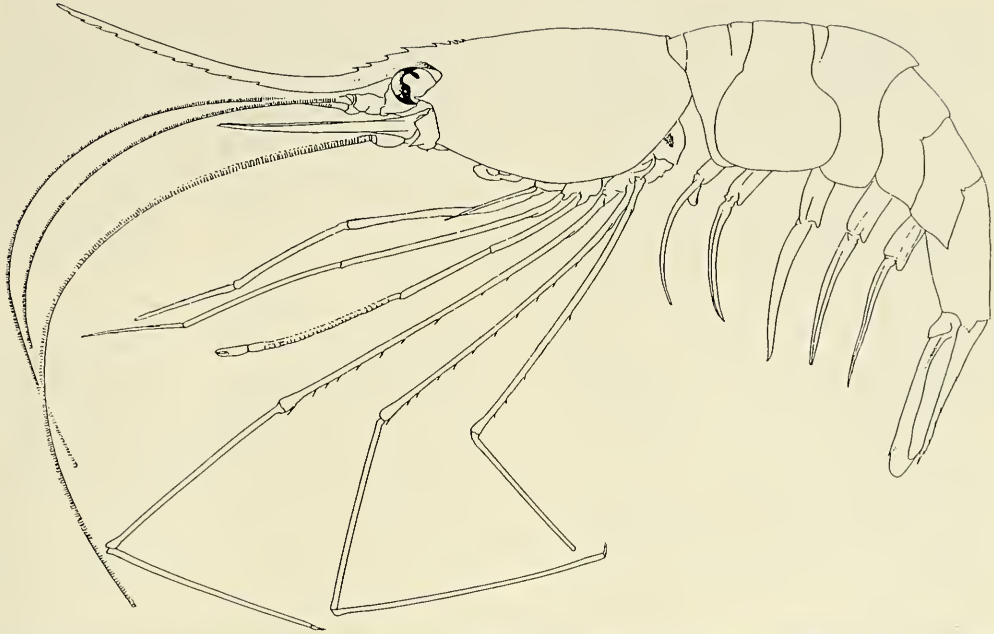


Fig. 4. *Plesionika macropoda,* female holotype from West Puerto Rico, carapace length 21.3 mm (Magnification: ×4.9).

rine invertebrate systematics and biology in the Department of Marine Sciences, University of Puerto Rico at Mayaguez.

Plesionika macropoda Chace, 1939
Figs. 4, 5

Plesionika macropoda. Chace, 1939:37.—Springer & Bullis, 1956:12.—Bullis & Thompson, 1965:8.

Material examined.—USNM, 1 ♂, 5 ♀ (3 ovig.), off Fredericksted, St. Croix, U.S. Virgin Islands, 320 m, 27 Aug 1982, coll. W. Tobias; USNM, 3 ♂, 1 ♀, north of Mona Island, Puerto Rico, 18°14.3′N, 67°52.7′W, 500 m, 10 Mar 1984, coll. O. Monterrosa; UPR, 5 ♀ (2 ovig.), south Puerto Rico, 17°54.3′N, 66°51.0′W, 500 m, 28 Mar 1985, coll. O. Monterrosa; UPR, 2 ♀ (1 ovig.), north St. Thomas, U.S. Virgin Islands, 550–650 m, Jun–Jul 1985, coll. I. Clavijo; MNHP, 5 ♂, 2 ♀, south Puerto Rico, 17°53.6′N, 66°55.1′W, 475 m, 7 Oct 1985, R/V *Chapman,* NMFS, cruise no. 507, sta 28; UPR, 1 ♀, south Puerto Rico, 17°53.2′N, 66°54.6′W, 615 m, 11 Oct 1985, R/V *Chapman,* NMFS, cruise no. 507, sta 34.

Size of material examined (carapace length): males, 16.4–20.8 mm (n = 9); females, 9.5–21.3 mm (n = 10); ovigerous females, 20.6–22.1 mm (n = 6).

All specimens were captured in baited, wire-mesh fish traps, except 1 ♀ from R/V *Chapman,* sta 34, which was collected in a bottom trawl.

Geographic range.—Collections of *Plesionika macropoda* have been few but the species appears to be distributed throughout the Greater and Lesser Antilles (Cuba, Chace 1939; Gulf of Mexico, Springer & Bullis 1956; Guadeloupe, Crosnier, pers. comm.; and Puerto Rico and the U.S. Virgin Islands).

Bathymetric range.—Specimens have been collected between 320–650 m.

Remarks.—Apart from *Plesionika mac-*

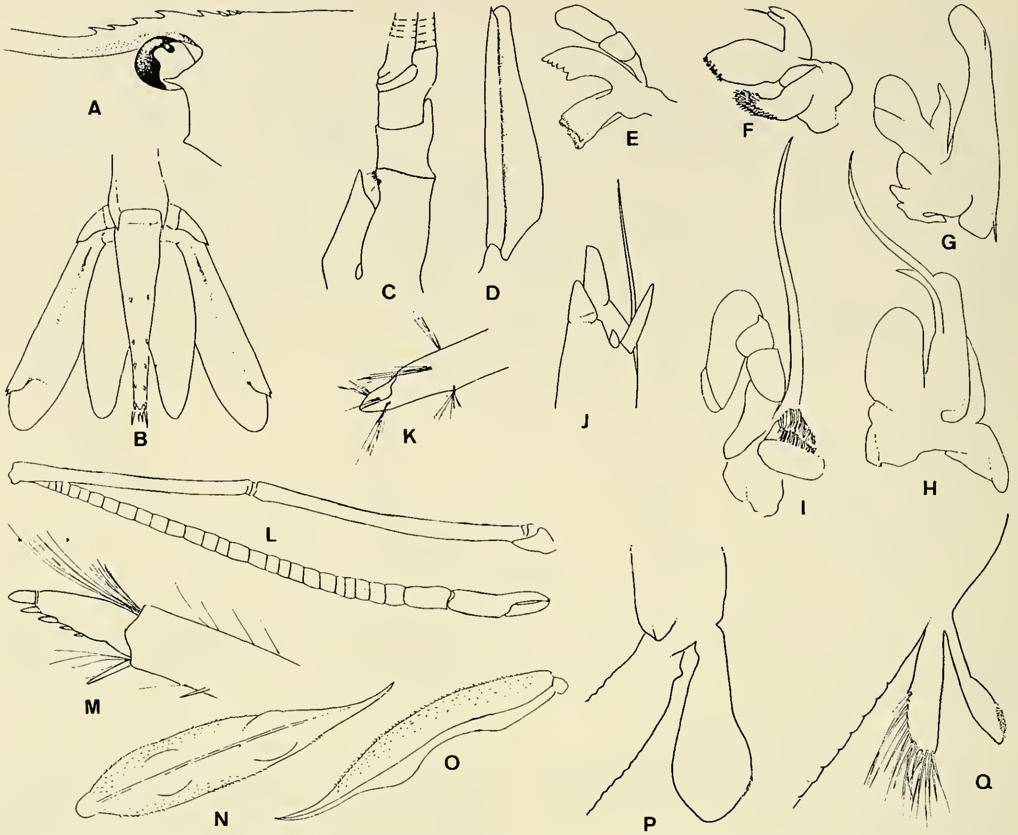


Fig. 5. *Plesionika macropoda,* A–O, female holotype; P, Q, male paratype from West Puerto Rico: A, Left eye and orbit; B, Telson and uropods, dorsal aspect; C, Left antennule, mesiodorsal aspect; D, Left antennal scale, dorsal aspect; E, Left mandible; F, Left 1st maxilla; G, Left 2nd maxilla; H, Left 1st maxilliped; I, Left 2nd maxilliped; J, Distal end of left 3rd maxilliped; K, Chela of left 1st pereopod; L, Left 2nd pereopod; M, Dactyl and distal end of propodus of left 4th pereopod; N, Tegumental scale from posterodorsal area of carapace; O, Same, lateral aspect; P, Endopod of left 1st pleopod; Q, Left appendices masculinae and internae, mesial aspect (Magnifications: A, B, D, ×3.2; C, E–I, L, ×6.4; P, ×13.2; K, M, Q, ×25; J, ×165; N, O, ×323).

ropoda Chace, 1939, other western Atlantic members of the genus having a rostrum that is dorsally smooth (excluding the basal crest) include *P. polyacanthomerus* Pequegnat, 1970 and *P. martia* (A. Milne-Edwards, 1883). *Plesionika polyacanthomerus* is easily differentiated by the presence of a broad curved ridge on the lateral surface of the carapace (Pequegnat 1970). *Plesionika martia* on the other hand, has a rostrum with fewer dorsal teeth at the basal crest (5–9 vs. 8–10 for *P. macropoda*) and considerably more ventral teeth (34–56 vs. 9–14 respectively) (Pequegnat 1970; Crosnier & Forest 1973, fig. 63d). In addition, dactyls of the walking legs of *Plesionika martia* are armed with a single terminal tooth (A. Milne-Edwards 1883, pl. 21), dactyls of *P. macropoda* have 5 teeth.

To my knowledge, *Plesionika edwardsii* (Brandt, 1851) and *P. macropoda* are the only two species within the genus to have multiple teeth along the posterior margin of the dactyls, *P. edwardsii* having 4 (Chace

1985, fig. 26e) and *P. macropoda* with 5 (includes terminal tooth in both cases). Features distinguishing *P. macropoda* from *P. edwardsii* respectively, include longer walking legs, a rostrum with fewer dorsal teeth (8–10 vs. 28–34), color of the eggs (red-brown vs. blue), and well-formed versus vestigal epipods.

Acknowledgments

I am grateful to Dr. Fenner A. Chace, Zoologist Emeritus, National Museum of Natural History, for his invaluable and unselfish assistance throughout the course of this study. In addition, Dr. Alain Crosnier of the Division of Crustacea, Museum of Natural History in Paris, contributed important suggestions to the revision of the manuscript. My sincere thanks to the Smithsonian Institution, especially to members of the Division of Crustacea, and to Prof. C. Cutress, Mrs. B. Cutress, and Dr. R. Appeldoorn of the University of Puerto Rico at Mayaguez, who provided helpful comments and assistance.

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101(3), 1988, pp. 640–643

NOTES ON THE FRESHWATER CRABS OF THE GENUS *MORITSCHUS* PRETZMANN, 1965 (CRUSTACEA: DECAPODA: PSEUDOTHELPHUSIDAE) WITH DESCRIPTION OF *M. NARINNENSIS* FROM SOUTHERN COLOMBIA

Martha R. Campos and Gilberto Rodríguez

Abstract.—*Moritschus narinnensis,* n. sp. adds a second species to a genus of pseudothelphusid crabs previously considered to be monotypic. The distribution of the genus appears to be confined to the high mountains of the Pacific slope of the Western Cordillera of Colombia and Ecuador, in areas neighboring the boundary between them, but their closest affinities are with *Hypolobocera henrici* from the Amazonian drainage of Ecuador and Perú. The generic diagnosis is redefined to accommodate the new species and a key is given to separate the two taxa.

In 1897, Mary J. Rathbun, following the system of genera of freshwater crabs then in use, described a sample of small crabs collected by H. Deyrolle near Quito, Ecuador, which she named *Pseudothelphusa ecuadorensis.* Almost 70 years later, Pretzmann (1965) created the monotypic subgenus *Moritschus* of the genus *Hypolobocera,* to receive this species. In his monograph of the Pseudothelphusidae, Rodríguez (1982) gave generic status to *Moritschus* and mentioned the similarity of its gonopod to that of *Hypolobocera henrici,* a species from the Amazonian drainage of Ecucador and Perú. The species is fairly common around Quito and has been collected repeatedly in that area. Recent intensive collections in southern Colombia have revealed the presence there of a second, undescribed species of *Moritschus.*

The material is deposited at the Museum of Natural History, Universidad Nacional de Colombia, Bogotá (ICN-MHN), and in the reference collection of the Instituto Venezolano de Investigaciones Científicas (IVIC).

Tribe Hypolobocerini Pretzmann, 1971
Genus *Moritschus* Pretzmann, 1965
Moritschus ecuadorensis (Rathbun, 1897)

Material examined.—Alluriquin, affluent of Rio Toachi, SE of Santo Domingo de los Colorados, Pichincha Province, Ecuador; 31 Nov 1980; H. Díaz; 12 males, the largest cb. 22.0 mm, cl. 13.9 mm (IVIC).

Remarks.—These specimens agree well with the description and illustration of the species given by Rathbun (1897) and Rodríguez (1982). The border of the marginal lobe of the gonopod has a band of very tiny spinules, barely visible with the stereoscopic microscope at a magnification of 500 times. The 5th abdominal sternites of the males are deeply invaginated to form gonopodial receptacles where the apices of the gonopods are lodged. However, the mature males usually carry the gonopods outside the abdominal fossa, protruding on each side of the folded abdomen. The large gonopodial receptacles and the extrusion of the gonopods are also characteristic of *Hypolobocera henrici*; in other pseudothelphusids the gonopodial receptacles are shallower and the gonopods are folded inside the abdominal fossa.

The known distribution of the species covers the Pacific slope of the Western Cordillera of Eucador, between the Guayllabamba and Toachi rivers, tributaries of the Esmeraldas River, at altitudes between 880 and 2740 m above sea level.

Moritschus narinnensis, new species
Fig. 1

Material examined.—Quebrada Taibai, Vereda Piedra Verde, Inspección Buena Vista, Municipio Barbacoas, 1140 m above sea level, Nariño Department, Colombia; 16 Aug 1987; G. Arango; 1 male holotype, cb. 25.2 mm, cl. 15.5 mm, 12 male paratypes, the largest cb. 24.4 mm, cl. 15.0, 16 female paratypes, the largest cb. 24.2 mm and cl. 15.3 mm (ICN-MHN No. CR 0605).

Description.—The cervical groove is straight and shallow, it reaches the margin of the carapace. The anterolateral margin has a conspicuous notch behind the orbit; it does not meet the outer orbital angle, but curves upward above the orbital margin; it is smooth, except for a faint crenulation near its midlength. The postfrontal lobes are ill defined, their presence being indicated only by 2 small scars. The median groove is obsolescent. The surface of the carapace behind the front is moderately inclined anteriorly and towards the mid-line. The upper border of the front is arched and bilobed in dorsal view, bearing a row of tubercles; the lower margin is strongly sinuous in frontal view and conspicuously marginated; it lies a little in front of the upper one. The front between the upper and lower margins is high. The surface of the carapace is smooth, covered by papillae not visible to the naked eye; for the most part, the regions are clearly defined.

The palm of the larger cheliped is inflated. The fingers have a strong gape between them; the mobile finger is strongly arched. The walking legs are slender and elongate, the longest being the third pair (total length greater than the breadth of carapace); in this pair the merus is 3.2 times longer than wide. The exopod of the third maxilliped is 0.32 the length of the ischium of the endognath. The orifice of the efferent branchial channel is open.

The male gonopod is slender and strongly arched laterally; the lateral lobe, which is elongate and moderately prominent, occupies the distal half of the appendage; the apex is strongly elongate in the meso-lateral plane and strongly arched, the caudal end produced in a strong fingerlike process directed proximally. The elongate process over the field of spines, which in all species of *Hypoloberini* has 2 rudimentary papillae, in this species is entire, with its distal margin bordered with minute spines. In addition to the spines surrounding the spermatic aperture, other small closely-set ones cover the lateral margin of the apex and the fingerlike process.

Etymology.—The species is named after the Nariño Department in Southern Colombia.

Remarks.—The locality of the present species is on the Pacific slope of the Western Cordillera of Colombia, which is a continuation of the Western Cordillera of Ecuador, but 170 km to the North of the area frequented by *Moritschus ecuadorensis,* in the basin of the Paita River.

The species of *Moritschus* are among the smallest within the Pseudothelphusidae. *M. narinnensis* can be easily distinguished from *M. ecuadorensis* by details of the male gonopod given in the key below.

Key to the Species of the Genus *Moritschus*

1. Gonopod with caudal end produced in short beak. Elongate process over field of spines with 2 rudimentary papillae directed laterally. Lateral margin of apex unarmed .... *M. ecuadorensis*
   – Gonopod with caudal end pro-

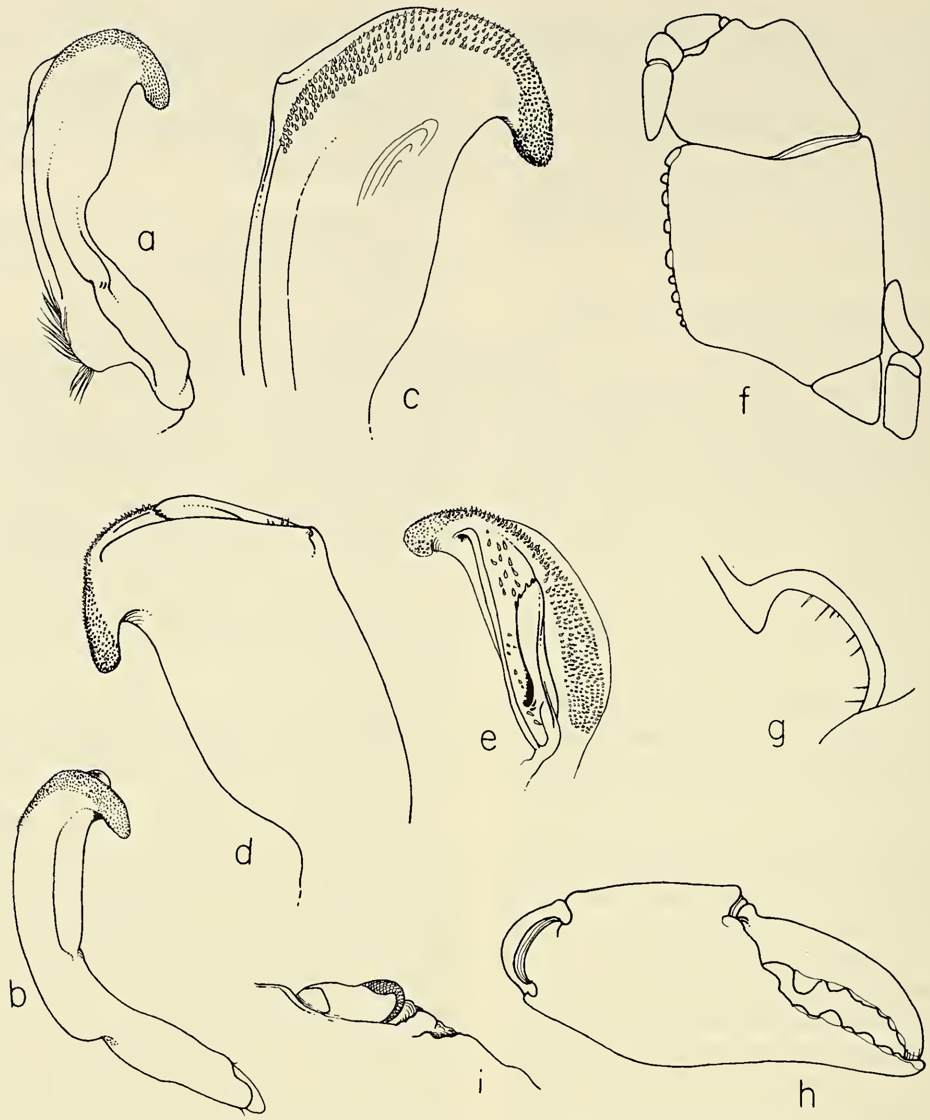

Fig. 1. *Moritschus narinnensis,* holotype, ICN 0605: a–e, Left gonopod (a, Caudal view; b, Same lateral view; c, Apex in caudal view; d, Apex in mesial view; e, Apex in distal view); f, Third maxilliped, left; g, Aperture of efferent channel; h, Larger chela; i, Detail of anterolateral margin of carapace at the outer orbital angle.

duced in strong fingerlike process directed proximally. Elongate process over field of spines entire, its distal margin bordered with minute spines. Lateral margin of apex and fingerlike process covered with small closely-set spines. .... *M. narinnensis*

Since the gonopod type found in *Moritschus* somewhat resembles the gonopod of some *Hypolobocera,* particularly *H. henrici,* a revised definition of *Moritschus* is given below to distinguish between the genera and to accommodate the new species described above.

Moritschus Pretzmann, 1965

Pseudothelphusid crabs of small size (carapace breadth usually less than 26 mm). The anterolateral margin of the carapace does not meet the outer orbital angle, but curves upward above the orbital margin. The exognath of the third maxilliped is less than half the length of the lateral margin of the ischium of the endognath. The male gonopod is slender and strongly arched laterally; the lateral lobe occupies the distal half of the appendage; it is elongate and moderately prominent; the apex is strongly elongate in the meso-lateral plane and strongly arched; its caudal end is produced in a beak or strong fingerlike process directed proximally.

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101(3), 1988, pp. 644–652

CAMBARUS (*EREBICAMBARUS*) *MACULATUS,* A NEW CRAYFISH (DECAPODA: CAMBARIDAE) FROM THE MERAMEC RIVER BASIN OF MISSOURI

Horton H. Hobbs, Jr., and William L. Pflieger

Abstract.—*Cambarus* (*Erebicambarus*) *maculatus* is described from the Meramec River and its tributaries in eastern Missouri. Its speckled color pattern, which is unique in the genus *Cambarus,* prompted the vernacular name, "Freckled Crayfish." It may be distinguished from its closest relatives, *C.* (*E.*) *hubbsi* Creaser (1931) and *C.* (*E.*) *rusticiformis* Rhoades (1944), by the color pattern and by the tapering central projection of the first pleopod of the first form male.

So long as the crayfish described here retains its color pattern, it is one of the most easily recognized of any of the American species. Only one other, *Procambarus* (*Girardiella*) *tulanei* Penn (1953), an inhabitant of the Ouachita River Basin in Arkansas and Louisiana, exhibits a similar freckled pattern, but the chelae of the males of that species bear a heavy beard on the mesial surface of the palm; moreover, the pleura of members of both sexes are broadly rounded rather than being acute as they are in this crayfish from Missouri.

Closely allied to the new species from the Meramec River Basin, and occupying contiguous, if not overlapping, ranges are the troglobitic *Cambarus* (*Erebicambarus*) *hubrichti* Hobbs (1952) and a probable ecological equivalent, *C.* (*E.*) *hubbsi* Creaser (1931), which seems to be limited to the White and St. Francis watersheds of Missouri and Arkansas.

Cambarus (*Erebicambarus*) *maculatus,* new species
Figs. 1, 2

Cambarus hubbsi.—Williams 1954:908, fig. 233 [in part]. Freckled Crayfish, Pflieger, 1987a:23; 1987b:7.

Diagnosis.—Body pigmented; eyes well developed. Rostrum, with thickened lateral carinae, broad basally, tapering gradually to base of acumen where studded with paired, conspicuous, dorsally projecting, corneous tubercles; apex of acumen with similar, dorsally directed, strong tubercle. Postorbital ridges thickened and capped at anterior extremity with prominent, corneous, sometimes spiniform tubercle. Suborbital angle obtuse, usually rounded. Cervical spines represented by rounded, inconspicuous tubercles. Areola of adults 3.8 to 5.9 times as long as wide and comprising 37.0 to 40.6% of entire length of carapace (43.8 to 49.0% of postorbital carapace length), and bearing 3 to 6 punctations across narrowest part. Chela with single row of 9 to 12 (usually 10) often poorly defined tubercles on mesial surface of palm, remainder of which punctate. Fingers with tubercles restricted to opposable margins; fixed member with third tubercle from base distinctly larger than others on either finger (size difference not evident in regenerated chelae); both fingers with well defined dorsomedian longitudinal ridges. Prominent subacute hook on ischium of third pereiopod distinctly overreaching basioischial articulation, and opposed by tubercle on basis. Pleura of second through fifth abdominal segments tapering to acute or subacute apices. First pleopod

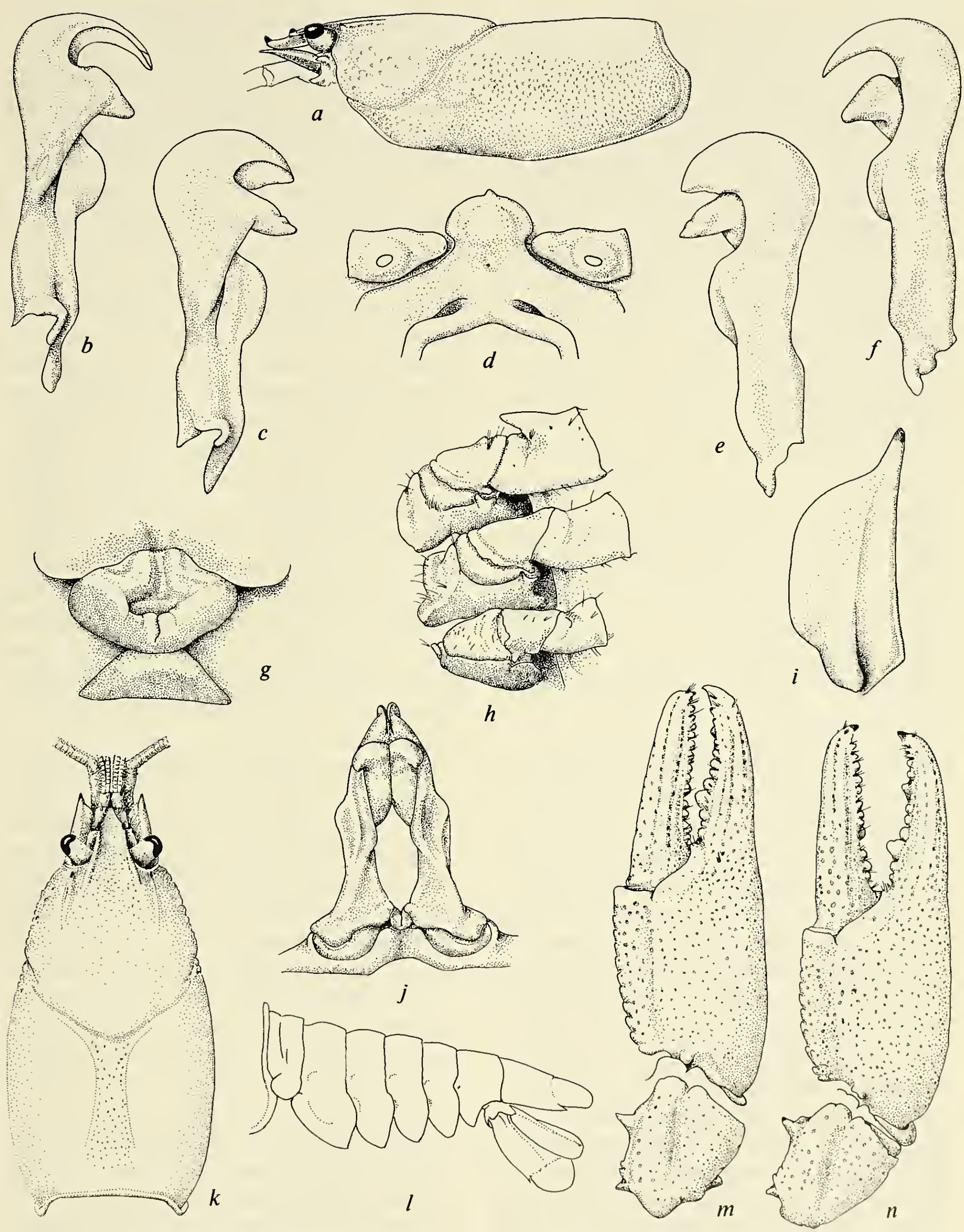

Fig. 1. *Cambarus* (*Erebicambarus*) *maculatus* (all from holotype except c and e which are from paratypic male, form II, and g, m which are from allotype): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Epistome; e, f, Lateral view of first pleopod; g, Annulus ventralis and adjacent sternites; h, Basal podomeres of third, fourth, and fifth pereiopods; i, Antennal scale; j, Caudal view of first pleopods; k, Dorsal view of carapace; l, Dorsolateral view of abdomen; m, n, Dorsal view of distal podomeres of cheliped.

of first form male terminating in two elements: gently curved, scythelike, tapering central projection with apex, lacking subapical notch, directed caudoproximally; and mesial process inflated and directed caudolaterally with apex situated lateral to apex of central projection although reflexed somewhat mesially. Color tan to olive tan with darker brown to almost black spots. First pleopods present in female.

Holotypic male, form I.—Cephalothorax subovate in cross section; carapace rather strongly depressed (Fig. 1a, k), its greatest width decidedly broader than height at caudodorsal margin of cervical groove (20.1 and 13.0 mm). Rostrum with conspicuously thickened, elevated, and tapering lateral carinae studded with obliquely set, dorsally disposed, corneous tubercles, latter clearly marking base of acumen which, bearing prominent corneous, dorsally directed tip, reaching about midlength of ultimate podomere of antennular peduncle. Subrostral ridges rather weak and evident in dorsal aspect along slightly less than basal third of rostrum. Suborbital angle obtuse. Postorbital ridges weak except anteriorly where bearing upturned, corneous tip. Branchiostegal spine obsolete. Areola 5 times as long as broad, with 4 or 5 punctations across narrowest part; length of areola 38.7% of total length of carapace (46.5% of postorbital carapace length). Cervical spine represented by inconspicuous tubercle no larger than others nearby. Carapace densely punctate dorsally, becoming granulate to tuberculate laterally, especially from area of cervical tubercle anteriorly.

Abdomen shorter than carapace (33.7 and 37.7 mm); pleura (Fig. 1l) tapering ventrally, all acute. Cephalic section of telson with lateral margins comparatively strongly converging posteriorly and bearing single prominent, fixed spine in each caudolateral corner; caudal section narrow and appearing remarkably small. Proximal podomere of uropod lacking spines on both lobes; distally subtruncate mesial ramus with poorly developed median keel ending in small premarginal spine.

Cephalomedian lobe of epistome (Fig. 1d) broadly rounded with small cephalomedian projection, margin somewhat thickened, and central part of lobe elevated ventrally; main body with distinct fovea, and epistomal zygoma rather weakly arched. Ventral surface of proximal podomere of antennule with very small tubercle at about base of distal fourth and slightly lateral to median line of podomere. Antennal peduncle devoid of spines and tubercles; flagellum broken, but probably reaching fifth or sixth abdominal tergum. Antennal scale (Fig. 1i) about 2.5 times as long as broad with mesial and lateral margins subparallel for more than half length, distomesial margin of lamellar area tapering to join prominent distolateral spine which attaining about same level anteriorly as apex of rostrum. Mesial half of ischium of third maxilliped with linear clusters of tubercles bearing long, stiff setae; setae scattered over lateral half short and inconspicuous; distolateral extremity of podomere not produced.

Right chela (Fig. 1n) about 2.5 times as long as wide, moderately depressed; palm, with length of mesial margin subequal to greatest width of podomere and bearing row of 10 very low tubercles; remainder of palm densely punctate and lacking tubercles other than usual ones associated with articulation of adjacent podomeres. Both fingers with low but clearly defined dorsal and ventral median longitudinal ridges. Arched fixed finger rather smaller than those of some of its congeners and with row of 9 (10 on left) tubercles, third from base largest, rather evenly distributed along opposable margin; usual additional large tubercle situated below row just proximal to distal 3 tubercles of row; finger otherwise unremarkable. Typically heavy dactyl with row of 11 (12 on left) tubercles on opposable margin and offset larger one slightly below row and immediately distal to gap between third and fourth (fourth and fifth on left) tubercles from base; gap lying almost opposite largest tubercle on opposable margin of fixed finger. Minute denticles abundant on opposable margins of fingers of chelae of many crayfishes sparse and largely limited to single fine, short row extending between distalmost tubercle and corneous tip of finger. Mesial surface of dactyl lacking tubercles, even basally; podomere entirely punctate except for those on opposable margin.

Carpus of cheliped longer than broad (13.4 and 9.5 mm), with moderately deep, oblique, longitudinal furrow dorsally flanked by punctations; mesial surface with prominent mesiodistally directed spine and single (2 on left) small tubercle near proximomesial base; ventral surface polished and with single tubercle situated on distal margin mesial to ventrolateral articular knob. Merus with 2 small dorsodistal tubercles; ventral surface with mesial row of 7 (left with 9) corneous tipped spines and 2 (1 on left) representing lateral row of other crayfishes; lateral and mesial surfaces sparsely punctate. Basioischial podomere with row of 4 poorly developed tubercles ventromesially.

Hook on ischium of third pereiopod only (Fig. 1h), acute, overreaching basioischial articulation, and opposed by tubercle, flanked by setiferous punctations, on basis. Coxa of fourth pereiopod with prominent caudomesial boss, caudal face of which in almost same plane as remainder of caudal surface of podomere. Boss absent from coxa of fifth pereiopod. First pleopods (Fig. 1b, f, j) reaching coxae of third pereiopods, symmetrical, and with small gap between their bases. See "Diagnosis" for description of terminal elements.

Allotypic female.—Excluding secondary sexual characteristics, differing in only few minor respects from holotype: telson and uropods decidedly hirsute; mesial lobe of proximal podomere of uropod produced caudally in spine; tubercle on ventral surface of basal podomere of antennule situated slightly more proximally; chela (Fig. 1m) proportionately narrower, about 2.7 times as long as wide; mesial margin of palm with row of 11 ill-defined tubercles. Fixed finger with row of 13 (left with 12, proximalmost lacking) tubercles along opposable margin, fifth from base largest; opposable margin of dactyl with row of 13 (left with 14) tubercles and offset 1 following gap; ventral surface of merus of cheliped with mesial row of 8 tubercles (9 on left) and lateral row represented by only 1 tubercle. (See Table 1.)

Table 1.—Measurements (mm) of *Cambarus* (*E.*) *maculatus*.

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	37.7	36.0	32.0
Postorbital length	31.4	29.0	26.6
Width	20.1	18.9	17.2
Height	13.0	12.7	11.2
Areola:			
Width	2.9	2.4	2.1
Length	14.6	14.2	11.5
Rostrum:			
Width	5.2	5.2	5.0
Length	6.3	7.0	5.4
Right chela:			
Length, palm mesial margin	14.2	13.2	10.5
Palm width	14.5	11.9	11.1
Length, lateral margin	37.1	32.6	25.6
Dactyl length	18.3	16.6	13.2
Abdomen:			
Width	17.6	17.7	13.5
Length	33.7	31.6	27.7

Annulus ventralis (Fig. 1g) firmly fused to sternite XIII, irregularly ovate with greater axis lying transversely, about 1.7 times as broad as long; cephalomedian trough moderately deep but not flanked by conspicuous cephalolateral prominences; transverse sulcus well defined with tongue extending dextrally, disappearing under high, longitudinally creased caudal wall. Postannular sclerite only slightly narrower than annulus and only little more than half as long.

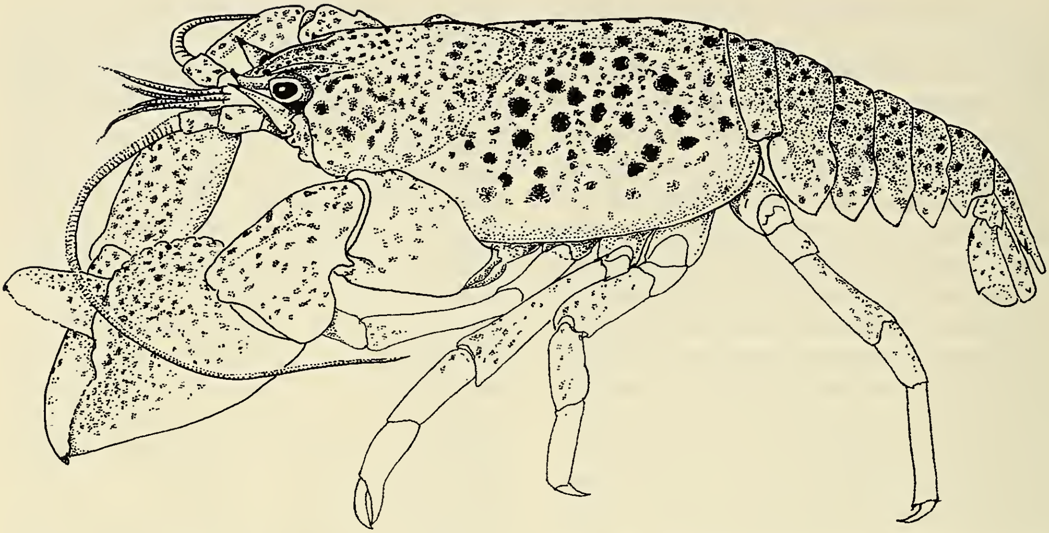

Fig. 2. Dorsolateral view of first form male of *Cambarus* (*E.*) *maculatus* from Huzzah Creek, Crawford County, Missouri.

Morphotypic male, form II.—Differing from holotype in following respects: apical spines on postorbital ridges directed cephalolaterally and only slightly dorsally; telson with less convergent margins, and anterior section with pair of movable spines mesial to fixed ones in caudolateral corners; mesial lobe of basal podomere of uropod with prominent caudally projecting spine; mesial margin of palm of chela with row of 14 tubercles (left with 10); opposable margin of fixed finger with row of 8 tubercles (left with 10); opposable margin of dactyl with row of 11 tubercles and offset one (left with 10 and 1); row of minute denticles on opposable margins of both fingers longer and more conspicuous; ornamentation of more basal podomeres within ranges noted in holotype; hooks on ischia of third pereiopod much less well developed, not reaching basioischial articulation, but small opposing tubercle on basis clearly evident. First pleopods (like Fig. 1c, e) differing from that of holotype chiefly in structure of central projection which much more massive, comparatively shorter, and non-corneous. (See Table 1.)

Color notes (Fig. 2).—Carapace yellowish tan to pale orange tan with very dark brown to black spots, largest of which subcircular and occurring dorsolaterally over branchiostegites and in posterior part of areola. Dorsal surface of abdomen, telson, and uropods with yellow or tan base infused with brown, thus yellowish to orange brown, with dark spots similar to, but smaller than, those on carapace. Background color of chelipeds often much paler, sometimes almost cream, and, except ventrally, bearing dark brown to black spots of varying sizes and shapes; only few of those on dorsal part of carpus and merus as large as those on branchiostegites. Second through fifth pereiopods similarly colored but with spots small and more sparse.

Size.—The largest specimen available is a first form male from Huzzah Creek in Crawford County having a carapace length of 44.4 (postorbital carapace length 37.2) mm. The smallest first form male, from Washington County, has corresponding lengths of 24.6 and 20.4 mm. The smallest ovigerous female available has a carapace length of 32 mm (postorbital length 27.8

mm), the largest, 36 and 30.6 mm, respectively.

Type locality.—Hazel Creek at Route C, 8 miles (12.8 km) northeast of Courtois, Washington County, Missouri (T. 36N, R. 1W, SE¼ Sec. 24). The specimens collected there were found beneath rocks in the plunge pool just below the concrete road crossing. At low water this pool measured 14 m in width and 8.4 m in length, with a maximum depth of 1 m. At this locality, *C.* (*E.*) *maculatus* occurred in association with *Orconectes* (*Procericambarus*) *punctimanus* (Creaser 1933), *O.* (*P.*) *luteus* (Creaser, 1933) and *O.* (*P.*) *medius* (Faxon, 1884). The latter species comprised 73.2% of our collections, while *C.* (*E.*) *maculatus* comprised 5.5%, the least common of the four species.

Disposition of types.—The holotype, allotype, and morphotype (USNM 219292, 219293, and 219280, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution. Of the paratypes, 3♂I, 2♂II, 1♀, and 1j♀ are in the collection of Ronald D. Oesch; the remaining ones are in the National Museum of Natural History.

Range and specimens examined.—This new crayfish appears to be restricted to the Meramec River and its tributaries in eastern Missouri (Fig. 3) where it has been found in the following localities: Crawford County: (1) Huzzah Creek at end of Rte E (T. 38N, R. 3W, Sec. 11), 1♂I, 4 Mar 1977, W. L. Pflieger, A. Buchanan; (2) Meramec River at Cooks Station (T. 36N, R. 5W, NE¼ Sec. 6), 2♀, 12 Oct 1984, WLP, 1♂I, 1♂II, 18 Jul 1985, WLP, 1♂I, 6 May 1986, WLP; (3) Meramec River at Hwy 8, 8.75 mi (14 km) W of Steelville (T. 37N, R. 5W, SW¼ Sec. 6) 2♀, 1j♀, 25 Aug 1968, J. E. Cooper, M. R. Cooper, 3♂I, 2♂II, 24 Oct 1985, WLP, 3♂II, 2♀, 5 May 1986, WLP, 1♂I, 16 Apr 1987, R. D. Oesch; (4) Huzzah Creek (T. 37N, R. 2W, Sec. 6), 3♂I, 1♀, 23 Oct 1986, WLP; (5) Trib of Huzzah Creek 1.5 mi (2.4 km) N of Dillard, 1♂II, 10 Sep 1955, Nell Crenshaw, John Crenshaw; (6) Huzzah Creek below Hwy 8, 1♂I, 1♂II, 1♀, 1j♂, 9 May 1987, RDO. Franklin County: (7) Meramec River at Meramec State Park (T. 40N, R. 2W, Sec. 13), 1♂I, 4 Mar 1977, WLP, AB. Washington County: (8) Type locality, 5♂I, 2♀, 18 Oct 1984, WLP, 1♂I, 2♀, 5 May 1986, WLP, 1♂I, 2♀, 4j♂, 25 Mar 1985, WLP; (9) Big River at Hwy 21, 3 mi N of Caledonia (T. 36N, R. 2E, Sec. 25), 1j♀, 25 Aug 1968, JEC, MRC, 1♀, 1j♂, 17 Oct 1984, WLP; (10) Mill Creek at Rte N (T. 36N, R. 3E, NE¼ Sec 22) 2♂I, 25 Mar 1985, WLP; (11) Fourche Renault Creek at Rte AA, 1 mi W of Summer Lake (T. 38N, R. 1E, SW¼ Sec 34), 1♂I, 22 Oct 1986, WLP; (12) Mine Breton Creek at Hwy 8, 1♂I, 11 Apr 1984, RDO; (13) Cedar Creek at Hwy 32, 1.5 airmi (2.4 km) ESE of Caledonia, 1j♂, 18 Aug 1948, ABW, ABL, 1♀, 21 Jun 1987, RDO; (14) Big River, 8.6 mi (13.8 km) S of Potosi, 1♂II, 2j♂, 18 Aug 1948, ABW, ABL; (15) Mineral Fork at W Hwy 57 bridge, 1♂II, 7 Jul 1979, J. F. Payne; (16) Big River at Hwy 21, 1♂II, 1♀, 7 Jul 1979, JFP.

Variations.—Barring variations that have almost certainly resulted from injury, regeneration, or abrasion that often appear to be commensurate with the length of the period since the most recent molt, our specimens exhibit remarkable uniformity in both mensural and meristic qualities. Such ratios as length of areola/total length of body yielded a mean of 38.6 ± 1.653; length of the areola/postorbital carapace length, 46.3 ± 1.125; and areola length/areola width, 4.9 ± 0.597. Moreover, ratios involving the length of the chela, its maximum width, and length of the palm, even when regenerated chelae were considered, show little variation. Similarly the differences in the numbers of tubercles on the body and the various podomeres of the chelipeds are comparatively small, hardly exceeding the variations pointed out in the descriptions of the primary types. Perhaps the most conspicuous variation occurs in the relative development and numbers of tubercles on the regenerated chelipeds. Such chelae can be

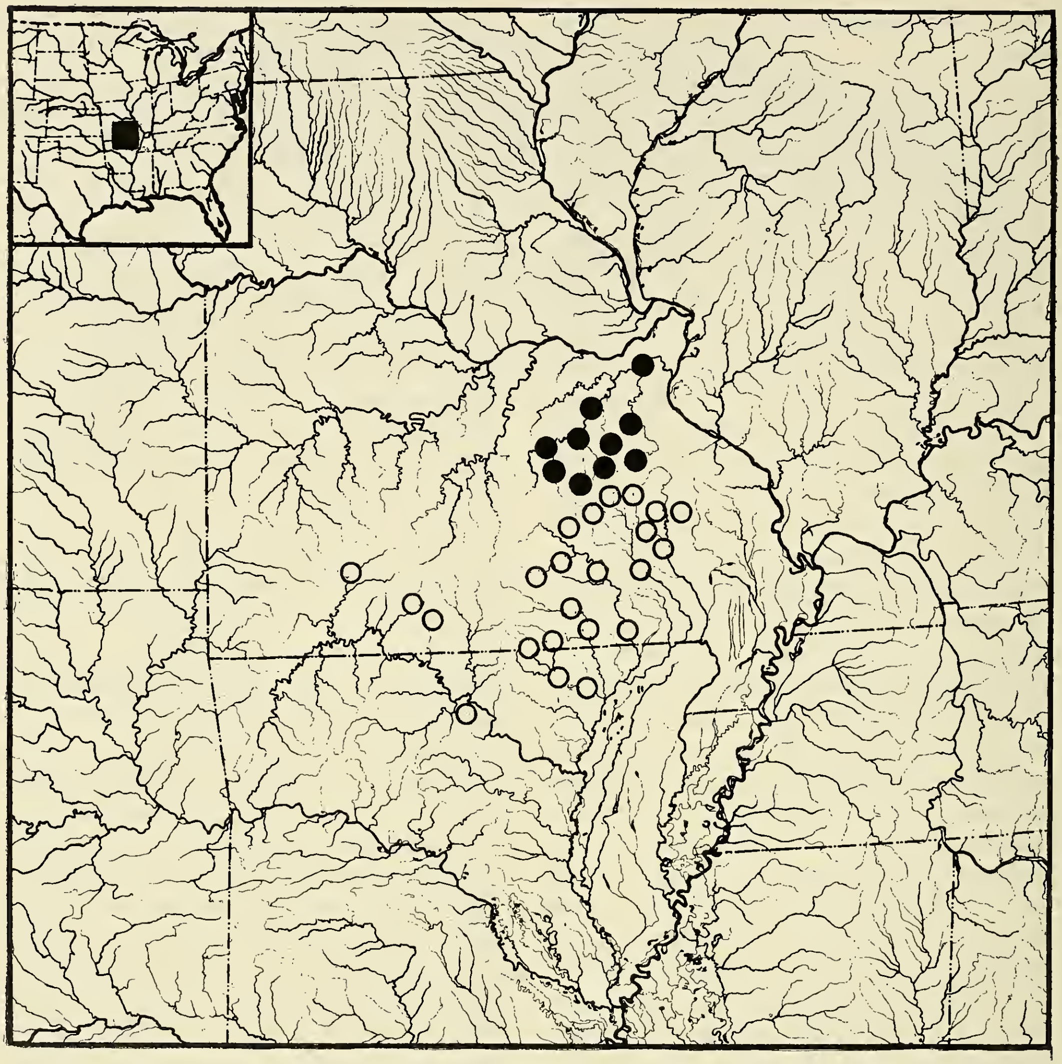

Fig. 3. Distribution of *Cambarus* (*E.*) *maculatus* (black circles) and *Cambarus* (*E.*) *hubbsi* (open circles).

recognized by the absence of an enlargement of the third, fourth, or fifth tubercle from the base on the opposable margin of the fixed finger. While it is likely that such a difference does not exist in a cheliped that was lost and regenerated in the earlier instars, should a large tubercle be wanting on the opposable margin of that finger, one may be sure that the appendage is a regenerated one, and is likely to bear a larger number of tubercles on that and the corresponding margin of the dactyl.

Ecological notes.—*Cambarus* (*E.*) *maculatus* is largely restricted to a deeply dissected region of the eastern Ozarks known as the Coutois Hills. The bedrocks of this region consist principally of limestones and dolomites of the Gasconade and Potosi formations. Chert gravel weathered from these rocks is the principal bottom type in the streams. Much of the region is sparsely populated and is within the boundaries of the Mark Twain National Forest. The streams are very clear, with permanent flow maintained by numerous springs. *C.* (*E.*) *maculatus* occurs in streams ranging in size from order 3 to 7, but is most abundant in those of order 4 or 5. It is usually found in pools, at depths of 20 cm or more, beneath rocks that are well seated in gravel. Its presence is often revealed by small piles of gravel pushed out of the shallow cavities that it excavates. The habitat and habits of this species are not notably different from those of *C.* (*E.*) *hubbsi.*

In 12 collections made by one of us (WLP), five other species of crayfishes, all belonging to the genus *Orconectes* occurred. The species and number of collections were: *O.* (*Procericambarus*) *luteus,* 12; *O.* (*P.*) *punctimanus,* 9; *O.* (*P.*) *medius,* 8; *O.* (*Billecambarus*) *harrisonii* (Faxon 1884), 4; and *O.* (*P.*) *hylas* (Faxon 1890), 2.

Life history notes.—In our collections from the months of October, March, and April, 18 of 20 males were Form I, while 5 of 6 males collected during the months of July to September were Form II. Three ovigerous females occurred in collections made on 5 May 1986. These females measured 32, 34, and 36 mm carapace length and carried 67, 63, and 127 eggs, respectively. The eggs were about 1.8 mm in diameter and were grey to nearly black in color.

Relationships.—*Cambarus* (*Erebicambarus*) *maculatus* has its closest affinities with *C.* (*E.*) *hubbsi* and *C.* (*E.*) *rusticiformis* Rhoades (1944). Differing from their other congeners, these three crayfishes with strongly depressed bodies possess rostra, the lateral carinae of which end abruptly at the base of the acumen and usually bear marginal tubercles at their apices. The carinae are thickened and diverge at their bases. All three have rather broad, moderately densely punctate areolae. The rather weak tubercles along the mesial margin of the palms of their chelae are largely confined to a single row. All three exhibit a striking similarity in their abdominal pleura, which taper to acute angles (apices often rounded) that, when the abdomen is extended, are directed almost ventrally. Similarly structured pleura, which may be found to be associated with adaptations to lotic habitats, occur in the Astacidae and in members of the cambarid genera *Cambaroides* and the monotypic *Barbicambarus cornutus* Faxon (1884), all of which are at least primarily stream dwellers.

The "freckled" color pattern alone serves to distinguish this crayfish from *C.* (*E.*) *hubbsi* and *C.* (*E.*) *rusticiformis,* but in preserved specimens in which the pigment has completely faded, distinguishing between them becomes more difficult. First form males of the new species are unique among them in that the central projection of the first pleopod tapers to an acute tip, whereas in the other two the comparatively broad distal part of the element bears a subapical notch. Except for the color patterns, we have been unable to discover a single character that will serve consistently to distinguish the second form males, females, and juveniles of the three, although the obliquely set marginal spines of the rostrum that project dorsally rather than anterodorsally can usually be relied upon to recognize most members of *C.* (*E.*) *maculatus.* The recognition of the allopatric (with respect to the other two) *C.* (*E.*) *rusticiformis,* which is restricted to streams east of the Mississippi River (where it is largely, if not entirely, restricted to the Cumberland Basin, and thus their ranges are not even contiguous) presents no problem.

Although *Cambarus* (*E.*) *hubbsi* is restricted largely, if not entirely, to the White and St. Francis watersheds of Missouri and Arkansas, there is a Form I male of this species at the National Museum of Natural History (USNM 219315) which was reportedly collected from the Meramec River east of Eureka, Missouri, in 1934. If this record is valid, the range of *C.* (*E.*) *hubbsi* overlaps that of *C.* (*E.*) *maculatus,* and recognition of the identity of bleached second form males and females of the two, at least sometimes, might be problematical. Recent collections at this locality, however, included specimens of only the latter species.

There can be little doubt that before the ancestral *Erebicambarus* stock crossed the Mississippi River (Hobbs 1969:110) to become established in the Meramec, St. Francis, and White river basins, it had already acquired a mien shared by the segment of the stock that was left behind and that gave rise to the modern *C.* (*E.*) *rusticiformis.* In our view then, the close resemblance existing between the latter, *C.* (*E.*) *maculatus,* and *C.* (*E.*) *hubbsi,* has resulted from a retention of features that have been little altered during the course of their long-time, continuous occupancy of similar ecological niches rather than from convergence in the three undergoing similar adaptations independently. Of the three *Erebicambarus* occurring west of the Mississippi River (Ozark Region), only *C.* (*E.*) *hubrichti* exhibits features that appear to us to be markedly different from those we believe to have been characteristic of the pioneering ancestor, and we suggest that these are associated with its ancestors becoming adapted to a spelean environment.

At least two features of *C.* (*E.*) *maculatus,* unique in the subgenus *Erebicambarus,* suggest that this crayfish is farther removed from the ancestral stock than is *C.* (*E.*) *hubbsi.* These are the speckled color pattern and the tapered central projection of the first pleopod in first form males.

Acknowledgments

Appreciation is extended to Ronald D. Oesch, who is associated with the Cooperating Schools of the St. Louis Suburban Area, for lending us specimens of *C.* (*E.*) *maculatus* from his collection and to other collectors mentioned under "Range and specimens examined" who have donated specimens to the Smithsonian Institution. For their helpful comments on the manuscript, acknowledgment is also made with thanks to C. W. Hart, Jr., of the National Museum of Natural History, and to Douglas G. Smith, of the University of Massachusetts.

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TYPES OF STOMATOPOD CRUSTACEANS IN THE ZOOLOGICAL SURVEY OF INDIA

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Abstract.—A list of the types of stomatopod crustaceans in the Zoological Survey of India is presented. This historically important collection includes type specimens of 42 species, including primary types (holotype, lectotype, or syntype) of 36 species.

The collection of types of stomatopod crustaceans held by the Zoological Survey of India forms comprises the most important collection of types of Indo-West Pacific species in the world, with no less than 42 species, or about 10% of the known stomatopods, represented in the collection by type specimens. The collection is based largely on material reported on by James Wood-Mason and Stanley W. Kemp between 1875 and 1921, supplemented by a few additions since then. Kemp prepared the first major regional monograph of the stomatopods, and his work remains today as an essential tool for anyone studying the group.

Species are first listed alphabetically under their original combination. Then species are listed by current names, cross-referenced to the original combination.

The following information is included under each species represented in the collection: catalogue number, location, date, collector or source of material, and number of specimens. Condition of material is good unless otherwise specified.

For some localities, coordinates or alternate spellings, taken from gazetteers of the U.S. Board on Geographic Names, have been added; these always are given in square brackets. Where possible we have added station data from "Biological collections of the R.I.M.S. "*Investigator.*" List of stations 1884–1913." Pages 1–35. Indian Museum, Calcutta. 1914. Station data that we have added also is given in square brackets.

Under each species, the material is listed in the same order as listed by Kemp (1913).

We thank B. K. Tikader, former Director of the Zoological Survey of India, for his permission to undertake the preparation of this catalogue.

STOMATOPOD TYPES IN THE ZOOLOGICAL SURVEY OF INDIA, CALCUTTA

(Listed alphabetically under
original combination)

Chorisquilla andamanica Manning, 1975

Chorisquilla andamanica Manning, 1975: 258, fig. 3 [=*Chorisquilla excavata* (Miers, 1880)].

Holotype.—9177/6, off Andaman Islands [12°30′N, 92°45′E], India, 20 fm (=37 m), *Investigator,* 1 male.

Paratypes.—9177/6, off Andaman Islands, 20 fm (=37 m), *Investigator,* 4 females (one specimen broken in middle).—9850–3/6, off Little Andaman Island [10°45′N, 92°30′E], 10.5 fm (=19 m), *Investigator,* 1 male, 3 females.—9846–9/6, off Table Island [14°12′N, 93°22′E], Coco Group, Andaman Islands, 5 fm (=9 m), *Investigator,* 1 male, 3 females.

Clorida decorata Wood-Mason, 1875

Clorida decorata Wood-Mason, 1875:231.

Holotype.—3086/5, Andaman Islands [12°30′N, 92°45′E], India, J. Wood-Mason, 1 female (delicate, broken).

Remarks.—Kemp (1913) gave Port Blair as the type locality.

Coronis spinosa Wood-Mason, 1875

Coronis spinosa Wood-Mason, 1875:232 [=*Heterosquilla tricarinata* (Claus, 1871)].

Lectotype (selected by Holthuis 1967: 11).—3052/5, Port Blair [11°36′N, 92°45′E], Andaman Islands, India, J. Wood-Mason, 1 female (very delicate, dactylus missing).

Paralectotype.—3053/5, Dunedin [45°52′S, 170°30′E], New Zealand, Capt. F. W. Hutton, 1 female.

Remarks.—This is a cold water species known to be common in New Zealand; the specimen from the Andaman Islands may have been labelled incorrectly.

Gonodactylus chiragra var. *platysoma* Wood-Mason, 1895

Gonodactylus chiragra var. *platysoma* Wood-Mason, 1895:11, pl. 3, figs. 3–9) [=*Gonodactylus platysoma* Wood-Mason, 1895].

Lectotype.—3033/5, Society Islands, Otago Museum, 1 female.

Paralectotypes.—3039/5, Mauritius [20°18′S, 57°35′E], purchased, 2 females.

Remarks.—Although Kemp (1913:163) considered three specimens from Port Blair, Andamans, to be the types, Wood-Mason did not mention these specimens or material from the Andamans in his original account. The female from the Society Islands is here selected as the lectotype.

Gonodactylus choprai Manning, 1967

Gonodactylus choprai Manning, 1967:16, fig. 6.

Paratypes.—C 1334/2, Indian Ocean, off Somali coast, 9°36′N, 51°01′E, 78–82 m, 16 Dec 1964, International Indian Ocean Expedition, *Anton Bruun* sta 9-444, exchange from Smithsonian Institution, 1 male, 1 female.

Gonodactylus furcicaudatus Miers, 1880

Gonodactylus furcicaudatus Miers, 1880: 124, pl. 3, figs. 13–16 [=*Mesacturus furcicaudatus* (Miers, 1880)].

Syntype.—7225/10, type locality unknown, H.M.S. *Alert,* exchange from British Museum (Natural History), 1 male.

Gonodactylus glyptocercus Wood-Mason, 1875

Gonodactylus glyptocercus Wood-Mason, 1875:232 [=*Haptosquilla glyptocercus* (Wood-Mason, 1875)].

Holotype.—3038/5, Nicobar Islands [8°00′N, 93°30′E], India, S. Kurz, 1 female.

Gonodactylus lanchesteri Manning, 1967

Gonodactylus lanchesteri Manning, 1967:11, fig. 4.

Paratype.—C 1337/2, Junghi Bay, Ibo Archipelago [12°20′S, 40°36′E], Mozambique, 5–18 fm (=9–33 m), A. Patience, exchange from Smithsonian Institution, 1 female.

Gonodactylus nefandus Kemp, 1911

Gonodactylus nefandus Kemp, 1911:93 [=*Haptosquilla nefanda* (Kemp, 1911)].

Syntypes.—3045/5, Andaman Islands [12°30′N, 92°45′E], India, J. Wood-Mason, 6 males, 16 females.—3040/5, same data, 1 female.—9025/6, same data, 20 fm (=37 m), *Investigator,* 1 female.—2825–6/7, Port Blair [11°36′N, 92°45′E], Andaman Islands, G. H. Booley, 2 males.—2546/3, Cheduba [Cheduba Island = 18°48′N, 93°38′E], Arakan coast, Burma, 7 fm (=13 m), *Investigator,* 3 females.

Gonodactylus proximus Kemp, 1915

Gonodactylus proximus Kemp, 1915:183, pl. 1, figs. 9, 10 [=*Haptosquilla proxima* (Kemp, 1915)].

Syntypes.—9296/10, Port Galera [Puerto Galera = 13°30′N, 120°57′E], Mindoro, Philippine Islands, Philippine Bureau of Science, 1 male, 1 female.

Lophosquilla tiwarii Blumstein, 1974

Squilla costata.—Kemp, 1913:84 [specimen from Burmese coast only]. [Not *Squilla costata* De Haan, 1844.]

Squilla sp. prox. *costata.*—Tiwari & Biswas, 1952:354, fig. 2.

Lophosquilla tiwarii Blumstein, 1974:123, fig. 8.

Paratype.—C 332/1, 4 miles NNE of Kabusa Island [Kabosa Island = 12°49′N, 97°53′E], Mergui Archipelago, Burma, *Investigator* [? sta 550, 33 fm (=60 m), 22 Oct 1913], 1 female.

Remarks.—This specimen from the Mergui Archipelago is a paratype of Blumstein's species, as she referred to the accounts of both Kemp and Tiwari & Biswas in her original description.

Lysiosquilla insignis Kemp, 1911

Lysiosquilla insignis Kemp, 1911:94 [=*Heterosquilloides insignis* (Kemp, 1911)].

Holotype.—7568/10, off North Andaman Island, India, 14°27′N, 93°50′E, 235 fm (=430 m), 19 Apr 1907, *Investigator* sta 375, 1 male (condition delicate, dactylus missing).

Remarks.—Kemp (1913) gave 50°7′N, 79°7′E as the coordinates for the *Investigator* station at which this species was taken. His coordinates apparently are in error.

Lysiosquilla maculata var. *sulcirostris* Kemp, 1913

Lysiosquilla maculata var. *sulcirostris* Kemp, 1913:116, pl. 8, figs. 92, 93 [=*Lysiosquilla sulcirostris* Kemp, 1913].

Holotype.—7564/10, Andaman Islands [12°30′N, 92°45′E], Homfray and Tytler, 1 male.

Lysiosquilla multifasciata Wood-Mason, 1895

Lysiosquilla multifasciata Wood-Mason, 1895:1, pl. 1, figs. 4–7 [=*Acanthosquilla multifasciata* (Wood-Mason, 1895)].

Holotype.—3342/7, Bombay [18°58′N, 72°50′E], India, Bombay Natural History Society, 1 female (both dactyli missing).

Manningia andamanensis Ghosh, 1975

Manningia andamanensis Ghosh, 1975:33, fig. 1.

Holotype.—C 1268/2, Aerial Bay Rock Reef, Diglipur, North Andaman Island [13°15′N, 92°55′E], India, 22 Feb 1970, A. G. K. Menon, 1 female.

Odontodactylus southwelli Kemp, 1911

Odontodactylus southwelli Kemp, 1911:94 [=*Odontodactylus brevirostris* (Miers, 1884)].

Syntypes.—3526/10, Andaman Islands [12°30′N, 92°45′E], India, *Investigator,* 1 female.—3502/10, Andaman Islands, 53 fm (=97 m), *Investigator,* 1 male, 1 female.—9751/6, off Cinque Island, Andaman Islands, 20 fm (=37 m), *Investigator,* 1 female.—9747/6, off Interview Island [12°55′N, 92°43′E], Andaman Islands, *Investigator,* 1 male.—7313/10, N. Cheval Paar [Cheval Bank = 08°40′N, 79°46′E], Ceylon [=Sri Lanka], 1 female.

Remarks.—Although Kemp (1913) considered the specimens from lot 3526/10 as the types, in his original description he did not specify a holotype. All of the specimens assigned to this species by him in 1913 appear to be syntypes.

Oratosquilla hindustanica Manning, 1978

Oratosquilla hindustanica Manning, 1978: 15, figs. 7, 15e.

Holotype.—7037–41/10, Tuticorin [8°47′N, 78°08′E], Madras, Gulf of Manaar, South India, J. Hornell leg., 1 male.

Paratypes.—ex. 7037–41/10, same data, 12 males, 17 females.

Remarks.—These specimens also are paralectotypes of *Squilla oratoria* var. *perpensa* Kemp, 1911 (see Manning 1978: 15,16).

Oratosquilla pentadactyla Manning, 1978

Oratosquilla pentadactyla Manning, 1978: 19, fig. 10.

Paratype.—8107/10, Kilakarai [9°14′S, 78°47′E], Ramnad District, India, from fishermen's nets, 17 Feb 1913, S.W. Kemp, 1 male.

Oratosquilla subtilis Manning, 1978

Oratosquilla subtilis Manning, 1978:33, fig. 19.

Holotype.—7536/10, off Vizagapatam coast [Visakhapatnam = 7°42′N, 83°18′E], Madras, India, 20 fm (=37 m), *Investigator,* 1 female.

Paratypes.—ex. 320/1, off Kabusa Island [Kabosa Island = 12°49′N, 97°53′E], lower Burma, 25–35 fm (=46–64 m), *Investigator,* 1 male, 1 female.

Remarks.—The holotype is also a syntype of *Squilla gonypetes* Kemp, 1911.

Squilla annandalei Kemp, 1911

Squilla annandalei Kemp, 1911:99 [=*Harpiosquilla annandalei* (Kemp, 1911)].

Syntypes.—7563/10, Gulf of Martaban, Burma, 14°46′N, 95°52′E, 61 fm (=112 m), 7 Mar 1901, *Investigator* sta 328, 1 female.—1748/10, same area, 14°26′N, 96°23′E, 67 fm (=123 m), *Investigator* [sta 226, 24 Mar 1897], 1 male.—1749/10, same area, 14°38′12″N, 96°24′30″E, 53 fm (=97 m), *Investigator* [sta 225, 14°38′15″N, 96°24′30″E, 24 Mar 1897], 1 female.

Remarks.—As Kemp (1911) did not designate a holotype in the original description of this species, but did mention that he had studied four specimens, all of the four specimens reported by him in 1913 must be considered to be syntypes, in spite of his suggestion in 1913 that the type was the female from 7563/10.

Squilla bengalensis Tiwari & Biswas, 1952

Squilla bengalensis Tiwari & Biswas, 1952: 352, fig. 1b, c [=*Cloridopsis bengalensis* (Tiwari & Biswas, 1952)].

Holotype.—C 3013/1, Salt Lakes, Lower Bengal, India, T. N. Poddar, 1 male.

Paratype.—C 3014/1, Piali River, Uttarbhag, Lower Bengal, India, 23 May 1934, S.L. Hora, 1 male.

Squilla boopis Kemp, 1911

Squilla boopis Kemp, 1911:97 [=*Busquilla quadraticauda* (Fukuda, 1911)].

Holotype.—1710/10, Gulf of Martaban, Burma, 14°26′N, 96°23′E, 67 fm (=123 m), *Investigator* [sta 226, 24 Mar 1897], 1 female.

Squilla bombayensis Chhapgar & Sane, 1967

Squilla bombayensis Chhapgar & Sane, 1967:1, fig. 1 [=*Clorida bombayensis* (Chhapgar & Sane, 1967)].

Holotype.—C 4621/1, Bombay [18°58′N, 72°50′E], India, intertidal water, 19 Apr 1963, S. R. Sane, 1 female.

Squilla brasiliensis Calman, 1917

Squilla brasiliensis Calman, 1917:139, figs. 1–3.

Paratype.—C 243/1, Atlantic Ocean, near Cabo Frio, Brazil, 22°56′S, 41°34′W, 40 fm (=73 m), 2 May 1913, *Terra Nova* sta 42, exchange from British Museum (Natural History), 1 male.

Squilla denticauda Chhapgar & Sane, 1967

Squilla denticauda Chhapgar & Sane, 1967: 4, fig. 2 [=*Clorida denticauda* (Chhapgar & Sane, 1967)].

Holotype.—C 4622/1, Bombay [18°58′N, 72°50′E], India, intertidal water, 17 Jan 1963, B. F. Chhapgar, 1 male.

Squilla foveolata Wood-Mason, 1895

Squilla foveolata Wood-Mason, 1895:2, pl. 2, fig. 1 [=*Dictyosquilla foveolata* (Wood-Mason, 1895)].

Syntypes.—3332/9, Hong Kong [Hong Kong Island = 22°15′N, 114°11′E], G. Dennys, 1 male, 4 females.

Squilla gilesi Kemp, 1911

Squilla gilesi Kemp, 1911:95 [=*Lenisquilla gilesi* (Kemp, 1911)].

Syntypes.—7514–18/10, off Madras coast, India, 14°18′15″N, 80°18′30″E, 88–110 fm (=161–201 m), *Investigator* [sta 154, 3 Jan 1894], 1 male, 3 females.—488/10, Madras coast, India, *Investigator,* 1 male.—5800/9, off Orissa coast, India, 19°49′N, 86°43′E, *Investigator,* 1 female.—3077/5, northeast Bay of Bengal, 20°18′N, 90°50′E, 65 fm (=119 m), *Investigator,* 4 males.—7519/10, Persian Gulf, 26°20′30″N, 54°52′30″E, 35 fm (=64 m), *Investigator* [sta 345, 20 Oct 1904], 1 female.

Squilla gonypetes Kemp, 1911

Squilla gonypetes Kemp, 1911:96 [=*Oratosquilla gonypetes* (Kemp, 1911)].

Lectotype (selected by Manning 1978: 13).—3359/7, off Cheduba [Cheduba Island = 18°48′N, 93°38′E], Arakan coast, Burma, 7 fm (=13 m), *Investigator,* 1 male.

Paralectotypes.—3476/10, off Andaman Islands [12°30′N, 92°45′E], India, 60 fm (=110 m), *Investigator,* 1 male, 1 female.—4421/10, Persian Gulf, 26°24′N, 56°02′E, 47 fm (=86 m), *Investigator* [? sta 296, 26°4′N, 56°2′E, 12 Apr 1902], 1 female.

Remarks.—The latitude for this station may have been cited erroneously by Kemp.

Squilla hieroglyphica Kemp, 1911

Squilla hieroglyphica Kemp, 1911:96 [=*Alima hieroglyphica* (Kemp, 1911)].

Holotype.—7327/10, type locality unknown, 1 female.

Squilla holoschista Kemp, 1911

Squilla holoschista Kemp, 1911:97 [=*Oratosquilla holoschista* (Kemp, 1911)].

Syntypes.—7926/9, Sandheads, Ganges delta, India, A. J. Milner, 1 male.—7301/10, Puri [19°48′N, 85°51′E], Orissa coast, India, N. Annandale, F. H. Gravely, and S. W. Kemp, 6 males, 2 females.—3147/5, Madras, Madras Museum, 7 males, 12 females.—7445–50/10, Cuddalore [11°45′N, 79°45′E] and Porto Novo [11°29′N, 79°46′E], south India, T. H. Hill, 7 males, 13 females.—3062/5, Ceylon [=Sri Lanka], Colombo Museum, 1 male, 2 females (specimens completely fragmented).

Remarks.—Although Kemp (1913) reported that the large lot from Madras (3147/5) were types, apparently all of the specimens reported by him are syntypes. In his original account (1911:98) he remarked that "In all, several hundreds of specimens have been examined."

Squilla interrupta Kemp, 1911

Squilla interrupta Kemp, 1911:98 [=*Oratosquilla interrupta* (Kemp, 1911)].

Syntypes.—9827–8/6, Hong Kong [Hong Kong Island = 22°15′N, 114°11′E], Hong Kong Museum, 1 male, 1 female.—3329/9, same locality, G. Dennys, 3 males, 3 females.—4743–5/9, Singapore? [1°17′N, 103°51′E], Malaysia, Raffles Museum, 3 males.—3095/5, Camorta [Camorta Island

= 8°08′N, 93°30′E], Nicobar Islands, India, F. Stoliczka, 1 female.—3094/5, Akyab [20°09′N, 92°54′E], Arakan coast, Burma, W. Dodgson, 1 female.—7982–91/9, Sandheads, Hughli delta, India, Commissioners of H. M. Pilot Brigs., 5 males, 5 females.—1284–6/7, same data, 2 males, 1 female.—7783/10, Ghapa Natta, Mutlah River, near Calcutta, India, S. B. Nath, 1 male.—7268–74/10, mouth of River Hughli, India, J. Munro, 5 males, 5 females.—3080/5, off Mutlah Light, Hughli River, India, G. M. Giles, 1 male.—8043/10, Puri [19°48′N, 85°51′E], Orissa coast, India, F. H.Gravely, 1 male, 1 female.—3335–7/7, off Ganjam coast, Madras, India, 7 fm (=13 m), *Investigator,* 3 males.—5830/9, off Vizagapatam coast, Madras, India, 7.5–9 fm (=14–16 m), *Investigator* [? sta 87, 10 Feb 1890], 1 male.—7557/6, 7559/9, Bombay [18°58′N, 72°50′E], India, Bombay Natural History Society, 4 males, 14 females.—7272–8/10, Panvel Creek, Bombay, India, J. Caunter, 2 males, 4 females.—7004/10, Karachi? [24°52′N, 67°03′E], Pakistan, Karachi Museum, 1 male, 1 female.—3047/5, 3067/5, Arabian Sea, Karachi Museum and A. O. Hume, 4 males, 4 females.—647/10, Persian Gulf, F. H. Townsend, 1 female.—7282–3/10, Persian Gulf, F. H. Townsend, 1 female.—7282–3/10, Persian Gulf, 29°20′N, 48°47′E, 13 fm (=24 m), *Investigator* [sta 352, 19 Nov 1905], 2 males.—7279–81/10, same area, 28°59′N, 50°5′E, 25 fm (=46 m), *Investigator* [sta 349, 8 Oct 1905], 2 males, 1 female.

Remarks.—Kemp (1911:99) remarked that he had examined "very numerous specimens." Apparently all of the specimens listed by him in 1913 are syntypes, although in 1913 he considered the specimens from lot 7982–91/9 as types.

Squilla investigatoris Lloyd, 1907

Squilla investigatoris Lloyd, 1907:7, 10 [=*Natosquilla investigatoris* (Lloyd, 1907)].

Syntypes.—5354–65/10, Arabian Sea, off the southeast coast of Arabia, 15°8′30″N, 51°52′15″E, 110 fm (=201 m), sandy mud, *Investigator* sta 364, 27 Mar 1906, 9 males, 5 females.

Squilla lirata Kemp & Chopra, 1921

Squilla lirata Kemp & Chopra, 1921:303, figs. 3, 4 [=*Lophosquilla lirata* (Kemp & Chopra, 1921)].

Syntypes.—C 306/1, Singapore [1°17′N, 103°51′E], Malaysia, Capt. Hutcheson leg., 1 male, 1 female.

Squilla mauritiana Kemp, 1913

Squilla mauritiana Kemp, 1913:66 [in synonymy], 68 [=*Oratosquilla mauritiana* (Kemp, 1913)].

Syntypes.—4269/4, Mauritius [20°18′S, 57°35′E], purchased, 1 male, 1 female (badly mutilated).

Squilla merguiensis Tiwari & Biswas, 1952

Squilla merguiensis Tiwari & Biswas, 1952: 350, fig. 1a [=*Clorida merguiensis* (Tiwari & Biswas, 1952)].

Holotype.—C 302/1, 4 miles NNE of Kabusa Island, Burma, 33 fm (=60 m), *Investigator* [sta 550, 12°52′N, 97°54′E, 22 Oct 1913], 1 male.

Squilla mikado Kemp & Chopra, 1921

Squilla mikado Kemp & Chopra, 1921:301, fig. 2 [=*Kempina mikado* (Kemp & Chopra, 1921)].

Holotype.—7685/10, Misaki [Misaki Harbor = 33°23′N, 132°07′E], Shikoku Island, Japan, A. Owston leg., 1 male.

Paratype.—C 304/1, Misaki, Japan, K. Aoki leg., 1 male.

Squilla oratoria var. *perpensa* Kemp, 1911

Squilla oratoria var. *perpensa* Kemp, 1911: 98 [=*Oratosquilla perpensa* (Kemp, 1911)].

Lectotype (selected by Manning, 1978: 23).—ex. 4851–72/9, Hong Kong [Hong Kong Island = 22°15′N, 114°11′E], G. Dennys leg., 1 female.

Paralectotypes.—4851–72/9, 6728/10, data same, 13 males, 16 females.—9817–20/6, Hong Kong, Hong Kong Museum, 1 male, 5 females.—8179/7, Mergui Archipelago, Burma, museum collector, 1 female.—5776–80/9, off Irrawaddy delta, Burma, 15°20′N, 94°55′E, 20 fm (=37 m), *Investigator* [sta 60, 23 Nov 1889], 2 males, 1 female.—5769/9, 6729/10, Sandheads, Hughli delta, India, A. J. Milner, 2 females.—7266–7/10, Madras coast, India, 1 male, 1 female.—4520/10, Persian Gulf, 26°20′N, 53°54′W, 53 fm (=124 m), *Investigator* [sta 292, 2 Nov 1901], 1 female.

Remarks.—Manning (1978:23) pointed out that Kemp's (1913) material of this species included representatives of at least two other species, *O. hindustanica* Manning, 1978, and *O. solicitans* Manning, 1978.

Apparently all of the specimens listed by Kemp (1913) were syntypes of *S. oratoria* var. *perpensa*; in his original description of this species (1911:98) he remarked that he had seen "Very numerous specimens."

Squilla scorpio var. *immaculata* Kemp, 1913

Squilla scorpio var. *immaculata* Kemp, 1913:45, pl. 2, fig. 31 [=*Cloridopsis immaculata* (Kemp, 1913)].

Syntypes.—3090/5, E of Terribles [19°24′N, 93°18′E], Arakan coast, Burma, 13 fm (=24 m), *Investigator,* 1 male.—1317/7, Bay of Bengal, V. Ball, 1 male.—3093/5, Calcutta [22°32′N, 88°22′E], India, J. Wood-Mason and V. Ball, 6 males, 5 females.—7531/10, Pratapnagar, Calcutta, India, B. L. Chaudhuri, 1 male.—7784/10,Ghaga Nata, Mutlah River, near Calcutta, India, brackish water, S. B. Nath, 14 males, 7 females.—7532/10, Saugor Island, mouth of Hughli River, India, J. Munro, 1 male.—1407–9/7, Hughli estuary, India, museum collector, 1 male, 1 female.—3091/5, Port Canning, Ganges delta, India, R. D'Cruz, 1 female.—7533/10, Karachi [24°52′N, 67°03′E], Pakistan, 1 male.—7528/10, locality unknown, 2 males, 4 females.

Squilla stridulans Wood-Mason, 1894

Squilla stridulans Wood-Mason, in Alcock, 1894:409 [=*Kempina stridulans* (Wood-Mason, 1894)].

Syntypes.—7035–40/9, Masulipatam coast, Madras, India, 15°56′20″N, 81°26′10″E, 95 fm (=174 m), *Investigator* [sta 120, 24 Dec 1890], 6 females.—6935–6/9, same area, 15°56′50″N, 80°30′30″E, 240 fm (=439 m), *Investigator* [sta 119, 24 Dec 1890], 2 females.

Remarks.—In his original description, Wood-Mason (in Alcock 1894:411) listed material from two *Investigator* stations: sta 119, 95 fm, and sta 120, 240 fm. Specimens from these stations are syntypes, in spite of Kemp's indication (1913:80) that two specimens from the Orissa coast of India were types.

Squilla supplex Wood-Mason, 1875

Squilla supplex Wood-Mason, 1875:232 [=*Alimopsis supplex* (Wood-Mason, 1875)].

Holotype.—3048/5, Bombay [18°58′N, 72°50′E], India, F. Stolizcka, 1 male (delicate).

Squilla tenuispinis Wood-Mason, 1891

Squilla tenuispinis Wood-Mason, in Wood-Mason & Alcock 1891:271 [=*Squilloides tenuispinis* (Wood-Mason, 1891)].

Syntypes.—5801/9, off Ganjam coast, Madras, India, 18°40′N, 84°46′E, 98–102 fm (=179–187 m), *Investigator* [sta 96, 18°30′N, 4 Mar 1890], 1 male.—3081/5, off Cheduba [Cheduba Island = 18°48′N, 93°38′E], Arakan coast, Burma, *Investigator,* 1 female.

Remarks.—In the original description, Wood-Mason (in Wood-Mason & Alcock 1891:272) mentioned two specimens taken by the *Investigator*: one from sta 96 in 90 to 100 fm and one from off Cheduba [Island], Arakan coast of Burma, in about the same depth. Of the specimens listed by Kemp (1913:49), these two specimens are syntypes; Kemp listed them as types.

The latitude given by Kemp for the material from sta 96 is incorrect by 10 minutes.

Squilla wood-masoni Kemp, 1911

Squilla wood-masoni Kemp, 1911:99 [=*Oratosquilla woodmasoni* (Kemp, 1911)].

Syntypes.—7513/10, Port Jackson [33°51′S, 151°15′E], New South Wales, Australia, Australian Museum, 1 female.—7294/10, Pondicherry, India, purchased, 1 female.—3098/5, Madras [13°05′N, 80°17′E], India, 3 males, 2 females.—3078/5, 3087/5, Madras, India, Madras Museum and purchased, 2 males.—7295/10, off Madras coast, India, 14°4′57″N, 80°20′50″E, 23 fm (=42 m), *Investigator* [sta 158, 10 Jan 1894], 1 female.—7297–8/10, Puri [19°48′N, 85°51′E], Orissa coast, India, N. Annandale, F. H. Gravely, and J. Caunter, 9 males, 3 females.—7992/9, Sandheads, Ganges delta, India, W. M. Daly, 1 female.

Remarks.—In his original account, Kemp (1911:99) stated that he had seen "Numerous examples." Apparently all of the specimens listed by him in 1913 are syntypes.

Types of Stomatopoda in the Zoological Survey of India, Listed by Current Name

Acanthosquilla multifasciata (Wood-Mason, 1895)
See *Lysiosquilla multifasciata*
Alima hieroglyphica (Kemp, 1911)
See *Squilla hieroglyphica*
Alimopsis supplex (Wood-Mason, 1875)
See *Squilla supplex*
Busquilla quadraticauda (Fukuda, 1911)
See *Squilla boopis*
Chorisquilla excavata (Miers, 1880)
See *Chorisquilla andamanica*
Clorida bombayensis (Chhapgar & Sane, 1967)
See *Squilla bombayensis*
Clorida decorata Wood-Mason, 1875
Clorida denticauda (Chhapgar & Sane, 1967)
See *Squilla denticauda*
Clorida merguiensis (Tiwari & Biswas, 1952)
See *Squilla merguiensis*
Cloridopsis bengalensis (Tiwari & Biswas, 1952)
See *Squilla bengalensis*
Cloridopsis immaculata (Kemp, 1913)
See *Squilla scorpio* var. *immaculata*
Dictyosquilla foveolata (Wood-Mason, 1895)
See *Squilla foveolata*
Gonodactylus choprai Manning, 1967
Gonodactylus lanchesteri Manning, 1967
Gonodactylus platysoma Wood-Mason, 1895
See *Gonodactylus chiragra* var. *platysoma*
Haptosquilla glyptocercus (Wood-Mason, 1875)
See *Gonodactylus glyptocercus*
Haptosquilla nefanda (Kemp, 1911)
See *Gonodactylus nefandus*
Haptosquilla proxima (Kemp, 1911)
See *Gonodactylus proximus*
Harpiosquilla annandalei (Kemp, 1911)
See *Squilla annandalei*
Heterosquilla tricarinata (Claus, 1871)
See *Coronis spinosa*
Heterosquilloides insignis (Kemp, 1911)
See *Lysiosquilla insignis*
Kempina mikado (Kemp & Chopra, 1921)
See *Squilla mikado*
Kempina stridulans (Wood-Mason, 1894)
See *Squilla stridulans*
Lenisquilla gilesi (Kemp, 1911)
See *Squilla gilesi*
Lophosquilla lirata (Kemp & Chopra, 1921)
See *Squilla lirata*
Lophosquilla tiwarii Blumstein, 1974
Lysiosquilla sulcirostris (Kemp, 1913)
See *Lysiosquilla maculata* var. *sulcirostris*
Manningia andamanensis Ghosh, 1975
Mesacturus furcicaudatus (Miers, 1880)
See *Gonodactylus furcicaudatus*
Natosquilla investigatoris (Lloyd, 1907)
See *Squilla investigatoris*
Odontodactylus brevirostris (Miers, 1884)
See *Odontodactylus southwelli*

Oratosquilla gonypetes (Kemp, 1911)
See *Squilla gonypetes*
Oratosquilla hindustanica Manning, 1978
Oratosquilla holoschista (Kemp, 1911)
See *Squilla holoschista*
Oratosquilla interrupta (Kemp, 1911)
See *Squilla interrupta*
Oratosquilla mauritiana (Kemp, 1913)
See *Squilla mauritiana*
Oratosquilla pentadactyla Manning, 1978
Oratosquilla perpensa (Kemp, 1911)
See *Squilla oratoria* var. *perpensa*
Oratosquilla subtilis Manning, 1978
Oratosquilla woodmasoni (Kemp, 1911)
See *Squilla woodmasoni*
Squilla brasiliensis Calman, 1917
Squilloides tenuispinis (Wood-Mason, 1894)
See *Squilla tenuispinis*

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PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS IV. ON SOME SPECIES FROM THE RYUKYU ISLANDS

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Abstract.—A small collection of Pycnogonida from the southern Ryukyus and miscellaneous specimens from Okinawa are recorded with their zoogeography. One new species, *Callipallene tridens,* is described and figured and 11 known species are recorded for the first time in the Ryukyus. A high incidence of juveniles and larvae suggests that the months of collection, May and June, may be the peak of the breeding and hatching season in these islands.

Only two species of pycnogonids were known from the Ryukyu Islands prior to this report. The specimens reported here were taken in the Sakishima Group of the southern Ryukyus and from Okinawa. The first pycnogonid described from Okinawa was *Pycnogonum benokianum* Ohshima (1935:137–139), from Benoki (=Benochi, 26°48′N, 128°14′E). The second species reported from the Ryukyus was *Endeis mollis* (Carpenter), also by Ohshima (1935:139), taken at Ishigaki Island in the Sakishima Group south of Okinawa. Specimens of *E. mollis* are reported from the Sakishima Group, but *P. benokianum* has not been recorded since the type specimens were described. Hedgpeth (1949:304–397, fig. 49) subsequently redescribed this species from Ohshima's notes and a preserved type specimen in his paper on collections taken in Japan by the *Albatross.* Utinomi (1971:327) also repeated Ohshima's record in his list of Japanese pycnogonids.

There are now 13 species known from the Ryukyus with one of them, *Callipallene tridens,* described herein as new. At least two and probably three other species are represented in these collections but the questionable specimens are juveniles or larvae and do not have characters sufficiently developed for recognition or description.

The known Ryukyu Islands species have their strongest faunal affinity with the Philippines where six of the species are also known, suggesting some form of transport by shallow northward-flowing currents. Three of the species are also found in Japan while three are found to the south in Indonesia and beyond. There are also three species found in the Marshall, Hawaii, and Samoa Island groups while a more distant distribution occurs for two species recently described from Aldabra Atoll in the Indian Ocean. Two other widely distributed species are known from the western Indian Ocean while one additional species, *Pigrogromitus timsanus,* is known to be pantropical. The distribution of most of these species is so incompletely known that their true distribution can not be suggested at this time. They are all shallow-water species.

Family Phoxichilidiidae

Genus *Anoplodactylus* Wilson, 1878

Anoplodactylus pectinus Hedgpeth

Anoplodactylus pectinus Hedgpeth, 1948: 234–236, fig. 34.—Child, 1982a:372–373 [literature]; 1988a:20.

Material examined.—Sakishima: Funauki Bay, Iriomote Island, 5 m, 7 Jun 1987; 1 ♂ with eggs, 2 ♀, 1 juv. Southwest Ishigaki Harbor, Ishigaki Island, 2–4 m, 10 Jun 1987; 1 ♂.

Distribution.—This species was first described from specimens taken in the Florida Keys and is now known from many localities in Florida and the Caribbean. It has also been taken in Madagascar and more recently in the northern Philippines. Its occurrence in the southern Ryukyus constitutes only a small range extension from the Philippines, but the range of collections in which the species appears suggests that it may be another pantropical species. All known depths of capture are shallow, the deepest being 27 meters.

Remarks.—The moderately large size (leg span about 12 mm) of this species in relation to other tropical members of this genus, its slender appearance, and the fairly long cribriform cement gland slit of the male along with the serrate major heel spine in both sexes all serve to make this an easily identified species.

Anoplodactylus perforatus Nakamura & Child

Anoplodactylus perforatus Nakamura & Child, 1982:288–291, fig. 3; 1983:49; (in press).

Material examined.—Sakishima: southwest Ishigaki Harbor, Ishigaki Island, 8–12 m, 4 Jun 1987; 1 ♂, 1 ♀.

Distribution.—This species is often taken in large numbers per capture effort in western Sagami Bay, Japan, while another similar large aggregation was recently reported from Western Samoa. These 2 Ryukyu specimens serve to help bridge the wide distributional gap between Japan and Samoa while contributing nothing new to the known depth range of 7–113 meters.

Remarks.—This is an easily recognized species, at least in the male, by its many cement gland pores (17 to 25) per femur and the long slender oviger having an incongruously tiny terminal segment. Both sexes have a very short propodal lamina and long chelae fingers lacking teeth.

Anoplodactylus, species indeterminate

Material examined.—Sakishima: Funaura Bay, Iriomote Island, night, at surface, 10 May 1986; 2 juv, 1 larva. Same locality, depth, 3 Jun 1986; 4 juv, 5 larvae. Funauki Bay, Iriomote Island, 5 m, 7 Jun 1987; 1 larva. Iriomote Island, 11–20 m, 7 Jun 1987; 1 ♀ juv. Southwest Ishigaki Harbor, Ishigaki Island, 2–4 m, 10 Jun 1987; 1 ♀.

Remarks.—There are at least two species represented by these females and young but none of them is sufficiently developed or was taken with adult males to permit identification. The relatively large number of *Anoplodactylus* young in relation to the total number of pycnogonids taken during collecting in the Sakishima Islands group is possibly significant in suggesting that May and June represent the breeding-hatching season for the genus.

Family Endeidae

Genus *Endeis* Philippi, 1843

Endeis nodosa Hilton

Endeis (*Phoxichilus*) *nodosa* Hilton, 1942: 47–48, fig. 4.

Endeis nodosa.—Stock, 1968:59 [key].—Child, 1982b:275–277, fig. 2g–i.

Material examined.—Okinawa: Naha Harbor, on breakwater, 1.5 m, 27 Jun 1987; 1 subadult.

Distribution.—This species is rare because it is found on islands seldom or never exposed to collecting for marine microinvertebrates. Its type locality is Hawaii and it has subsequently been taken at Enewetak Atoll in the Marshall Islands. Okinawa is only the third known locality where it has been found and it is apparently not common in any of these places. All known collecting depths are littoral or very shallow waters.

Remarks.—This species is fairly easily distinguished from others of the genus by the presence of a large node or low conical tubercle on the midventral femur and for the many diverticula or blind pockets of the central intestinal branches in the legs. The integument is usually opaque so that the gut branches and diverticula are easily seen. There are sometimes many more finger-like diverticula on the intestines than are figured by Child (1982b:276, fig. 2h).

Endeis mollis (Carpenter)

Phoxichilus mollis Carpenter, 1904:182–183, figs. 1–7.

Endeis mollis.—Utinomi, 1971:327 [literature].—Stock, 1975a:1083–1085; 1975b:76.—Child, 1979:66.—Nakamura & Child, 1983:41.—Stock, 1986:440.—Child, 1988a:20–21.

Material examined.—Sakishima: Funaura Bay, Iriomote Island, 3 Jun 1986; 2 juv. Same locality and date, night, at surface; 1 juv.

Distribution.—This is a pantropical-temperate species found as far north as Sagami Bay, Japan. Ohshima reported it from the Sakishima Group at Ishigaki Island (Ohshima 1935:139), the only pycnogonid found in the southern Ryukyus, but it could also be expected to inhabit Okinawa. It is a shallow-water species, having been taken from the shoreline down to 60 meters.

Remarks.—This species does not have the small side pockets along its gut diverticula in each leg nor does it have the conspicuous conical ventral tubercle on the femorae as does *E. nodosa.*

Family Ammotheidae

Genus *Eurycyde* Schiödte, 1857

Eurycyde, species indeterminate

Material examined.—Sakishima: Iriomote Island, 11–20 m, 7 Jun 1987; 1 juv.

Remarks.—This juvenile specimen is indeterminable although it has several characters reminiscent of *Eurycyde setosa* Child (1988a:8–10, fig. 3), from the Philippines. This recently described species has 7 large spines at the ocular tubercle apex, but the abdomen of the unique type is missing. The Iriomote specimen has 4–5 large spines at the ocular apex and several similar spines on the curved abdomen. The lateral processes are also closely spaced as in *E. setosa.* The proboscis of this juvenile has not yet divided into the characteristic 2 segments and the specimen otherwise has no visible identifying characters.

Family Callipallenidae

Genus *Callipallene* Flynn, 1929

Callipallene novaezealandiae (Thomson)

Pallene novae-zealandiae Thomson, 1884:246–247, pl. 14, figs. 1–4.

Callipallene novaezealandiae.—Child, 1983:708 [literature].

Material examined.—Sakishima: Funaura Bay, Iriomote Island, night, at surface, 3 Jun 1986; 2 ♂, 1 juv. Southwest Ishigaki Harbor, Ishigaki Island, 3 m, 4 Jun 1987; 4 ♂ with eggs, 2 ♂, 4 ♀, 8 juv, 15 larvae. Same locality, 2–4 m, 10 Jun 1987; 2 ♂, 3 ♀, 7 juv, 1 larva.

Distribution.—This species is known from eastern Africa, Australia, Japan, New Zealand, and from Palau and Enewetak Atoll in Micronesia, all from shallow localities. This series of specimens extends its distribution to an intermediate locality between Japan and islands to the south and east.

Remarks.—These specimens, particularly the males, have the same variation in oviger denticulate spine counts per segment as seen in the Micronesian specimens, but otherwise agree with these specimens in diagnostic characters.

Callipallene tridens, new species

Fig. 1

Material examined.—Sakishima: southwest Ishigaki Harbor, Ishigaki Island, 3 m, 4 Jun 1987; 1 ♂ with eggs (holotype, USNM 234430), 5 ♂, 5 ♀, 2 juv (paratypes, USNM 234431).

Description.—Size very tiny, leg span only 3.6 mm. Trunk fairly elongate, segmentation lines faint, incomplete. Lateral processes no longer than wide, distally separated by their own diameter or less, glabrous. Neck very short, without parallel sides, expansion before chelifores no wider than long. Ocular tubercle very broad-based, only half as tall as basal width, eyes large, slightly pigmented, lateral papillae present, not prominent. Proboscis short, 1.5 times longer than diameter, with low rounded ventrodistal bulges, constricted distally just posterior to flat lips. Abdomen very short, less than length of 4th lateral processes, distally rounded, armed with 2 short lateral setae.

Chelifore scape moderately slender, 3 times longer than its diameter, armed with 3 dorso- and laterodistal setae longer than scape diameter. Chela palm subtriangular, with 10–11 ectal and lateral setae longer than palm diameter. Fingers longer than palm, carried anaxially, slender, overlap strongly at tips, armed with 4–5 long sharp teeth on immovable finger and 6 similar teeth on movable finger. Movable finger longer and more curved than immovable finger.

Oviger short, 4th segment only slightly longer than 3rd, 0.6 as long as 5th which is armed with rounded distal apophysis bearing 2–3 short setae. Strigilis segments each shorter than last, armed with 1–2 ectal short setae distally and dimorphic denticulate spines endally in the formula 5:5:5:6. Proximal spines with many tiny lateral serrations, distal serrations slightly larger; distal spines with tiny serrations on proximal side, long finger-like serrations on distal side of spines. Egg size very large, 4 times larger than 5th segment diameter.

Legs fairly short, slightly inflated, cement gland tubes or pores not evident. Second and 3rd coxae armed with very long ventrodistal setae, each 2–3 times longer than segment diameter. Femur with slight ventrodistal bend, armed with several distal and lateral setae not as long as segment diameter. Tibiae slightly shorter than femur, 1st tibia armed with few lateral and distal setae shorter than segment diameter, 2nd tibia with more setae, some longer than segment diameter. Tarsus very short, armed with dorsal and ventral setae, some longer than segment diameter. Propodus slightly inflated, straight, without heel but with 4 stout heel spines and 7–8 sole spines, very short distal lamina, and few lateral and distal setae. Claw moderately curved, half propodal length, with very short auxiliary claws shaped like tridents bearing broad pointed spatulate median spine flanked by 1 or 2 tiny pointed lateral serrations. Auxiliaries slightly inflated, curved in lateral view.

Female paratype: propodal claw longer, 0.7 propodus length, more curved distally. Trunk and legs slightly larger than those of male, oviger reduced, without distal apophysis on 5th segment.

Measurements (holotype in mm).—Trunk length, 0.6; trunk width (across 2nd lateral processes), 0.29; proboscis length, 0.2; abdomen length, 0.05; third leg, coxa 1, 0.08; coxa 2, 0.19; coxa 3, 0.1; femur, 0.33; tibia 1, 0.29; tibia 2, 0.31; tarsus, 0.04; propodus, 0.22; claw, 0.11.

Distribution.—Known only from the type locality, Ishigaki Harbor, Ishigaki Island, in the southern Ryukyus, in 3 meters.

Etymology.—The name *tridens* (Latin: forked with 3 tines) refers to the 3-lobed "trident" auxiliary claws of this species.

Remarks.—The presence of short trident-like auxiliary claws is unique among known pycnogonid species. Auxiliary claws are used as a usually reliable diagnostic character among pycnogonid genera and some have them while some do not. They are usually simple curved claws, but some species have tiny endal setules or spinules. These are most often found among *Callipallene* species and these trident-like claws add another form to the seemingly endless variety of characters.

This new species does not conform in other ways to most *Callipallene* species; the chelae are atypical in having very slender fingers placed anaxially on the palm and bearing long slender teeth, the ocular tubercle is broader based and is shorter than

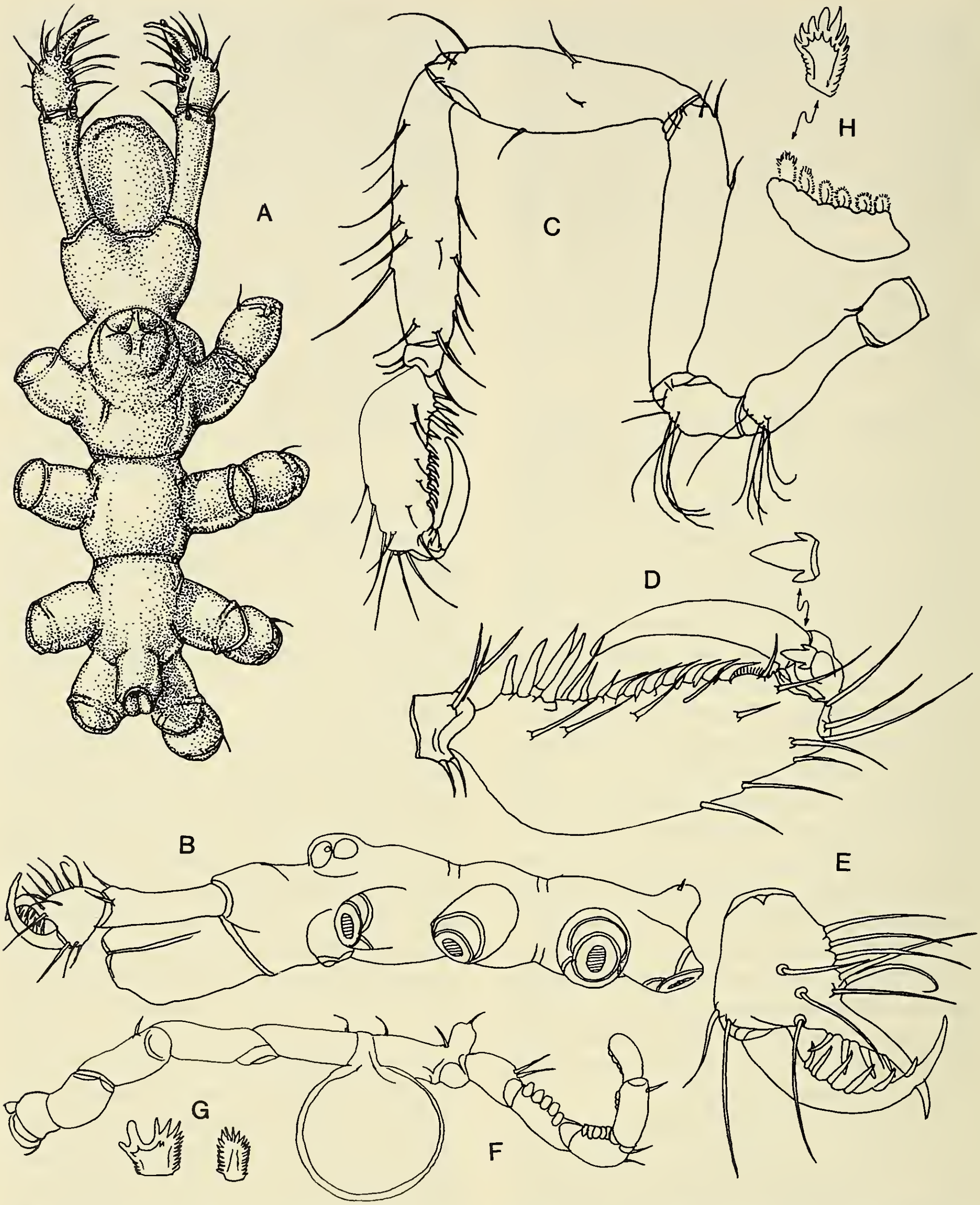

Fig. 1. *Callipallene tridens,* holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg; D, Distal segments of third leg with auxiliary claw enlarged; E, Chela; F, Oviger with single egg attached; G, Oviger distal and proximal denticulate spines, enlarged; H, Oviger terminal segment, distal spine enlarged.

in almost any other species known, and the propodus has a short distal sole lamina, a character unknown to this genus but common among species of the genus *Anoplodactylus.* These atypical and unique characters are sufficient to permit description of this as a new species and they continue to expand the diversity of characters found among the Pycnogonida.

Genus *Cheilopallene* Stock, 1955
Cheilopallene hirta Child

Cheilopallene hirta Child, 1988b:63–66, fig. 5.

Material examined.—Sakishima: Funaura Bay, Iriomote Island, night, at surface, 3 Jun 1986; 1 ♂, 1 ♀. Funauki Bay, Iriomote Island, 5 m, 7 Jun 1987; 1 ♀. Southwest Ishigaki Harbor, Ishigaki Island, 5 m, 4 Jun 1987; 1 juv.

Distribution.—This species is known only from Aldabra Atoll, western Indian Ocean, its type locality, in 0–21 meters. The Sakishima specimens greatly extend this distribution eastward into the Pacific and northward to the southern Ryukyus in similarly shallow waters.

Remarks.—There is remarkably little difference between these specimens and the type series. The male fourth oviger segment is very slightly longer than with the Aldabra specimens and there are the usual 1–2 spine differences in the denticulate spine counts among specimens. The four stout spines next to the chela immovable finger of the type are reduced to three with several additional slender setae on the adjacent raised pad, but the specimens agree exactly otherwise, including the hirsute distal proboscis.

Genus *Pigrogromitus* Calman, 1927
Pigrogromitus timsanus Calman

Pigrogromitus timsanus Calman, 1927:408–410, fig. 104a–f.—Child, 1982a:367–368; 1988a:21 [literature].

Material examined.—Okinawa: Maeda Misaki, reef flat, on *Lybia tesellata* [Xanthidae: Crustacea], 15 Nov 1985; 1 juv.

Distribution.—This species has a pantropical but scattered distribution in many varied localities. It has been taken in Hawaii and is known from the Philippines, so it is not surprising to find it in Okinawan waters. It inhabits shallow depths, the deepest capture being 108 meters.

Remarks.—This is an easily recognized species in a monotypic genus. It superficially looks like several species of the genus *Pycnogonum* in habitus, but has chelifores with small functional chelae, and has an oviger without denticulate spines but with a terminal claw having a proximal spine in a forcipulate arrangement with the large claw. Live specimens of this species have a uniform whitish-tan coloration.

Genus *Propallene* Schimkewitsch, 1909
Propallene curtipalpus Child

Propallene curtipalpus Child, 1988a:21–23, fig. 9.

Material examined.—Sakishima: Iriomote Island, 11–20 m, 7 Jun 1987; 2 ♂, 1 ♀, 2 juv.

Distribution.—This species was originally described from material taken in the Visayan Islands, central Philippines, from depths of 2 meters or less. The presence of the species in the southern Ryukyus is not surprising considering the supposed corridor of pycnogonid genera thought to inhabit islands from New Zealand north along the western Pacific archipelagoes as far as Japan (Child 1983:713). The corridor hypothesis was originally proposed to include the predominantly Antarctic genus *Austrodecus* which has several species found from New Zealand to Japan. It now appears that the corridor should include other genera, among them *Propallene,* with the majority of its species found from the Indian Ocean (including South Africa) and Australia north along the corridor to Japan. The genus *Scipiolus* with representatives from South Africa, Indonesia, and Japan, and the genus *Hemichela* having species known from Australia, Indonesia, and the Philippines, should possibly be included as members of this corridor fauna. There are several endemic genera known to the East Indies, but none of the above genera nor any families are confined to the western Pacific corridor as endemics although the majority of their species are known from parts of the corridor and Indian Ocean-Australian localities. Our knowledge of the pycnogonids of this vast region remains very fragmentary and the distribution of any of these genera may be greatly expanded to more distant parts of the Pacific in future collecting.

The known depth at which this species has been taken is now extended to 20 meters by the Ryukyu records. It has not been taken on Okinawa Island.

Remarks.—This is the only known species in a genus with very look-alike members to have a reduced number of cement gland tubes (4–5) arranged on the femur (1) and both tibiae (1–2 each), and a very reduced palp which is less than half the proboscis length. Where specimens are sympatric, they can not be differentiated to species with only females in hand. The males with palps and cement glands bear the only characters with which to separate any two species. Necks have some variation in length among a large suite of females. The only instance of sympatry in this genus, to our knowledge, is in *P. longiceps* and *P. saengeri,* both of which appear in Sagami Bay collections (Nakamura & Child 1983:61–62).

Propallene longiceps (Böhm)

Pallene longiceps Böhm, 1879:59–60.
Propallene longiceps.—Nakamura & Child, 1983:61–62 [literature].—Kim & Hong, 1986:41.—Hong & Kim, 1987:158.

Material examined.—Okinawa: Heanza Shima, 30 Apr 1987; 11 ♂ with eggs.

Distribution.—This species was believed to be endemic to the main Japanese Islands until it was reported from the Korean coast by Kim & Hong (1986:41). This record is the first for the species from the Ryukyus. Further collecting in these many islands will possibly yield other endemics from the main islands to the north.

Remarks.—One of the most common pycnogonids in Sagami Bay, this species has more than 10 cement gland tubes per leg which are usually confined to the ventral femur and has a palp almost as long as the proboscis with a constriction in the second or longest segment.

Family Nymphonidae

Genus *Nymphon* Fabricius, 1794

Nymphon diabolus Child

Nymphon diabolus Child, 1988a:23–25, fig. 10; 1988b:75.

Material examined.—Sakishima: Funaura Bay, Iriomote Island, night, at surface, 3 Jun 1986; 1 ♀.

Distribution.—This species was described from specimens taken in Negros Oriental Province, central Philippines, and was subsequently found on Aldabra Atoll, Indian Ocean. All collecting depths are very shallow. Its distribution is extended northward to the Ryukyus by the above record. This is the first known record of the species being taken in a night plankton haul at the surface.

Remarks.—This specimen is very much like the adult female listed under other material from the Philippines. The species is notable for its reduced anterior size (chelae, proboscis and palps) in relation to its trunk, for the "horns" at the ocular tubercle apex, for the short main and auxiliary claws as related to the length of the propodus, and for the slender graceful chelae having long fingers bearing from 9 to 12 long pointed teeth. This female has the marked horns of the Philippine specimen, but there are slight variations in the tarsus-propodus ratio and the oviger denticulate spine count.

Nymphon, species indeterminate

Material examined.—Sakishima: Iriomote Island, 11–20 m, 7 Jun 1987; 1 juv.

Remarks.—This juvenile is close to *N. micronesicum* Child, but is insufficiently developed for determination. It has the tiny lateral tubercles on the ocular tubercle, but without horns, and has short auxiliaries and a main claw with rugosities. The bifurcate chelae teeth are on much more slender fingers which strongly overlap at the tips, unlike those of the type specimen. The ovigers are not sufficiently developed to permit comparison.

Family Austrodecidae
Genus *Austrodecus* Hodgson, 1907
Austrodecus tubiferum Stock

Austrodecus gordonae (part).—Stock, 1954: 153, fig. 76e.

Austrodecus tubiferum Stock, 1957:75–77, fig. 43.

Material examined.—Okinawa: Horseshoe Cliffs, 1 km WNW of Onna Village, 73.2 m, coll. R. F. Bolland, 28 Sep 1981; 1 ♀.

Distribution.—This species is only known from off Okinose in Sagami Bay, Japan, at 183 meters (type locality) and the above specimen extends this distribution south to the Ryukyus in shallower water.

Remarks.—This female conforms very well to the figures given for the type (a male), except that the median trunk tubercles and those of the first coxae are smaller, the oviger is very similar, and the palp has the deep cleft in its terminal segment although there is apparently no indication of a suture line beyond the cleft as shown for the type (Stock 1957:76, fig. 43c).

Acknowledgments

We wish to thank Mr. Hiroaki Akishige, captain of the *Kakuyo Maru,* and the crew of the vessel for their many kindnesses to the first author (K.N.) in collecting specimens, Mr. Nobuhiro Ooshiro of the Yaeyama Branch of the Okinawa Prefectural Fisheries Experimental Station for pycnogonids from his night tow samples, and Mr. Norikazu Shikatani of the Department of Marine Science, University of the Ryukyus, for bringing specimens from sortings of Fishery Bureau material to the attention of one of us (K.N.).

All specimens are deposited in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the old U. S. National Museum system.

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POECILOCHAETUS KOSHIKIENSIS, A NEW POLYCHAETE SPECIES FROM SHIMO-KOSHIKI ISLAND, JAPAN

Tomoyuki Miura

Abstract.—A new species of polychaetous annelid, *Poecilochaetus koshikiensis,* collected at a depth of 200 m off Shimo-Koshiki Island, Kyushu, southern Japan, is described. The new species is characterized by posterior notopodial hooks and basally fused anal cirri.

The genus *Poecilochaetus* Claparède, 1875 consists of 16 nominal species (Pilato & Cantone 1976, Read 1986). Their main diagnostic characters include the epidermal smoothness, the distribution of flask-shaped (ampullaceous) postsetal lobes (dorsal and ventral cirri), the length and number of nuchal organs, and the occurrence and distribution of several types of setae. Despite the small number of species and the large interspecific variability in morphology, some difficulties in the identification of species arise from the insufficient descriptions of most species, their intraspecific variability (Milligan & Gilbert 1984) and the confused terminology of the setae. For example, "plumose setae" called by Hartman (1939) corresponds to "pinnate setae" by Milligan & Gilbert (1984), while "plumose setae" by the latter refers to "spinose setae" by the former. In this study, the terminology of setae by Read (1986, Table 2) is chiefly followed. The worms are very fragile and complete specimens are rarely collected, even from shallow bottoms. The extensive morphology and habitat were described only on few particular species, such as *Poecilochaetus serpens* Claparède from England by Allen (1904), *P. australis* Nonato from Brazil by Nonato (1963), and *P. johnsoni* Hartman from Florida by Taylor (1966).

Only a single species, *Poecilochaetus japonicus* Kitamori, 1965, has been reported from Japanese coasts. In this study, a new species of *Poecilochaetus* is described based on a complete female and two additional mature specimens collected in Japan. The types are deposited in the National Museum of Natural History, Smithsonian Institution (USNM), and the National Science Museum, Tokyo (NSMT).

The specimens were fixed in 10% formalin-seawater and preserved in 70% alcohol. Parapodia of the holotype were observed by a scanning electron microscope after dehydration in ethyl alcohol and critical drying in CO_2.

Family Poecilochaetidae Hannerz, 1956
Poecilochaetus Claparède, in Ehlers, 1875
Poecilochaetus koshikiensis, new species
Figs. 1–3

Material.—Japan, off Shimo-Koshiki Island, Kagoshima Prefecture, 31°40.0′N, 129°40.7′E, 200 m, muddy sand, 4 Jun 1987, *Nansei-Maru* Cruise 1987-TR5, holotype, complete female (USNM 104126), paratype, incomplete male (USNM 104127), paratype, incomplete female (NSMT-Pol. P-249).

Types.—Holotype consisting of 68 setigers, 43 mm long, 1.5 mm wide without parapodia, 2.6 mm with parapodia. Mature types with gametes in coelom.

Description.—Prostomium small, rounded, with 2 pairs of eyes, anterior left eye

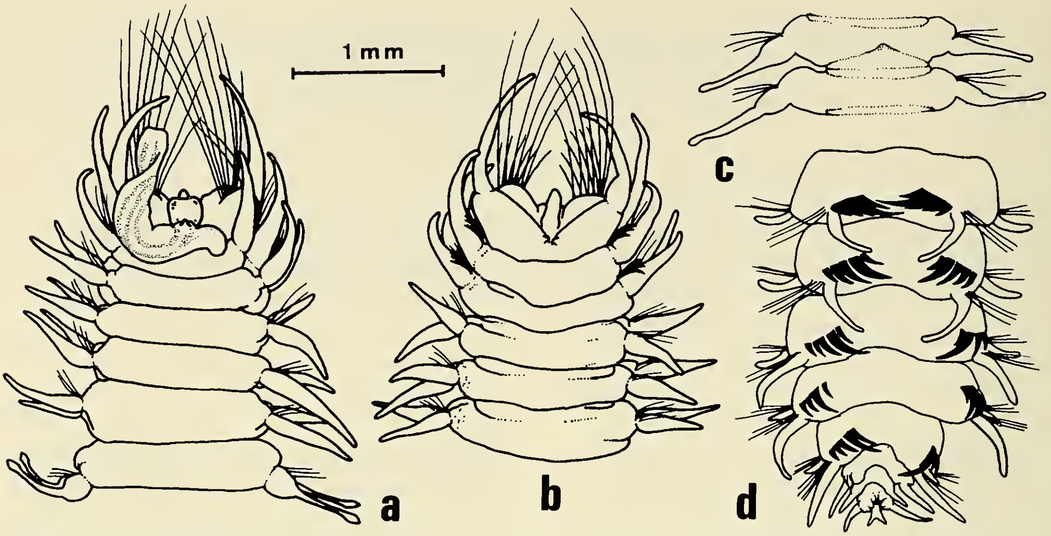

Fig. 1. *Poecilochaetus koshikiensis,* holotype: a, Anterior end, dorsal view; b, Same, ventral view; c, Dorsal view of setigers 9, with chitinized plate, and 10; d, Posterior end, dorsal view.

consisting of several pigment spots (in holotype, Fig. 1a). Nuchal organ trilobed, middle lobe extending posteriorly to setiger 4, flattened laterally with ciliated margin, lateral lobes small and discoid (Fig. 1a) and tentacular palps missing. Facial tubercle present in front of ventral mouth and directed anteriorly (Fig. 1b). Stout setae of setiger 1 directed forward, forming cephalic cage; parapodial postsetal lobes of anterior 3 setigers directed more or less forward (Fig. 1a, b). Weakly chitinized middorsal elevated plate present on setiger 9 (Fig. 1c). Pygidium with pair of cylindrical dorsal cirri and pair of short ventral cirri fused in single Y-shaped structure (Fig. 1d). Posterior segments well marked by stout notopodial spines.

Parapodia all biramous. First parapodium with very short notopodial and very long neuropodial postsetal lobes (Fig. 2a). Notopodial postsetal lobes longer than neuropodial ones on parapodia 2–6, both cylindrical (Fig. 2c). Notopodial postsetal lobes of setiger 5 longer than those of setigers 3, 4, and 6. Both postsetal lobes of parapodia 7–13 flask-shaped (ampullaceous) with swollen tips (Fig. 2d). Succeeding parapodia on middle of body with long conical postsetal lobes (Fig. 2e, f). Far posterior postsetal lobes again cylindrical but smaller, notopodial ones with many conical tubercles (Fig. 2h, i). Numerous papillae present on anteroventral sides of anterior parapodia of setigers 1, 2, 6–8 (Fig. 2a, c, d). Interramal parapodial sensory organs present on all setigers except for setigers 6–9. A well-developed sensory organ cup-shaped with cilia in distal hole (Fig. 2b). Sensory organs varying in size and sometimes withdrawn and detected only by their cilia (Fig. 2g). Sensory organs of anterior 5 setigers well developed, those of others smaller. Branchiae absent.

First parapodium with stout cephalic setae forming cephalic cage, very long, surface covered with numerous short spines (Figs. 1a, b, 2a, 3c, d). Parapodia 2 and 3 with slender hispid capillaries, spiral setae (membranous capillary) and 3 or 4 neuropodial falcate spines (Fig. 2c). Falcate spines curved posteriorly to body axis, distal tip smooth in SEM observation, but finely hirsute in LM observation (Fig. 3a, b). Spiral setae with spirally fringed pectinate margin, present on all parapodia except for first setiger, their margins with long stout teeth on

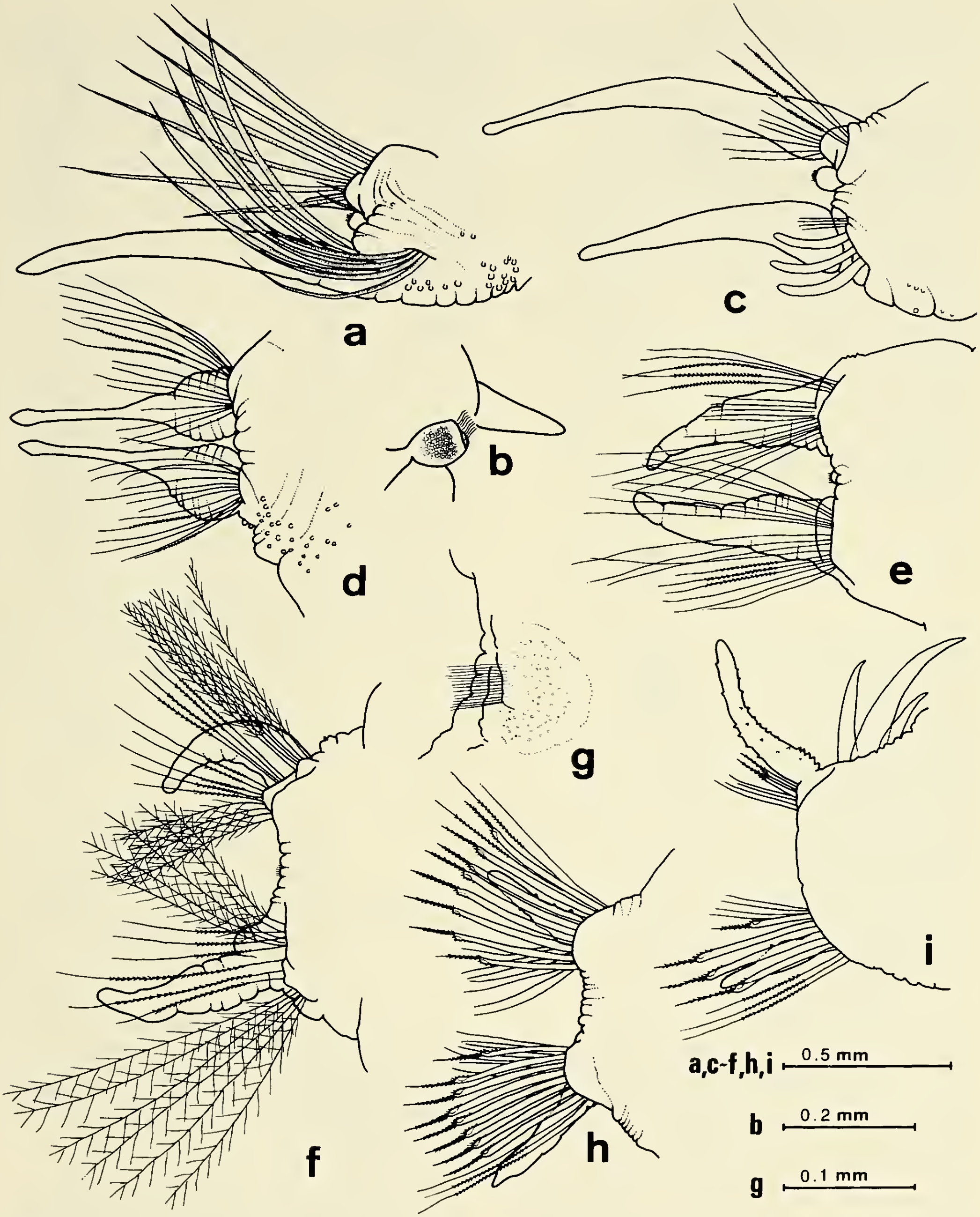

Fig. 2. *Poecilochaetus koshikiensis*: a, Parapodium 1, anterior view; b, Sensory organ below notopodial postsetal lobe of same; c, Parapodium 2; d, Parapodium 7; e, Parapodium 14; f, Parapodium 17; g, Sensory organ of same; h, Parapodium 54; i, Parapodium 61.

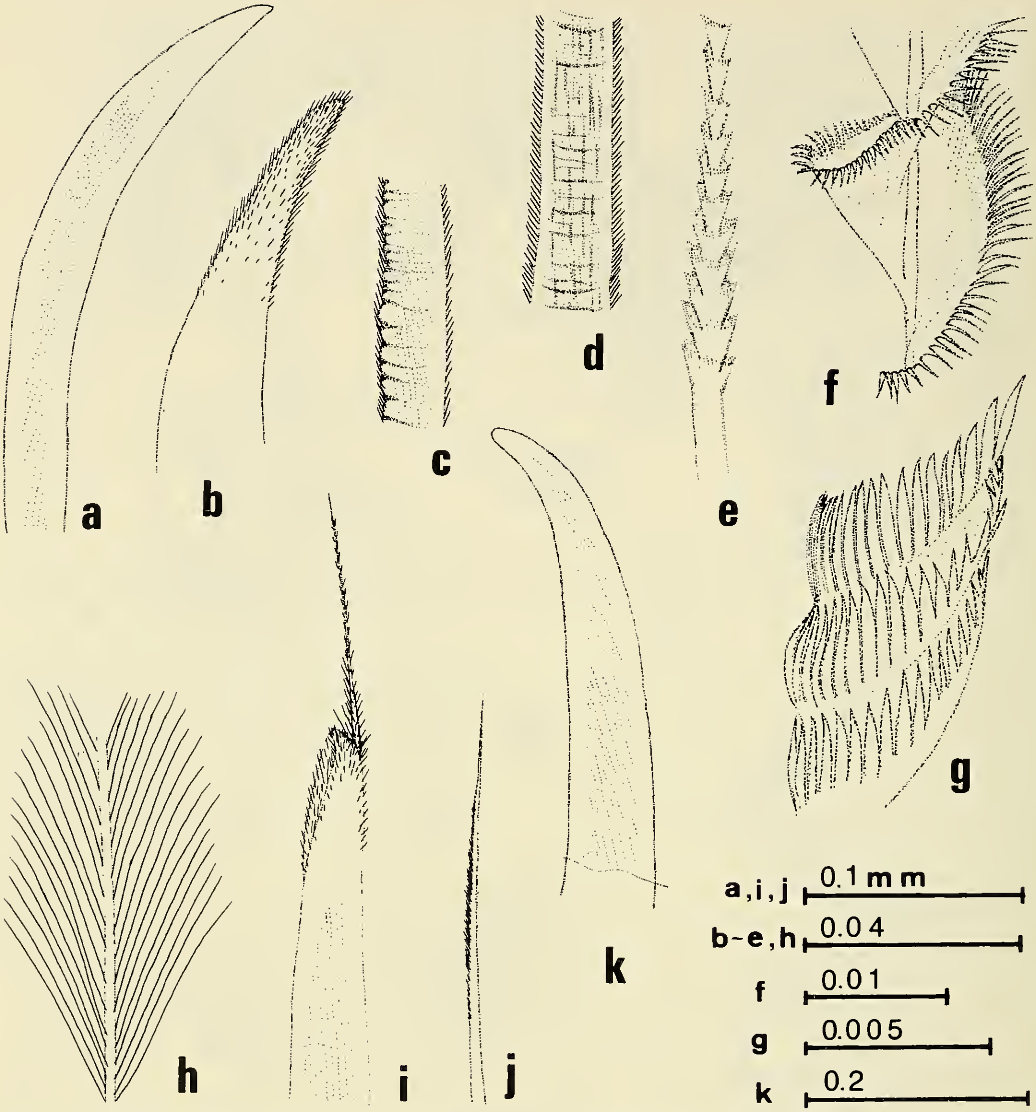

Fig. 3. *Poecilochaetus koshikiensis*: a, Neuropodial falcate spine from setiger 2; b, Enlarged tip of same; c, Section of cephalic seta from setiger 1 in lateral view; d, Same, convex side; e, Spiral seta; f, Distal part of same; g, Proximal part of same; h, Pappose seta; i, Aristate seta; j, Slender hispid seta; k, Posterior notopodial hook.

proximal part and fine teeth on distal part (Fig. 3e–g). Parapodia 4–16 with slender hispid capillaries and spiral setae (Fig. 2d, e). Parapodia 17–50 with pappose setae covered with long, fine flexible spinules on distal part and stout spinules on proximal part (Figs. 2f, 3h). Aristate setae first present on parapodia 48, unidentate with hoods covered with numerous short spines (Figs. 2h, 3i). Posterior parapodia with slender hispid setae (Fig. 3j). Stout smooth notopodial hooks forming prominent dorsal shield in posterior 10 segments (Figs. 1d, 2i, 3k).

Remarks.—In the genus *Poecilochaetus,* seven species have flask-shaped cirri on parapodia 7–13. Of these seven species, two species and a subspecies, *P. serpens* Allen, 1904, *P. serpens honiarae* Gibbs, 1971, and *P. tropicus* Okuda, 1935, 1937, have branchiae, differing easily from the abranchiate new species. *P. johnsoni* Hartman, 1939 and *P. australis* Nonato, 1963 differ from *P. koshikiensis* in lacking stout notopodial hooks which make remarkable dorsal shields of several preanal segments in the new species. *P. fauchaldi* Pilato & Cantone, 1976 differs from the new species in lacking aristate spines and interramal sensory organs on segments posterior to setiger 5. *P. paratropicus* Gallardo, 1968 has well-developed lateral lobes on the nuchal organ, while *P. koshikiensis* has only small discoidal ones. *P. japonicus* Kitamori, 1965, the only species recorded from Japan, and known only from anterior fragments, has a very short middle lobe on the nuchal organ, reaching setiger 2, compared to the new species with middle lobe extending back to setiger 4.

Etymology.—The species name is derived from the type locality, Shimo-Koshiki Island.

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NEOPILINA GOESI, A NEW CARIBBEAN MONOPLACOPHORAN MOLLUSK DREDGED IN 1869

Anders Warén

Abstract.—A new monoplacophoran species, *Neopilina goesi,* dredged NW of the Virgin Islands, from the upper part of the continental slope, is described. This new species resembles *N. oligotropha* Rokop and *N. zografi* (Dautzenberg & Fischer), but has a more marginal apex than the former and a finer sculpture than the latter species.

Axel Theodor Goës (1835–1897) was a Swedish physician and zoologist whose main zoological interest was Foraminifera. During 1862–1870 he was employed at the garrison at St. Barthelemy, Leeward Islands, then a Swedish colony. In 1866 and 1869 Goës dredged around St. Barthelemy at depths down to 400 fathoms (720 m). This yielded rich material of different groups of animals. A very brief description of the dredgings was given by Goës (1882:8). These collections were given to the Swedish Museum of Natural History in 1870 (Theel 1916:205) and formed the base for several reports on Caribbean invertebrates. The molluscs, however, were only roughly sorted to species by N. Odhner and never published upon, although he labelled many species with manuscript names. A considerable part of the molluscan species collected by Goës is undescribed and will probably remain so until better material becomes available, because most of it consists of broken juveniles extracted from shell gravel. The monoplacophoran, here described as a new species, had been labelled "*Acmea sp.,*" by Odhner, an irony of fate, as it was Odhner who named the class Monoplacophora (*in* Wenz 1940; not Wenz *in* Knight 1952, as often is quoted).

Neopilina Lemche, 1957
Neopilina goesi, new species
Figs. 1–3, 6–11

Type material.—Holotype, Swedish Museum of Natural History type collection no. 3635a, the shell figured in Figs. 2, 6, 7. Paratype, type collection no. 3635b, the shell figured in Figs. 1, 3, 8–11.

Type locality.—"Windward off the eastern keys of the Virgin Islands, 200–300 fathoms (360–540 m)," upper continental slope of the western Caribbean.

Distribution.—Known only from the type locality and type material.

Description.—Shell very small, colorless, fragile, regularly ovate and depressed, with apex reaching slightly outside margin. Apical region consisting of central part without sculpture, but rather rough and with signs of wear, 0.13 × 0.16 mm (Figs. 3, 6); surrounded by smooth area, diameter 0.3 mm, sculptured only by numerous pores or pits and 2 or 3 incomplete anterior concentric ridges. Outside this area more regular sculpture of concentric and radial ridges starting, giving surface distinctly reticulated appearance, with distinct tubercules at intersections of concentric and radial ridges. Concentric ridges somewhat more close-set and irregular at edge of shell, but very regular at central part of shell. Shell interior very smooth with no muscle scars visible and only some traces of radial sculpture apparent by transparency. Shape regularly convex with apex distinctly overhanging anterior ventral margin.

Dimensions: Holotype 1.79 × 1.40 × 0.56 mm. Paratype 1.54 × 1.21 × 0.46 mm.

Remarks.—The two specimens are smaller than the maximum dimensions known for any other monoplacophoran species (smallest species: *Laevipilina hyalina* (McLean, 1979), 2.28 mm), but the more crowded concentric radial sculpture at the edge indicates that the specimens are approaching full-grown size.

The inside of the shell does not show any muscle scars, although the condition of the shell is good enough to have shown them if they had been present. This agrees with other recent monoplacophorans (Wingstrand 1985:47). The reason for considering this limpet a monoplacophoran is the similarity in shell characters to *N. oligotropha* Rokop, 1972, and *N. zografi* (Dautzenberg & Fischer, 1896), which from anatomy and shell structure, respectively, are known to belong to this group.

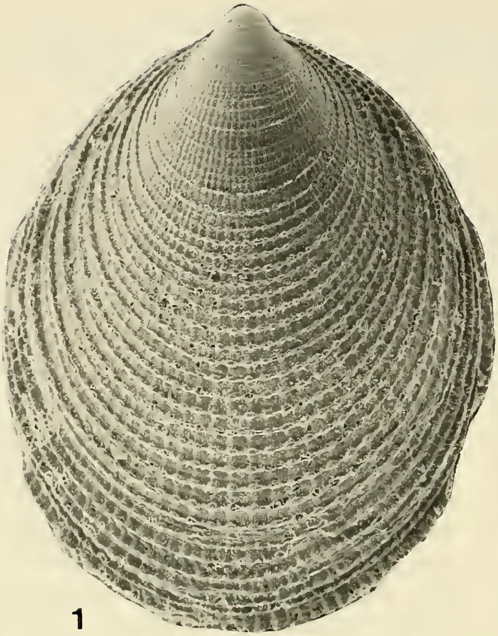
A part of the shell is covered by tracks or shallow furrows about 1 μm wide, similar to those made by beetles under the bark of trees (Figs. 9–10). These furrows occur on the area equipped with pores and on the early part of the area with adult sculpture. They appear to be too regular to be caused by corrosion, but their origin is unknown.

The presence of three different sculptural areas on the shell, in accordance with the growth lines, indicates that *N. goesi* passes through three different ontogenetic growth stages in its life history. I cannot, however, presently correlate these with the different phases in the shell development of gastropods or lamellibranchs with planktotrophic larvae. Nor is it possible to conclude that the bowl-shaped initial part which lacks pores is a larval shell although this seems possible. Wingstrand (1985) concluded that the old description by Lemche & Wingstrand (1959) of a spirally coiled larval shell was erroneous. He supported this on a report by Menzies (1968) where a young mollusc supposed to be a monoplacophoran was figured with a large bulbous larval shell. However, the identification of Menzies's specimen may be questioned. It closely resembles the young of many Lepetellacea Dall, 1881 (Archaeogastropoda), but his photo indistinctly shows a prismatic structure of the shell, not present in Lepetellacea. Wingstrand concluded that it probably represented a monoplacophoran and that this larval shell is later rejected, possibly as in *Patella* (Linné, 1758). Menzies's figure is, however, too poor to allow any conclusions about whether the larval shell is spirally coiled as in the Docoglossa, where it consists of half a whorl, or simply bowl-shaped as assumed by Wingstrand.

I have seen the process of larval shell rejection in *Patella coerulea* (Linné, 1758) (Figs. 12–14). Here a narrow zone around the larval and part of the first postlarval shell is dissolved, evidently actively (Warén unpubl. data, see also Gardner 1986), after which the larval shell falls off at the slightest touch. The place where the larval shell has been attached is marked by a distinct scar with a large pore, now closed. These observations agree with Smith's (1935) description of the larval development of *Patella,* based on sectioned material. His fig. 29b shows a small apical chamber, cut off from the main part of the body by a septum and connected to the body by a narrow string of tissue. Behind the scar is a second impression from the overhanging part of the larval shell. A very similar mode of rejection of the larval shell has also been observed in the Lepetellidae (Warén, unpubl. data).

The absence of a pronounced scar from the larval shell (compare Figs. 3, 5 and 14), the shape of the apex, and the presence of three well-marked apical zones seem to argue against Wingstrand's hypothesis about rejection of the larval shell, but it is possible that there occur different modes of larval development among monoplacophorans.

Pores like those obvious in Figs. 6–9 have not previously been reported from any recent monoplacophoran. I have, however, seen them also in *N. zografi,* although they are less obvious in that species, probably because the shells available of *N. zografi* were less well preserved. These pores are most numerous in the smooth area around the scar of the protoconch, but occur less



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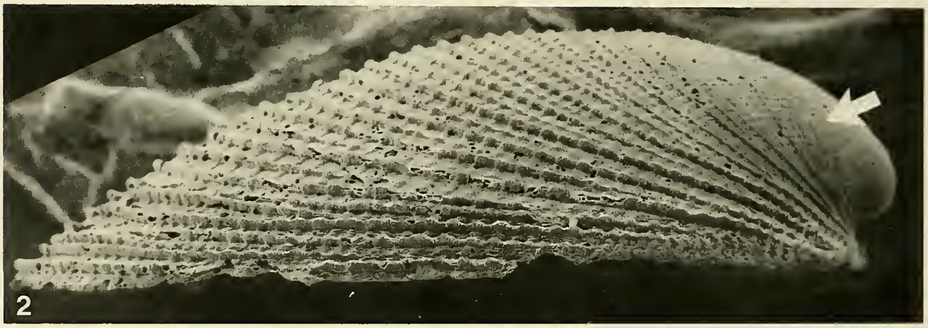

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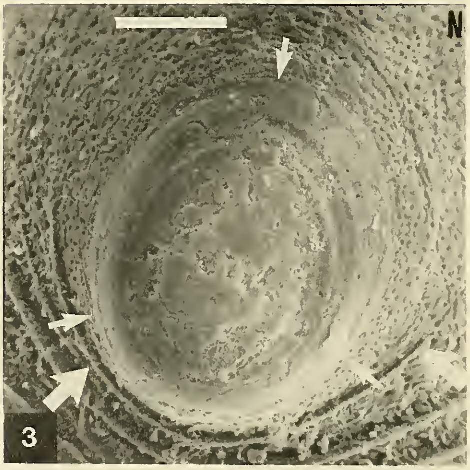

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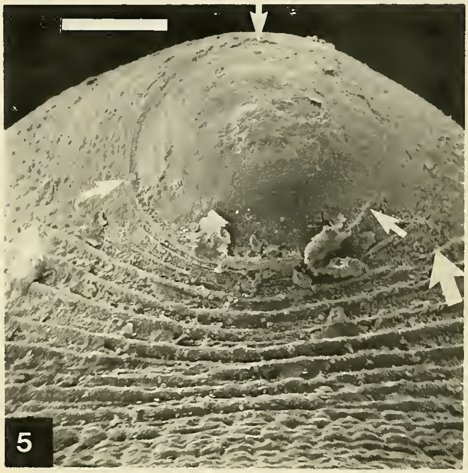

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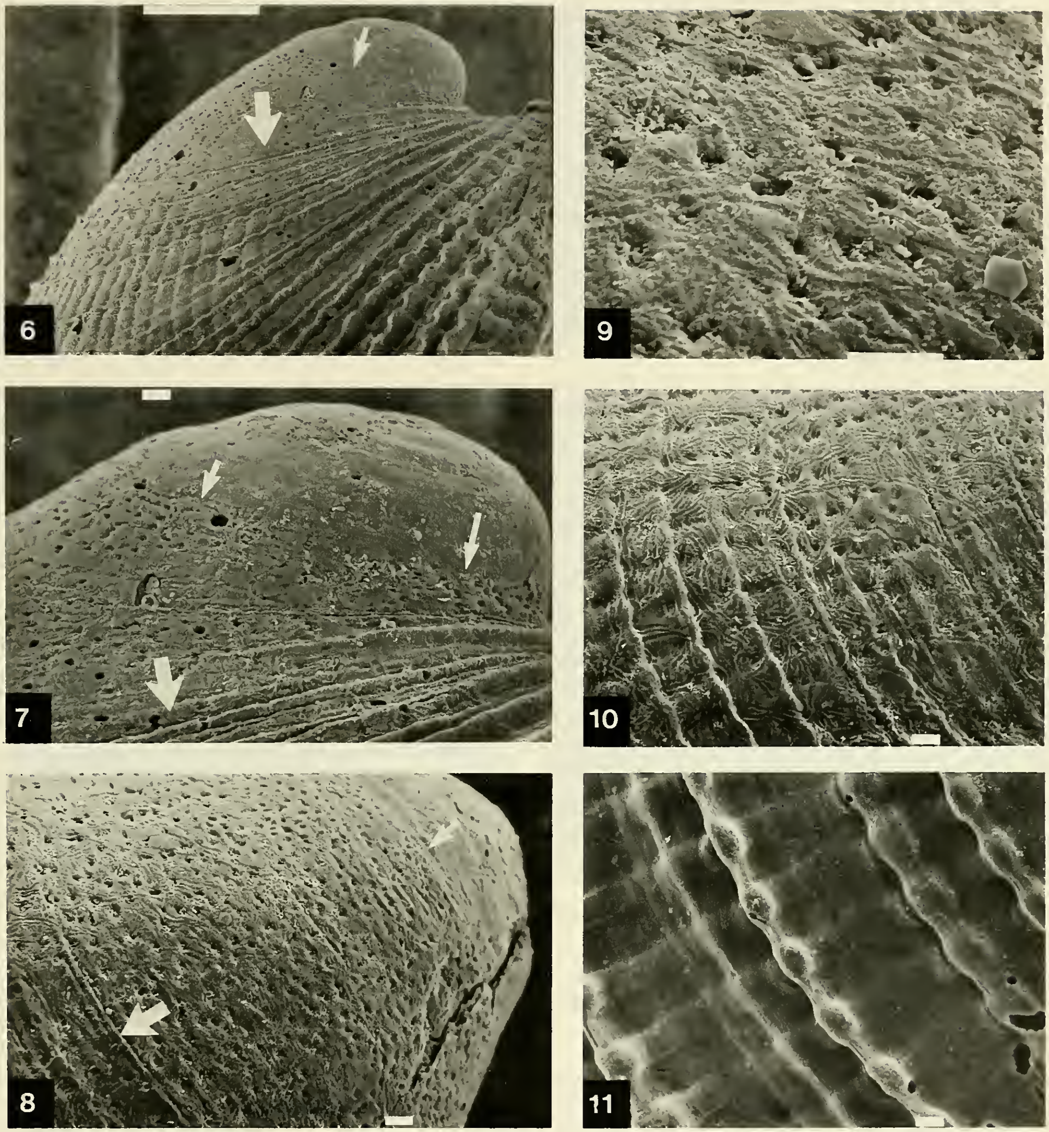

Figs. 6–11. *Neopilina goesi,* details of sculpture: 6, 7, Apical area of holotype, side view, showing bowl-shaped apex; 8, Apical area of paratype, showing distribution of pores; 9, Detail of pores; 10, Transition from part with pores to adult sculpture; 11, Adult sculpture on central part of shell. Scale lines: Fig. 6, 100 μm; Figs. 7–11, 10 μm. Arrows indicate transition between different sculptural zones.

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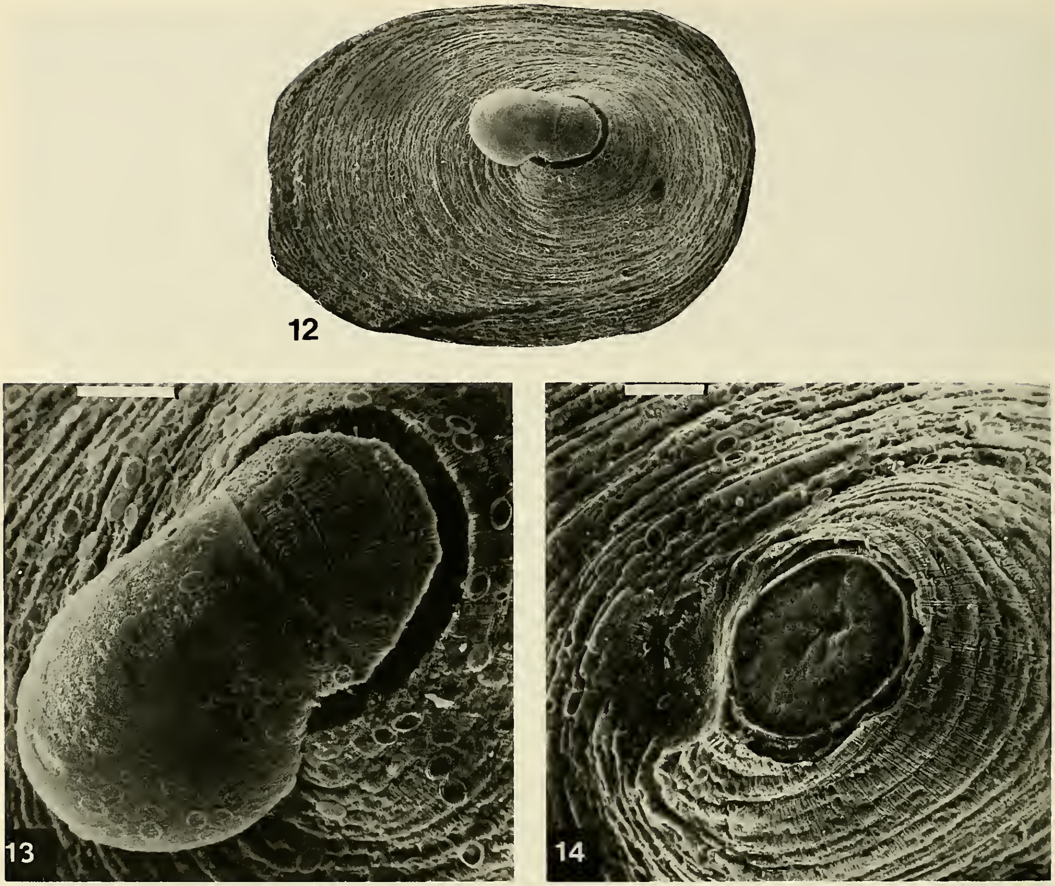
Figs. 1–5. *Neopilina goesi* and *N. zografi*: 1, *N. goesi,* paratype, maximum diameter 1.54 mm; 2, *N. goesi,* holotype, lateral view, length 1.79 mm; 3, *N. goesi,* paratype, apical area; 4, *N. zografi,* paratype, in Muséum National d'Histoire Naturelle, Paris, maximum diameter 3.9 mm; 5, *N. zografi,* apical area of specimen in Fig. 4. Scale lines 50 μm. Arrows indicate the different sculptural zones.



Figs. 12–14. *Patella coerulea* (L.), from Calvi, Corsica, taken at the pier of Station de Recherche Sousmarines et Océanographiques: 12, Juvenile shell, diameter 0.8 mm; 13, Larval shell (smooth) and part of initial teleconch ready to fall off; 14, Larval shell lost. In the center of the calcareous plug that seals off apex, a closed pore can be seen. This pore is the last connection to the larval shell and may in some way assist in the active dissolution of the zone of breakage. Scale lines: Fig. 13, 30 μm, Fig. 14, 20 μm.

densely all over the shell. I did not study them in detail and their significance is not known. Pores are known in the Silurian genus *Tryblidium* Lindström, 1880 (Erben et al. 1968). In that genus they branch inwards, something that could not be examined in *N. goesi* because of lack of material.

There are two known species of Monoplacophora that resemble *N. goesi* in shell morphology, viz. *N. zografi,* from the bathyal zone of the Azores, and *N. oligotropha,* from abyssal depths north of the Hawaiian Islands.

Neopilina oligotropha differs from *N. goesi* in having the apex placed well behind the anterior margin of the shell. Other differences are impossible to discern because of the poor illustrations of that species, except that *N. oligotropha* evidently has a coarser sculpture; *N. goesi* has 28 concentric ridges behind the apex at a size of 1.79 mm, while *N. oligotropha* has 32 at a size of 3.0 mm.

Neopilina zografi differs mainly in having a blunter apex, the sides of which form a wider angle in dorsal view and perhaps also by reaching a larger size, 3.9 mm.

The systematic position of *N. goesi* within Monoplacophora is uncertain, as no soft parts are known. From the shell, it is obvious that it does not belong to *Laevipilina* McLean, 1979, whose species have a rather smooth shell, with a low but dense nodular sculpture, caused by the large prisms that build up the shell. Prisms are also obvious in *Vema* Clarke & Menzies, 1959, where *Laevipilina* was described as a subgenus. *Monoplacophorus* Moskalev, Starobogatov, & Filatova, 1983, may be related to the present new species, but the description of the shell and the illustrations do not allow any conclusions. Therefore, I have followed Rokop (1972) and Bouchet, McLean, & Warén (1983) and included this small, strongly sculptured species in *Neopilina*.

Acknowledgments

I want to thank Dr. Philippe Bouchet, Dr. James H. McLean, Dr. H. Mutvei, and Prof. K. G. Wingstrand for discussions about this species and Dr. Bouchet, also, for preparing some of the SEM photos at "Centre de microscopie du CNRS, Paris."

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NOTES ON SOME *RHYSSOPLAX* FROM THE PACIFIC OCEAN (MOLLUSCA: POLYPLACOPHORA: CHITONIDAE)

Robert C. Bullock

Abstract.—Taxonomic comments are presented for the following *Rhyssoplax* from the Pacific Islands: *R. discolor* (Souverbie, 1866), *R. ectypa* (Rochebrune, 1884), and *R. rhynchota* (Rochebrune, 1884) from New Caledonia; *R. spinosetata* (Bergenhayn, 1930), from the Fiji Islands; *R. whitleyi* Iredale & Hull, 1932, from the Cook Islands; *R. perviridis* (Carpenter, 1865) from the Society Islands; *Rhyssoplax* sp. from the New Hebrides east to the Samoan Islands; and the widespread *R. pulcherrima* (Sowerby, 1842), which ranges from Southeast Asia to New Caledonia. The latter species is conspecific with *R. excellens* Iredale & Hull, 1926, *C. excellens capricornensis* Ashby, 1928, and *R. nierstrasziana* Kaas, 1957. *Rhyssoplax ectypa,* which has been considered a junior synonym of *R. discolor* for nearly a century, is recognized as a separate species. *Chiton* (*Clathropleura*) *pacificus* Thiele, 1910, is a junior synonym of *R. perviridis.* Thiele's (1910) published description and figure of the type specimen of *R. rhynchota* were erroneously based on *R. crawfordi* (Sykes) from South Africa.

Species of the polyplacophoran genus *Rhyssoplax* Thiele, 1893, are sporadically represented among malacological collections from the islands of the central Pacific Ocean, and their taxonomy is poorly understood. The predominant reason for this situation is the inadequate collections available for study. Large, well preserved collections from all major island groups will be required before sound taxonomic conclusions can be reached.

Study of many Pacific *Rhyssoplax* is also perplexing due to the inadequate published work of the past. The works of Rochebrune (1884 and other papers) especially have proved to be troublesome. Pilsbry (1893: 151), in a discussion of Rochebrune's use of the controversial name *Gymnoplax,* correctly observed the outcome of Rochebrune's efforts: "It should be noted that the irrepressible Rochebrune still uses *Gymnoplax* in a generic sense, in order presumably, to disguise his species;—an unnecessary precaution, for his diagnoses of Chitons generally defy identification of either genus or species." Iredale & Hull (1932:158) commented on the problems associated with type material in the Muséum National d'Histoire Naturelle in Paris: "Rochebrune ran riot among these shells in the Paris Museum. Using a classification of his own which has defied interpretation, he lost, mislaid and transferred labels and specimens, describing the types of former workers under different genera and then renaming his own new species until there is no confidence in any specimens of this class in that Museum." Bullock (1972) noted that some of this material is present in the Dautzenberg collection at the Institut Royal des Sciences Naturelles de Belgique in Brussels.

The zoogeography and phylogenetic relationships of Pacific Island *Rhyssoplax* will prove to be of great interest. Preliminary examination of the distributional patterns indicate that a few species, for example *R.*

pulcherrima (Sowerby, 1842), are broadly distributed across several island groups, while a larger numer of species appear to be endemic to a single island group. Examples of the latter group include: *R. discolor* (Souverbie, 1866), known only from New Caledonia; *R. whitleyi* Iredale & Hull, 1932, found only in the Cook Islands; and *R. spinosetata* (Bergenhayn, 1930), reported only from the Fiji Islands. Major conclusions, however, must be made only after the taxonomy of the group is better known.

Materials and Methods

Specimens were examined from the major collections of the U.S. and Europe listed below. Additional material was received from the Western Australian Museum and the Australian Museum. Girdle scales of selected specimens were prepared for scanning electron microscopy (SEM) following procedures described by Bullock (1985). Samples were mounted on aluminum stubs using double coated tape, and coated with carbon and gold/palladium in a Denton DV-502 vacuum evaporator. All work was done using an ISI MSM-3 SEM located in the Department of Zoology at the University of Rhode Island.

The following abbreviations are used: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; ICZN, International Code of Zoological Nomenclature; IRSN, Institut Royal des Sciences Naturelles de Belgique, Brussels; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MHNB, Muséum d'Histoire Naturelle de Bordeaux; MNHNP, Muséum National d'Histoire Naturelle, Paris; NRS, Naturhistoriska Riksmuseet, Stockholm; USNM, National Museum of Natural History, Washington, D.C.; WAM, Western Australian Museum, Perth; ZMA, Zoölogisch Museum, Amsterdam; ZMHU, Zoologischen Museum, Humboldt-Universität, Berlin; ZMK, Universitetets Zoologiske Museum, Copenhagen; ZMU, Uppsala Universitets Zoologiska Museum, Uppsala.

Genus *Rhyssoplax* Thiele, 1893

Rhyssoplax Thiele, 1893:368. Type species, *Chiton affinis* Issel, 1869, by declaration of the ICZN, Opinion 951.

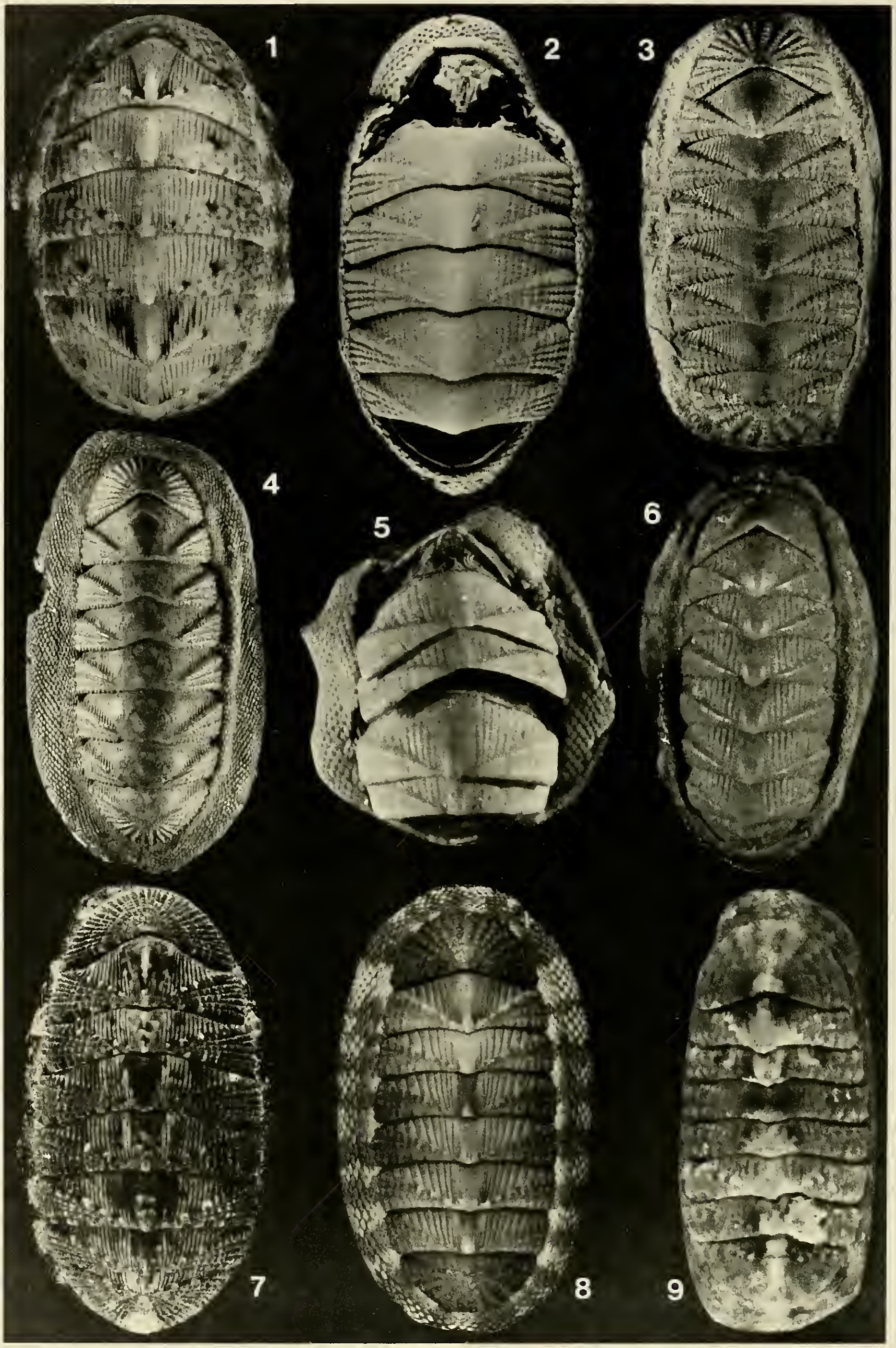
Remarks.—In general, the name *Rhyssoplax* has been used for small to moderate-sized, non-New World polyplacophorans that are otherwise similar in shell and girdle scale morphology to the genus *Chiton* from the New World. Employment of *Rhyssoplax* at the generic level is not accepted by all polyplacophoran workers. Malacologists from Australia and New Zealand for the most part have championed this use, while others, for example Kaas & Van Belle (1981), have used *Rhyssoplax* as a subgenus of *Chiton* Linnaeus, 1758. Substantial radular differences exist between *Chiton* and *Rhyssoplax*: in *Chiton* the distal edge of the centro-lateral tooth is perpendicular to the longitudinal axis of the animal, while in all *Rhyssoplax* the distal edge is parallel to the longitudinal axis. Furthermore, the denticle cap of the major lateral tooth of *Rhyssoplax* is rather short with a circular black tab distally on the anterior surface. In *Chiton* the denticle cap tends to be elongate and the black tab is usually elongate. It is advisable to consider these groups as separate genera within the subfamily Chitoninae.

Rhyssoplax discolor (Souverbie, 1866)
Fig. 13

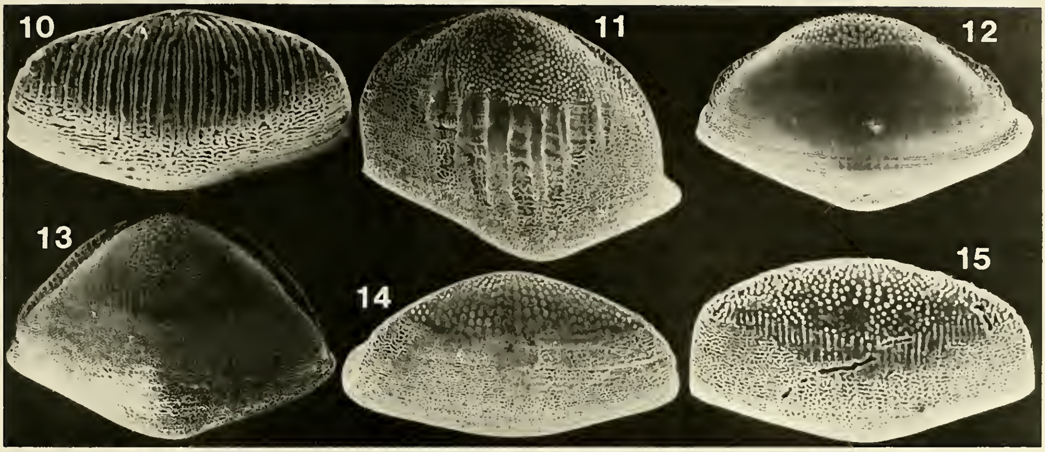
Chiton discolor Souverbie [in Souverbie & Montrouzier], 1866:252, pl. 9, figs. 1, 1a (ins. Art, l'Archipel calédonien; lectotype, selected by Strack [1986], in MHNB).

Chiton tuberculosus Souverbie [in Souverbie & Montrouzier], 1866:251, pl. 9, fig. 3 (ins. Art, l'Archipel calédonien; holotype in MHNB).

Chiton (*Rhyssoplax*) *discolor* Souverbie.—



Figs. 1–9. Shells of Pacific *Rhyssoplax*: 1, *Rhyssoplax perviridis* Carpenter, Arue, Society Islands, 11 mm [curled] (USNM 672794); 2, Holotype of *Chiton perviridis* Carpenter, Tahiti, Society Islands, 11 mm (MCZ 141125); 3, *Rhyssoplax ectypa* (Rochebrune), New Caledonia, 20.5 mm (BMNH); 4, Syntype of *Lepidopleurus ecyptus* Rochebrune, 20 mm (MNHNP); 5, *Chiton rhynchotus* 'Rochebrune' Thiele [=*R. crawfordi* (Sykes)], 9.5 mm



Figs. 10–15. Scanning electron micrographs of girdle scales of Pacific *Rhyssoplax*: 10, *Rhyssoplax rhynchota* (Rochebrune), W end, Ricaudy Reef, Noumea, New Caledonia, 291× (ANSP 271045); 11, *Rhyssoplax pulcherrima* (Sowerby), 3 mi [4.8 km] S of Airport Beach, Phuket Is., Thailand, 81× (ANSP 286765); 12, *Rhyssoplax spinosetata* (Bergenhayn), Korolevu, Viti Levu, Fiji Islands, 95× (ANSP 236891); 13, *Rhyssoplax discolor* (Souverbie), near radio station, Baie Ouemo, Noumea, New Caledonia, 46× (ANSP 271200); 14, *Rhyssoplax ectypa* (Rochebrune), 0–4 ft [0–1.2 m], Thio, New Caledonia, 107× (ANSP 238361); 15, *Rhyssoplax* sp., E side of Vailele Bay, Upolu Is., Western Samoa, 169× (ANSP 198086).

Strack, 1986:195, fig. 4a, b [description; types fig'd.].

Remarks.—*Rhyssoplax discolor* is a common species that varies considerably in color. Risbec (1946), who reported on the anatomy of this species, noted that on the rocks at Noumea *R. discolor* is second in abundance only to *Acanthopleura gemmata* (Blainville, 1825).

Pilsbry (1894) erroneously believed that *Lepidopleurus ectypus* Rochebrune is conspecific with this species, and all subsequent authors have accepted this conclusion. However, an examination of syntype material of *L. ectypus* [IRSN and NMHNP] (Fig. 4) revealed that it is distinct and not at all closely related to *R. discolor* (see remarks under *R. ectypa*).

The New Caledonian *R. discolor* is not very similar to *R. coryphea* (Hedley & Hull, 1912) from Norfolk Island, as Iredale & Hull (1932) suggested. *Rhyssoplax coryphea* is more highly elevated, more elongate, and has longitudinal ribs which only partly extend across the valve. The girdle scales of *R. discolor* (Fig. 13) characteristically exhibit a broad shelf across the apical surface and have many apical pustules; in *R. coryphea* this shelf is nearly lacking and the pustules are limited to a narrow region at the apex.

Locality records.—New Caledonia: Koe Reef, 2 mi [3.2 km] SSE Touho; Touho Bay; Koe, near Touho; Thio; Yate (all ANSP); Noumea Harbour (AMS); Port Ngéa, Magenta, Noumea (ANSP); Baie des Isoles,

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[curled] (MNHNP); 6, *Rhyssoplax rhynchotus* (Rochebrune), barrier reef, 5 mi [8 km] WSW Gatope Is., Voh, New Caledonia, 9.5 mm (ANSP 269722); 7, *Rhyssoplax spinosetata* (Bergenhayn), N shore of Port Ellington, NNE Viti Levu, Fiji Islands, 17.5 mm (MCZ 279505); 8, *Rhyssoplax whitleyi* Iredale & Hull, 0.25 mi [0.4 km] N of Matavera, NE Rarotonga, S Cook Islands, 11 mm (MCZ 252808); 9, *Rhyssoplax* sp., E side of Vailele Bay, Upolu Is., Western Samoa, 7 mm (ANSP 198086).

Ouemo, Magenta, Noumea (AMS); S side, Baie de Citron; Baie de Citron, Noumea, in 1–6 ft [0.3–1.8 m] (both ANSP); Île Cesar, Anse Vata, Noumea (AMS); mouth of stream entering Anse Vata Bay, Noumea, in 2–6 ft [0.6–1.8 m]; Tonghouen Bay, 45 km N of Noumea; Plage de Poe, Bourail; S side, Gatope Is., Voh; SW side, Isle Mouac, Poume; 2 mi [3.2 km] N of Poume (all ANSP).

Rhyssoplax ectypa (Rochebrune, 1884)
Figs. 3, 4, 14

Lepidopleurus ectypus Rochebrune, 1884:37 (Nouvelle Calédonie; syntypes in IRSN and MNHNP).

Description.—Animal medium in size, up to 38 mm in length, 19 mm in width. Valves subcarinate, angle about 90°. Anterior valve straight to convex; post-mucral slope of posterior valve abrupt, concave at first, convex ventrally. Mucro moderately sharp, often worn, centrally located on posterior valve. Jugal region smooth. Central areas with numerous, fine, slightly irregular, longitudinal ribs, up to 28 per side; dorsal edge somewhat sloping, ventral edge more abrupt; first few dorsal ribs not reaching preceding valve. Lateral triangle sharply elevated, with 3–6 nodular, radiating ribs; nodes on posterior rib longitudinally elongate. Terminal areas with similar radial sculpture, up to 25 on anterior and posterior valves. New radial ribs begin anew between existing ribs. Shell color grayish white with a few darker speckles at jugum or, more commonly, cream orange or reddish brown. Girdle very light orange or alternately banded white and light orange. Interior of valves white to dull greenish white.

Insertion plates: Intermediate valves with a single slit per side; insertion teeth well grooved, but not deeply pectinate. Anterior valve with 10 teeth; posterior valve with 13 teeth.

Hypostracum: Jugal tract in central depression with numerous transverse slits and continuous over callus as small holes in posterior depression. Primary slit-ray with longitudinally elongate slits on callus, more circular, smaller slits in posterior depression. Secondary slit-ray absent.

Girdle scales: Moderate in size, rather ovate, with reticular sculpture predominate except near apex where large, fairly close-packed nodules are arranged in rows. Apical shelf lacking (Fig. 14).

Remarks.—*Rhyssoplax ectypa* is distinguished from *R. discolor* by its more sharply defined lateral triangle, more abrupt post-mucral slope on the posterior valve, narrower ribs of the central area which are strongest near the lateral triangle, and by the fact that as the animal grows, additional ribs of the lateral triangle and end valves begin separately between existing ones, not as bifurcations of previous ribs. The girdle scales of the two species greatly differ (Figs. 13, 14). In *R. ectypa* the scales are ovate rather than roundly triangular and the characteristic apical shelf of *R. discolor* is lacking. The apical pustules of *R. ectypa* are linearly arranged, not random as in *R. discolor.* Certain structural aspects, such as the sharply defined lateral triangle and the manner by which new ribs are added, indicate that *R. ectypa* is most closely related to the more northern *R. komaiana* (Is. & Iw. Taki, 1929), which may be differentiated by its more inflated girdle scales and more pronounced ribs of the central areas of the intermediate valves.

Rhyssoplax ectypa has not been recognized as a valid taxonomic entity since its original description by Rochebrune (1884). At least five species of *Rhyssoplax* are now reported from New Caledonia: *Rhyssoplax subassimilis* (Souverbie, 1866), known only by the holotype (Strack 1986); the abundant *R. discolor* (Souverbie); and the uncommon *R. ectypa, R. rhynchota* (Rochebrune, 1884), and *R. pulcherrima* (Sowerby, 1842). *Gymnoplax ludoviciae* Rochebrune, 1884 [syntype IRSN], stated to be from New Caledonia, is *Chiton* (*Chondroplax*) *granosus*

Frembly, 1827, from the Pacific coast of South America. *Gymnoplax alphonsinae* Rochebrune, 1884 [syntypes IRSN and MNHNP], also stated to be from New Caledonia, is actually *Rhyssoplax aerea* (Reeve, 1847) from New Zealand.

Distribution.—*Rhyssoplax ectypa* is known only from New Caledonia.

Locality records.—New Caledonia: (BMNH, IRSN, MNHNP); 0–4 ft [0–1.2 m], Thio, New Caledonia (ANSP).

Rhyssoplax sp.
Figs. 9, 15

Remarks.—The collections of the ANSP and USNM include a few examples of small *Rhyssoplax* that possibly are juveniles of one or more species. The shell sculpture is reminiscent of that of *R. ectypa* from New Caledonia. The girdle scales from the different localities vary in the size of the apical pustules, the linearity of these pustules, the existence of small riblets that extend from the pustular region ventrally to the reticular sculpture, and the presence in some cases of broader ribs. I figure an example from the Samoan Islands (Fig. 9) and a girdle scale from it (Fig. 15).

Locality records.—New Hebrides: rocky reef flat, ESE of Inyeung Is., Aneityum (USNM).—Tonga Islands: Niuafoou Is. (USNM).—Hoorn Islands: over the outside fringing reef, NW of Mua, Alofi (USNM).—Samoan Islands: Asili, Tutuila (USNM); Pago Pago, Tutuila (USNM); east side of Vailele Bay, Upolu Is. (ANSP).

Rhyssoplax pulcherrima (Sowerby, 1842)
Fig. 11

Chiton pulcherrimus Sowerby, 1842:103 (Gindulman, ins. Bohol, Philippinarum; type in BMNH).—Leloup, 1952:34, pl. 1, fig. 2; pl. 4, fig. 1; text-fig. 13 [girdle elements and esthetes fig'd.].

Ischnochiton pulcherrimus (Sowerby).—Pilsbry, 1893:130, pl. 27, fig. 47, 48.

Chiton reticulatus Nierstrasz, 1905:81, pl. 2, fig. 36; pl. 7, figs. 195–199 (Insel Sanguisiapo, 12 m; Saleyer; syntypes in ZMA). Non Reeve, 1847, nec Dupuis, 1918.

Rhyssoplax excellens Iredale & Hull, 1926: 181, pl. 19, figs. 22, 27, 40 (Darnley Island, Torres Strait; type in Macleay Museum, Sydney) [description].—Iredale & Hull, 1927:116, pl. 13, figs. 22, 27, 40.—Mackay, 1934:150, pl. 16

Chiton (*Rhyssoplax*) *excellens capricornensis* Ashby, 1928:169, pl. 12, figs. 1, 13 (Capricorn Group; location of type unknown).

Rhyssoplax nierstrasziana Kaas, 1957:85 (new name for *C. reticulatus* Nierstrasz, 1905, non Reeve, 1847).

Remarks.—*Rhyssoplax pulcherrima* differs from all other *Rhyssoplax,* and all other Chitoninae, by its cancellate sculpture of the central areas. This species has been redescribed on a number of occasions because it seems that authors have been unwilling to recognize its broad distribution. Australian workers in particular have maintained that their specimens represented a species different from the one in the Philippine Islands.

Pilsbry (1893) considered this species to be an *Ischnochiton,* but an examination of the radula, especially the denticle cap of the major lateral tooth, indicates its chitonid affinities. A study of the shell morphology of the Siboga Expedition material revealed that *Chiton reticulatus* Nierstrasz, 1905, is this species, and its renaming by Kaas (1957) was unjustified. *Rhyssoplax komaiana* (Is. & Iw. Taki, 1929), which occurs sympatrically with *R. pulcherrima* in at least Malaysia, the Philippines, and possibly south to the Admiralty Islands (ANSP 182204), differs by its rounded valves and lack of cancellate sculpture. The prominent central ribs on the girdle scales of *R. pulcherrima* (Fig. 11) easily distinguish this species from other carinate *Rhyssoplax.*

Distribution.—A tropical species, *Rhys-*

soplax pulcherrima occurs from Thailand to the Philippine Islands and south to Queensland, Australia, the New Hebrides, and New Caledonia.

Locality records.—Thailand: Pulau Tanga, Butang Group (USNM); coral rubble reef, 3 mi [4.8 km] S of Airport Beach, Phuket Is., Andaman Sea (ANSP); Koh Chang, Gulf of Siam (ZMK).—Malaysia: Pulau Siburu, N of Sipora, SW of Sumatra (USNM); Pisang Is. (IRSN); N shore of Toba Is., N end of Aru, Molucca Is. [5°21′S, 136°27′E] (WAM).—Philippine Islands: Gindulman, Bohol Is. (BMNH); rock shore at Cabcaben, SE Bataan, Luzon Is. (ANSP).—New Hebrides: Anelgauhat, Aneityum Is., on *Turbo marmoratus* L. (ANSP).—New Caledonia: 4–7 ft [1.2–2.1 m], barrier reef, 5 mi [8 km] WSW of Gatope Is., Voh, SW New Caledonia (ANSP).

Rhyssoplax spinosetata
(Bergenhayn, 1930)
Figs. 7, 12

Chiton spinosetatus Bergenhayn, 1930:24, pl. 1, figs. 17–28; pl. 2, figs. 29–31 (Viti Levu, Fiji Islands; type in NRS).

Description.—Animal medium to small in size, reaching a length of 22 mm, a width of 14 mm. Valves fairly carinate, angle about 100°. Anterior valve straight to convex; postmucral slope of posterior valve straight to slightly concave. Mucro rather blunt, slightly anteriorly acentric on posterior valve. Jugal region smooth; central area with up to 20 well formed longitudinal ribs per side, usually all reaching preceding valve; dorsal edge of each rib somewhat sloping, lateral edge abrupt. Lateral triangle with 5–8 radiating, occasionally bifurcating rows of low, broad nodules. Terminal areas with similar radial sculpture, up to 41 rows on anterior valve, 29 on posterior valve. Shell color variable. Some specimens dark brown with scattered lighter, maculated areas and dark girdle of yellowish white scales irregularly banded with dark brown. Other specimens much lighter, usually yellowish green maculated with small greenish brown markings, or yellowish white with similar maculations with lateral areas orange; girdle alternately banded yellowish white and dull green. Interior of valves blue or white with bluish green to dull green streak extending from mucro along slope of posterior depression.

Insertion plates: Intermediate valves with a single slit per side, occasionally doubly slit; insertion teeth highly grooved, not deeply pectinate. Anterior valve with 9–12 teeth; posterior valve with 11–15 teeth.

Hypostracum: Much of central depression with irregular thin grooves and slits. Primary slit-ray well developed, with prominent diagonal slits. Secondary slit-ray lacking.

Girdle scales: Moderately large, rather smooth; fine reticular sculpture ventrally; central area smooth with obsolete striations; apical area sharply defined by close-packed pustules of moderate size.

Remarks.—A comparison of Bergenhayn's type specimen of *R. spinosetata* with additional specimens collected from the Fiji Islands has firmly established the identity of *R. spinosetata,* although slight differences exist between populations. *Rhyssoplax spinosetata* appears to be related most closely to two New Zealand species, *R. stangeri* (Reeve, 1847) and *R. canaliculata* (Quoy & Gaimard, 1835).

Distribution.—*Rhyssoplax spinosetata* is apparently endemic to the Fiji Islands.

Locality records.—Fiji Islands: Kaba, Viti Levu (ZMU); N shore of Nananu-i-ra Is., 3 mi [4.8 km] N of Port Ellington, NNE Viti Levu (ANSP, MCZ); fringe reef, Korolevu, Viti Levu (ANSP, MCZ).

Rhyssoplax perviridis (Carpenter, 1865)
Figs. 1, 2

Chiton (*Lophyrus*) *perviridis* Carpenter, 1865:511 (Central Pacific [type locality here restricted to Tahiti, Society Islands]; holotype MCZ 141125).

Chiton (*Clathropleura*) *pacificus* Thiele, 1910:93, pl. 10, figs. 1–4 (Huahine and Anaa [Society Is.]; type in ZMHU).

Description.—Animal rather small, attaining a length of 13 mm, a width of 8.5 mm. Valves subcarinate, angle about 105°. Anterior valve straight; post-mucral slope of posterior valve concave. Mucro moderately sharp, anteriorly acentric on posterior valve. Jugal region smooth. Central areas with up to 17 longitudinal ribs, the more dorsal ones not reaching preceding valve; dorsal surface of each rib sloping, ventral edge abrupt. Lateral triangle elevated, with 4–6 weak, low-noduled ribs. Terminal areas with similar radial sculpture; ribs obsolete. Shell color usually yellowish white; lateral edge of each longitudinal rib translucent brown or dark green. Small, irregular greenish brown flecks on lateral triangle; larger splotches along anterior edge of lateral triangle and occasionally along posterior edge. Some immature specimens smoother, totally green. Girdle alternately banded light blue-green and yellowish white. Interior of valves white.

Insertion plates: Intermediate valves with a single slit per side; insertion teeth highly grooved, moderately pectinate. Anterior valve with 10–11 teeth; posterior valve with 11–12 teeth.

Hypostracum: Jugal tract of central depression with scattered transverse slits; entire central depression nearly transparent. Primary slit-ray with prominent slits on callus, a row of irregular small holes in posterior depression.

Girdle scales: Rather large, roundly triangular, moderately inflated; reticular sculpture ventrally; 14–17 broad ribs on central area, thinning near apex; small number of close-packed pustules at apex; apical shelf barely evident.

Remarks.—The unique type of *R. perviridis* (Fig. 2), formerly in the Pease collection, is in the Museum of Comparative Zoology. Although the label and the original description state the locality to be "Central Pacific," Pease (1872) mentioned that the specimen was from Tahiti. The type locality is therefore restricted to Tahiti, Society Islands. Thiele (1910), who was no doubt unaware of the identity of Carpenter's species, described *Chiton pacificus* on the basis of specimens from Huahine and Anaa, also in the Society Islands; an examination of Thiele's type indicates it is conspecific with *R. perviridis.*

Rhyssoplax perviridis differs from the *Rhyssoplax* of neighboring island groups, but appears to be most closely related to *R. linsleyi* Burghardt, 1973, from the Hawaiian Islands and *R. whitleyi* Iredale & Hull, 1932, from the Cook Islands. *Rhyssoplax linsleyi* has more even radial sculpture and the longitudinal ribs of the central areas are somewhat better formed. *Rhyssoplax perviridis* is easily differentiated from *R. whitleyi* by lacking the stronger longitudinal ribs of the central area and the low, but prominent, nodules of the lateral triangle. The girdle scales of all three species are quite similar, except that those of *R. linsleyi* have thin ribs in the central area while those of *R. perviridis* and *R. whitleyi* have broad ribs.

Distribution.—*Rhyssoplax perviridis* is known only from the Society and Tubuai Islands.

Locality records.—Society Islands: (MCZ, USNM); W of Motu Tapu, Bora Bora Is.; Arue, Tahiti; E side of Taunoa Pass, Tahiti (all USNM); fringe reef, opposite pass, Puneavia, Tahiti (ANSP, MCZ); Huahine; Anaa (both ZMHU).—Tubuai Islands: W of wharf, Moerai, Rurutu (USNM).

Rhyssoplax whitleyi Iredale & Hull, 1932
Fig. 8

[?] *Chiton* (*Clathropleura*) *alphonsinae* 'Rochebrune' Thiele, 1910:93 [in part]. Non Rochebrune, 1884.

Rhyssoplax whitleyi Iredale & Hull, 1932: 145, pl. 9, figs. 15, 16 (Rarotonga, Cook Islands; type in AMS [not seen]) [description].

Remarks.—*Rhyssoplax whitleyi* is distinguished from other *Rhyssoplax* from the central Pacific by its yellowish brown and blue coloration and by the prominent low nodules on the lateral triangle. Its girdle scales are moderately large, roundly triangular with reticular sculpture evident ventrally and at sides; there are 8–10 broad ribs on the central area and moderate-sized pustules on a flattened apical area. *Rhyssoplax whitleyi* differs from *R. perviridis* by having better formed longitudinal ribs on the central areas. In *R. spinosetata* from the Fiji Islands, the nodules are less pronounced and the scales (Fig. 12) very weakly striated, not distinctly striated as in *R. whitleyi*. Also, the apical pustules of the girdle scales of *R. spinosetata* are sharply limited to the apex, and not converging into the central area ribs as in *R. whitleyi* and *R. perviridis*.

Distribution.—*Rhyssoplax whitleyi* has only been recorded from the Cook Islands.

Locality records.—Cook Islands: Avatiu Harbor to Motu Toa, Rarotonga (USNM); 0.25 mi [0.4 km] N of Matavera, NE Rarotonga (ANSP, MCZ); Koromiri Is., SE Rarotonga (ANSP); Avaavaroa Passage, S Rarotonga (ANSP); fringe reef off Aroa Creek, SW Rarotonga (ANSP).

Subgenus *Anthochiton* Thiele, 1893

Anthochiton Thiele, 1893:377. Type species by monotypy, *Anthochiton tulipa* (Quoy & Gaimard, 1835).

Remarks.—The name *Anthochiton* has been used for *Rhyssoplax*-like species that have a smooth lateral triangle and end valves. It appears useful at this time to use this name to denote a separate lineage within the genus *Rhyssoplax* that is characterized by these features. The taxonomic status of nomina associated with *Rhyssoplax*, such as *Anthochiton*, *Tegulaplax* Iredale & Hull, 1926, *Delicatoplax* Iredale & Hull, 1926, and *Mucrosquama* Iredale & Hull, 1926, must await detailed radular and anatomical studies.

Rhyssoplax (*Anthochiton*) *rhynchota* (Rochebrune, 1884)
Figs. 6, 10

Gymnoplax rhynchotus Rochebrune, 1884: 39 (Nouvelle Calédonie; type not found in the MNHNP).—Pilsbry, 1894:100.

Rhyssoplax rhynchotus (Rochebrune).—Risbec, 1946:163, fig. 18 (anatomy, esthetes, radula).

Non *Chiton* (*Clathropleura*) *rhynchotus* 'Rochebrune' Thiele, 1910:92, pl. 9, figs. 52–55 [=*Rhyssoplax crawfordi* (Sykes, 1898)].

Description.—Animal rather small, reaching a length of 9.5 mm, a width of 5.5 mm. Valves subcarinate, angle about 90°. Mucro rather blunt, anteriorly acentric on posterior valve. Jugal region smooth. Central areas with up to 12 well formed longitudinal ribs per side. Lateral triangle smooth, often somewhat inflated. Terminal areas smooth. Shell color tan, yellowish green, or light orange, often with irregular darker markings. Girdle similarly colored. Interior of valves white.

Insertion plates: Intermediate valves with a single slit per side; insertion teeth appearing smooth but obsoletely grooved.

Hypostracum: Jugal tract with numerous, faint transverse grooves. Primary slit-ray with many longitudinally elongate slits.

Girdle scales: Moderate in size, ovate to rectangular; reticular sculpture ventrally, about 21 broad, close-packed ribs on central and apical areas (Fig. 10).

Remarks.—*Rhyssoplax rhynchota* is characterized by its small size, strong longitudinal ribs of the central areas, and slightly inflated lateral triangle. The specimen marked "type" in the MNHNP is not this species. This latter specimen was figured and described by Thiele (1910) as an example of Rochebrune's species, but an examination of the valves (Fig. 5), which clearly have a concave lateral triangle, and the girdle scales reveal it to be a young example of *R. crawfordi* (Sykes, 1898) from South Africa.

The nearly smooth insertion teeth of *R. rhynchota* are unusual for Chitoninae. A check of the radular proved it to be typically chitonid.

Distribution.—*Rhyssoplax rhynchota* occurs from the Bismarck Archipelago south to New Caledonia.

Locality records.—Bismarck Archipelago: New Ireland (BMNH).—New Caledonia: (MNHNP); Oubatche (AMS); N tip of Santa Marie (Isle Ngéa), Magenta, Noumea; 0–3 ft [0–0.9 m], W end, Ricaudy Reef, Noumea; 4–7 ft [1.2–2.1 m], barrier reef, 5 mi [8 km] WSW Gatope Is., Voh (all ANSP).

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A REVIEW OF THE MARINE NEMATODE GENERA *PLATYCOMA* AND *PROPLATYCOMA*, WITH A DESCRIPTION OF *PROPLATYCOMA FLEURDELIS* (ENOPLIDA: LEPTOSOMATIDAE)

W. Duane Hope

Abstract.—The taxonomic histories of the genera *Platycoma* Cobb, 1894 and *Proplatycoma* Platonova, 1976 are reviewed. *Proplatycoma fleurdelis*, n. sp. from Barbados West Indies, is described, and it is the first record of this genus in the western North Atlantic. The structure of the buccal capsule, amphidial flaps, spicula and gubernacula are discussed, and the genera *Proplatycoma* and *Platycoma* are redefined. An artificial key to the males of the species of *Platycoma* and *Proplatycoma* is provided.

The genus *Platycoma* was proposed by Cobb (1894:399) to receive a single new species, *P. cephalata* and named for the "Two flat hairs of unequal length that grow from the inner margin of the anterior border of each . . ." amphid of the males (Cobb 1894:400). Platonova (1976:138) and Platt & Warwick (1983:178) have identified these structures as setae. *Platycoma africana* (Gerlach, 1959) Gerlach, 1962, *P. curiosa* (Gerlach, 1955) Gerlach, 1962, and *P. sudafricana* Inglis, 1966 were subsequently added to the genus. Males of species whose descriptions were subsequent to those of the type species lack the pair of "hairs" or "setae" emerging from each amphid, but all possess what is presumed to be a modification of this character. The amphid in males of *P. africana* is covered by a flap that is broad at its posterior end and tapered anteriorly to a blunt, central point. The amphidial flap in males of *P. curiosa* and *P. sudafricana* is tapered to form a central, anteriorly directed lobe, and each has a dorsal and ventral lobe as well. The dorsal and ventral lobes in *P. curiosa* are highly branched, whereas in *P. sudafricana* they are not branched, but sloped posteriorly, giving the flap the appearance of an arrowhead.

Platonova (1976:139) proposed the genus *Proplatycoma* to which she transferred *P. curiosa*, *P. africana*, and *P. sudafricana*, with the latter designated as the type species. In the diagnosis of *Proplatycoma*, Platonova (1976:139) states that the amphids of the males are elongated anteriorly, sometimes with unique processes, and that cuticular, labial outgrowths are absent around the buccal aperture. Although Platonova (1976:138) did not give a formal diagnosis for *Platycoma*, it is stated in her key to the genera of Platycominae that there are two flat setae situated near each amphid, and cuticular, labial outgrowths are present. Platonova (1976:137) also proposed a new subfamily, Platycominae, for the genera *Platycoma*, *Proplatycoma*, *Platycomopsis* and *Pilosinema*.

A collection of marine nematodes from Barbados, West Indies, deposited at the National Museum of Natural History, Smithsonian Institution (USNM), contains two males, three females and three juveniles of *Proplatycoma fleurdelis*, n. sp. These specimens most closely resemble those of *P. sudafricana*, known only from males. The syntypes of *P. sudafricana* were studied for the purpose of making a comparison between members of the two species. The morpho-

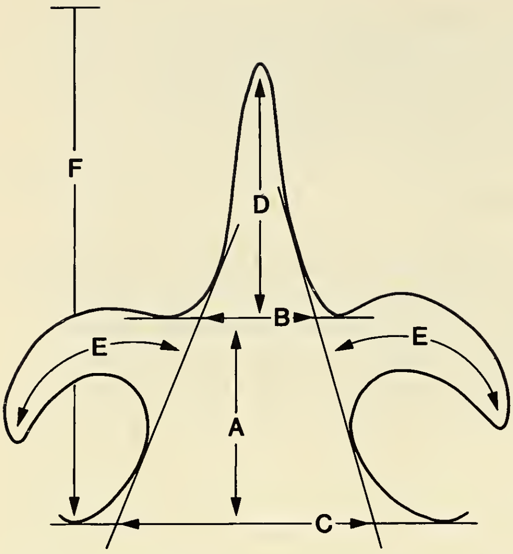

Fig. 1. Diagram showing location of measurements of amphidial flap of *Proplatycoma fleurdelis*: A, Length of flap; B, Minimum (anterior) width of flap; C, Maximum (posterior) width of flap; D, Length of anterior lobe; E, Length of dorsal and ventral lobes; F, Distance from oral surface of head to posterior margin of flap.

metric and meristic data for *P. sudafricana* presented in the discussion of *P. fleurdelis* are from original observations.

These specimens provided an opportunity to make detailed observations on the structure of the amphidial flap, the cuticular, labial outgrowths, and the spicula and gubernaculum. *Platycoma* and *Proplatycoma* are redefined on the basis of these observations.

Materials and methods.—Specimens were fixed in formalin and mounted in anhydrous glycerine between coverslips mounted on Cobb aluminum frames. Morphometric data were obtained by measuring camera lucida drawings and photographs of the specimens with a Sumagraphics Digitizing Pad. Morphometric and meristic data in the text are given first for the male holotype (USNM 77129), followed by that for the male paratype (USNM 77130). Some measurements were not possible for the male paratype; in those cases it is stated that the data is for the holotype. Similarly, for females the data is given for USNM 77131 followed by that for USNM 77132, and for juveniles the data is given for USNM 77133, USNM 77170, and USNM 77171, in that order. Where only two items of data are given for the juveniles, it is that for USNM 77170 that has been omitted, because the position of the head of that specimen made certain measurements impossible. Measurements of the male amphid were made as shown in Fig. 1. For each set of data, the mean ± one standard deviation is given in parentheses. Statistics are not calculated for the juveniles because the specimens are most likely at different stages of development.

After measurements were made on male specimen USNM 77130, it was removed from its slide mount, rehydrated, and freeze dried for scanning electron microscopy by a method described elsewhere (Hope 1982: 2). The specimen was precoated with carbon, coated with gold/palladium, and examined with an Hitachi S-570 SEM.

Platycoma Cobb, 1894

Platycoma Cobb, 1894:399.—Inglis, 1966: 85.—Gerlach & Riemann, 1974:482.—Platonova, 1976:137.

Type species.—*Platycoma cephalata* Cobb, 1894.

Diagnosis.—Leptosomatidae. Body slightly tapered from mid region toward each end; cuticle, at least in head region, with very fine transverse striae. Head region of males constricted at level of amphid, then cylindrical to level of cephalic sensilla; anterior end rounded, truncate or slightly concave. Head region of female uniformly tapered, without constriction. Amphid cyathiform; cuticle at posterior rim of amphidial aperture flap-like in males and extended anteriorly over amphidial aperture; each amphidial flap with 2 parallel, tapered lobes. Amphidial flap absent in females.

Oral aperture surrounded by 3 microlabia, each microlabium triangular in profile with apex anteriorly directed. Odontia, onchia or other forms of buccal armament absent. Anterior end of esophagus attached to cephalic cuticle; oral aperture dilated by labial retrodilator muscles in anterior end of esophagus. Subventral esophageal gland duct orifices open into buccal capsule at base of subventral microlabia. Spicula typical in structure and position, and with ventrolateral wedge- or rod-shaped accessory structure; gubernaculum with small, paired, dorsally directed apophyses.

Proplatycoma Platonova, 1976

Proplatycoma Platonova, 1976:139.

Type species.—*Proplatycoma sudafricana* (Inglis, 1966) Platonova, 1976.

Diagnosis.—Leptosomatidae. Body slightly tapered from mid region toward each end; cuticle with very fine transverse striae. Head region of males constricted at level of amphid, then cylindrical to level of cephalic sensilla; anterior end rounded to slightly concave. Head region of female uniformly tapered. Cephalic capsule present or absent. Amphid cyathiform; cuticle at posterior rim of amphidial aperture in males flap-like and extended anteriorly over amphidial aperture. Amphidial flap tapered to single, anteriorly directed point without dorsal and ventral lobes, or flap with single, central, anteriorly directed lobe and with dorsal and ventral lobes; amphidial flap absent in females.

Oral aperture surrounded by 3 microlabia, each microlabium triangular in profile with apex anteriorly directed. Odontia, onchia or other forms of buccal armament absent. Anterior end of esophagus attached to cephalic cuticle; oral aperture dilated by labial retrodilator muscles in anterior end of esophagus. Subventral esophageal gland duct orifices open into buccal capsule at base of subventral microlabia. Spicula typical in structure and position; wedge- or rod-shaped accessory structure ventrolateral to spicula; gubernaculum with paired caudally directed apophyses. Caudal glands absent.

Proplatycoma fleurdelis, new species
Figs. 1–5

Holotype.—Male, USNM 77129.

Paratypes.—Male, USNM 77130; two females (USNM 77131 and 77132); and three juveniles (USNM 77133, 77170, and 77171).

Type locality.—Barbados, West Indies. The type specimens were collected by Dr. Bjorn Urhammer in Jan and May 1968. Unfortunately, the type specimens came from a composite sample from the top 20 cm of sediment at high- and low-water marks at Skeete's Bay, the top 10 cm of sediment at the edge of Green Pond, and from the top 20 cm of sediment at the low-water mark in Bottom Bay. Therefore, it is not possible to identify the exact location(s) from which this material was obtained.

Description.—

Males.—

	a	b	c	Body length
USNM 77129	128	6.6	52	8.135 mm
USNM 77130	142	6.9	60	9.672 mm

Body diameter uniform except near anterior and posterior ends; midbody diameter 64 and 68 (66 ± 3) μm; body width at base of esophagus 62 μm (holotype); at level of nerve ring 55 μm (holotype); at level of cephalic sensilla 25 and 21 (23 ± 3) μm. Head region (Figs. 2A, C; 5A) constricted at level of amphid, cylindrical to level of cephalic sensilla, then rounded anteriorly from level of cephalic sensilla. Oral surface of head slightly concave to rounded.

Striae of cuticle (Fig. 2B) very shallow; periodicity of striae 400 nm. Head with 6 papilliform, inner labial sensilla (Figs. 2B; 5A). Single circle of 6 setiform, outer labial sensilla and 4 setiform cephalic sensilla (Figs. 2A; 5A), 8 μm from oral surface of head in both specimens; outer labial sensilla of holotype 20–25 (22 ± 3) μm and cephalic sen-

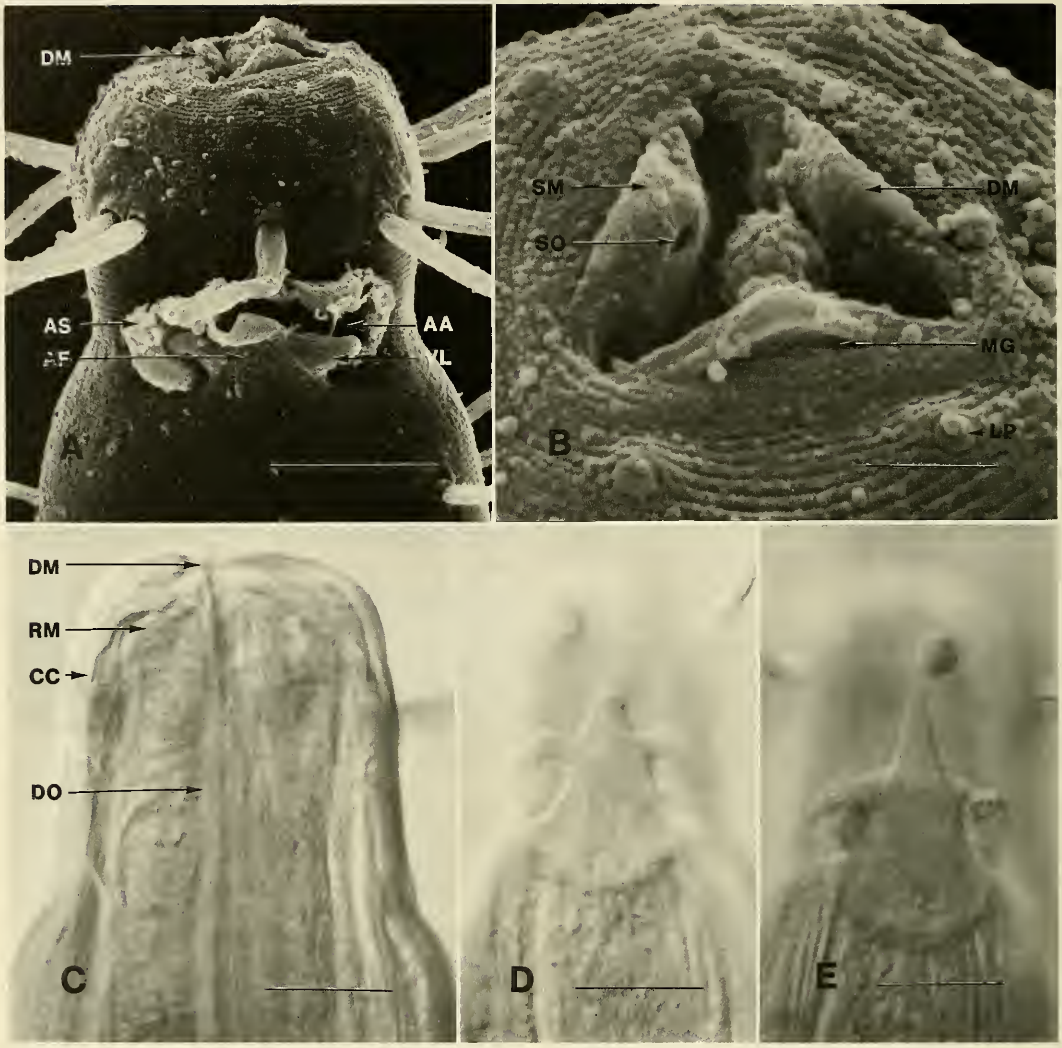

Fig. 2. *Proplatycoma fleurdelis*: A, SEM micrograph of lateral surface of head of male paratype, USNM 77130; scale equals 10 μm; B, SEM micrograph of oral surface of male paratype, USNM 77130; scale equals 3 μm; C, Photomicrograph of head of holotype male USNM 77129 in optical sagittal section; scale equals 10 μm; D, Photomicrograph of left amphidial flap of male holotype USNM 77129; scale equals 10 μm; E, Photomicrograph of right amphidial flap of holotype; scale equals 10 μm. Abbreviations.—AA, amphidial aperture; AF, amphidial flap; AS, amphidial gland secretion; CC, cephalic capsule; DM, dorsal microlabium; DO, level of dorsal esophageal gland orifice; LP, inner labial papillae; MG, microlabial groove; RM, retrodilator muscles of buccal aperture; SM, subventral microlabium; SO, subventral esophageal gland orifice; VL, ventral lobe of amphidial flap.

silla of holotype 20–22 (21 ± 1) μm long. Cervical region of holotype with 21 sensilla on right side of body, 20 on left. Length of cervical sensilla 14–19 (16 ± 2) μm. Cephalic capsule (Figs. 2C; 5A) 3 μm long on both specimens, visible only on dorsal and ventral sides of head when head viewed in sagittal, optical section.

Cuticle at posterior rim of amphidial aperture extended anteriorly, flap-like over aperture; amphidial flap (Figs. 2A, D, E; 5A) tri-lobed and with shape of fleur-de-lis. Sur-

Fig. 3. *Proplatycoma fleurdelis*: A, SEM micrograph of tail of paratype male USNM 77130; scale equals 20 μm; B, SEM micrograph of ventral, precloacal region of male paratype USNM 77130; scale equals 10 μm; C, SEM micrograph of a postero-lateral view of the posterior ventromedian supplement of paratype USNM 77130; scale equals 5 μm; D, Same as C, but in ventral view; scale equals 1 μm. Abbreviations.—AS, anterior ventromedian supplement; CS, subventral caudal seta; MD, depression produced by the contraction of copulatory muscles; PS, posterior ventromedian supplement; SS, subventral, setiform supplements.

face of flap striated; lobes nonstriated and more electron reflective than flap (Fig. 2A). Middle, anteriorly-directed lobe tapered to point with tip often bent outward; dorsal and ventral lobes arched with rounded ends directed posteriorly. Right and left amphidial flaps of holotype 7 μm long; width of flap at its anterior end 4 μm on right and left

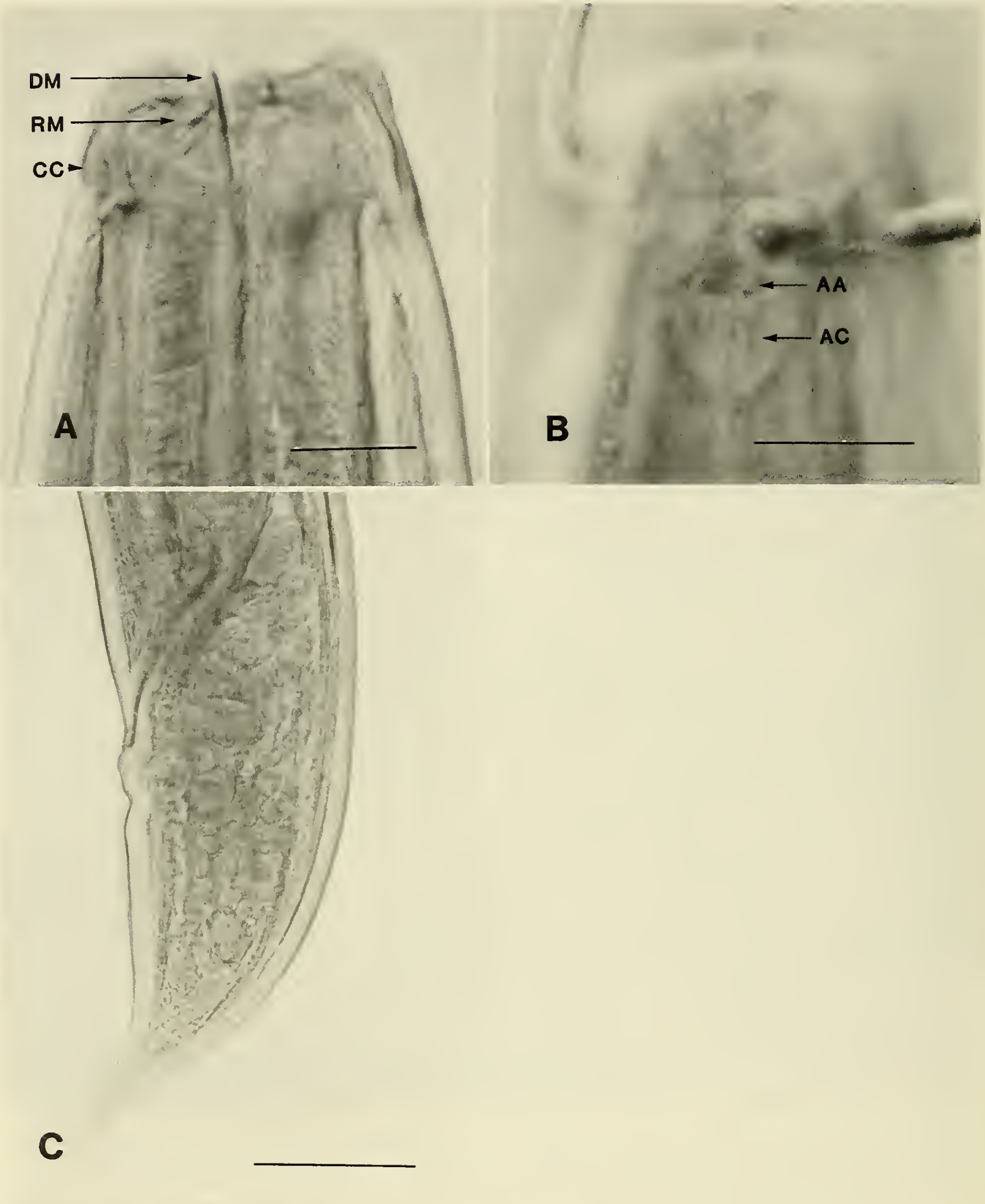

Fig. 4. *Proplatycoma fleurdelis,* photomicrographs of female paratype USNM 77131: A, Head in optical sagittal section, scale equals 10 μm; B, Right lateral surface of head; scale equals 10 μm; C, Optical sagittal section of tail; scale equals 40 μm. Abbreviations.—AA, amphidial aperture; AC, amphidial fovea; CC, cephalic capsule; DM, dorsal microlabium; RM, retrodilator muscles of the buccal aperture.

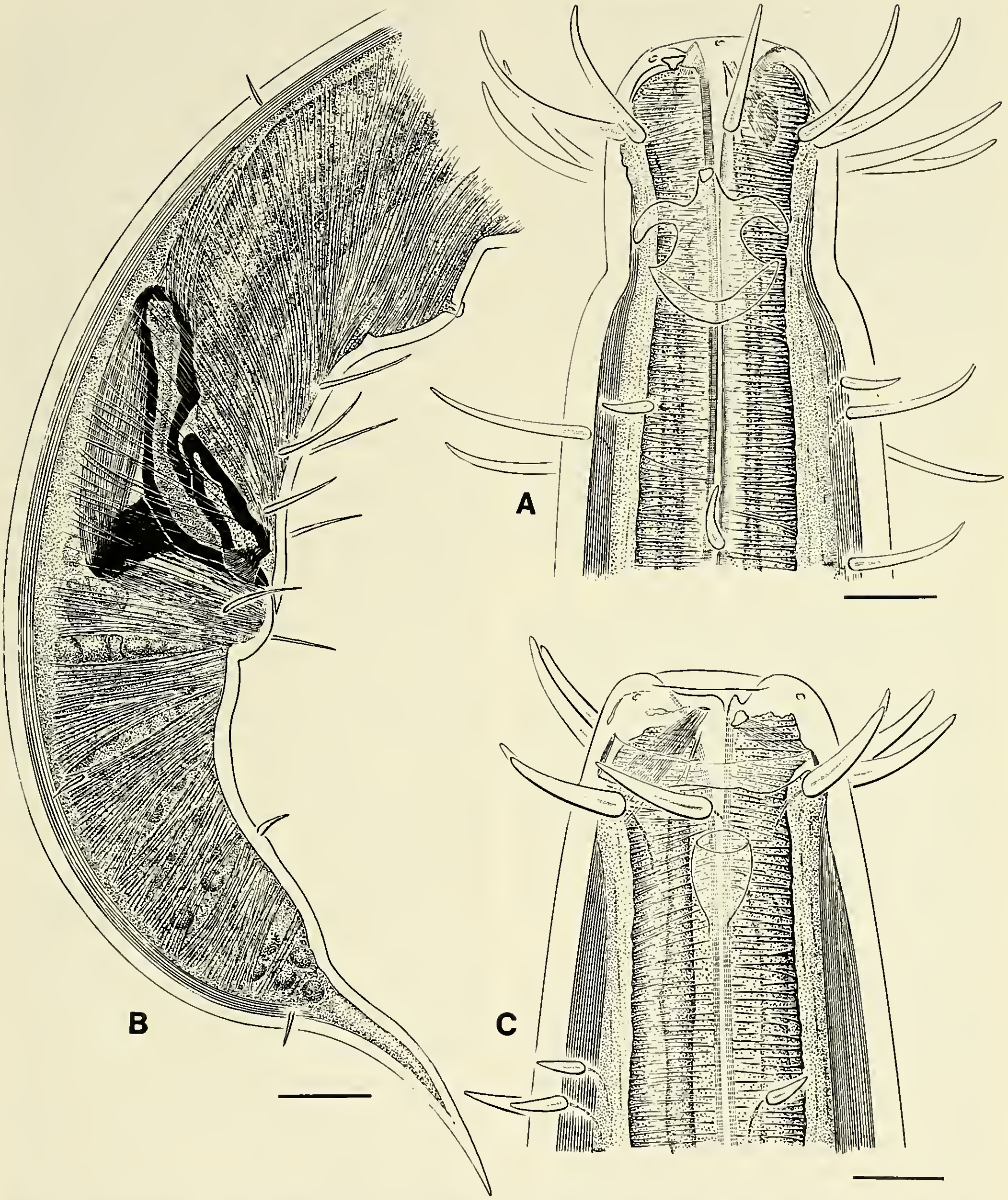

Fig. 5. *Proplatycoma fleurdelis*: A, Lateral view of head of holotype, USNM 77129; scale equals 10 μm; B, Lateral view of tail of holotype, USNM 77129; scale equals 20 μm; C, Lateral view of head region of female paratype, USNM 77131; scale equals 10 μm.

sides and width of flap at its posterior end 9 μm on right and left sides; anterior lobe of left flap 8 μm long; dorsal and ventral lobes of right and left amphidial flaps 7 μm long. Distance from oral surface of head to posterior margin of right and left flaps 24 and 26 (25 ± 1) μm, respectively. Amphidial glands well developed; posterior end of right gland of holotype 687 μm from oral surface of head.

Oral aperture (Fig. 2B) triradiate and surrounded by 3 microlabia (Figs. 2A, B, C; 5A). Microlabia triangular with apex directed anteriorly, and each set off from head by microlabial groove (Fig. 2B). Buccal capsule triradiate and dilated by 3 obliquely oriented, labial retrodilator muscles (Figs. 2C; 5A), 1 in each sector at anterior end of esophagus. Buccal armament absent. Orifice of dorsal esophageal gland (Figs. 2C; 5A) in lumen of esophagus, 18 and 20 (19 ± 1) μm posterior from oral surface. Orifices of right and left subventral esophageal glands on mesal surface of right and left microlabia, respectively (Fig. 2B). Esophagus 1240 and 1400 (1320 ± 114) μm long, cylindrical, slightly tapered anteriorly, and posteriorly crenate. Renette absent.

Somatic sensilla uncommon between level of nerve ring and near level of cloacal vent. Right lateral chord of holotype with 48 dorsolateral loxometanemes of type I with caudal filaments, and 28 without caudal filaments; in left lateral chord 58 with caudal filaments and 29 without. Hypodermal gland cells present in hypodermal chords, each gland cell opening on surface of cuticle at dorsolateral or ventrolateral margin of chord.

Testes paired and opposed, each on left of gut. Seminal vesicle highly convoluted. Ejaculatory duct enveloped with muscle cells, each cell oblique with dorsal margin anterior to ventral margin. Spicula (Fig. 5B) paired, curved ventrally; right spiculum of holotype 73 and left spiculum 76 (75 ± 2) μm long, measured on chord. Proximal end of each spiculum bluntly rounded without distinct capitulum; diameter of proximal third uniform, distal end tapered. Ventral surface of distal two-thirds of each spiculum recessed. Gubernaculum (Fig. 5B) with paired apophyses directed caudally; each apophysis keel-shaped, straight; right apophysis in holotype 18 and left 13 (16 ± 4) μm long. Wedge-shaped accessory structure (Fig. 5B) present in recessed area on ventrolateral surface of spiculum; proximal end narrow; distal end of right accessory structure in holotype 9 and distal end of left 11 (10 ± 1) μm wide and with 13 fine transverse striae on right and with 12 on left side of body. Copulatory muscles of body wall anterior to spicula (Fig. 5B) oblique and nearly in continuous sheets.

Setiform, subventral supplements (Figs. 3A; 5B) 18–24 (20 ± 2) μm long and in series of 4 and 4 on right side of body and 3 and 4 on left; anterior supplements 41 and 49 μm anterior to cloacal vent on right side of body and 35 and 36 (40 ± 6) μm on left; posterior subventral supplements approximately adanal. Posterior ventromedian supplement (Figs. 3A, B, C, D; 5B) disc-shaped and pedunculate, on raised surface of body 63 and 79 (71 ± 11) μm anterior to cloacal vent; center of disc with slightly raised, longitudinally oriented ridge (Fig. 3D); posterior end of ridge expanded and with central depression (sensory receptor ?). Anterior ventromedian supplement (Fig. 3A, B) with 4 and 3 pairs of setiform sensilla, 1 member of each pair on right and left sides respectively of sagittal plane; sensilla of paratype 3–5 (4 ± 1) μm long; posterior pair 112 and 108 (111 ± 2) μm from cloacal vent, and anterior pair 127 and 118 (123 ± 6) μm from cloacal vent. Dorsolateral, lateral and ventrolateral setiform sensilla sparsely distributed precaudally to near anterior limit of copulatory muscle.

Tail 158 and 160 (159 ± 1) μm long with terminal, conical spike (Figs. 3A; 5B). Paired, stout, subventral setiform sensilla (Figs. 3A; 5B), 8 and 9 (9 ± 1) μm long, present on tail 67 and 81 (74 ± 10) μm posterior from cloacal vent, or 45 and 51 (48 ± 4)% of tail length. One subdorsal setiform sensilla present on each side of tail near base of spike; additional subdorsal caudal setiform sensilla sparse or absent. Cloacal body diameter 59 and 48 (53 ± 8) μm. Caudal glands absent.

Females.—

	a	b	c	V	Body length
USNM 77131	133	8.5	86	63%	10.619 mm
USNM 77132	107	8.0	60	65%	7.718 mm

Body diameter at midlength 80 and 72 (76 ± 6) μm; at level of base of esophagus 70 and 68 (69 ± 1) μm; at level of nerve ring 65 and 63 (64 ± 1) μm; at level of cephalic sensilla 29 and 28 (29 ± 1) μm. Head (Figs. 4A; 5C) uniformly tapered from cephalic sensilla to oral surface, then truncate to slightly concave.

Head with 6 papilliform, inner labial sensilla (Fig. 5B). Single circle of 6 setiform, outer labial sensilla and 4 setiform, submedian, cephalic sensilla (Fig. 5C), 11 and 13 (12 ± 1) μm from oral surface. Outer labial sensilla 13–17 and 15–16 (15 ± 2) μm long, and 4 submedian cephalic sensilla 15–17 and 16–18 (17 ± 1) μm long. Cervical region with 22 and 19 (21 ± 1) sensilla on right side of neck and 20 and 17 (19 ± 2) on left. Cervical sensilla 3–14 (9 ± 4) and 4–14 (9 ± 4) μm long. Cephalic capsule 5 μm long on both specimens. Amphid (Figs. 4B; 5C) cyathiform; aperture transversely oval, 16 and 15 (16 ± 0.4) μm from oral surface; amphidial fovea 9 and 8 (9 ± 1) μm long and 7 and 6 (7 ± 0.4) μm wide.

Oral aperture triradiate and surrounded by 3 microlabia (Fig. 4A; 5C). Microlabia set off from head by microlabial grooves. Oral surface of head concave with contraction of retrodilator muscles (Figs. 4A; 5C). Buccal armature absent. Orifice of dorsal esophageal gland (Fig. 5C) 21 and 19 (20 ± 1) μm from oral surface. Orifices of subventral glands on mesal surface of subventral microlabia. Esophagus 1255 and 967 (1111 ± 204) μm long, cylindrical, slightly tapered anteriorly, and posteriorly crenate. Renette absent.

Somatic sensilla sparse. Hypodermal gland cells present in hypodermal chord, each gland cell opening on surface of cuticle at dorsolateral and ventrolateral margin of chord. Hypodermal chord in vulvar region without specialized gland cells. Reproductive system amphidelphic and antidromous. Gonads ventral to gut; anterior ovary on left side of oviduct, posterior on right.

Tail (Fig. 4C) tapered dorsally and ventrally; length 124 and 128 (126 ± 3) μm with 1 subdorsal sensillum and 2–4 sensilla at base of caudal spine on each side of body. Anal body diameter 59 and 60 (60 ± 1) μm. Caudal glands absent.

Juveniles.—

	a	b	c	Body length
USNM 77133	60.3	4.8	27.5	3.498 mm
USNM 77170	92.0	5.1	31.5	5.683 mm
USNM 77171	133.0	7.3	54.0	8.268 mm

Similar to females. Midbody diameter 58, 62, and 62 μm; body diameter at base of esophagus 61, 61, and 62; at level of nerve ring 59, 52, and 56; at level of cephalic sensilla 20, 22, and 23 μm. Head truncate to slightly concave on oral surface. Cephalic sensilla 11–14, 12–13, and 13–17 μm long and 10 and 8 μm from oral surface of head. Amphid cyathiform; aperture transversely oval; anterior rim of aperture 13 μm from oral surface of head in each of 2 specimens; amphidial fovea longitudinally ovoid, 9 by 6 μm in each of 2 specimens. Cephalic capsule 2.5 and 3.0 μm long. Distance from oral surface to orifice of dorsal esophageal gland 19 and 16 μm. Esophagus 730, 1108, and 1135 μm long. Cervical region with 15, 18, and 24 sensilla on right side; 10, 20, and 22 on left; cervical sensilla 6–14, 5–14, and 6–15 μm long.

Tail tapered on dorsal and ventral surfaces; length 127, 180, and 153 μm; terminal spike present. Each side of tail with 1 or 2 subdorsal setiform sensilla. Anal body diameter 47, 49, and 54 μm. Caudal glands absent.

Diagnosis.—*Proplatycoma fleurdelis* is most similar to *P. sudafricana,* with the amphidial flap of the males of each species having a median lobe and unbranched, dorsal and ventral lobes. The males of the new species differ from those of *P. sudafricana* in that the dorsal and ventral lobes of each amphidial flap are arched with their respective tips pointed dorso- and ventrocaudally so that the overall shape of the amphidial flap resembles the fleur-de-lis; the values for "a" and "b" are 135 ± 10 and 7 ± 0.2 respectively; the distances from the cloacal vent to the posterior and anterior ventromedian supplements are 71 ± 11 and 117 ± 29 μm respectively; the number of setiform subventral supplements are 3 or 4 on the right side of the body and 4 on the left. In *P. sudafricana* the dorsal and ventral branches respectively are sloped dorso- and ventrocaudally so that the overall shape of the amphidial flap resembles an arrowhead; the values of "a" and "b" for the only whole syntype specimen are 174 and 8 respectively; the distances from the cloacal vent to the posterior and anterior ventromedian supplements are 115 ± 17 μm and 185 ± 23 μm respectively; the number of setiform subventral supplements are 2 on the right and 2 on the left sides of the body.

Etymology.—The specific epithet is a noun derived from fleurdelis (middle French) for flower of the lily, which denotes the shape of the amphidial flap.

Discussion.—SEM observations reveal that the base of the amphidial flap in males of *P. fleurdelis* is covered with striated exocuticle, whereas the anterior and dorsal and ventral lobes are without striations and have the same relatively high electron-reflective appearance as the cephalic and cervical sensilla (Fig. 2A). This may be due to the fact that both the sensilla and lobes of the amphidial flaps are extensions of the meso- or endocuticle without the external covering of the exocuticle. Even if this is so, it does not necessarily imply that the branches of the amphidial flaps are derived from sensory sensilla, because, unlike the sensilla, each does not arise from a socket, and there is no evidence from light microscopy of a nerve passing into them. Although SEM observations have not been made on the amphidial flaps of the males of the other species of *Proplatycoma*, or those of *Platycoma cephalata,* it is assumed that the flaps are homologous. The only difference between them is assumed to be the number, shape and position of the lobes. The amorphic substance at the edge of the amphidial aperture (Fig. 2A) is assumed to be a secretion of the amphidial gland.

The 3 projections around the oral aperture are here interpreted to be microlabia, homologous with the microlabia among members of Leptosomatidae (Hope 1982: 12). Like microlabia, they are set off from the head region by a groove, the microlabial groove, to the base of which is attached the labial retrodilator muscle for the buccal capsule. It was not possible to determine if this muscle is attached to an apodeme, as it is in *Deontostoma* (Hope 1982:4). Also, as in other leptosomatids, there is an orifice of a subventral esophageal gland duct on the mesal surface of each subventral microlabium. However, in other members of Leptosomatidae, the subventral gland duct orifice opens into the mandibular groove on the mesal surface of the microlabium (Hope 1982:8). This groove separates the microlabium from the mandibular ridge, the latter being absent in members of *Proplatycoma.*

The microlabia of *P. fleurdelis* differ from those of Deontostomatinae (Leptosomatidae) in that they are triangular in profile, and tapered to a relatively thin anterior edge (Fig. 2A, B). When the labial retrodilator muscles are relaxed, the microlabia project anteriorly beyond the anterior surface of the head (Fig. 2A, B), but when these muscles are contracted, the buccal cavity is dilated and the microlabia are pulled posteriorly so that they no longer protrude beyond the oral surface (Figs. 2C; 4A; 5A, C). In this condition, microlabia may appear tooth-like, especially when the head is viewed laterally in optical longitudinal section. This interpretation applies to females as well. It is also apparent that complete contraction of the labial retrodilator muscles causes the oral surface of the head to become concave (Figs. 4A; 5C).

An examination of the syntypes of *P. sudafricana* during this study has revealed the presence of microlabia similar to those of *P. fleurdelis* and a complete absence of buccal armament. This is in contrast to the interpretations of Inglis (1966:83) who does not mention the presence of lips or microlabia and states that the buccal cavity has ". . . three small wholly cuticular onchia on each sector . . . ." A head remains on only one of the two syntypes of this species, and in that specimen the microlabia are pulled posteriorly into the buccal cavity. It is concluded that Inglis (1966:83) erroneously identified the microlabia as onchia. The structure and function of the labial region among members of *P. sudafricana* is identical to those among members of *P. fleurdelis.*

It is further postulated that the buccal aperture is surrounded by 3 microlabia, and the buccal cavity is without odontia or onchia in *Proplatycoma curiosa* and *P. africana,* as well as in *Platycoma cephalata.* Thus, in the illustrations of the male heads in the original description of *P. curiosa* and *P. africana,* the microlabia have probably been pulled posteriorly into the buccal capsule (Gerlach 1955:254; 1959:361). The illustration of the male head in the original description of *Platycoma cephalata* is without sufficient detail to allow conclusions concerning the structure of the labial region (Cobb 1894:400). However, in the illustrations of the head of a male of this species published by Bresslau & Schuurmans Stekhoven (1940:table II, figs. 6a, b, c), the tips of the microlabia are level with the oral surface of the head, whereas in the illustrations of a male of the same species published by Platt & Warwick (1983:179), the microlabia extend anterior to the oral surface. Even though the projections are interpreted in both publications as being teeth, they are undoubtedly microlabia, and the difference in the degree to which the microlabia are extended is attributable to the degree by which the labial retrodilator muscles are contracted. This applies to males and females.

The foregoing are relevant with regard to the diagnoses of *Platycoma* and *Proplatycoma.* Although the former genus was not redefined by Platonova (1976:139), she characterizes *Proplatycoma* as follows:

Nematodes characterized by sharp sexual dimorphism in structure of amphids. In females amphids typically cyathiform but slightly elongated in longitudinal direction. In males anterior end of amphids elongated anteriorly and sometimes with unique processes. Cuticular labial outgrowths absent. Cervical setae may be numerous and may be scattered over the preneural region in groups or singly. Tail wide, terminally acicular. Spicules small, blunt, and reduced. Gubernaculum significantly longer than spicules, curved in the middle, with large blunt dorsal process.

The cuticular labial outgrowths of the above diagnosis are the microlabia of this study. Because it has been demonstrated that specimens of *P. fleurdelis* and *P. sudafricana* do have microlabia, and that microlabia probably occur as well in *P. curiosa* and *P. africana, Platycoma* and *Proplatycoma* cannot be separated on the basis of this character.

Platonova's (1976:140) interpretation of the spicula and gubernacula in her diagnosis of *Proplatycoma* is probably based upon an earlier erroneous interpretation by Gerlach (1959:361; 1962:85) who regarded the straight, wedge-shaped structure ventrolateral to the spicula as being the spicula, and the spicula as being the gubernaculum with a caudal apophysis. This interpretation is in contrast to that made by Inglis (1966:83) in his original description of *P. sudafricana* and in the present study of *P. fleurdelis.* As may be seen in Fig. 5B, the structure of the spicula and gubernacula and the number and arrangement of the muscles associated with them are similar to those found in other leptosomatid species, especially in those cases where the gubernaculum possess a caudal apophysis. This interpretation for the structure and arrangement of the spicula and gubernacula corresponds to that made by Platt & Warwick (1983:178) in their redescription of *Platycoma cephalata.* The only difference that exists between males of *Platycoma* and *Proplatycoma* is that in the former the apophyses of the gubernaculum are smaller and directed dorsad, whereas in males of all species of *Proplatycoma* the apophyses are larger and directed caudad.

The remainder of the characteristics given by Platonova (1976:139) for *Proplatycoma* also apply to *Platycoma.* Furthermore, the presence or absence of the cuticular labial outgrowths is the only character by which Platonova (1976:138) separates *Platycoma* and *Proplatycoma* in her key. Therefore, the two genera cannot be distinguished from one another as they are defined by Platonova. In the new definitions given here, the males of the two genera may be distinguished by differences in 1.) the amphidial flap, which is comprised of two, anteriorly-directed, parallel lobes in the case of *Platycoma,* and by a single, anteriorly-directed lobe, with or without dorsal and ventral lobes, in *Proplatycoma*; and 2.) the apophyses of the gubernaculum, which are smaller and dorsally directed in *Platycoma,* and larger and caudally directed in *Proplatycoma.* There are no known characters by which the females of the two genera can be separated.

The subfamily Platycominae is retained, but it is recognized that at present it cannot be defined by a single synapomorphic character. Further study of members of *Platycomopsis* Ditlevsen, 1926 and *Pilosinema* Platonova, 1976 is needed.

The following key to the species of *Platycoma* and *Proplatycoma* is for the identification of males only, because adult females of *P. curiosa* and *P. sudafricana* have not been described, and females of other species of the genera are not sufficiently well known.

Artificial Key to the Males of the Species of *Platycoma* and *Proplatycoma*

1. Each amphidial flap tapered to a single anteriorly directed tip without dorsal and ventral lobes, or with a single, central, pointed lobe, and with dorsal and ventral lobes.
– Apophysis of gubernaculum caudally directed .... *Proplatycoma* 2
– Each amphidial flap with 2 parallel, anteriorly directed lobes; each lobe tapered anteriorly, without dorsal and ventral lobes; apophysis of gubernaculum dorsally directed .... *Platycoma cephalata* Cobb, 1894
2. Amphidial flap with single central and dorsal and ventral lobes 3
– Amphidial flap tapered to single, anteriorly-directed tip without dorsal and ventral lobes .... *P. africana* (Gerlach, 1959)
3. Dorsal and ventral lobes not branched 4
– Dorsal and ventral lobes branched .... *P. curiosa* (Gerlach, 1955)
4. Amphidial flap arrowhead-shaped; dorsal and ventral lobes sloped posteriorly; 2 subventral supplements on each side of body .... *P. sudafricana* Inglis, 1966
– Amphidial flap with shape of fleur-de-lis; dorsal and ventral lobes arched; 3 or 4 subventral supplements on each side of body .... *P. fleurdelis,* n. sp.

Distribution and ecology.—The original description of specimens of *Platycoma cephalata* was based on material extracted from sandy sediment collected in the Bay of Naples, Italy (Cobb 1894:399). This species was redescribed by Southern (1914: 33) from specimens obtained from a habitat of sand and shells at a depth of 44 m in

Clew Bay, Ireland, and by Bresslau & Schuurmans Stekhoven (1940:13) from specimens, including females, inhabiting Polygordius-sediment collected at Helgoland in the North Sea.

Proplatycoma africana was originally collected in coarse, intertidal sand on the Insel Abd el-Kuri, Gulf of Aden (Gerlach 1959: 360). Subsequently, it was found in medium sand in the intertidal zone of Fadiffollu Atoll, Maldive Islands (Gerlach 1962:85); coral sand in the littoral and supralittoral zones of Sarso Island, Red Sea (Gerlach 1967a: 15; 1967b:20); coarse sand between the low and mean water levels on the coast of India (Bay of Bengal) near Waltair (Rao & Ganapati 1968a:40; 1968b:97); fine to coarse sand between low and mean water levels on the coast of India (Bay of Bengal) near Puri and Konarak, Orissa (Nagabhushanam & Rao 1969:77; Rao 1969:94); medium sand between low and mid-tide levels on Pudimadaka Beach, Andhra Pradesh, India (Rao 1970:112).

Proplatycoma curiosa was originally collected from the intertidal zone on the coast of El Salvador near San Salvador (Gerlach 1955:253), and subsequently found in coarse sand on the coast of Brazil near Victoria and Macaé (Gerlach 1957:463).

Proplatycoma sudafricana is known only from its type habitat and locality, which is sand of the surf zone near Durban, Republic of South Africa (Inglis 1966:83).

In summary, the known distribution of *P. cephalata,* the only species of the genus, is the eastern North Atlantic and Mediterranean Seas, roughly between 40°N (Bay of Naples) and 54°N (Helgoland), and its depth range is to at least 44 m. Members of the genus *Proplatycoma,* on the other hand, range from about 20°N, as in the case of *P. africana* (Rao 1969:89) to almost 30°S, as in *P. sudafricana* (Inglis 1966:83). The known depth distribution for all members of *Proplatycoma* does not extend below the intertidal zone. It appears, therefore, that differences between *Platycoma* and *Proplatycoma* are to be found in geographic distribution and, possibly, habitat distribution. Members of *Platycoma* are temperate and are known to range into subtidal depths, whereas members of *Proplatycoma* are tropical to subtropical and limited to the intertidal zone; and John Lambshead of the British Museum (Natural History) for the loan of type specimens.

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101(3), 1988, pp. 707–708

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following Opinions were published on 25 March 1988 in vol. 45, part 1 of the *Bulletin of Zoological Nomenclature:*

Opinion No.

1464 *Calcarina calcar* d'Orbigny, 1839 (currently *Pararotalia calcar*; Protista, Foraminiferida): specific name conserved.
1465 *Laomedea gracilis* Sars, 1850 (currently *Clytia gracilis*; Cnidaria, Hydrozoa): specific name conserved.
1466 *Terebratula triangulus* Valenciennes, 1819, *T. catulloi* Pictet, 1867 and *T. janitor* Pictet, 1867 (Brachiopoda, Articulata): specific names conserved.
1467 *Criopus* Poli, 1791 and *Criopoderma* Poli, 1795 (Brachiopoda): suppressed.
1468 *Orbicula* Cuvier, 1798 (Brachiopoda, Inarticulata): suppressed.
1469 *Crania tuberculata* Nilsson, 1826 (Brachiopoda): conserved.
1470 SINUITIDAE Dall, 1913, MACLURITIDAE Carpenter, 1861 and EUMPHALIDAE de Koninck, 1881 (Gastropoda, Archaeogastropoda): conserved.
1471 *Aplysia* (originally *Laplysia*) *viridis* Montagu, 1804 (Mollusca, Gastropoda): specific name conserved.
1472 *Cyclaxyra* Broun, 1893 (Insecta, Coleoptera): conserved.
1473 *Tetropium* Kirby, 1837 (Insecta, Coleoptera): conserved.
1474 *Tropiphorus* Schönherr, 1842 (Insecta, Coleoptera): conserved.
1475 *Dexia* Meigen, 1826 (Insecta, Diptera): *Musca rustica* Fabricius, 1775 designated as the type species.
1476 *Agromyza* Fallén, 1810 (Insecta, Diptera): *Agromyza reptans* Fallén, 1823 designated as the type species.
1477 *Napomyza* Westwood, 1840 (Insecta, Diptera): conserved.
1478 *Lycaena mirza* Plotz, 1880 (currently *Azanus mirza*; Insecta, Lepidoptera): specific name conserved.
1479 *Antispila* Hübner [1825] (Insecta, Lepidoptera): *Antispila stadtmuellerella* Hübner [1825] designated as type species.
1480 *Apanteles ornigis* Weed, 1887 (currently *Pholetesor ornigis*; Insecta, Hymenoptera): specific name conserved.
1481 *Siphamia* Weber, 1909 and *S. permutata* Klausewitz, 1966 (Osteichthyes, Perciformes): conserved.
1482 *Heteroclonium bicolor* Cope, 1896 (currently *Bachia bicolor*; Reptilia, Squamata): specific name conserved.
1483 *Rhabdodon* Matheron, 1869 (Reptilia, Ornithischia): conserved.

Direction No.

122 *Bubo* Duméril, 1806 and *Surnia* Duméril, 1806 (Aves): Official List entries completed.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following applications, and one general article, were published on 25 March 1988 in vol. 45, part 1 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, ICZN, @ British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

General Article An appraisal of the Zoology of C. S. Rafinesque.

Case No.

2609 *Madrepora limax* Esper, 1797 (currently *Herpolitha limax*) and *Fungia talpina* Lamarck, 1801 (currently *Polyphyllia talpina*; both Cnidaria, Anthozoa): proposed conservation of the specific names.
2610 *Coenobita* Latreille, 1829 (Crustacea, Decapoda): proposed conservation
2613 *Sphaeroma hookeri* Leach, 1814 (currently *Lekanesphaera hookeri*; Crustacea, Isopoda): proposed conservation of the specific name.
2607 *Hydrobius* Leach, 1815 and *Berosus* Leach, 1817 (Insecta, Coleoptera): confirmation of type species.
2481 *Elachista* Treitschke, 1833 (Insecta, Lepidoptera): proposed conservation, and confirmation of type species designation.
2617 *Colias alfacariensis* Ribbe, 1905 (Insecta, Lepidoptera): proposed availability as a senior synonym of "*Colias australis* Verity, 1911."
2411 *Ludita* Nagy, 1967 (Insecta, Hymenoptera): proposed designation of *Tiphia villosa* Fabricius, 1793 as type species.
2608 *Vespa triangulum* Fabricius, 1775 (currently *Philanthus triangulum,* Insecta, Hymenoptera): proposed conservation of the specific name.
2598 *Ictiobus* Rafinesque, 1820 (Osteichthyes, Cypriniformes): proposed conservation.
2556 *Hydrolycus* Müller & Troschel, 1844 (Osteichthyes, Cypriniformes): confirmation proposée de *Hydrocyon scomberoides* Cuvier, 1819 comme espèce-type.
2621 *Ascalabotes gigas* Bocage, 1875 (currently *Tarentola gigas*; Reptilia, Squamata): proposed conservation of the specific name.
2605 *Euryotis brantsii* A. Smith, 1834 (currently *Parotomys brantsii*; Mammalia, Rodentia): proposed conservation of the specific name.

INFORMATION FOR CONTRIBUTORS

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Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

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CONTENTS

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CRYPTOTROCHUS, NEW GENUS AND TWO NEW SPECIES OF DEEP-WATER CORALS (SCLERACTINIA: TURBINOLIINAE)

Stephen D. Cairns

Abstract.—A new genus in the Turbinoliinae is described: *Cryptotrochus,* characterized by having an imperforate theca, a papillose columella, and well-developed P2. A partial key to the 21 recognized genera of Turbinoliinae shows it to be similar to *Kionotrochus,* but differing in corallum shape and in having well-developed P2. Two widely geographically separated new species are described in this genus: *C. carolinensis,* known only from 320–338 m off North Carolina, and *C. javanus,* known only from 585 m in the Java Sea.

Species of the subfamily Turbinoliinae have small, solitary, unattached coralla that are completely invested by the polyp. This complete investiture of the corallum by soft tissue allows for deep intercostal furrows from the calice to the base, which is characteristic of the subfamily. They are among the smallest of the Scleractinia; one species, *Oryzotrochus stephensoni* Wells, 1959, has an adult calicular diameter of 1.5 mm, and the genus is so named for its resemblance in size and shape to a grain of rice.

There are approximately 118 species of Turbinoliinae attributed to 21 genera, eight of which are exclusively fossil genera. Species in the subfamily are known from the Upper Cretaceous to the Recent and are worldwide in distribution (including the Antarctic), the Recent species recorded from depths of 9–835 m. Some species of Turbinoliinae are known to be interstitial in habitat. Species of Turbinoliinae are most common in the Australian-New Zealand and Indonesian regions, especially in the Miocene; only five species are described from the Atlantic Ocean.

While studying the deep-water coral collection of the R/V *Gosnold* at the National Museum of Natural History (USNM) in 1977, I discovered a species of Turbinoliinae from off North Carolina (*Gosnold* sta. 1811) that was very different from any yet described from the Atlantic but quite similar to an Indo-West Pacific species (i.e., *Notocyathus conicus* (Alcock, 1902)). Thinking that this single lot of specimens might be improperly labelled, I placed it aside. Several years later I discovered a damaged basal part of the same species from *Gosnold* sta. 1841, not far from *Gosnold* sta. 1811.

More recently, I diagnosed two specimens collected from the Java Sea by the R/V *Galathea* as having the same generic attributes. In reviewing all genera of the Turbinoliinae in preparation for a revision of the deep-water Scleractinia of the Philippine Islands (Cairns, in prep.), I determined that the *Gosnold* and *Galathea* samples are two new species and represent a new genus, described herein as *Cryptotrochus.* A key is provided for the imperforate paliferous genera of Turbinoliinae (9 of 21 genera in the subfamily) to help distinguish the new genus.

Order Scleractinia Bourne, 1900
Suborder Caryophylliina Vaughan and Wells, 1943
Family Caryophylliidae Dana, 1846
Subfamily Turbinoliinae Milne Edwards and Haime, 1848
Cryptotrochus, new genus

Diagnosis.—Solitary, conical, free corallum with pointed base. Imperforate theca.

Well-developed, discrete P2. Columella papillose. Ahermatypic.

Discussion.—Among the 21 genera of Turbinoliinae, nine can be characterized as having pali and an imperforate theca (see Key). Of these nine, only two genera have pali restricted to the second-cycle septa (P2): *Kionotrochus* and *Cryptotrochus.* Although the type species of *Kionotrochus, K. suteri* Dennant, 1906, was originally described as lacking pali, and Wells (1956) also defined the genus as lacking pali, Squires (1960) correctly noted that *K. suteri* does, in fact, have small, rod-like P2 that merge almost indistinguishably with the columella (Fig. 13). This is the basic difference between the two genera: *Kionotrochus* has indistinct rod-like P2, whereas *Cryptotrochus* has discrete lamellar P2. Another important difference is corallum shape: *Cryptotrochus* has a conical corallum with a pointed base; *Kionotrochus* has a bowl-shaped corallum with a rounded base (Fig. 14), often the result of transverse division (Squires 1964). Based on corallum shape, it is unlikely that *Cryptotrochus* reproduces by transverse division. Other less important differences are that species of *Cryptotrochus* have highly exsert S1–2 and four cycles of septa, wheras *K. suteri* has moderately exsert septa and only three cycles of septa. *Kionotrochus* was divided into two subgenera by Squires (1960): the nominal subgenus and *K.* (*Cylindrophyllia*). *Cylindrophyllia* is considered to be a junior synonym of *Peponocyathus* (Cairns, in prep.), resulting in *Kionotrochus* s. str. being monotypic. It is endemic to northeastern New Zealand, 48–241 m (Squires & Keyes 1967).

Although not apparent from the key, *Cryptotrochus* is very similar to *Notocyathus,* being similar in size, corallum shape, septal exsertness, costae, and columella. The only point of difference concerns the pali: *Cryptotrochus* has six P2, whereas *Notocyathus* has 12 P3, arranged in 6 V-shaped pairs, the P1 and P2 of *Notocyathus* usually being suppressed in the adult stage.

Two species are assigned to *Cryptotrochus, C. carolinensis* and *C. javanus*; however, two more undescribed species are known from off New Caledonia and the Chesterfield Islands (H. Zibrowius, pers. comm. and examination of specimens). One differs from *C. javanus* in having a more slender corallum, having only one row of granules per costa, and having less prominent pali. It is known from a similar depth range: 555–680 m. The second undescribed species differs from *C. javanus* in having prominent lateral granules on costal edges, S3 almost as large as S2, and highly granular septa. It is known only from 223–345 m.

Etymology.—*Cryptotrochus* is a combination of "*kryptos*" (Greek: hidden, concealed) and "*trochos*" (Greek: wheel), a common suffix of turbinoliid generic names, together alluding to the inconspicuous presence of these small corals, which are only now being described from the Atlantic. The gender is masculine.

Type species.—*Cryptotrochus carolinensis,* n. sp., here designated.

Distribution.—Currently known only from off North Carolina and Java Sea, 320–585 m. Also New Caldonia and Chesterfield Islands, 223–680 m (H. Zibrowius, pers. comm.).

Partial Key to the Genera of Turbinoliinae with Emphasis on the Imperforate Paliferous Genera (+ denotes exclusively fossil genera)

1. Corallum perforate ....
 +*Turbinolia* Lamarck, 1816; *Conocyathus* Orbigny, 1849; *Trematotrochus* Tenison-Woods, 1879; +*Bothrophoria* Felix, 1909
1′. Corallum imperforate 2
2. Columella absent ....
 .... +*Dominicotrochus* Wells, 1937
2′. Columella present 3
3. Pali absent ....
 Sphenotrochus Milne Edwards and

Haime, 1848; *Platytrochus* Milne Edwards and Haime, 1848; +*Koilotrochus* Tenison-Woods, 1878; *Holcotrochus* Dennant, 1902; +*Sphenotrochopsis* Alloiteau and Tessier, 1958; *Oryzotrochus* Wells, 1959; *Wellsotrochus* Squires, 1960

3′. Pali present 4

4. Only P2 present 5

4′. P1–2 present 6

4″. Pali before all but last cycle of septa (usually P1–3), but P1–2 suppressed in adult *Notocyathus* ... 8

5. P2 fused to columella, obscure; corallum bowl-shaped with rounded base ....*Kionotrochus* Dennant, 1906

5′. P2 independent and prominent; corallum conical with pointed base .... *Cryptotrochus,* n. gen.

6. Septa correspond to costae; transverse division lacking ....+*Coronocyathus* Alloiteau and Tessier, 1958

6′. Septa alternate with costae; transverse division present 7

7. Corallum discoidal; pali in one crown of 12 elements; columella spongy .... *Dunocyathus* Tenison-Woods, 1878

7′. Corallum cuneiform; pali in 2 crowns of 10–12 elements; columella papillose .... *Idiotrochus* Wells, 1936

8. Eighteen primary septa ....+*Monticyathus* Alloiteau and Tessier, 1958

8′. Typical hexameral symmetry (S1≥S2>S3>S4) 9

9. P3 fused to one another in V-shaped pairs; P2 usually suppressed in adult; septa independent; corallum conical, with pointed base .... *Notocyathus* Tenison-Woods, 1880

9′. P3 fused to intermediate P2; P2 well developed; higher cycle septa fuse with lower cycle septa; corallum of variable shape, but never with a pointed base 10

10. Corallum relatively large (adult calicular diameter over 10 mm), cuneiform; P1 well developed .. *Tropidocyathus* Milne Edwards and Haime, 1848

10′. Corallum small (adult calicular diameter less than 8 mm) and of variable shape (e.g., cylindrical, hemispherical); P1 often poorly developed .... *Peponocyathus* Gravier, 1915 (=*Cylindrophyllia* Yabe and Eguchi, 1937)

Cryptotrochus carolinensis, new species

Figs. 1–9

Types.—Holotype: *Gosnold* sta. 1811, USNM 46914.—Paratypes: *Gosnold* sta. 1811 (8) USNM 46915; *Gosnold* sta. 1841 (1) USNM 81082, 33°38.5′N, 76°29.3′W, 338 m. Type locality: *Gosnold* sta. 1811: 33°00.5′N, 77°16.2′W (off Cape Fear, North Carolina), 320 m.

Description.—Corallum conical, with pointed basal angle of 55°–65°, the corallum becoming cylindrical at height of about 5.5 mm. No evidence of asexual regeneration from basal fragments. Largest specimen (holotype) 6.4 mm in calicular diameter and 7.7 mm tall; calice circular. C1–2 measures 0.16–0.17 mm wide at calicular edge; C3–4 narrower, about 0.10 mm wide. Costae separated by intercostal furrows 0.17–0.21 mm wide and about 0.55 mm deep at calicular edge. Each costa bears a unilinear row of outward projecting triangular teeth, each about 0.14 mm in basal width and height, producing a serrate costal edge. Smaller cylindrical granules, 0.09 mm tall and 0.045 mm in diameter, adorn the lateral edges of costae. Costae arranged in typical turbinoliid fashion (Fig. 2): 12 C1–2 originate at the base, each C2 bifurcating into 2 C3 very close to the base (0.3 mm from epicenter), and each C3 bifurcating into 2 C4 about 1.5 mm from base epicenter, the original C2–3 continuing beyond points of bifurcation. At level of C3–4 bifurcation, the 12 C1–2 abruptly decrease in width to accommodate the doubled number of costae. Theca about 0.15 mm thick; corallum white.

Septa hexamerally arranged in 4 cycles according to the septal formula: $S1 > S2 \geq S3 > S4$. S1 highly exsert (up to 1.4 mm) and extend about 0.8 distance to columella. S1–3 have straight, vertical inner edges and rounded upper edges. S2 less exsert (about 1.1 mm) and extend slightly over ½ distance to columella. Each S2 bordered internally by a large, flat palus (P2), each about 0.60 mm deep and 0.3 mm thick. S3 slightly less exsert than S2 but extend an equal distance to columella, at which point their lower inner edges create a porous fusion with the P2. S4 slightly less exsert than S3 and extend toward columella only about ⅓ the distance, at which point their entire inner edges create a porous fusion with the adjacent S3. Septal faces covered by low (about 0.07 mm tall) triangular granules aligned in rows perpendicular to septal edges (Figs. 7–9). Granulation of pali coarser, with blunt granules up to 0.15 mm tall.

Fossa very shallow to nonextant, containing the 6 P2 and columella. Rounded upper edges of P2 extend above calicular edge but below the upper edges of the S4; inner edges of pali fused to columella. Columella composed of 7–9 tuberculate papillae, fused among themselves and to surrounding pali. Upper edges of columellar papillae stand above upper edges of pali, equally as high as the S4. Pali and columellar elements morphologically discrete.

Discussion.—C. carolinensis is distinguished from *C. javanus,* the only other species in the genus, by three characters: 1) the inner edges of the higher-cycle septa of *C. carolinensis* are fused to the lower-cycle septa or pali (S4 to S3, S3 to P2); septa of *C. javanus* are independent, 2) its costae bear a uniserial row of spines; costae of *C. javanus* bear up to three rows of granules per costa at the calicular margin, and 3) its pali have rounded upper edges that do not rise above the level of the columella; the pali of *C. javanus* have slender, pointed upper edges that rise well above the columella.

Etymology.—This species is named *carolinensis* for North Carolina, its type-locality.

Distribution.—Known only from off Cape Fear, North Carolina, 320–338 m.

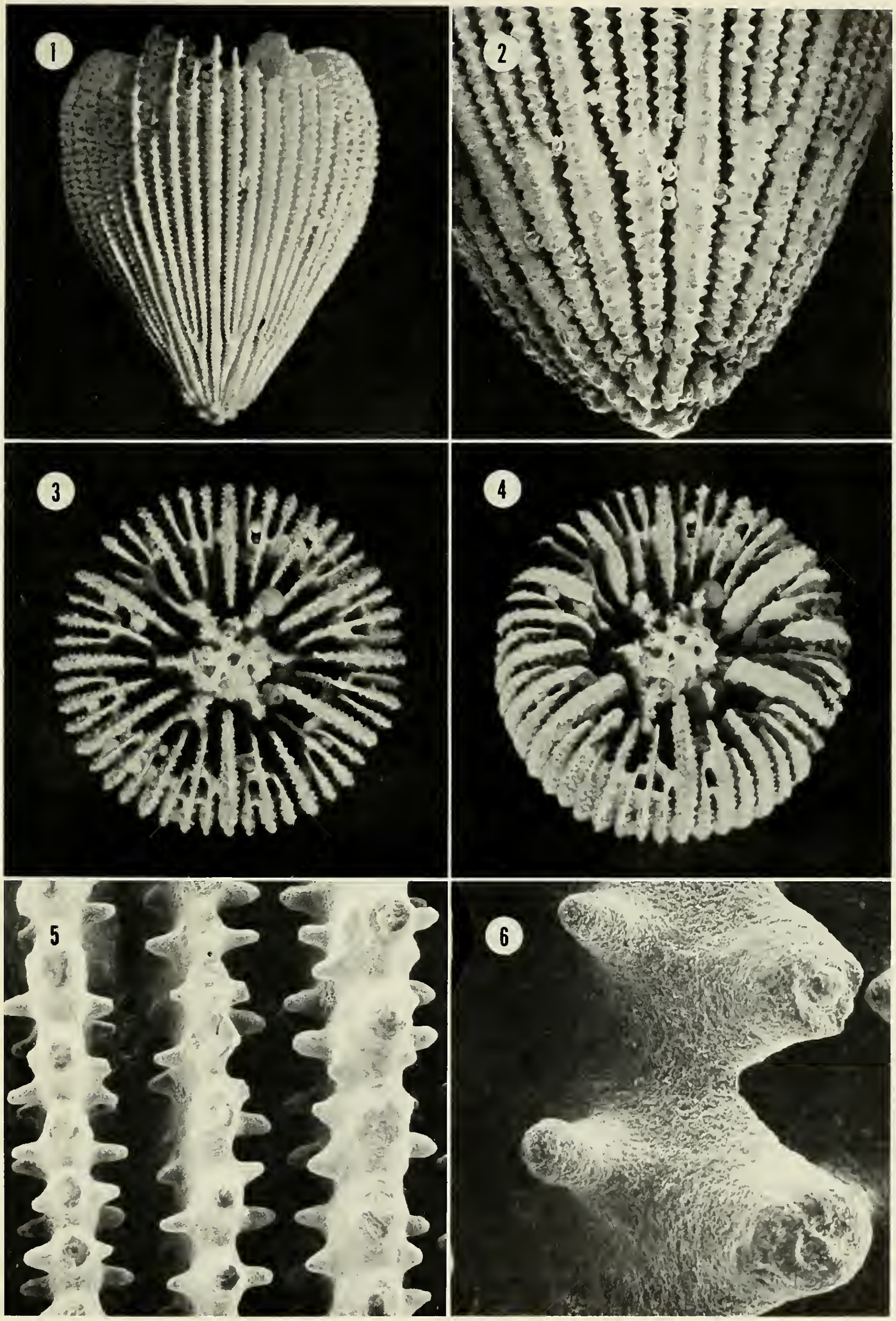
Cryptotrochus javanus, new species

Figs. 10–12

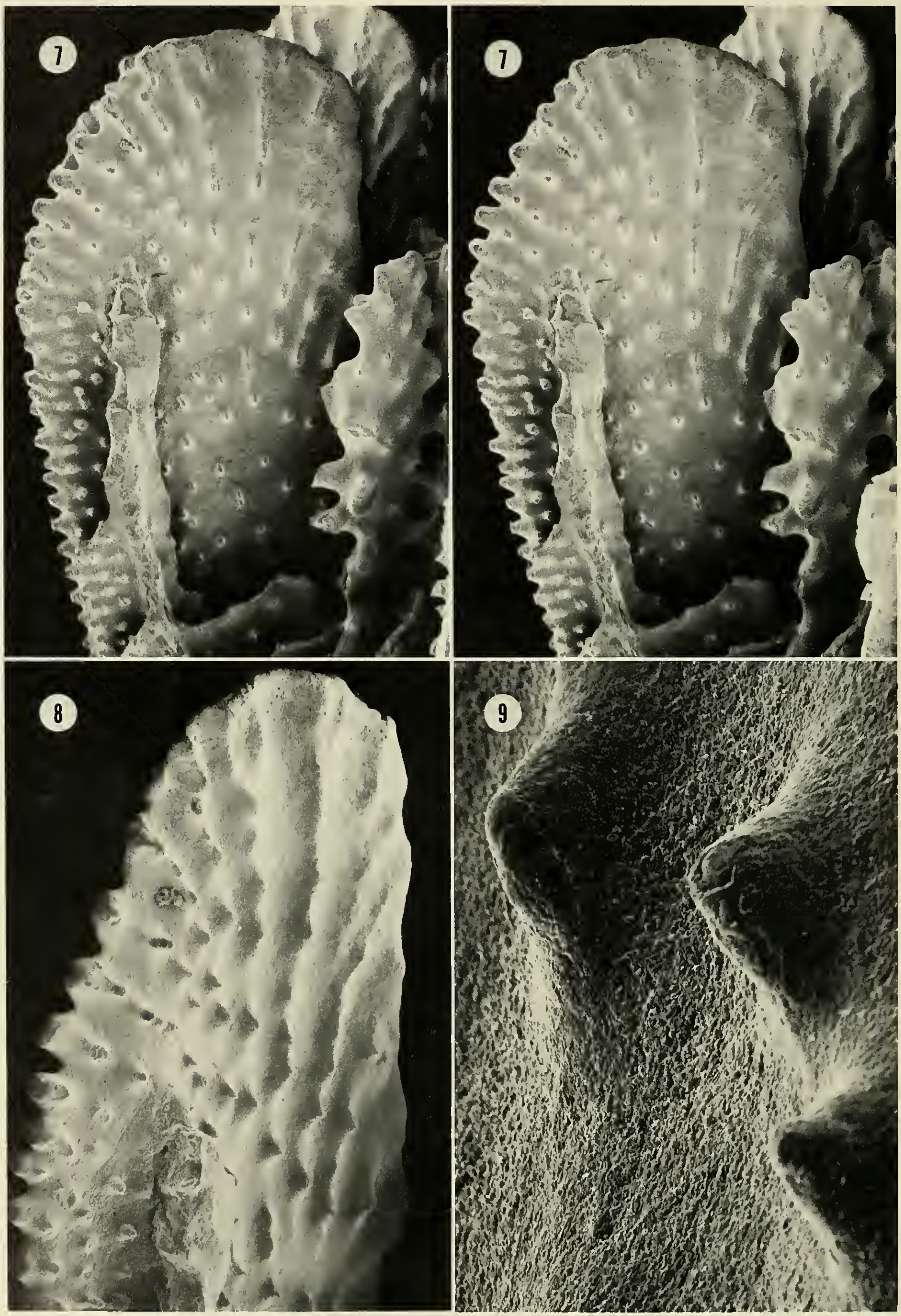
Types.—Holotype: *Galathea* sta. 490, Zoologisk Museum, Copenhagen.—Paratype: *Galathea* sta. 490 (1) Zoologisk Museum, Copenhagen. Type locality: 5°25'S, 117°03'E (eastern Java Sea), 585 m.

Description.—Corallum conical, with a pointed basal angle of 75°, the corallum becoming cylindrical at a height of about 6.0 mm. No evidence of asexual regeneration from basal fragments. Holotype 9.2 mm in calicular diameter and 10.0 mm tall; calice circular. Costae equal in width near calicular edge, about 0.32 mm wide, separated by deep intercostal furrows about 0.18 mm wide and 0.60 mm deep. Basally, each costa bears one row of coarse teeth; several mm from the base epicenter, each costa bears 2 rows of teeth; and near the calicular edge, the C1–2 each bear 3 rows of outward-projecting coarse teeth. Costal arrangement identical to that of *C. carolinensis.* Corallum white.

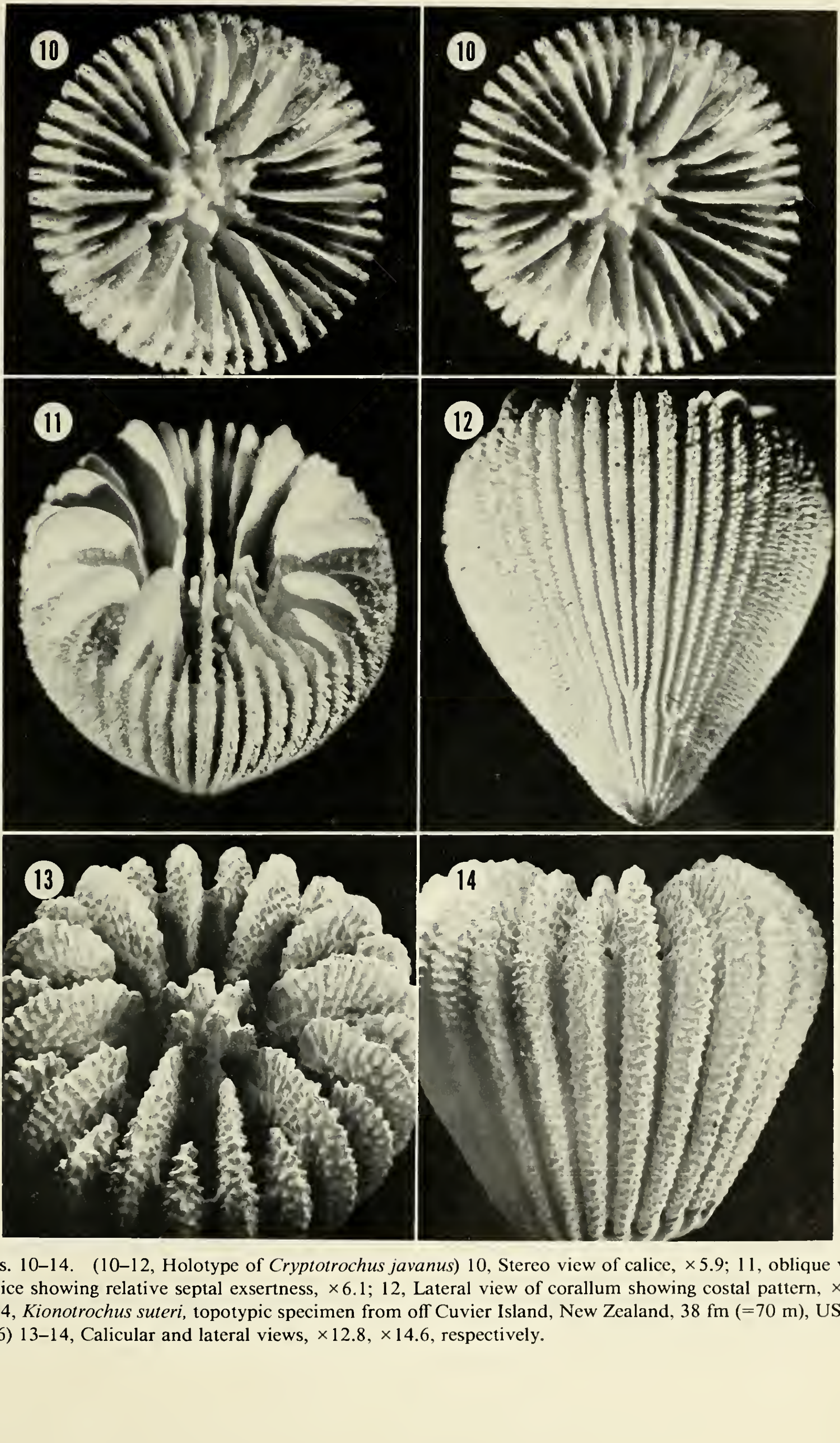
Septa hexamerally arranged in 4 cycles according to the formula: $S1 > S2 > S3 > S4$. S1 highly exsert (up to 1.5 mm) and extend about 0.8 distance to columella. S1–2 have straight, vertical inner edges and rounded upper edges. S2 slightly less exsert and extend about 0.7 distance to columella. Each S2 bordered internally by a tall, flattened,



Figs. 1–6. *Cryptotrochus carolinensis* (1, 3–4, Holotype, USNM 46914; 2, 5–6, Paratype from *Gosnold* sta. 1811, USNM 46915): 1, Lateral view of holotype, ×7.1; 2, Corallum base showing typical costal bifurcations, ×18; 3–4, Calicular views of holotype, ×7.8; 5–6, Costae, showing large triangular outward projecting teeth and smaller cylindrical lateral granules, ×56, ×202, respectively.



Figs. 7–9. *Cryptotrochus carolinensis,* paratype from *Gosnold* sta. 1811, USNM 46915: 7, Stereo view of broken corallum exposing septocostal face, aligned septal granules, palus, and cross section of theca, ×20; 8, Oblique view of septocostal face, ×34; 9, Enlargement of septal granules, ×260.



Figs. 10–14. (10–12, Holotype of *Cryptotrochus javanus*) 10, Stereo view of calice, ×5.9; 11, oblique view of calice showing relative septal exsertness, ×6.1; 12, Lateral view of corallum showing costal pattern, ×6.6. (13–14, *Kionotrochus suteri*, topotypic specimen from off Cuvier Island, New Zealand, 38 fm (=70 m), USNM 78586) 13–14, Calicular and lateral views, ×12.8, ×14.6, respectively.

sharp palus (P2) having a vertical inner edge. S3 less exsert than S2 and extend about 0.6 distance to columella; their inner edges are slightly sinuous and not fused to any other septa. S4 less exsert than S3 and extend about 0.3 distance to columella; their inner edges also free, not fused to adjacent septa. Upper septal faces smooth, without granulation, but lower septal faces sparsely covered by low pointed granules.

Fossa moderately deep, containing the 6 P2 and columella. Upper edges of pali extend just above calicular edge. Columella composed of 2 papillae, terminating below level of pali.

Discussion.—Comparisons to *C. carolinensis* are made in the account of that species.

Etymology.—This species is named *javanus* for the Java Sea, in reference to its type-locality.

Distribution.—Known only from the type-locality.

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SYRINGONOMUS DACTYLATUS, A NEW SPECIES OF BATHYAL MARINE NEMATODE (ENOPLIDA: LEPTOSOMATIDAE) AND A SUPPLEMENTARY DESCRIPTION OF *SYRINGONOMUS TYPICUS* HOPE AND MURPHY, 1969

W. Duane Hope

Abstract.—The taxonomic history of the genus *Syringonomus* is reviewed, and the genus is redefined. A supplementary description of the males of *Syringonomus typicus* is given, and *Syringonomus dactylatus* is described. The structure of the amphidial flap of the males is compared and contrasted between both species of *Syringonomus,* and between species of *Syringonomus, Platycoma* and *Proplatycoma.* The geographic distribution and ecology of *Syringonomus* is discussed and compared with that of *Platycoma* and *Proplatycoma.*

The genus *Syringonomus* has, until now, contained a single species, *S. typicus* Hope & Murphy, 1969. The description of the type species was based upon specimens collected in the North Atlantic at a depth of 3806 m, which remains the only record of its occurrence. The report that *S. typicus* had been collected from near Recife, Brazil (Bongers 1983:855) is based upon misidentified specimens of the new species, *Syringonomus dactylatus.*

Syringonomus was assigned by Hope & Murphy (1969) to the subfamily Leptosomatinae (Leptosomatidae). However, the sexually dimorphic males of *Syringonomus* are unique among members of this subfamily in that the neck is slightly narrowed and the cuticle is thickened between the amphid and cephalic sensilla. Also, the amphids were originally described as having the shape of an "inverted lyre," with a fringed border, and with or without a tapered process directed posteriorly from the center of the anterior edge of the lyre. An amphid by this description, in fact, is not known among other marine nematodes.

The males of *Syringonomus dactylatus,* which in other regards resemble the males of *S. typicus,* have a lobed flap, obvious even in light microscopic observations, that covers the amphidial aperture. This observation made it necessary to question the original interpretation of the amphid of *S. typicus.* Consequently, the amphid was studied with the SEM, and the results are included in the following supplementary description of the type species.

Materials and methods.–The original description of the males of *S. typicus* was based upon the holotype (USNM 39489) and three paratypes (USNM 39490–39492) (USNM = National Museum of Natural History). Of the three paratypes, one has been sectioned for histological examination, and another is a young male that was moulting when fixed and is in poor condition. Therefore, of the original type material, only the holotype (USNM 39489) and one paratype (USNM 39490) were used in this redescription of *S. typicus.* However, three additional males (USNM 77178–77180) have been included in this redescription. They were not part of the original type series, but were sorted, for the purposes of this study, from the same samples as those from which the type material had originally been obtained. One

Table 1.—Morphometric and meristic data for males of *Syringonomus typicus*.

USNM number	39489	39490	77178	77179	77180
Midbody diameter	83	95	—	77	100
Body width at base of esophagus	70	80	—	74	82
Body width at level of nerve ring	69	74	—	70	74
Head width at level of cephalic sensilla	32	30	22	33	28
Length of cephalic capsule on dorsal and ventral sides of head, d/v	5/3	5/4	—/—	6/5	3/2
Distance from oral surface to outer labial and cephalic sensilla	17	15	13	16	15
Length of outer labial sensilla	3,3,4,4	3,3	3,3,3,4	3,4,4,4,5	4,5
Length of cephalic sensilla	5,5,5	5,6	4,4,4,5	5,5,6,6	5,6
Number cervical sensilla anterior end to nerve ring; right/left	2/3	1/2	—/—	4/2	5/4
Length of amphidial flap, r/l	3/3	3/5	—/3	6/—	5/6
Anterior width of amphidial flap; r/l	7/7	7/7	—/4	5/—	5/5
Posterior width of amphidial flap; r/l	10/10	9/11	—/9	15/9	8/9
Length of amphidial lobes; r/l	5/5	6/5	5/4	—/3	5/6
Distance from oral surface to posterior margin of flap; r/l	27/31	27/31	—/24	32/30	32/31
Distance from oral surface to posterior end of amphidial gland (% of esophagus length); r/l	677/706 (92/96)	762/700 (107/98)	—/— —/—	840/849 (96/97)	800/792 (91/90)
Distance from oral surface to orifice of dorsal esophageal gland	43	31	—	39	34
Distance from oral surface to nerve ring	300	305	—	368	344
Length of esophagus	736	715	—	872	879
Position of testes relative to gut (v = ventral; l = left); anterior/posterior	v/l	v/l	—/—	l/l	v/l
Length of spicula; r/l	80/77	80/73	—/—	—/72	52/55
Length of lateral accessory component; r/l	14/13	—/—	—/—	15/16	11/13
Cloacal body diameter	79	83	—	88	85
Tail length	142	138	—	143	132

"—" indicates data that were not obtainable.

of these three topotype males (USNM 77178) was critical point dried for SEM by a method described elsewhere (Hope 1982: 2). The technique differs from the original in that a graded series of acetone was used for dehydration, and amyl acetate was excluded from the process. The specimen was precoated with carbon, coated with gold/palladium, and examined with an Hitachi S-570 scanning electron microscope.

The description of *S. dactylatus* is based upon specimens collected with an epibenthic sled at station 167, cruise 31 of *Atlantis II,* and donated to the National Museum of Natural History by the Woods Hole Oceanographic Institution.

All specimens of both species were fixed in 4% formalin in sea water. Those employed in light microscopic observations are mounted in anhydrous glycerin between coverslips on Cobb aluminum frames. Morphometric data were obtained by measurements from camera lucida drawings or electron micrographs. Morphometric and meristic data for each specimen of *S. typicus* are given in Table 1, and for each specimen of *S. dactylatus* in Table 2. In some cases, several data are given for one character, such as the length of each of several outer labial or cephalic sensilla, which are separated from one another by commas. The range, mean, and plus or minus one standard de-

Table 2.—Morphometric and meristic data for *Syringonomus dactylatus.*

	Males		Females		Juv
USNM number	77172	77173	77174	77175	77176
Midbody diameter	87	84	124	103	76
Body width at base of esophagus	78	79	88	82	68
Body width at level of nerve ring	70	77	70	73	59
Head width at level of cephalic sensilla	30	30	30	28	29
Length of cephalic capsule on dorsal and ventral sides of head, d/v	NA	—/3	6/4	6/5	4/5
Distance from oral surface to outer labial and cephalic sensilla	23	14	13	15	15
Length of outer labial sensilla	2,2,3,3,3	2,2,2,3	2,3,3	2,3,3,3	3,3
Length of outer cephalic sensilla	3,3,3	3,3,3,3	4,5,5	3,4,5	4,4,5
Number of cervical sensilla anterior end to nerve ring; right/left	5/3	3/4	5/3	6/5	7/6
Length of cervical sensilla	2,3	2,2	2,3,3,4	2,4	3,5
Length of amphidial flap; r/l	5/4	4/3	NA	NA	NA
Anterior width of amphidial flap; r/l	5/5	7/6	NA	NA	NA
Posterior width of amphidial flap; r/l	10/11	11/11	NA	NA	NA
Length of anterior amphidial lobes; r/l	8,8/8,8	8,8/8,8	NA	NA	NA
Length of dorsal amphidial lobes; r/l	9/9	8/6	NA	NA	NA
Length of ventral amphidial lobes; r/l	7/8	7/7	NA	NA	NA
Distance from oral surface to posterior margin of flap (males); to amphidial aperture (females); r/l	39/29	30/30	17/18	21/20	20
Distance from oral surface to posterior end of amphidial gland (% of esophagus length); r/l	846/884 (86/90)	707/740 (73/76)	NA	NA	NA
Distance from oral surface to orifice of dorsal esophageal gland	31	23	26	21	24
Distance from oral surface to nerve ring	331	333	295	307	235
Length of esophagus	988	970	851	943	673
Distance from oral surface to excretory pore	119	148	NA	NA	NA
Position of gonads relative to gut (r = right; v = ventral); anterior/posterior	v/r	r/r	v/v	v/v	NA
Length of spicula on arc; r/l	93/84	79/69	NA	NA	NA
Length of lateral accessory component; r/l	14/15	14/—	NA	NA	NA
Cloacal and anal body diameters	79	79	83	75	63
Tail length	121	123	120	103	82

NA indicates data that are not applicable; "—" indicates data that were not obtainable.

viation of the data are given in the text. The points between which the various measurements of the amphidial flaps and lobes were made is depicted in Fig. 1A and B.

Syringonomus Hope & Murphy, 1969

Syringonomus Hope & Murphy, 1969:511.

Type species.—*Syringonomus typicus* Hope & Murphy, 1969:512.

Emended diagnosis.—Leptosomatidae. Body elongate and spindle-shaped. Anterior end bluntly rounded. Neck slightly reduced in width at level of amphid, slightly tapered from amphid to level of cephalic sensilla, and head rounded anteriorly from level of cephalic sensilla. Tail bluntly conical. Cuticle with fine transverse striae, at least posterior to amphid. Cuticle of neck in males thickened between level of amphids and cephalic sensilla; not thickened in females. Cephalic capsule present or absent in males; present in females. Amphidial aperture of males wide, slit-like, and covered with lobed amphidial flap; cephalic cuticle fringed at edge of amphidial flap and outside edge of lobes. Amphid of females cyathiform with small, pore-like aperture; amphidial flap absent. Amphidial glands well developed in males, apparently absent in females. Lips short, flap-like, directed anteriorly and not set off by microlabial groove. Buccal capsule unarmed. Anterior end of esophagus attached to cephalic cuticle; cephalic cuticle at anterior end of esophagus not thickened. Oral aperture dilated by retrodilator muscles in anterior end of esophagus. Dorsal esophageal gland orifice in lumen of esophagus; subventral esophageal gland orifices apparently at anterior end of buccal capsule. Dorsolateral and ventrolateral orthometanemes present; some with, others without, caudal filaments. Spicula with paired, ventrolateral, accessory structures. Gubernaculum absent and ventromedian supplements absent. Caudal glands well developed, and extended anteriorly beyond level of cloacal and anal vents.

Syringonomus typicus Hope & Murphy, 1969

Figs. 1A; 2A–C

Nec *Syringonomus typicus* sensu Bongers, 1983:855.

Material examined.—

Holotype.—Male, USNM 39489.

Paratype.—Male, USNM 39490.

Topotypes.—Males, USNM 77178, 77179 and 77180.

Type locality.—Sediment from epibenthic trawl collected between 39°37.0′N, 66°47.0′W and 39°37.5′N, 66°44.0′W at 3806 m on 24 Aug 1966. Although males, USNM 77178 thru 77180 are not paratype specimens, they are from the type locality.

Supplementary description of males.—

	a	b	c	Total length
USNM 39489	65.9	7.3	37.9	5.377 mm
USNM 39490	65.3	8.7	44.9	6.206 mm
USNM 77179	89.4	7.8	47.9	6.844 mm
USNM 77180	58.2	6.6	44.1	5.824 mm

Body elongate, gradually tapered from midbody to level of nerve ring and anal vent. Midbody diameter 77–100 (89 ± 11) μm; body width at base of esophagus 70–82 (77 ± 5.5) μm, at level of nerve ring 69–74 (72 ± 2.6) μm, and at level of cephalic sensilla 22–33 (29 ± 4.4) μm. Cervical region slightly constricted at level of amphid, then slightly tapered to level of cephalic sensilla. Head (Fig. 2A) rounded anteriorly. Cuticle thickened at level of amphid. External surface of cuticle posteriorly from amphid with very shallow, transverse striae (Fig. 2A, C); periodicity of striae 300 nm. Cephalic capsule apparent when head viewed in optical sagittal section; length of cephalic capsule 3–6 (5 ± 1.3) and 2–5 (4 ± 1.3) μm on dorsal and ventral sides of head respectively.

Inner labial papilliform sensilla not observed. Head with single circle of 6 setiform, outer labial sensilla and 4 setiform cephalic sensilla (Fig. 2A), 13–17 (15.2 ± 1.5) μm from oral surface of head. Outer labial sensilla 3–5 (3.7 ± 0.7) μm long; cephalic sensilla 4–6 (5.1 ± 0.7) μm long. Cervical region between cephalic sensilla and nerve ring with 1–5 (3 ± 1.8) setiform sensilla on right side, and 2–4 (2.8 ± 1.0) on left; length of cervical sensilla ca. 4 μm.

Cuticle at posterior rim of amphidial aperture extended anteriorly, flap-like over aperture (Figs. 1A; 2A–C); anterior end of each flap with paired, anteriorly directed, finger-like lobes (Fig. 2A–C), tapered and rounded at tip. Length of flap (Fig. 1A) on right side of head 3–6 (4.3 ± 1.5) μm, and 3–6 (4.3 ± 1.5) on left. Width of anterior end of flap on right side of head 5–7 (6.0 ± 1.2), and on left side 4–7 (5.8 ± 1.5) μm; width at posterior end of flap on right side

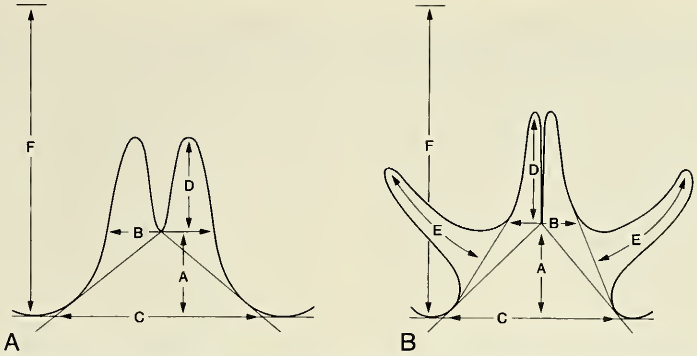

Fig. 1. Diagram showing location of measurements of the amphidial flap of 1A.) *Syringonomus typicus* and 1B.) *S. dactylatus* A. Length of flap. B. Minimum (anterior) width of flap. C. Maximum (posterior) width of flap. D. Length of central anteriorly directed lobes. E. Length of dorsal and ventral lobes. F. Distance from oral surface of head to posterior margin of flap.

of head 8–15 (10.5 ± 3.1), and on left 9–11 (9.6 ± 0.9) μm; length of lobes on right side of head 5–6 (5.3 ± 0.5), and on left 3–6 (4.9 ± 0.9) μm. Distance from oral surface of head to posterior margin of flap on right side of head 27–32 (29.5 ± 2.9), and on left 24–31 (29.4 ± 3.1) μm. Cephalic cuticle with fringed border (Fig. 2B) at edges of amphidial flaps and lobes. Amphidial glands well developed; distance from oral surface of head to posterior end of right amphidial gland (% of esophagus length) 677 (92%) to 840 (107%) (770 ± 70 μm; 97 ± 7%), and to posterior end of left amphidial gland 700 (90%) to 849 (98%) (762 ± 72 μm; 95 ± 4%). Edges of amphidial aperture dorsal and ventral from flap and lobes often with presumed secretion of amphidial gland (Fig. 2A, B).

Buccal aperture (Fig. 2C) triradiate and surrounded by 3 anteriorly directed, oral flaps (Fig. 2A, C). Anterior to posterior length of each flap greatest midway between corners of oral aperture; flaps not set off from head by groove. Buccal armature absent. Orifice of dorsal esophageal gland in cuticular wall of esophageal lumen 31–43 (37 ± 5.3) μm from oral surface of head. Subventral esophageal glands apparently with orifices at anterior end of buccal capsule.

Esophagus cylindrical, slightly narrower anteriorly; external surface of esophagus smooth. Distance from oral surface of head to anterior edge of nerve ring 300–368 (329 ± 33) μm. Length of esophagus 715–879 (801 ± 87) μm. Renette not observed.

Orthometanemes present at dorsal and ventral margins of lateral hypodermal chords; caudal filaments present in most metanemes, absent in others. Hypodermal glands absent.

Testes paired and opposed; testes on ventral or left side of gut. Spicula paired, curved ventrally; right spicula 52–80 (71 ± 16.2) and left 55–77 (70 ± 8.6) μm long, measured on arc; capitulum not distinct. Lateral accessory component at distal end of each spiculum; right accessory component 11–15 (13 ± 2.1) and left 13–16 (14 ± 1.7) μm long. Gubernaculum not apparent. Dorsoventral copulatory muscles on each side of body separated from one another. Precaudal, subventral, setiform sensilla present; not distinguishable from somatic setae. Ventromedian supplement absent.

Tail bluntly conical, 132–143 (139 ± 5) μm long, with subdorsal and subventral setiform sensilla. Cloacal body diameter 79–88 (84 ± 3.9). Cuticle of tail terminus with median, crescent-shaped lamella penetrated by spinneret. Cell bodies of each of 3 caudal glands extend anteriorly beyond cloacal vent.

Syringonomus dactylatus, new species
Figs. 1B; 3A–C; 4A, B

Syringonomus typicus sensu Bongers, 1983: 855.

Material examined.—

Holotype.—Male, USNM 77172.

Paratypes.—Male, USNM 77173; females USNM 77174 and 77175; juvenile USNM 77176.

Type locality.—Approximately 52 km off coast of Recife, Brazil, 7°58.0′–7°50.0′S; 34°17.0′W at a depth of 943–1007 m. Collected 20 Feb 1967.

Description.—

Males.–

	a	b	c	Total length
USNM 77172	76.3	6.7	54.3	6.613 mm
USNM 77173	78.1	6.7	53.1	6.528 mm

Body elongate, slightly tapered from midbody to level of nerve ring and anal vent. Midbody diameter 84–87 (85.5 ± 2.1) μm; body width at base of esophagus 78–79 (78.5 ± 0.7) μm, at level of nerve ring 70–77 (73.5 ± 4.9) μm, and at level of cephalic sensilla 30 μm in both specimens. Neck region (Fig. 3A) slightly constricted and cuticle thickened between level of amphid and cephalic sensilla. Thickness of cuticle posterior to amphids 4 μm, and between amphid and cephalic sensilla 7 μm in both specimens. Head rounded anteriorly. Cuticle posterior from head with fine transverse striae; periodicity of striae ca. 550 μm. Cephalic capsule absent in holotype (Fig. 3A), apparent only on ventral side in optical sagittal section of male paratype; length 3 μm.

Papilliform, inner labial sensilla not observed. Outer labial sensilla and cephalic sensilla setiform (Fig. 3A) and in single circle of ten, 14–23 (18.5 ± 6.4) μm from oral surface. Outer labial sensilla 2–3 (2.4 ± 0.5) μm long; all cephalic sensilla in both specimens 3 μm long. Cervical region between amphid and nerve ring with 3–5 setiform, sensory sensilla on right side of body, and 3–4 on left (3.8 ± 1.0); length of cervical sensilla 2–3 (2.3 ± 0.5) μm.

Cuticle at posterior rim of amphidial aperture extended anteriorly, flap-like over aperture; amphidial flap (Figs. 1B; 3A) with 2 central, anteriorly directed lobes and 1 dorsal and 1 ventral lobe; dorsal and ventral lobes directed obliquely towards anterior; all lobes tapered slightly and distally rounded. Edge of aperture extended dorsally and ventrally beyond posterior end of flap. Cephalic cuticle apparently with fringe at edge of flap and lobes. Length of flap (Fig. 1B) 4–5 (4.5 ± 0.7) μm on right side of head and 3–4 (3.5 ± 0.7) μm on left; width of posterior end of flap 10–11 (10.5 ± 0.7) μm on right, and 11 μm on left in both specimens; width at anterior end of flap 5–7 (6 ± 1.4) μm on right and 5–6 (5.5 ± 0.7) μm on left; length of anterior lobes 8 μm on both sides of both specimens; length of dorsal lobes 8–9 (8.5 ± 0.7) on right side and 6–9 (7.5 ± 2.1) μm on left side; and length of ventral lobes 7 μm on both specimens on right side and 7–8 (7.5 ± 0.7) μm on left side. Distance from oral surface of head to posterior margin of flap 30–39 (34.5 ± 6.4) μm on right side, and 29–30 (29.5 ± 0.7) μm on left side. Amphidial glands (Fig. 4A) well developed; distance from oral surface of head to posterior end of gland (in μm and % of esophagus length) on right side 707 (73%) to 846 μm (86%) (777 ± 98 μm; 80 ± 9%) and on left 740 (76%) to 884 μm (90%) (812 ± 102 μm; 83 ± 10%).

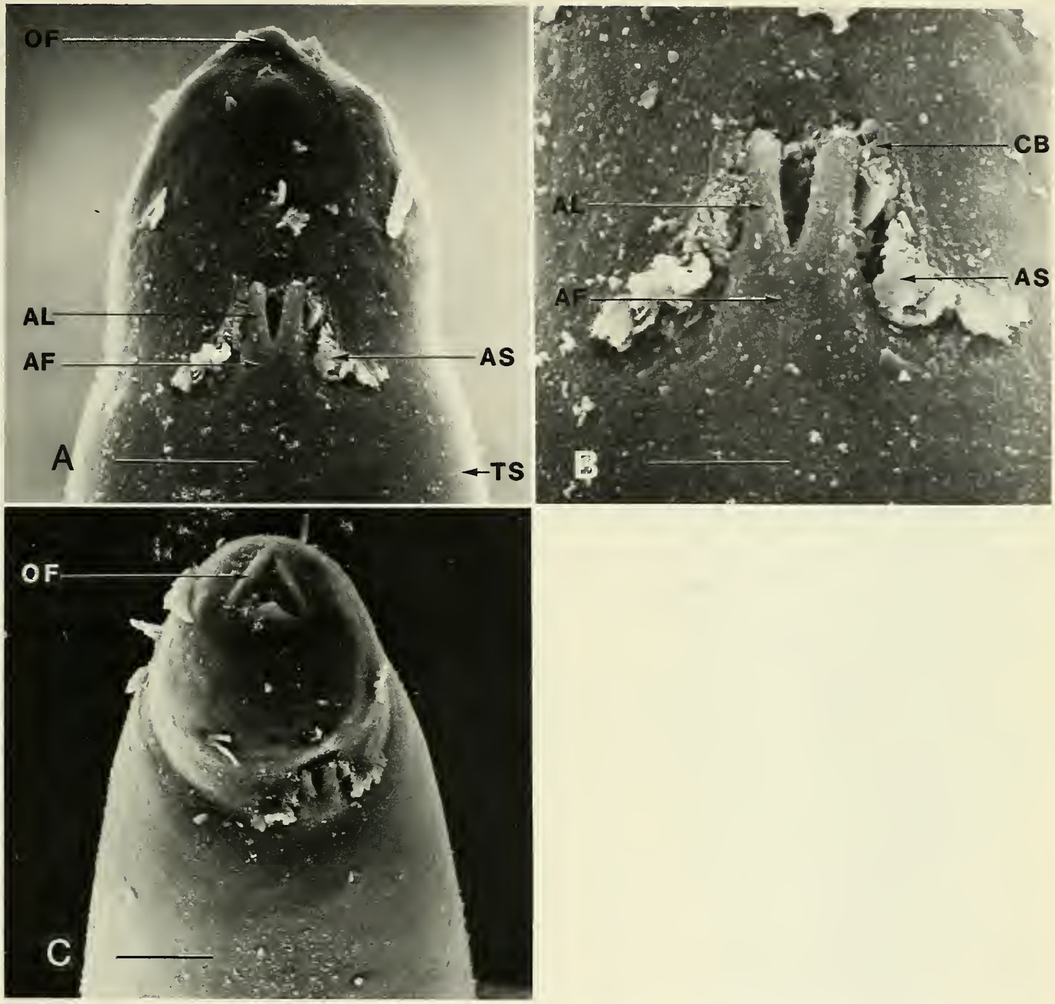

Fig. 2. *Syringonomus typicus.* Scanning electron micrographs of male topotype, USNM 77178. A. Left side of head; scale equals 10 μm. B. Left amphidial flap; scale equals 5 μm. C. Anterior view of head and left side of cervical region; scale equals 10 μm. Abbreviations.—AF, amphidial flap; AL, amphidial lobe; AS, amphidial secretion; CB, fringed border of amphidial aperture; OF, oral flap; TS, transverse striae.

Buccal aperture triradiate; microlabia or oral flaps not evident in light microscopic observations (Fig. 3A). Buccal capsule triradiate and dilated by 3 obliquely oriented, labial retrodilator muscles (Fig. 3A), one in each sector of esophagus. Buccal armature absent. Orifice of dorsal esophageal gland (Fig. 3A) in lumen of esophagus 23–31 (27 ± 5.7) μm from oral surface of head. Subventral esophageal glands (Fig. 3A) apparently with orifices at anterior end of buccal capsule.

Esophagus cylindrical, slightly narrower anteriorly; exterior surface of esophagus smooth. Distance from oral surface of head to anterior edge of nerve ring 331–333 (332 ± 1) μm. Length of esophagus 970–988 (979 ± 13) μm. Renette present and excretory pore 119–148 (134 ± 20.5) μm from oral surface of head.

Dorso- and ventrolateral orthometanemes present; some with caudal filaments, others without. Hypodermal gland cells absent.

Testes paired and opposed; testes on ventral or right of gut. Seminal vesicle straight without convolutions. Spicula (Fig. 3B) paired, curved ventrally; right spicula 79–93 (86 ± 10) and left 69–84 (77 ± 11) μm long, measured on arc; capitulum well developed. Lateral accessory component (Fig. 3B) at distal end of each spiculum; right accessory component 14 μm long on both specimens, and left 15 μm on only specimen measured; distal end thick-walled and narrow; proximal end thin-walled and slightly flared. Gubernaculum not apparent. Dorsoventral copulatory muscles on each side of body (Fig. 3B) separated.

Precaudal, subventral, setiform sensilla present (Fig. 3B); not distinguishable from other somatic setae. Length of setiform supplements 1 to 3 μm on both specimens. Ventromedian supplement absent.

Tail (Fig. 3B) bluntly conical, 121–123 (122 ± 1) μm long, with dorsolateral, subventral and subterminal setiform sensilla. Cloacal body diameter 79 μm in both specimens. Cuticle on ventral surface of tail of holotype, 85 μm posterior from anal vent, penetrated by hypodermis without evidence of setae or glands (Fig. 3B); not observed in paratype. Cuticle of tail terminus (Fig. 3B) with median, crescent-shaped lamella penetrated by spinneret. Cell bodies of each of 3 caudal glands extend anteriorly beyond cloacal vent (Fig. 3B).

Females.—

	a	b	c	V	Body length
USNM 77174	42	6	43	62%	5.156 mm
USNM 77175	56	6	56	64%	5.791 mm

Midbody diameter 103–124 (114 ± 15) μm; body width at base of esophagus 82–88 (85 ± 4) μm, at level of nerve ring 70–73 (71.5 ± 2) μm, and at level of cephalic sensilla 28–30 (29 ± 1) μm. Neck region uniformly tapered; head region (Fig. 3C) slightly constricted at level of amphid, but cuticle not thickened. Head rounded anteriorly (Fig. 3C). Striae of cuticle shallow, periodicity ca. 550 nm. Cephalic capsule (Fig. 3C) apparent only in optical sagittal section of head; length of cephalic capsule on dorsal side of head 6 μm in both specimens, and length on ventral side 4–5 (4.5 ± 0.7) μm.

Papilliform, inner labial sensilla not observed. Six outer labial and 4 cephalic setiform sensilla in single circle of ten (Fig. 3C), 13 to 15 (14 ± 1.4) μm from oral surface of head. Outer labial sensilla 2–3 (2.7 ± 0.5) μm long; cephalic sensilla 3–5 (4.3 ± 0.8) μm long. Cervical region (Fig. 4A) between amphid and nerve ring with 5 or 6 setiform sensilla on right side of body and with 3–5 (4 ± 1.4) on left; length of cervical sensilla 2–4 (3 ± 0.9) μm. Amphid (Fig. 3C) cyathiform with pore-like aperture 17–21 (19 ± 2.8) μm from oral surface on right side of head, and 18–20 (19 ± 1.4) μm on left side. Amphidial flap absent; amphidial glands not evident.

Buccal cavity and anterior end of esophagus as in males. Distance from oral surface of head to orifice of dorsal esophageal gland duct (Fig. 3C) 21–26 (23.5 ± 3.5) μm; to anterior edge of nerve ring 295–307 (301 ± 8.5) μm. Length of esophagus 851–943 (897 ± 65) μm. Renette not observed.

Somatic sensilla uncommon between level of nerve ring and near level of cloacal vent. Dorso- and ventrolateral orthometanemes present; some with caudal filaments, others without. Hypodermal gland cells absent.

Gonoducts opposed and ovaries antidromus. Anterior and posterior gonads ventral to gut in both specimens; both ovaries on right side of oviduct in both specimens. Tail (Fig. 4B) bluntly conical, 103–120 (112 ± 12) μm long. Anal body diameter 75–83 (79 ± 5.7) μm. Cuticle of tail terminus with median, crescent-shaped lamella penetrated

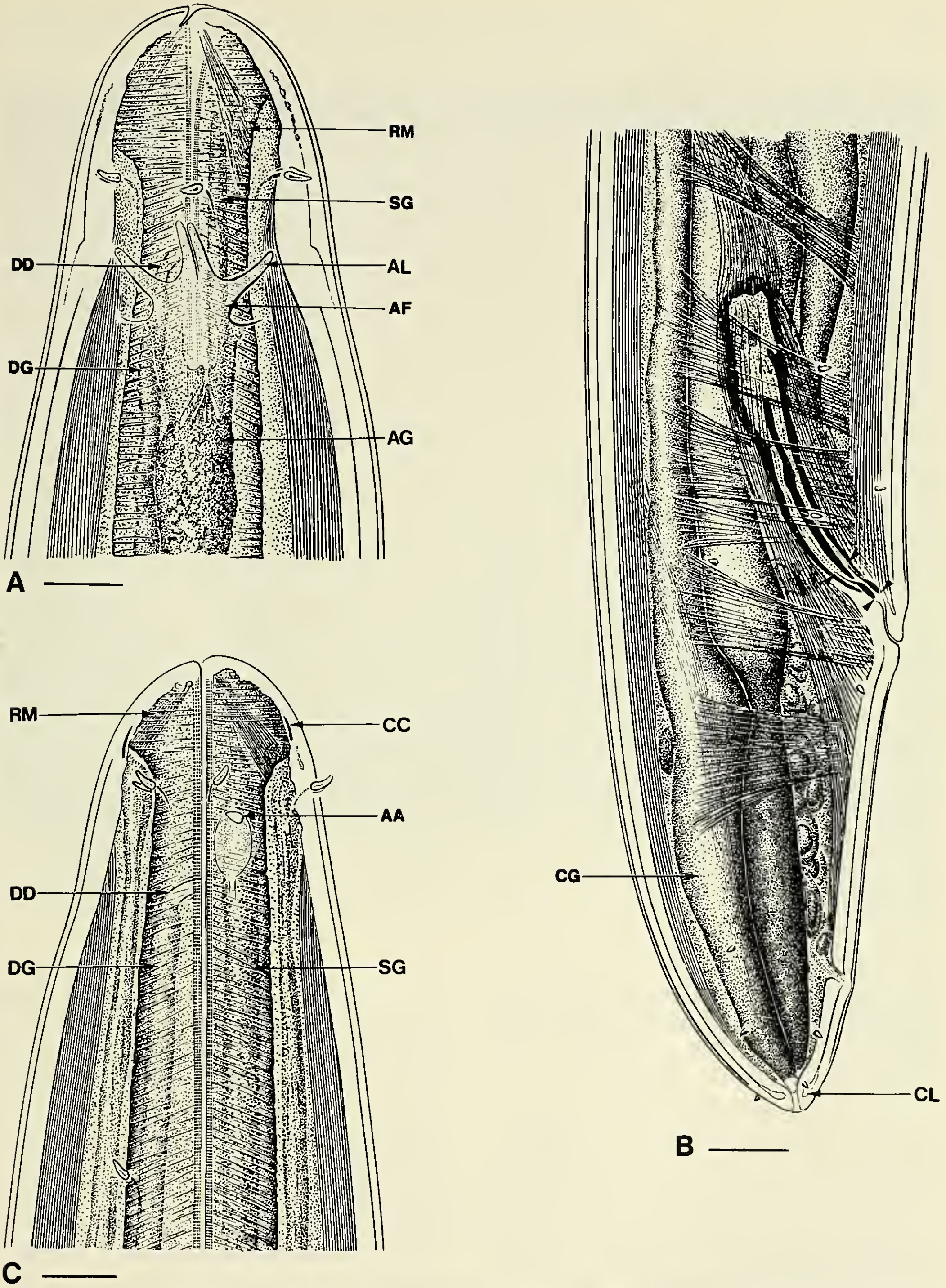

Fig. 3. *Syringonomus dactylatus.* A. Illustrated lateral view of the head of the holotype, USNM 77172; scale equals 10 μm. B. Illustrated lateral view of the tail of the holotype, USNM 77172; lateral accessory component is situated between 4 arrow heads at distal end of spiculum; scale equals 20 μm. C. Illustrated lateral view of the head of the female paratype USNM 77175; scale equals 10 μm. Abbreviations.—AA, amphidial aperture; AF, amphidial flap; AG, amphidial gland; AL, amphidial lobe; CC, cephalic capsule; CG, caudal gland; CL, crescent-shaped layer of cuticle; DD, duct of dorsal esophageal gland; DG, dorsal esophageal gland; RM, retrodilator muscle; SG, subventral esophageal gland.

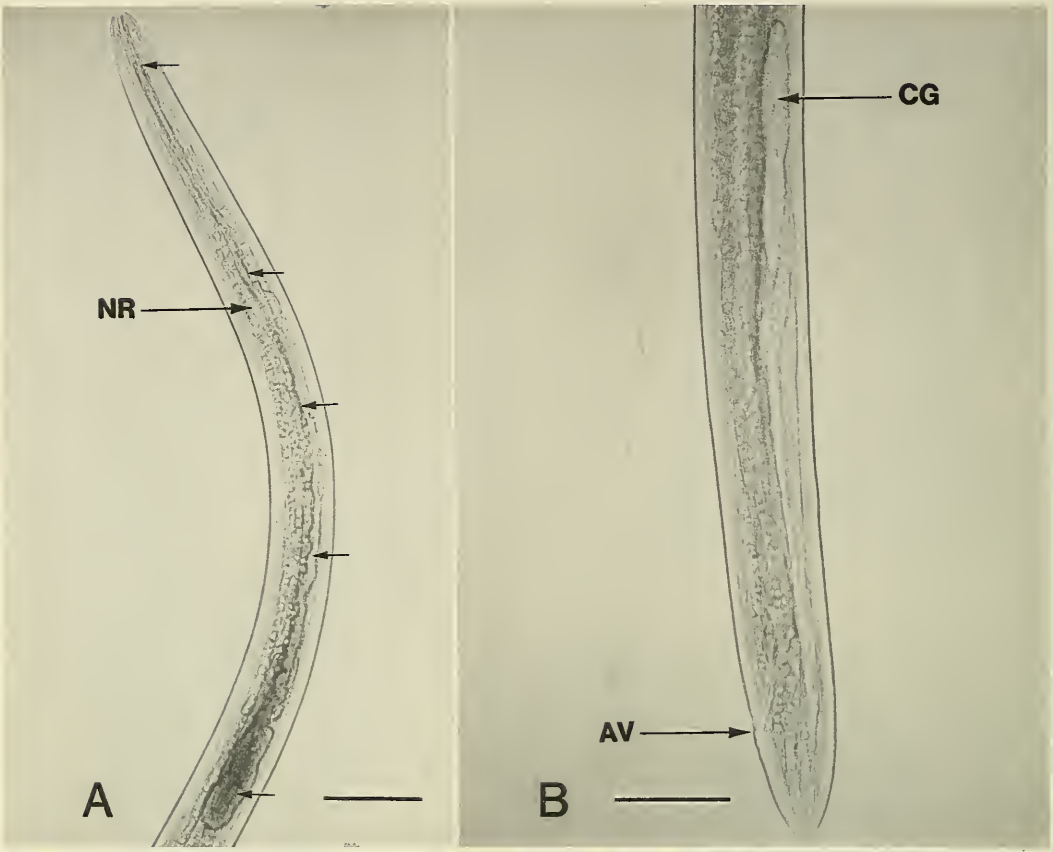

Fig. 4. *Syringonomus dactylatus.* A. Photomicrograph of the cervical region of the holotype, USNM 77172; unlabeled arrows point to amphidial gland; scale equals 100μm. B. Photomicrograph of the posterior body region and tail of the paratype USNM 77175; scale equals 100 μm. Abbreviations.—AV, anal vent; CG, caudal gland; NR, nerve ring.

by spinneret. Cell bodies of each of 3 caudal glands (Fig. 4B) extend anterior beyond anal vent.

Juvenile.—

	a	b	c	Body length
USNM 77176	52	6	49	3.984 mm

Midbody diameter 76 μm; body width at base of esophagus 68 μm, at level of nerve ring 59 μm, and at level of cephalic sensilla 29 μm. Neck region uniformly tapered; head region not constricted nor cuticle thickened at level of amphid. Cuticle with fine transverse striae; periodicity of striae ca. 500 nm. Cephalic capsule apparent on dorsal and ventral sides of head in optical sagittal section; length of cephalic capsule on dorsal side 4 μm and on ventral side 5 μm.

Papilliform, inner labial sensilla not observed. Six outer labial and 4 cephalic setiform sensilla in single circle of ten, 15 μm from oral surface of head. Outer labial sensilla 3 μm long; cephalic sensilla 4 to 5 (4.5 ± 0.7) μm long. Right cervical region between amphid and nerve ring with 7 setiform sensilla, and left with 6; cervical sensilla 3 to 5 (4 ± 1.4) μm long. Amphid cyathiform with pore-like aperture, 20 μm posterior from oral surface of head; amphidial flap absent. Amphidial glands not observed.

Buccal cavity and anterior end of esophagus as in adults. Distance from oral surface of head to orifice of dorsal esophageal gland duct 24 μm; to anterior edge of nerve ring 235 μm; to posterior end of esophagus 673 μm. Renette not observed.

Dorso- and ventrolateral orthometanemes present, with and without caudal filaments. Hypodermal gland cells absent. Tail bluntly conical, 82 μm long. Anal body diameter 63 μm. Cuticle of tail terminus with median, crescent-shaped lamella penetrated by spinneret. Cell bodies of each of 3 caudal glands extend anterior beyond anal vent.

Diagnosis.—The males of *S. dactylatus* may be distinguished from the males of the only other species of the genus, *S. typicus,* by the presence of a dorsal and a ventral lobe on each amphidial flap.

The females of *S. dactylatus* have a body length of 5.156–5.791 (5.474 ± 0.449) mm and the esophagus is 851–943 (897 ± 65) μm. The corresponding values for females of *S. typicus* are 3.320–4.940 (4.230 ± 0.510) mm and 556–717 (664 ± 45) μm. Although these values are likely to overlap if obtained from larger populations, they are the only characters known at present by which the females may be distinguished from one another.

Etymology.—The specific epithet is Greek, masculine gender, for finger, referring to the finger-like processes of the amphidial flap.

Discussion.—As noted in the introduction of this work, it is stated in the original description of *S. typicus* that the amphid has the shape of an inverted lyre, with or without a posteriorly directed central process. It is apparent from the present study that the inverted lyre corresponds to the outline of the paired lobes of the flap, and the posteriorly directed process corresponds to the space between the lobes when they are separated. The "process" is obscure when the lobes are together. Thus, the description of an inverted lyre-shaped structure was a misinterpretation of what has been demonstrated in this study to be a bilobed amphidial flap.

The misinterpretation of the amphidial flap in the original description had made it difficult to relate the structure of the amphid to that of any other taxon, especially in Leptosomatidae. From the new interpretation, it is apparent that the amphidial flaps of the males of *Syringonomus* resemble those found in males of *Platycoma* and *Proplatycoma,* (Platycominae: Leptosomatidae) in position, presence of lobes, and in that they occur in males only. In particular, the amphidial flap in males of *S. typicus,* with its paired, anteriorly directed lobes, is similar to the amphidial flap in the males of *Platycoma cephalata* Cobb, 1894. Also, the amphidial flaps of males of *S. dactylatus* are similar to those of *Proplatycoma sudafricana* Inglis, 1966 and *P. fleurdelis* Hope, 1988 in having unbranched dorsal and ventral lobes in addition to those that are central.

There are obvious differences as well. The ends of the dorsal and ventral lobes of the flaps of *P. sudafricana* and *P. fleurdelis* are directed posteriorly, whereas they are directed anteriorly in the case of *S. dactylatus.* Also, each flap in the males of each species of *Proplatycoma* has a single, anteriorly directed, central lobe, instead of the paired, central lobes that occur in the males of both species of *Syringonomus* and males of *Platycoma cephalata.* Another difference apparent from the SEM observations of *S. typicus* and *P. fleurdelis* is that the lobes of flaps in the former species have electron reflective qualities similar to those of the surrounding cephalic and cervical cuticle. By contrast, the lobes in males of *P. fleurdelis* are more electron reflective than is the cuticle of the surrounding head and neck regions (Hope 1988). Finally, there is no evidence that the amphidial flaps are framed by a fringe on the cephalic cuticle, as is the case in the males of both species of *Syringonomus.*

For obvious phylogenetic reasons, it is important to determine if the amphidial flap of *Syringonomus* is homologous with that of *Platycoma* and *Proplatycoma.* Its similarity among all three genera in position, general structure, and occurrence in males only is convincing evidence that they are homologous. The differences concerned with the number, position and shape of the lobes of the amphidial flaps within *Proplatycoma,* or between *P. cephalata* on the one hand and *Proplatycoma* on the other, are similar to the differences between either genus and *Syringonomus.* Therefore, differences of this nature are not regarded as evidence against homology. The fringe bordering the amphidial flap in males of both species of *Syringonomus* is a feature of the adjacent cuticle of the neck region, and so is not concerned with the question of the homology of the flap itself. Finally, because a difference in electron reflective properties has been observed between males of *S. typicus* and males of *P. fleurdelis* only, it is at best a weak argument against homology. Therefore, it is concluded from the available evidence that the amphidial flap of *Platycoma, Proplatycoma,* and *Syringonomus* are homologous.

A lobed amphidial flap is not known to occur in any other taxon within the Order Enoplida, and so it is interpreted to be an apomorphic character within the family Leptosomatidae. By this character, it is assumed that *Platycoma, Proplatycoma,* and *Syringonomus* share a common ancestor not known to be shared by any other taxon. Males of *Proplatycoma fleurdelis* Hope, 1988, *P. sudafricana* Inglis, 1966, and both species of *Syringonomus* have prominent amphidial glands that extend to near the posterior end of the esophagus. According to Bongers (1983), the amphidial glands are enlarged in males of *Leptosomatum,* and it may be that this is a unique (synapomorphic) character state indicative of a monophyletic relationship among the genera that share this character. However, taxonomic changes are deferred until after a more exhaustive morphological and phylogenetic analysis of Leptosomatidae.

Distribution and ecology.—The localities from which specimens of *S. typicus* and *S. dactylatus* have been collected are limited to their respective type localities. Therefore, representatives of this genus are at this time known to inhabit only the western North and South Atlantic, although members of the former species were collected at temperate latitudes, whereas specimens of the latter were collected at tropical latitudes. This is in contrast to the much wider distribution known for representatives of the genera *Platycoma* and *Proplatycoma* (Hope 1988). However, the apparently limited geographic distribution for the genus *Syringonomus* in comparison to *Platycoma* and *Proplatycoma* is likely to be a function of the relatively inaccessible depths inhabited by representatives of the genus *Syringonomus.*

All known specimens of *S. typicus* have been collected at 3806 m, and *S. dactylatus* at 943–1007 m. This is in contrast to all nominal species of *Proplatycoma* whose known depth distributions do not extend below the intertidal zone, and the maximum known depth for *Platycoma cephalata* Cobb, 1894, the only nominal species of the genus, is 44 m (Hope 1988). Therefore, from available data it appears that the species of *Platycoma* and *Proplatycoma* are limited to very shallow depths, whereas known species of *Syringonomus* are inhabitants of bathyal sediments.

A review of the literature has revealed that, where data is available, specimens of *Platycoma* and *Proplatycoma* inhabit fine to coarse, sandy sediment (Hope 1988). There is no published data on the sediment from the sites at which *S. typicus* and *S. dactylatus* were collected. However, according to George Hampson of the Woods Hole Oceanographic Institution (personal communication), the sediment from station 167 of *Atlantis II*'s cruise 31 is silty mud. It is likely that the sample from which *S. typicus* was sorted also contained substantial amounts of mud given that it was collected at abyssal depths. However, the sediment from which the latter species was sorted also contained tests of the foraminiferan *Rhabdamina abyssorum.* These tests were constructed of fine particles of sand, so sand also must have been present in this sample. Although definitive data is lacking, it appears that specimens of *Syringonomus* inhabit sediments muddier than those inhabited by specimens of *Platycoma* and *Proplatycoma.* It is very possible that *S. typicus* does not in its natural environment inhabit tests of *Rhabdamina abyssorum,* but may have done so upon being sorted live from the sediment.

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NOTES ON *ANTROSELATES* HUBRICHT, 1963 AND *ANTROBIA* HUBRICHT, 1971 (GASTROPODA: HYDROBIIDAE)

Robert Hershler and Leslie Hubricht

Abstract.—*Antroselates* Hubricht, 1963 and *Antrobia* Hubricht, 1971, monotypic cavesnail genera from eastern United States, are redescribed. The presence of a spermathecal duct in the female reproductive system of these snails indicates that, contrary to earlier opinions, they belong to the Hydrobiidae: Littoridininae. Both genera are well-differentiated members of the *Cochliopina* Morrison, 1946 group, characterized by possession of trochoidal shells and simple penes.

The monotypic genera *Antroselates* and *Antrobia* are poorly known members of the North American aquatic cavesnail (Gastropoda: Hydrobiidae) fauna. Initial descriptions of these unusual-shelled snails lacked critical details from soft-part morphology and speculations on their affinities have varied considerably. *Antroselates,* for instance, was initially considered a hydrobiid (Hubricht 1963:138), but also has been placed in the Micromelaniidae (Taylor 1966: 171, Burch 1982:3). During the course of an ongoing review of North American cavesnails, we examined what may be the only alcohol-preserved material available for these genera and determined that, contrary to all previous assertions, both are well-differentiated members of the *Cochliopina* group of Hydrobiidae: Littoridininae (Hershler 1985). Redescriptions of *Antroselates* and *Antrobia* follow.

Antroselates Hubricht, 1963

Antroselates Hubricht, 1963:138. Type species, *Antroselates spiralis* Hubricht, 1963, by monotypy and original designation.

Diagnosis.—Shell small, solid, trochoid-low conic, with 4.5 rounded whorls sculptured with numerous elevated spiral lines. Protoconch tilted or depressed, with punctate surface lined by spiral grooves. Aperture enlarged, with expanded outer lip. Umbilicus narrowly to broadly open. Operculum paucispiral, with rapidly expanding whorls. Animal blind, unpigmented. Basal cusps of central radular teeth emerging from lateral angles. Cephalic tentacles without hypertrophied ciliary tufts. Ctenidium broad and elongate, with ca. 25 filaments. Intestine with coil in pallial roof. Penis simple, flagellate, non-glandular; surface of distal portion striated. Females oviparous. Spermathecal duct present, connecting posteriorly with albumen gland and anteriorly with capsule gland. Oviduct opening into ventral surface of albumen gland. Bursa copulatrix large, positioned partly posterior to albumen gland.

Remarks.—Placement of this genus in the Micromelaniidae was based on the incorrect observation that the central radular teeth lacked basal cusps (Hubricht 1963:138). We assign the genus to the Hydrobiidae: Littoridininae on the basis of possession of a spermathecal duct in the female reproductive system (see Davis et al. 1982, Hershler 1985). The globose shell and simple penis indicate assignment to the informal *Cochliopina* group (Hershler 1985). Affinity with *Antrobia* is indicated by similarity of protoconch sculpture and duct arrangements in the pallial oviduct complex (including unique connection between spermathecal duct and albumen gland). These snails are, however, separable by differences in shell, penial and radular morphology.

Antroselates spiralis Hubricht
Figs. 1, 2, 3a–c, 4

Antroselates spiralis Hubricht, 1963:138–139, pl. 8, figs. a, b; (Holotype FMNH 116916).—Burch 1982:108, fig. 108.

Material examined.—Kentucky. Edmondson County: Echo River Spring, Mammoth Cave National Park, USNM 673526 (paratypes), USNM 673527 (paratypes); River Styx, Mammoth Cave, Mammoth Cave National Park, UF 40624 (alcohol series [unrelaxed]).

Description.—Shell (Fig. 1) 4.3–5.2 mm in height, slightly taller than wide. Whorls shouldered adapically, sutures slightly indented. Body whorl enlarged, spire relatively small. Shell white-clear, translucent, with amber periostracum. Surface typically eroded with small holes. Protoconch surface slightly pitted; spiral grooves (Fig. 1d) fairly broad and slightly depressed. Spiral lines of irregular height crossing strong growth lines on teleoconch (Fig. 1b, c). Aperture ellipsoidal, longer than wide, rounded above and somewhat angled below, and tilted relative to coiling axis, with anterior side advanced. Inner lip somewhat thickened and reflected below, broadly adnate to body whorl above. Outer lip thin. Operculum (Fig. 2a) thin, amber-colored, with pronounced growth lines.

Animal of three whorls (Fig. 1b). Proximal portions of tentacles without any externally visible vestiges of eyespots. Generalized formulae of radular teeth (Fig. 4): central, 5(6)-1-5(6)/3-3; lateral, 4(5)-1-4(5); inner marginal, 15–18; outer marginal, 12–16. Central teeth trapezoidal; basal cusps small, central cusps only slightly enlarged. Lateral teeth with enlarged, hoe-like central cusps (Fig. 4b). Stomach slightly longer than style sac. Posterior edge of stomach without caecal chamber. Intestinal loop filling posterior half of pallial roof (Fig. 2b). Osphradium filling 25–33% of ctenidium length.

Testis (Ts, Fig. 2b) massive, covering stomach and extending from posterior edge of prostate gland (overlapping most of stomach) almost to posterior end of animal. Branches of testis bearing numerous grape-like lobes and draining to narrow, thin vas efferens. Seminal vesicle consisting of a few thickened coils ventral to anterior testis. Prostate gland (Fig. 2d) thickened, near-circular in outline; almost entire length positioned in pallial roof. Vas deferens entering and exiting antero-ventral portion of gland; anterior portion of duct having thickened coil. Penis emerging from behind right cephalic tentacle, large relative to head (Fig. 2c), with a tight clockwise coil. Penis (Fig. 3a) unciliated, vermiform, with short distal-most section tapering gently. Vas deferens having thickened coils in base of penis; duct undulating in penis. Distal half of structure striated (Fig. 3a), with surface consisting of broad ridges alternating with narrow furrows (Fig. 3b). Terminus (Fig. 3c) thickened, smooth. Opening of vas deferens terminal, simple.

Ovary a simple lobed mass filling about one half whorl behind posterior edge of stomach. Albumen and capsule glands (Ag, Cg, Fig. 2e) about equal in length; capsule gland bipartite (posterior section much longer). Oviduct (Ov) with single, thickened coil on left side of albumen gland. Kidney-shaped bursa copulatrix pressed against and slightly overlapping posterior edge of albumen gland. Bursa duct narrow (Dbu). Seminal receptacle (Sr) small, almost ductless, pear-shaped, positioned on left side of albumen gland and slightly overlapping bursa. Oviduct without connection to albumen gland. Communication to latter achieved by short duct emerging from spermathecal duct (Dsd, Fig. 2f) slightly anterior to point where oviduct joins seminal receptacle duct. This unique arrangement implies that oocytes travel (anteriorly) a short dis-

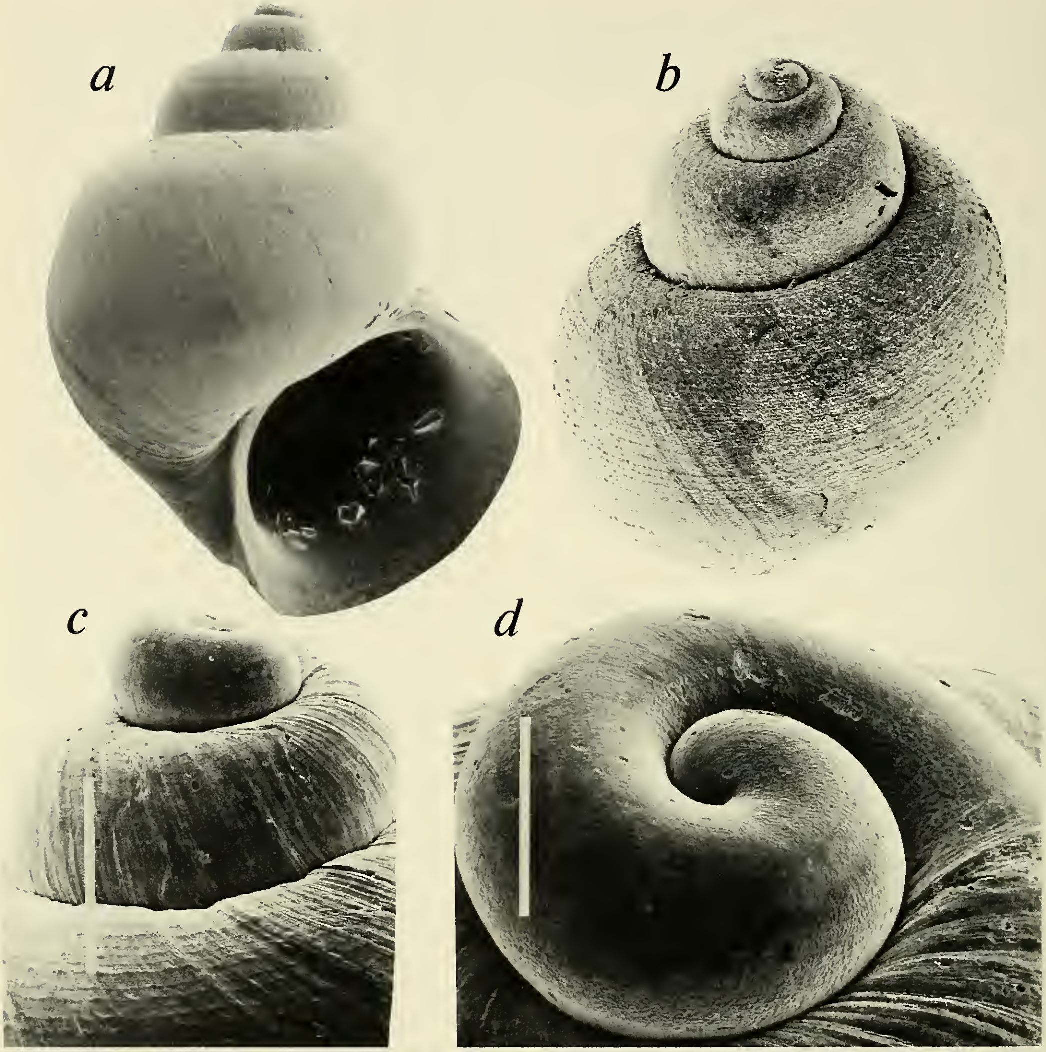

Fig. 1. SEM micrographs of shells of *Antroselates spiralis* Hubricht, USNM 673527 (paratypes): a, (Shell height, 4.95 mm); b, Dorsal aspect, showing well-developed spiral lines (shell height, 3.12 mm); c, Apical whorls (bar = 0.43 μm); d, Protoconch (bar = 176 μm).

tance through the spermethecal duct before entering duct to albumen gland. Spermathecal duct (Sd) fairly wide, pressed against capsule gland. Spermathecal duct entering anterior capsule gland; genital aperture (Ga) simple, terminal.

Distribution.—Found in a few caves and springs in vicinity of Mammoth Cave National Park, Kentucky, as well as in a cave stream in adjacent Indiana (Fig. 5; Hubricht 1963). Snails "found on the undersides of large stones in running water" (Hubricht 1963:139). The species was not found by the senior author during a 1987 trip to the Mammoth Cave area.

Antrobia Hubricht, 1971

Antrobia Hubricht, 1971:95. Type species, *Antrobia culveri* Hubricht 1971, by monotypy and original designation.

Diagnosis.—Shell small, low conical,

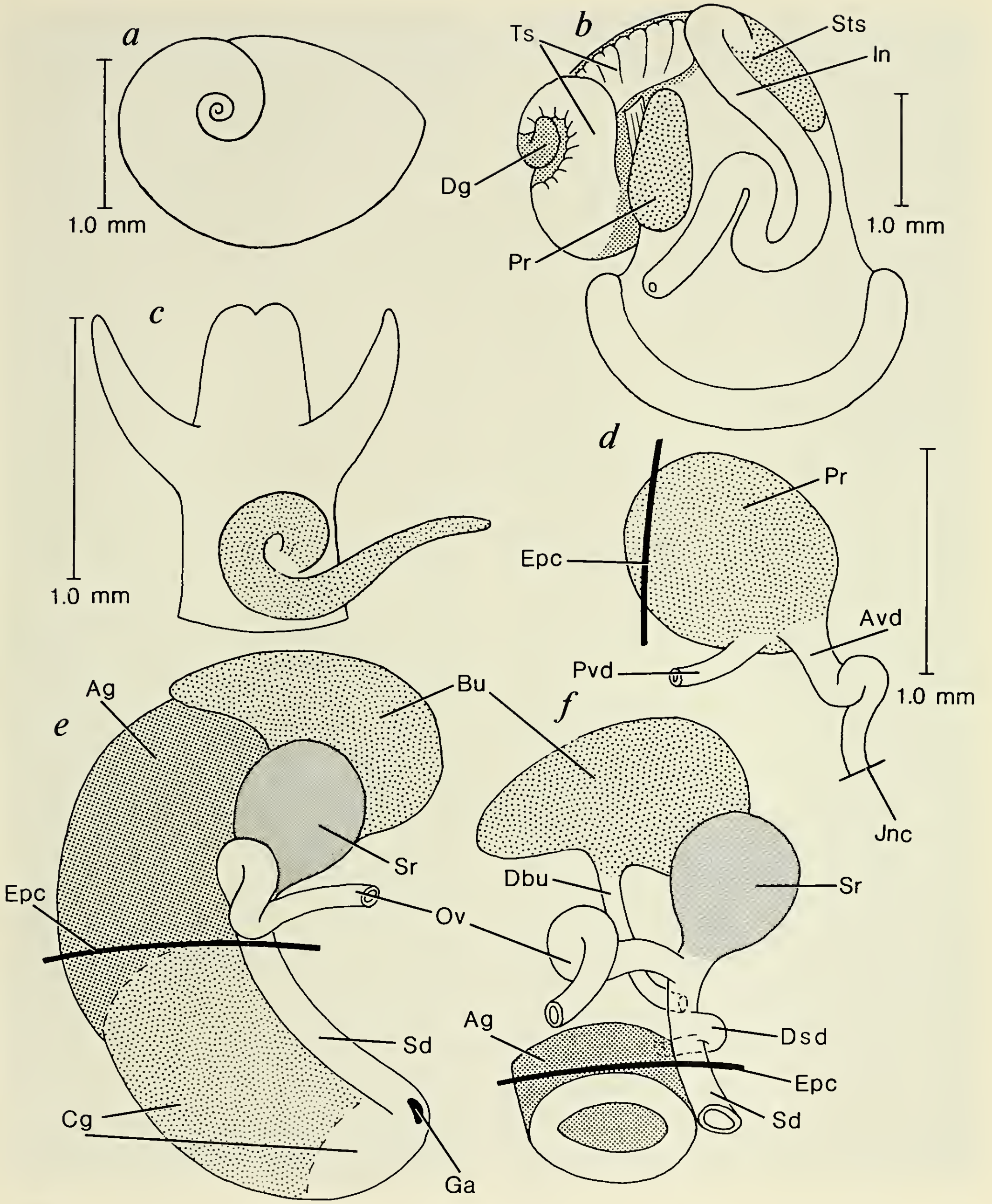

Fig. 2. Morphology of *Antroselates spiralis* Hubricht, UF 40624: a, Dorsal view of operculum; b, Dorsal view of male (head–foot removed); c, Dorsal view of head and penis; d, Right lateral view of prostate gland; e, Left lateral view of pallial oviduct complex; f, Left lateral view of bursa copulatrix, seminal receptacle (rotated to expose underlying structures), and associated ducts. Only the anterior portion of the albumen gland is shown. Ag = albumen gland; Avd = anterior vas deferens; Bu = bursa copulatrix; Cg = capsule gland; Dbu = duct from bursa copulatrix; Dg = digestive gland; Dov = duct connecting oviduct and spermathecal duct; Epc = posterior end of pallial cavity; Ga = genital aperture; In = intestine; Jnc = juncture between anterior vas deferens and "neck"; Ov = oviduct; Pr = prostate gland; Pvd = posterior vas deferens; Sd = spermathecal duct; Sr = seminal receptacle; Sts = style sac; Ts = testis.

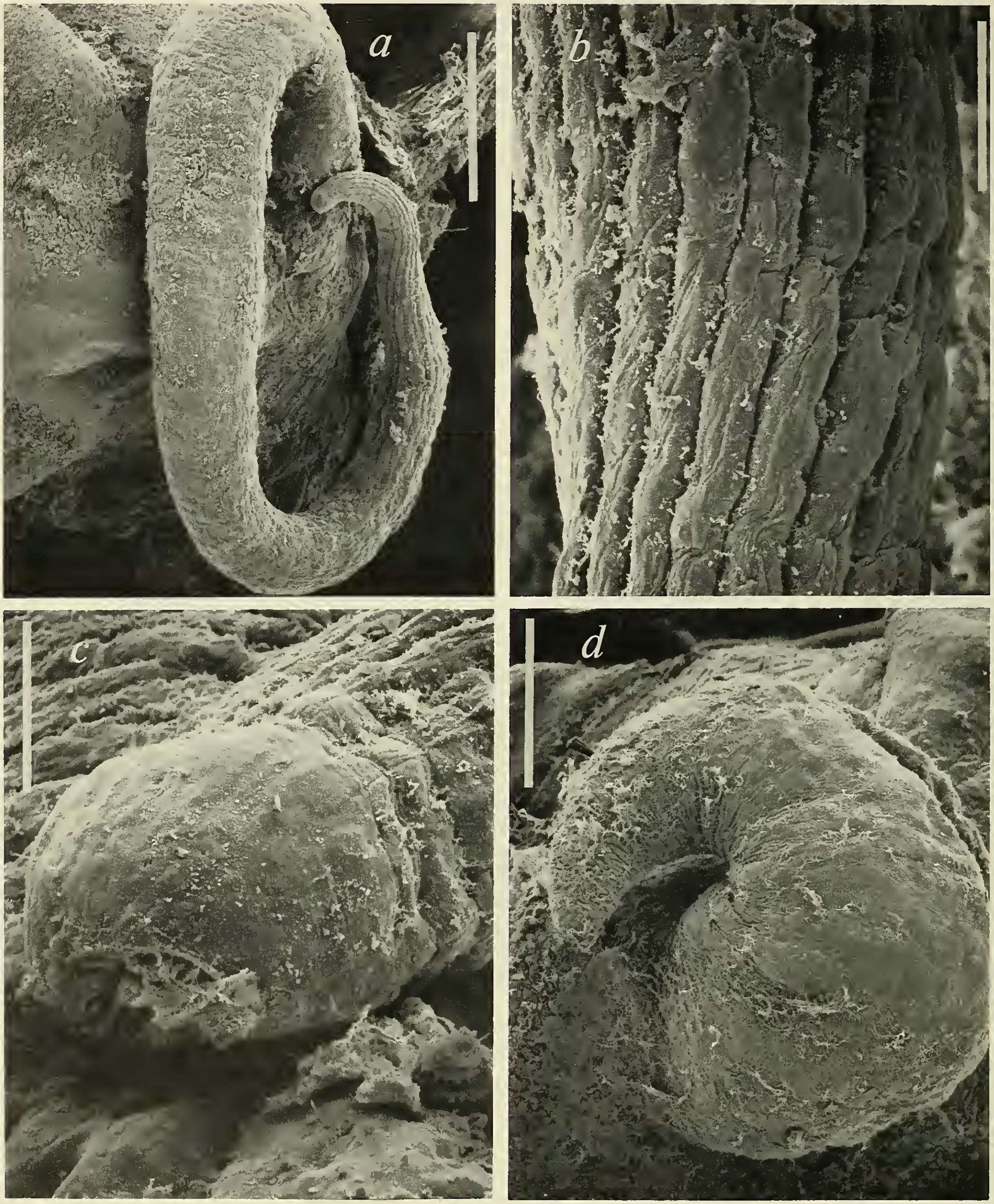

Fig. 3. SEM micrographs of critical point dried penes of *Antroselates spiralis* Hubricht, UF 40624 (a–c) and *Antrobia culveri* Hubricht, LH coll. (d): a, Dorsal view of penis (bar = 37 μm); b, Close-up of striated surface (bar = 213 μm); c, Close-up of penial tip, showing simple terminal opening (bar = 25 μm); d, Dorsal view of penis showing irregular ciliation (bar = 136 μm).

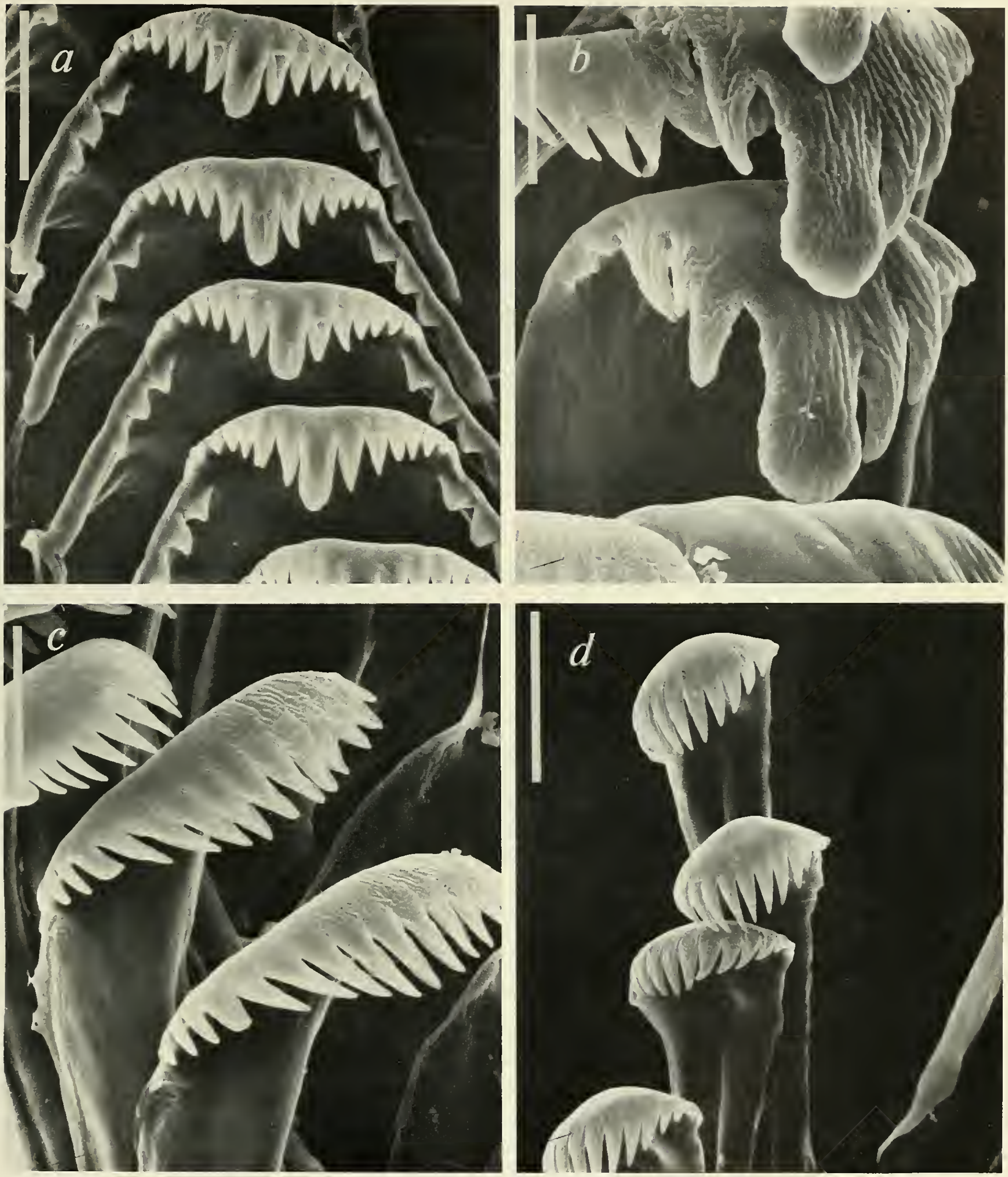

Fig. 4. Radula of *Antroselates spiralis* Hubricht, UF 40624: a, Centrals (bar = 17.6 μm); b, Laterals (bar = 12 μm); c, Inner marginals (bar = 13.6 μm); d, Outer marginals (bar = 15 μm).

broadly umbilicate, with 3.5 well-rounded whorls having indented sutures. Protoconch and teleoconch lined with regularly spaced shallow spiral grooves. Aperture simple, subcircular. Operculum multispiral, with slowly expanding whorls. Animal blind, unpigmented. Cusps numerous on all radular teeth; central teeth broadly trapezoidal with elongate lateral angles. Cephalic tentacles without hypertrophied ciliary tufts. Ctenidium reduced, consisting of ca. eight small filaments. Penis simple, non-glandular, dag-

Fig. 5. Drainage map of eastern United States showing distributions of *Antroselates spiralis* Hubricht and *Antrobia culveri* Hubricht.

ger-like. Females oviparous. Spermathecal duct present, connecting posteriorly with albumen gland and anteriorly with capsule gland. Bursa copulatrix positioned partly posterior to albumen gland.

Remarks.—Burch (1982:3) placed this genus in the Lithoglyphinae, presumably based on its low-conical "lithoglyphine-like" shell. Given the presence of a spermathecal duct in the female reproductive system (absent from lithoglyphines; Thompson 1984), these snails are more appropriately placed in the Hydrobiidae: Littoridininae. *Antrobia* is distinguished from other members of the *Cochliopina* group by its radular morphology (similar to that of *Fontigens* Pilsbry, 1933) and teleoconch sculpture.

Antrobia culveri Hubricht
Figs. 3d, 6–8

Materials examined.—Missouri. Taney County: stream in Tumbling Creek Cave, 4.5 mi NE of Protem, FMNH 164171 (Holotype), FMNH 164170 (Paratypes); Leslie Hubricht coll. 38780 (alcohol series [relaxed]).

Description.—Shell (Fig. 6) 1.9–2.2 mm high, very slightly taller than wide. Sutures indented. Shell white-clear, translucent, with amber periostracum. Surface typically partly covered by white deposits. Protoconch (Fig. 6d, e) with 1.0–1.25 whorls, having a slightly pitted surface with well-spaced, spiral grooves. Grooves sometimes ending af-

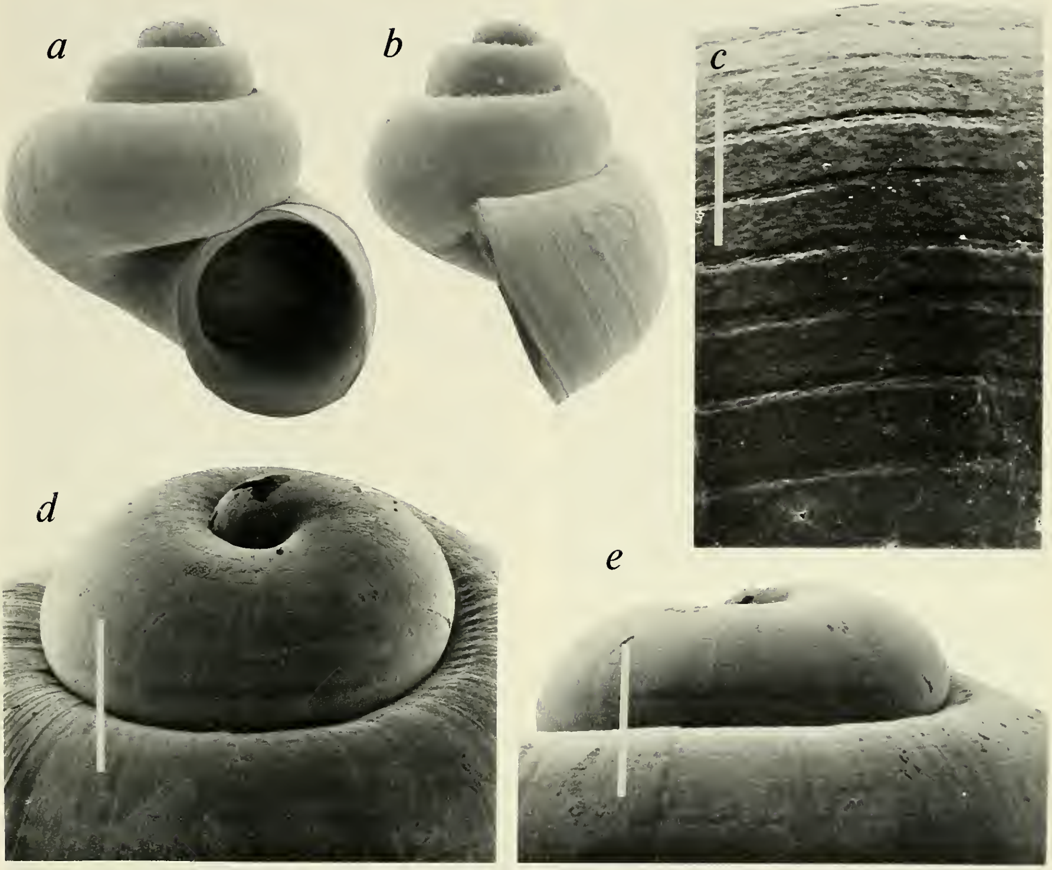

Fig. 6. SEM micrographs of shells of *Antrobia culveri* Hubricht, FMNH 164170 (paratypes): a, b (Shell heights, 1.9, 2.0 mm, respectively); c, Close-up showing spiral grooves (bar = 0.43 μm); d, e, Views of apex (bars = 176 μm).

ter first teleoconch whorl (erosion?). Teleoconch roughened with collabral growth lines. Aperture longer than wide, near-planar, adnate to a small portion of the body whorl above, and slightly tilted relative to coiling axis (adapical side advanced; Fig. 6b). Inner lip reflected, somewhat thickened; outer lip thin. Operculum (Fig. 7a) thin, amber.

Animal of two whorls. Proximal portion of tentacles without any externally obvious eyespot vestiges. Generalized formula of radular teeth (Fig. 8): central, 6(7)-1-6(7)/3-3; lateral, 16–17; inner marginal, 29; outer marginal, 21. Cusp morphology very similar for all tooth types: note absence of enlarged central cusps on centrals and laterals. Basal portion of central teeth well excavated between lateral angles and basal process. Stomach considerably longer than style sac. Posterior stomach edge without caecal chamber. Intestinal loop undulating gently in pallial roof. Osphradium about 33% of ctenidium length.

Testis a single, unlobed mass, filling one-half whorl of animal and partly overlapping the posterior stomach. No vas efferens not-

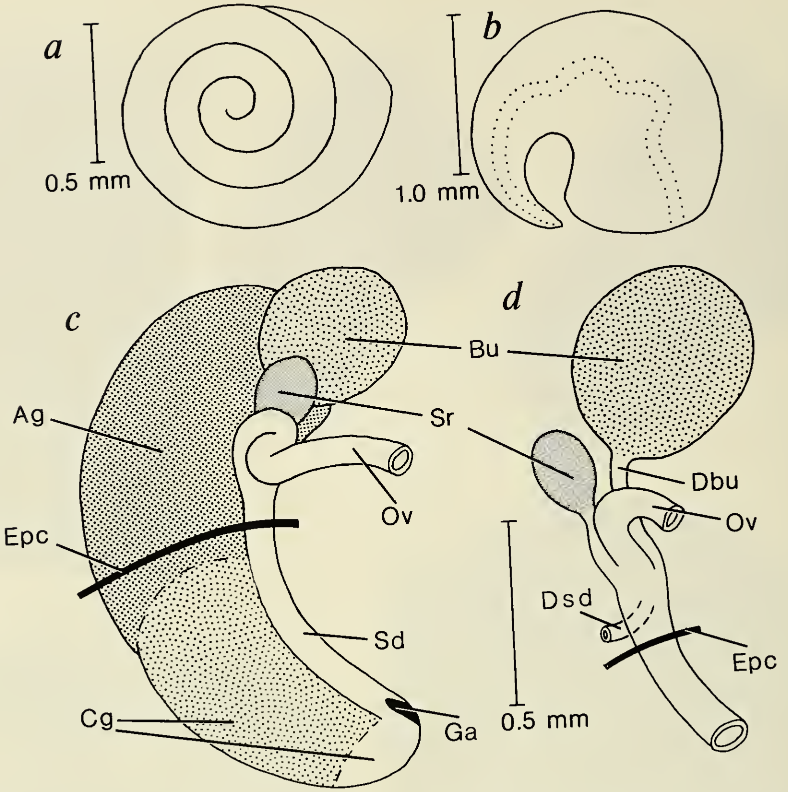

Fig. 7. Morphology of *Antrobia culveri* Hubricht, LH coll.: a, Dorsal view of operculum; b, Dorsal view of penis showing course of vas deferens (dotted line); c, Left lateral view of pallial oviduct complex; d, Left lateral view of bursa copulatrix, seminal receptacle (rotated to expose underlying structures), and associated ducts. Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Dbu = duct from bursa copulatrix; Dov = duct between oviduct and spermathecal duct; Epc = posterior end of pallial cavity; Ga = genital aperture; Ov = oviduct; Sd = spermathecal duct; Sr = seminal receptacle.

ed; seminal vesicle consisting of a few thickened coils entering anterior edge of testis. Prostate gland small, with 50% of length in pallial roof. Vas deferens entering and exiting central area of prostate. Penis (Fig. 7b) small, with tight clockwise coil, well-tapered. Surface irregularly ciliated (Fig. 3d), with cover particularly heavy distally. Distal end of penis undifferentiated; terminal pore simple. Vas deferens undulating slightly within penis.

Ovary an unlobed mass filling a relatively small portion of digestive gland posterior to the stomach. Albumen gland slightly longer than capsule gland (Ag, Cg, Fig. 7c). Capsule gland bipartite with posterior section much larger. Oviduct (Ov) with single coil on left side of albumen gland. Bursa (Bu) sac-like, with a narrow duct (Dbu, Fig. 7d). Seminal receptacle (Sr) small, positioned partly anterior to bursa. Oviduct without connection to albumen gland. Communication to latter achieved by short duct emerging from spermathecal duct (Dsd, Fig. 2f) anterior to point where oviduct joins seminal receptacle duct. Spermathecal duct (Sd) moderately wide, pressed against capsule gland and entering gland near anterior terminus. Genital aperture (Ga) simple, terminal.

Distribution.—Endemic to underground

Fig. 8. Radula of *Antrobia culveri* Hubricht, LH coll.: a, Centrals (bar = 7.5 μm); b, Laterals (bar = 7.5 μm); c, Inner marginals (bar = 6 μm); d, Outer marginals (bar = 3.8 μm).

stream of Tumbling Creek Cave in SE Missouri (Fig. 5). Snails are currently uncommon in the cave (pers. comm. 1986, T. J. Aley, Ozark Underground Laboratory).

Acknowledgments

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A REVISION OF THE GENUS *THEMISTE* (SIPUNCULA)

Edward B. Cutler and Norma J. Cutler

Abstract.—The 31 putative species of the sipunculan genus *Themiste* and the morphological characters used to differentiate them are critically reviewed. The monograph of Stephen & Edmonds (1972) is used as a starting point and all changes made in the intervening years are reiterated. All available type material was studied and new collections of Hawaiian and Californian material are used to analyze within-deme variation. Four characters are determined to be useful at the species level and three at the subgeneric level. A key to and a discussion of each of the 10 remaining species (plus one reduced to subspecies) with the newly designated synonyms are presented. A brief statement of the known distribution and an overall summary of the zoogeography of the two subgenera (largely non-overlapping) are given.

This is a continuation of our series in which we reevaluate the species of sipunculan worms (e.g., Cutler & Cutler 1985a, b, 1986, 1987). With this work we complete our survey of the genera in the Class Sipunculida. The monograph of Stephen & Edmonds (1972) is the starting place for this work (25 species names). In that same work there were three names listed as species inquirendae or incertae sedis that subsequently were considered members of this genus and are addressed herein. The one species and the subgenera erected and the two species transferred into this genus since that time are also included (Table 1).

The genus *Themiste* was erected by Gray in 1828, but this name dropped from sight for over a century. The name *Dendrostomum* (Grube & Oersted, 1858) took its place until 1964 when Stephen resurrected Gray's name. The genus has been placed in its own family, Themistidae of the order Golfingiiformes by Cutler & Gibbs (1985).

While no formal subgenera exist in Stephen & Edmonds (1972), there were six groups that Edmonds later (1980) converted into three subgenera. These subgenera were considered in Gibbs & Cutler (1987), and the one with four retractors (*Stephensonum*) was determined to be a junior synonym of the genus name *Golfingia.* One of its two species (*Themiste pinnifolia* Keferstein, 1865) was regarded as nomen dubium and the other (*T. stephensoni* Stephen, 1942) was a mixture of *Golfingia capensis* and *T. lageniformis* (see below). The remaining two subgenera (based on differences in contractile vessel villi or tubules) are used here. We do question the presumed homologous nature of these tubular extensions. They are very different in size, distribution, and number. It seems likely that these elaborations resulted from two different evolutionary events (homoplasy).

The type (10 mm trunk), and only specimen of *Themiste spinifera,* Sluiter, 1902 is not in the museum collections (ZMUA) with the other *Siboga* material. Certain aspects of the figures and description make us doubt the generic affinity, and, with no way to verify this, we reduce its status to that of incertae sedis.

Whenever possible we have obtained type material to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to better evaluate the traditionally used morphological characters. Collecting

Table 1.—Species considered and proposed taxonomic changes.

Present name	Proposed name
Subgenus *Themiste*	
Themiste alutacea (Grube & Oersted, 1858)	no change
Themiste blanda (Selenka et al, 1883)	no change
Themiste dyscrita (Fisher, 1952)	no change
Themiste hennahi Gray, 1828	no change
Themiste hexadactyla (Sato, 1930)	*Themiste pyroides*
Themiste lissa (Fisher, 1952)	*Themiste hennahi*
Themiste orbiniensis (de Quatrefages, 1865)	*Themiste alutacea*
Themiste perimeces (Fisher, 1928)	*Themiste hennahi*
Themiste petricola (Amor, 1964)	*Themiste alutacea*
Themiste pyroides (Chamberlin, 1920)	no change
Dendrostomum ramosum Quatrefages, 1865	*Themiste hennahi*
Sipunculus rapa Quatrefages, 1865	*Thimiste hennahi*
Themiste rosacea (Amor, 1964)	*Themiste alutacea*
Themiste schmitti (Fisher, 1952)	*Themiste hennahi*
Themiste spinifera (Sluiter, 1902)	incertae sedis
Themiste zostericola (Chamberlin, 1920)	*Themiste hennahi*
Subgenus *Lagenopsis*	
Themiste cymodoceae (Edmonds, 1956)	no change
Themiste dehamata (Kesteven, 1903)	no change
Themiste elliptica (Sato, 1934)	*Themiste dehamata*
Themiste fisheri (Amor, 1964)	*Themiste dehamata*
Themiste fusca (Edmonds, 1960)	*Themiste minor minor*
Themiste glauca (Lanchester, 1905)	*Themiste lageniformis*
Themiste huttoni (Benham, 1904)	*Themiste minor huttoni*
Themiste lageniformis (Baird, 1868)	no change
Themiste minor (Ikeda, 1904)	*Themiste minor minor*
Themiste pyriformis (Lanchester, 1905)	*Themiste lageniformis*
Themiste robertsoni (Stephen & Robertson, 1952)	*Themiste lageniformis*
Themiste tropica (Sato, 1935)	*Themiste lageniformis*
Themiste variospinosa Edmonds, 1980	no change
Subgenus *stephensonum* (now void)	
Themiste pinnifolia (Keferstein, 1865)	nomen dubium
Themiste stephensoni (Stephen, 1942)	*Golfingia capensis*

trips to Hawaii and California have greatly facilitated this effort. The opportunity to see the differences in the habitat of these animals and to observe living material is invaluable.

We first discuss the morphological characters in light of our recent analyses. Next a key to all the species we consider valid and a section where each of these species is discussed; this includes a synonymy, a discussion of newly added junior synonyms, and a summary of their distribution. Within each subgenus the species are grouped according to whether or not hooks are present. A short zoogeographical summary is also presented.

The following abbreviations are used in this text for the museums from which we borrowed material: Bernice P. Bishop Museum, Homolulu (BPBM); British Museum (Natural History) (BMNH); Museum of Comparative Zoology, Harvard (MCZH); Museum für Naturkunde der Humboldt-Universitat zu Berlin (MNHU); Royal Scottish Museum, Edinburgh (RSME); Santa Barbara Museum of Natural History (SBNH); University Zoological Museum, Cambridge (UZMC); National Museum of Natural History, Washington, D.C. (USNM); Zoologisk Museum, Copenhagen (UZMK); Zoological Institute, Tohoku University, Sendai (ZITU); Zoological Museum, Hamburg (ZMUH); Zoology Museum, University of Tokyo (ZMUT).

Morphological Characters

Historically the following characters have been used to differentiate *Themiste* species. Earlier descriptions were not always based on a good understanding of possible variation within a population (species). In this section we evaluate these characters in light of our experience with large sample sizes. It must be emphasized that if the specimens are not relaxed prior to fixation the measurements of diverse parts can be misleadingly different. For instance, in the Hawaiian *T. lageniformis* population we had access to one collection with completely retracted introverts and another which was preserved with introverts extended. The length of the introverts did vary considerably (Fig. 1), but this is partly an artifact of preservation technique. Introverts of retracted specimens were measured by dissecting the body wall and determining the distance from the nephridiopores to the base of the tentacles.

We have observed other differences that are not of the classical type but worth mentioning. The niche concept is particularly applicable in the Californian species; we found one (*T. hennahi*) lives in unconsolidated sediments (various mixtures of silt/sand/gravel), and a second (*T. dyscrita*) lives in discrete holes made by other animals in shales or sandstones. These also have different sporozoan parasites in their intestine (F. Hochberg, pers. comm.) and respond very differently to anesthesia (*T. hennahi* is much more likely to extend its introvert in response to refrigeration or menthol). The third species (*T. pyroides*) lives in fissures/crevices in granitic rock, is much more eurybathyal, and does not relax easily. A similar case (ill-defined but different niches) seems to exist for the Australian complex (S. J. Edmonds, pers. comm.).

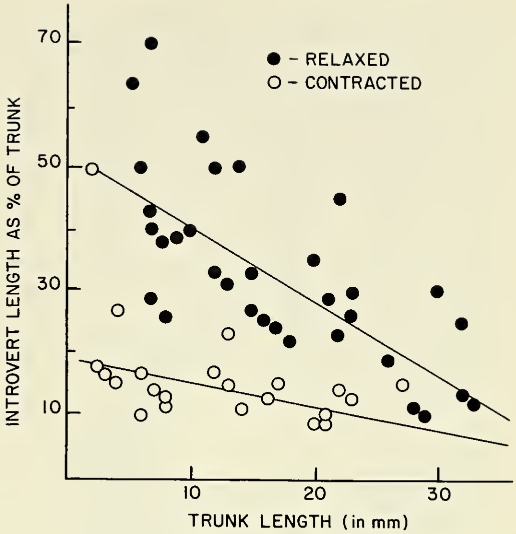

Fig. 1. Introvert length of *T. lageniformis* to show how such measurements can differ between relaxed and contracted worms. As in other genera, the relative length of this body part becomes shorter with age (in linear regression b = −1.2 and − 0.27).

Karyology may be an attribute that biologists can use to differentiate species. A more detailed statement will be published separately, but, based on a preliminary analysis of three species, it appears that the members of this genus have ten pairs of chromosomes. The apparent similarities preclude using this as a diagnostic character at the species level. Information about developmental pathways and parasites might be useful, but at this time the data base is far from complete.

1. *Contractile vessel villi.*—In sipunculans a closed, fluid filled, tubular system extends into the tentacles from one or two vessels running along the esophagus functioning as a circulatory system helping in the exchange of gases between the external and internal

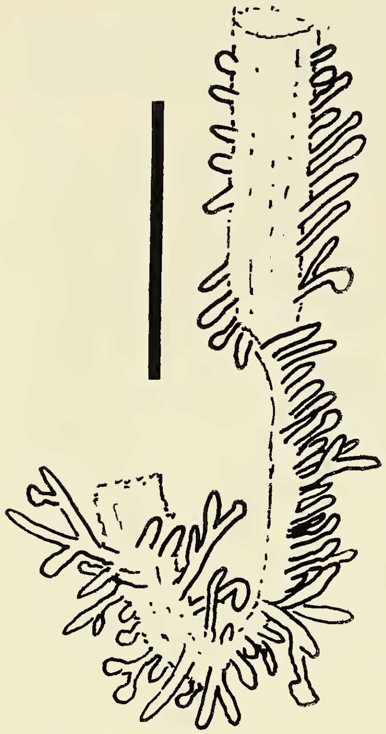

Fig. 2. Contractile vessel villi from a 5 mm *T. lageniformis* showing bifurcations in a small specimen and the increasing frequency of bifurcations toward the posterior end (bottom of figure). Scale line is 1 mm.

environments. It may also be a turgor pressure system not unlike the polian vessels in echinoderms aiding in the expansion of the tentacular crown. In five genera, digitiform villi along this vessel increase the volume and the surface area for internal gas exchange. In this genus are two rather different configurations, and this character is used to separate the two subgenera (Edmonds 1980). The more common pattern (found in other genera) of many (more than 100) short villi is found in *T.* (*Lagenopsis*). In *T.* (*Themiste*) a unique design exists: few (usually 8–14) long threadlike extensions off the posterior quarter of the vessel, often with a corkscrew or beads-on-a-string shape.

A question that has been raised about the shorter villi is whether or not the individual units bifurcate; a few species have been alleged to lack any bifurcating villi. Our examination of recently collected Hawaiian *T. lageniformis,* ranging in size from 2–33 mm, shows that while more bifurcation exists in larger worms, all those over 3 mm show at least some evidence of bifurcation (Fig. 2). One must look carefully in smaller worms. In addition to an ontogenetic change, we have observed an anterior/posterior gradient. The branching complexity (and size of villi) increase towards the posterior end—sometimes more than three terminal branches can be seen.

In the subgenus *T.* (*Themiste*) none of the tubular extensions (villi seems inappropriate here) bifurcates in the same manner. In some larger specimens a complex branching occurs near the base (see Fisher 1952 pl. 30, fig. 3). The variable, occasionally used in species descriptions, is the number, e.g., more than 10 vs. 10 or less. The exact number of tubules is difficult to determine, and our data suggest that smaller worms (under 30 mm) have less than 10 while larger worms (same population) usually have more than 10 tubules. To use this difference as a species specific character is unwise.

Only a few references to anastomosing "networks" of the vessel around the esophagus exist, but our examination shows this feature to be age dependent, thus rarely developed in smaller worms (see *T. pyroides* section for more detail). Therefore, its use as a taxonomic character is limited.

2. *Introvert hooks.*—In both subgenera some species carry dark, horny, chitinoid hooks scattered on the introvert. In some genera hooks appear to be deciduous, but that does not seem to be the case here. However, we know very little about the ontogeny of those species lacking hooks as adults. The one such species we do have information on is *T. lageniformis.* Awati & Pradhan (1935) reported hooks on early stages and Pilger (1987) reported hooks in a five day specimen. Also, Williams (1977:38) observed that 13 day old Hawaiian specimens

(about 0.5 mm) have "... several rows of hooks." We saw no hooks on our 2–3 mm worms from Hawaii.

One record suggests the reverse pattern exists in one species that has hooks as adults: Fisher's (1952) discussion of *T. pyroides* includes the observation that smaller worms have fewer hooks (no hooks in those less than 18 mm, 4–18 hooks in two 18 mm worms, 50 hooks in a 24 mm worm). One must remember that Fisher's measurements include both the trunk and the introvert, the later being about ⅓ the total. Our recent collections from the same area (Carmel and Monterey) included only a few small worms and all of these have hooks (30–80 hooks in worms with a total length of 15–21 mm; trunks from 10–14 mm). In the *T. blanda* we collected in Japan only one with a 2 mm trunk has no hooks; those 3 mm and larger carried them.

These data suggest that all *Themiste* species, as early juveniles, have hooks which are soon lost. While some species never replace these, other species do so in later stages of ontogeny. This hypothesis needs more testing, but Rice (1967) did observe one row of hooks in one month old specimens of *T. pyroides,* the same species Fisher was referring to above. She has also recorded (Rice 1975b) the presence of a row of hooks at one month in *T. alutacea.* Nevertheless, a presence/absence dichotomy in adult worms exists and therefore, this character can be helpful to the systematist. If these early juvenile hooks are real and are arranged in rings, we may have reason to reverse our earlier assumptions about the polarity of this character in our cladistic analyses, i.e., this may be the plesiomorphic not the apomorphic state.

The adult hooks are often large, sparse, and arrayed over a wide band on the proximal part (⅓–⅔) of the introvert (Fig. 3). Descriptions sometimes include comments on their number, size, and arrangement. As shown above, the number changes with trunk size. We originally thought that the amount of introvert covered by hooks (most animals have less than 45% covered, but in others the hooked region seems to cover more than 50% of the introvert) as genetically determined. Observations from our field work in California strongly suggest that those animals living in areas of high energy (open rocky intertidal) have fewer hooks covering a smaller area with many more broken hooks than other members of the same species at more protected or subtidal depths (e.g., *T. pyroides*). It now seems clear that, within limits, this trait is partly an environmentally determined feature. The arrangement is not constant within a species or species specific, generally being scattered and oriented posteriorly (one exception is *T. variospinosa*). Hook size also changes with trunk size: In the Japanese *T. blanda* population we analyzed, a 5 mm worm had hooks about 50 μm tall, an 8 mm worm had 75 μm hooks, and an 11 mm worm had hooks about 100 μm tall. The upper limit in this genus is about 450 μm in large adults.

3. *Tentacular crown.*—The diverse interpretations of this feature have been one of the most troublesome aspects of *Themiste.* The dendritic branching pattern is unique within Sipuncula and makes the identification of these worms to the generic level easy (if the tentacles are extended). However, the question of how many tentacular "stems" exist has led to some unfortunate confusion. Perhaps the classic (but not only) case is the holotype of *T. hennahi.* Gray (1828) saw five main stems; Stephen (1964) reported only four main branches; but, when Rice and Stephen (1970) reexamined the same worm, they reported six tentacular stems.

The lack of consistency in language describing these tentacles has compounded the confusion. We are defining the terms as follows: The four structures arising from the oral disc are the stems; these stems divide into branches (primary, secondary, etc.); the final subdivisions or terminal units are tentacules. Finally, one tentacle is the entire

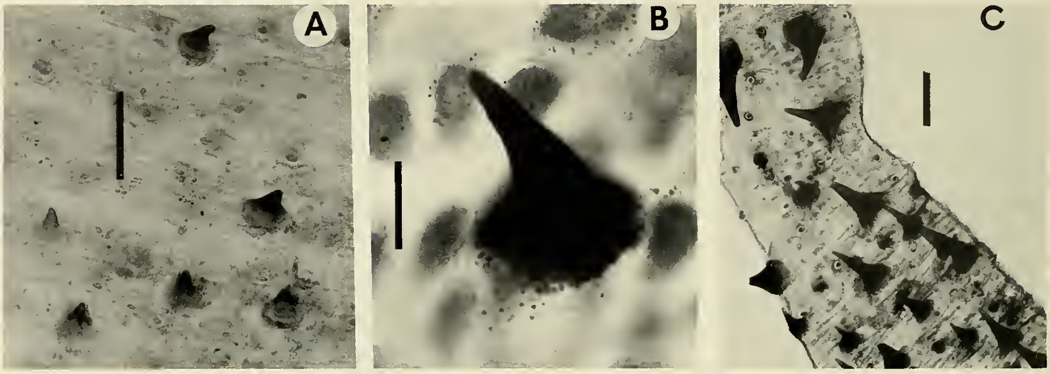

Fig. 3. Introvert hooks showing different sizes and orientation among species: A. *T. minor minor*; B. *T. pyroides*; C. *T. variospinosa*. Scale lines all equal 200 μm.

array of subunits beginning with one stem. While this is somewhat arbitrary, it is consistent with several earlier authors (Fisher 1952, Edmonds 1980).

The basic plan in this genus is four stems, but most of the problems arise when the first dichotomy appears close to the base of a stem. During the ontogeny of these worms different species exhibit different patterns vis-a-vis the timing of the "splitting." Two adult patterns result—either 4 or 6 (occasionally 5) putative stems. Those animals with 5 or 6 may have a developmental pathway that involves an early post-larval subdivision of the dorsal pair. At times the dorsal stems will be longer/larger than the ventrals. Our work with the Hawaiian and Californian populations supports the hypothesis that as these worms increase in size a corresponding increase in the complexity of the tentacular crown occurs, more branches and more tentacules (Fig. 4). Therefore, the number of apparent tentacular stems varies and should not be considered species specific.

A separate issue relates to the branching pattern that has been asserted to be either dendritic, pinnate, or palmate by different authors, sometimes for the same species. These adjectives have been used with minimal precision and suggest differences that do not exist. In the subgenus *Lagenopsis* the four stems divide into smaller branches relatively few times (1–3), depending on their age/size (Fig. 4). On all of these branches as well as the main stems, terminal tentacules are given off along the entire length from near the branch points to the tip. The length of these tentacules exhibits some consistency within a species. We measured the longest ones in *T. lageniformis,* 2–4 mm; shorter in *T. cymodoceae,* 1–2 mm; and shortest in *T. dehamata,* 0.5–1 mm). The trunk lengths of the measured specimens, in order, are 10–30 mm, 79–85 mm, and 45–68 mm.

In the subgenus *Themiste* each stem branches dichotomously several times with discrete internodes. In small individuals (less than 15 mm) the dendritic crown exists but with fewer branches and shorter internodes (see Fig. 4 and Fisher 1952 for more detail). The terminal tentacules are present as clusters near the tips of the terminal branches. Tentacules are widely spaced (what Fisher (1952) illustrated and called processes) along the branches. In small worms the relative size of the parts gives the crown a more *Lagenopsis*-like appearance. In general, the complexities and variations in the branching patterns mitigate against using it for taxonomic purposes at the species level. The exception (helpful in particular species com-

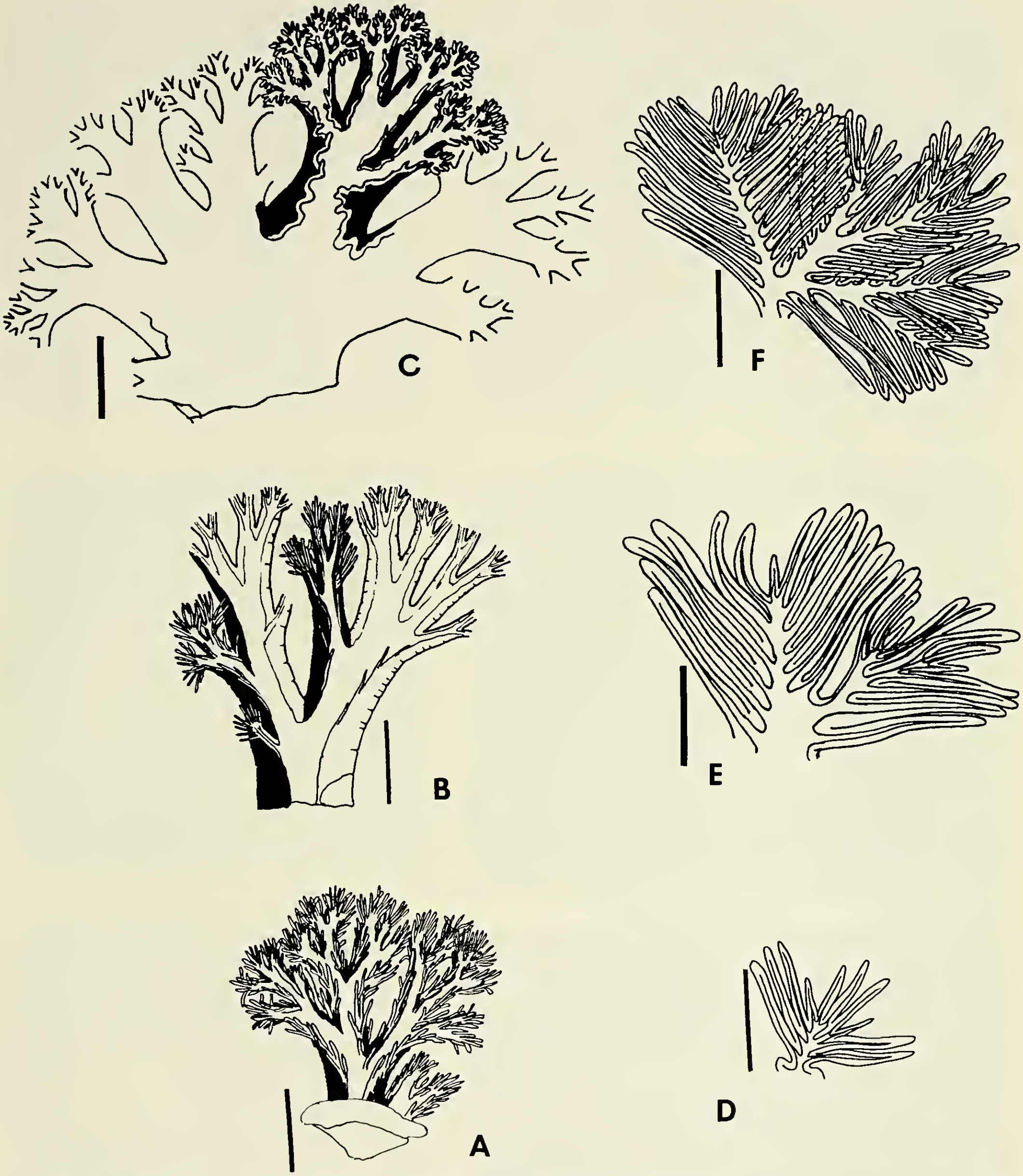

Fig. 4. Left dorsal tentacle from two *Themiste* species showing size-related changes in branching pattern in the two subgenera: A–C are *T.* (*Themiste*) *hennahi* trunk lengths are 25, 80 and 140 mm. D–F are *T.* (*Lagenopsis*) *lageniformis*; trunk lengths are 6, 16 and 30 mm. Scale line is 1 mm.

plexes), is unequal length of dorsal vs. ventral stems and whether or not the ventral stems split at the same time as dorsals.

4. *Anus-nephridia relationship.*—As in other genera the relative anterior/posterior relationship of these openings has been reported and sometimes used to differentiate species. The language is often general; these

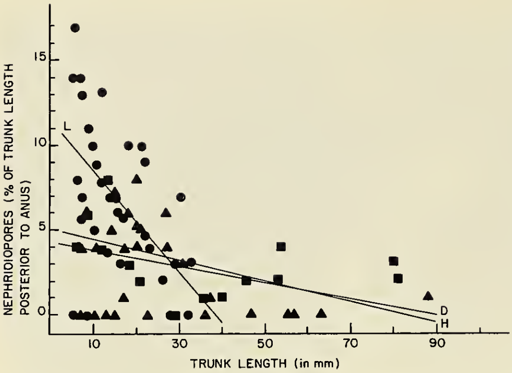

Fig. 5. Distance nephridiopores are posterior to anus as percentage of trunk length. Circles are *T. lageniformis,* squares are *T. dyscrita,* triangles are *T. hennahi.* This distance decreases with size but with much overlap among species.

are at the same level, nearly the same level, or the nephridiopores open posterior to the anus. In our study of the Hawaiian *T. lageniformis* population, the nephridia are almost always posterior to the anus, commonly at a distance equal to 3–7% of the trunk length, occasionally up to 12–15%, but a few at the same level (Fig. 5). In one Californian population of *T. hennahi* this distance is usually only 0–1% but in a few small worms it is 5%. In a population of *T. dyscrita* this distance is 1–4%. Fisher (1952) weighted this heavily in the California complex to distinguish his *T. lissa* from its neighbors, but our measurements of Fisher's material show that only in the holotype is this distance 10% while in four of the paratypes this value ranged from 4–6%.

Our conclusion is that since this distance is small, not easy to measure precisely, and, most importantly, since there can be much variation within demes, it has very little taxonomic significance and should not be used.

5. *Trunk size and shape.*—While this kind of information is often reported imprecisely (large vs. small or slender vs. stout), it may have some meaning. Based on our observations there do appear to be two size classes for adult worms. Those that generally inhabit soft substrata commonly have trunks exceeding 60 mm (some over 200 mm) while those living in rock or coral rarely exceed 30 mm. However, the north Pacific *T. pyroides* may reach 150 mm. Most of the smaller worms have a similar pyriform shape. Shape of preserved material is partly dependent on the animal's unique set of circumstances prior to fixation (physical microhabitat and anesthesia, if any). However, worms living in unconsolidated sediments are cylindrical and elongate while those from rock/fissures/coral have stouter and more pyriform bodies. When these occupy holes made by boring bivalves the body is shaped by the mold chosen by the juvenile worm (Fig. 6). This shape is difficult to quantify and therefore difficult to communicate without ambiguity. Our observations on living, freshly-collected material lead us to conclude that trunk shape is partly environmentally determined. Nevertheless, this character (especially as an indicator of niche) can be used by the taxonomist.

6. *Fixing muscle attachments.*—Small threadlike muscles connect some part of the digestive tract to the body wall. The general pattern in *Themiste* is three muscles labeled F1, F2, F3. In the subgenus *Themiste,* F1 anchors the esophagus in the area of the long contractile vessel villi to the body wall of the mid-trunk, while in *Lagenopsis* it anchors the esophagus near the posterior part of the trunk where the esophagus turns forward and may take the form of several threads or a membrane. F2 is generally on the posterior esophagus or first gut coil while F3 is more often on the last intestinal coil or the rectum. The precise insertion of these muscles has been asserted to be constant and taxonomically meaningful (Fisher 1952 compares *T. hexadactyla* to *T. pyroides* or *T. dyscrita* to *T. zostericola*). However, Fisher did illustrate variations and Foster (1974:856) working with several hundred *T. dyscrita* from one deme commented on the novel and abnormal arrangement of the F2, other than that described by Fisher. Our

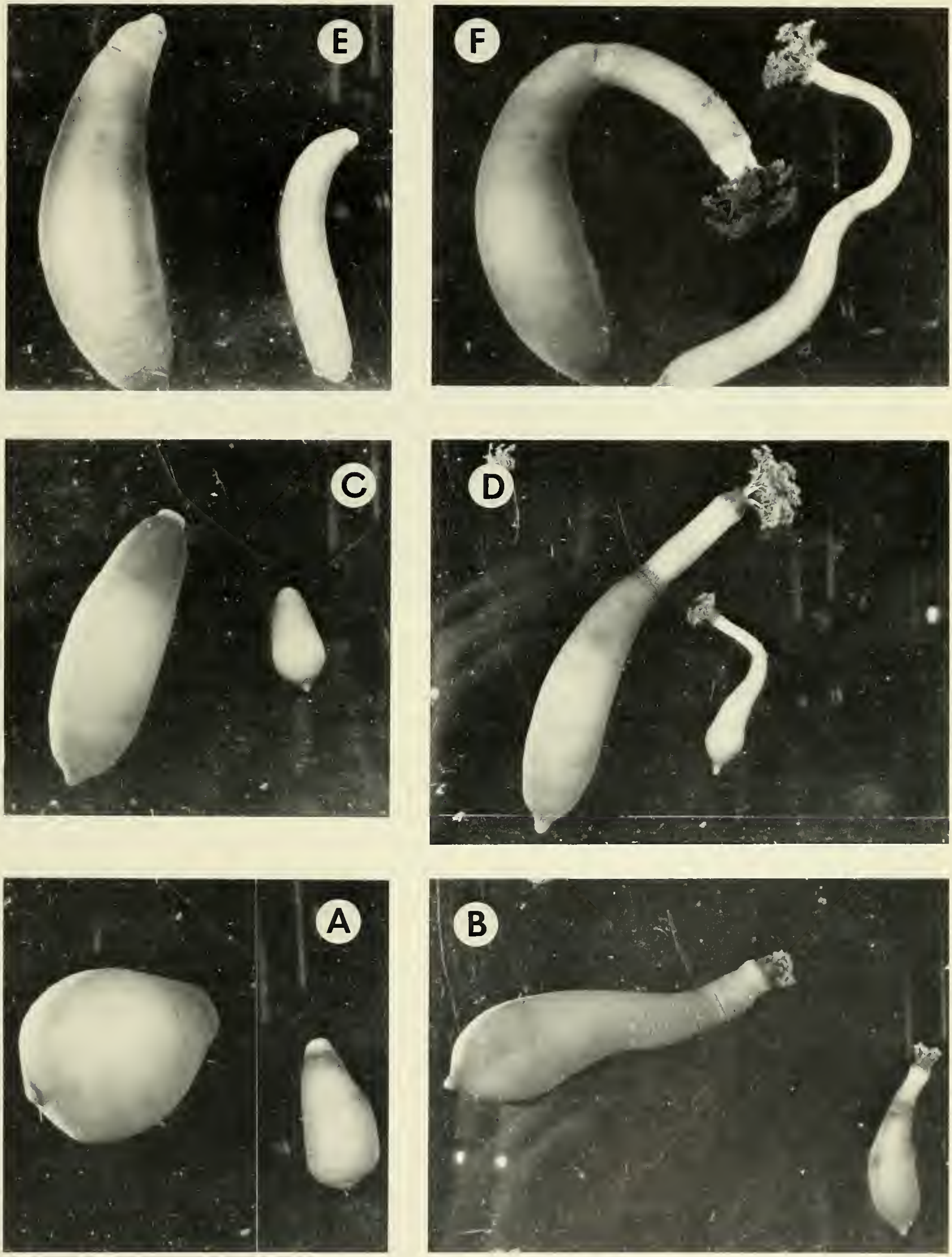

Fig. 6. Comparison of fully contracted (A, C, and E) with extended (B, D, and F) body shape in three pairs of living worms from different Californian microhabitats: A–B. *T. dyscrita* from boring mollusc (pholid) holes in shale at Santa Barbara; C–D. Same species from burrows in sandstone at Santa Cruz; E–F. *T. hennahi* from coarse sand at Santa Barbara.

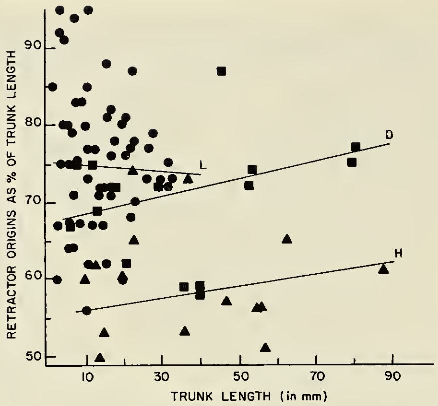

Fig. 7. Introvert retractor muscle origins on body wall as percentage of trunk length towards the posterior end in three species. Circles are *T. lageniformis,* squares are *T. dyscrita,* triangles are *T. hennahi.* This is not a size related character (all values for b (linear regression) are less than 0.1).

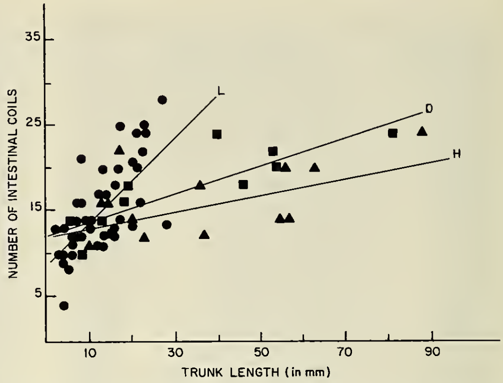

Fig. 8. Number of intestinal coils showing varying increases in number with increase in size for the same species as Fig. 7. The positive slopes (b in the linear regression) are 0.5, 0.16 and 0.09.

own analysis shows variation within populations (some lacking the full complement or the insertion of F2 being at different points and sometimes branched with several points of attachment). Therefore, as this variation also overlaps among species, it can only be used in a general manner.

7. *Retractor muscle origins.*—In adults one pair of muscles functions to retract the introvert into the trunk. These muscles have their origins on the body wall on either side of the ventral nerve cord and insert in the cephalic region. The anterior/posterior location of these origins has sometimes been used by systematists to describe a species using phrases like "in the middle third" or "in the last quarter." One must also determine whether the author is talking about the whole body (including the introvert) or just the trunk when giving measurements. In order to standardize these data we record it as a percentage of the trunk length using the nephridiopores to mark the anterior border of the trunk. Our analysis shows that the vast majority of individuals have their retractor origins from 60–80% of the distance towards the posterior end. In two California populations that we examined (*T. dyscrita* and *T. hennahi*), there is a smaller size related shift in the point of origin than that noted in other genera (Fig. 7). As this figure shows *T. dyscrita* is generally more anterior than *T. hennahi,* which is more anterior than *T. lageniformis.* The linear regression is a very poor fit because of much overlap, especially in smaller worms, and so much scatter of the data points.

8. *Number of intestinal coils.*—As in other genera the number of coils is directly correlated with the size of the worm: commonly 12 to 24 coils (Fig. 8). One apparent exception to this is: some larger individuals (over 200 mm) in the California population of *T. hennahi* may have more than 80 coils. Four species seem to have irregular, loosely wound gut coils; however, since we find much within-deme variation and overlap among species, this is not a useful character.

9. *Pigmentation on tentacles and introvert.*—Some species have dark bluish pigment in a collar-like band around the introvert and others have dark purple/blue pigmented patches on the tentacles (Fig. 9). The presence or absence of the dark collar on the introvert is consistent. Pigment on the branches is inconsistent, but its presence or absence on the tentacules of certain species is reliable and helpful to the systematist.

10. *Papillae size and shape.*—As with

Fig. 9. Distal introverts of two species; *T. dyscrita* on left with pigmented collar region and pale tentacules; *T. hennahi* on the right with unpigmented collar and dark tentacules.

other genera, these worms have glandular secretory papillae on the introvert and trunk. These are more numerous and larger near both ends of the trunk. While some authors have used the size and/or shape of these bodies to distinguish species we do not concur. The morphology of these papillae is simply too variable to be useful.

11. *Spindle muscle.*—As in other sipunculans, a thread-like muscle runs through the center of the gut coil, connected along its length to help anchor the intestinal coils. It originates anteriorly in all genera but does not insert on the body wall posteriorly in this genus. Some authors have described it as terminating on the rectum in certain species. After carefully analyzing this character, we conclude that all *Themiste* species are similar: after originating from the body wall anterior to the anus it appears to become part of the rectal wall, is difficult to trace but can be seen posteriorly attached to the caecum before entering the gut coil.

Summary.—Of these characters, the type of contractile vessel villi, branching pattern of the tentacular crown, and the origin and insertion of F1 are useful at the subgeneric level only. The presence or absence of hooks, trunk size and shape, pigmented collar on the introvert, and tentacule pigmentation can be useful at the species level. The remaining characters exhibit too much within-deme variation or among species overlap to have value for the systematist.

Key to *Themiste* Species

1\. Contractile vessel with numerous (more than 40) short digitiform villi (subgenus *Lagenopsis*) 2

— Contractile vessel with few (less than 20) long thread-like tubular extensions (subgenus *Themiste*) 6

2\. Introvert without hooks 3

— Introvert bearing dark scattered hooks 5

3\. Small (trunk <35 mm); introvert with purple "collar"; lives in hard substrates .... *T. lageniformis*

— Large (trunk commonly >40 mm); unpigmented introvert "collar"; lives in sand/mud 4
4. Trunk pyriform; undivided tentacle stems of equal length and less than 4% of trunk length .... *T. cymodoceae*
— Trunk elongate, cylindrical; undivided tentacle stems longer (>4.5% of trunk) and of unequal length (dorsal pair longer than ventrals) .... *T. dehamata*
5. Introvert hooks oriented posteriorly; 50–100 μm tall .... *T. minor*
— Introvert hooks point in all directions; 30–400 μm tall .... *T. variospinosa*
6. Introvert without hooks 7
— Introvert bearing dark scattered hooks 8
7. Introvert collar purple; tentacules white; lives in rocks .... *T. dyscrita*
— Introvert collar unpigmented; tentacules with pigment spots; lives in unconsolidated sediments .... *T. hennahi*
8. Introvert collar unpigmented; tentacules with pigment spots; Atlantic Ocean .... *T. alutacea*
— Introvert collar purple; tentacules unpigmented; Pacific Ocean 9
9. Tentacular crown appears to have 6 stems; many subdivisions of branches, tentacules mainly at distal tips .... *T. pyroides*
— Tentacular crown with 4 stems each dividing once to give 8 branches; tentacules appear all along branch .... *T. blanda*

Taxonomic Section

Genus *Themiste* Gray, 1828

Type species.—*Themiste hennahi* Gray, 1828 by monotypy.

Diagnosis.—Introvert shorter than trunk; body wall with continuous muscle layers; oral disc carries tentacles basically surrounding mouth but extending with growth along margins of branching stemlike outgrowths of oral disc; with or without hooks; two introvert retractor muscles; contractile vessel with villi or tubules; spindle muscle not attached posteriorly; two nephridia; species small to large sized (adults 4–400 mm).

Subgenus *Themiste* (*Themiste*) Edmonds, 1980

Diagnosis.—Contractile tubules (villi) few (less than 20), long and threadlike.

Within this subgenus one finds two subsets: those with and those without hooks as adults. The two species lacking hooks live in the eastern Pacific Ocean. The three species that bear hooks are similar to one another. Two of these live in the mid latitudes of the northern Pacific Ocean, and one lives in the western Atlantic.

Those without hooks:

Themiste dyscrita (Fisher, 1952)

Dendrostomum dyscritum Fisher, 1952:417–419, fig. 87 B–E; pl. 30, fig. 3, pl. 34.
Themiste dyscrita.—Stephen & Edmonds, 1972:199.—Oglesby, 1968:155–177.—Foster, 1974:856.—Rice, 1980:493–494.

Material examined.—USNM, Fisher's California material (holotype, 21221; and 21538, 27680, 27682) and Rice's Oregon specimens (35935); SBNH, Hollister Ranch (42496M); our 1987 Santa Barbara and Santa Cruz, California material.

Discussion.—Purple pigment on the smooth "collar" region just behind the tentacles but lacking pigment on the tentacules distinguishes this species from *T. hennahi.* The nephridiopores commonly open 2–3% of the trunk length posterior to the anus. Fixing muscle F2 is more often (but not always) found on the rectum and the retractors commonly originate at 65–75% of the distance to the posterior end of the trunk. Another difference from *T. hennahi* is its subspherical trunk. *T. dyscrita*'s ecology is also different; it lives in burrows made by other animals, commonly pholid bivalves, in intertidal shales or sandstones. It does not appear to coexist with the hooked *T. pyroides,* which may live in the same bay but occupies a different niche. The body color ranges from pale cream in small worms to dark brown in larger ones.

Distribution.—The U.S. west coast from Oregon to southern California at intertidal depths (one record at 18 m).

Themiste hennahi Gray, 1828

Themiste hennahi Gray, 1828:8, pl. 6, figs. 4, 4a.—Baird, 1868:98.—Stephen, 1964: 458; 1967:92–94.—Rice & Stephen, 1970: 53–56.—Amor, 1970:495–504; 1975:21–23.—Stephen & Edmonds, 1972:201–203.—Tarifeno, 1975:251–266; 1976:29–37.—Tarifeno & Rojas, 1978:118–119.

Dendrostomum lissum Fisher, 1952:419–422, pl. 35.

Themiste lissa.—Stephen & Edmonds, 1972: 206.—(Not Cutler & Cutler, 1979a:966–967).

Dendrostoma mytheca Chamberlin, 1920: 30.

Dendrostoma perimeces Fisher, 1928:196–198, pl. 6, figs. 3, 3a, pl. 7, fig. 1, pl. 8, figs. 2, 2a; 1952:415–417.—MacGinitie, 1935:631–682.

Themiste perimeces.—Stephen & Edmonds, 1972:207–209.

Dendrostoma peruvianum Collin, 1892:179–180.—Fischer, 1914b:12–13.

Dendrostomum peruvianum.—Wesenberg-Lund, 1955:12–13.

Dendrostomum ramosum Quatrefages, 1865:629.—Leroy, 1936:425.

Themiste ramosa.—Baird, 1868:98.—Stephen & Edmonds, 1972:340 (in list of incertae sedis, etc.).—Saiz Salinas, 1984: 184–185.

Sipunculus (*Aedematosomum*) *rapa* Quatrefages, 1865:627.—Saiz Salinas, 1984: 172–173.

Phascolosoma rapa.—Baird, 1868:86.

Dendrostomum schmitti Fisher, 1952:422, fig. 87F.

Themiste schmitti.—Amor, 1970:499.—Stephen & Edmonds, 1972:212.

Dendrostoma zostericolum Chamberlin, 1920:30.—Peebles & Fox, 1933:201.

Dendrostomum zostericolum.—Fisher, 1952:411–415, pl. 30, fig. 1, text-fig. 87A, pls. 31–32.—Gross, 1954:403–423.

Themiste zostericola.—Stephen & Edmonds, 1972:213–214.—Rice, 1980:493.

Material examined.—BMNH, paralectotype (1965.16.2/5); RSME, two Peru specimens identified by Stephen (1965.27.2); our own 1987 Santa Barbara and Monterey Bay, California material. *T. lissa*: USNM, Fisher's holotype (21222) and (27671). *T. perimeces*: USNM, Holotype (19615), paratype (21547), and other California material (26446, 27612); SBNH (42493, 42494, 47660); specimens at Moss Landing Marine Lab. *D. peruvianum*: MNHU, Collin's syntypes (Nr. 2087); ZMUH, Fischer's from Chile (V6184). *D. ramosum* and *D. rapa*: MNHN, Quatrefages' types (V25). *T. schmitti*: USNM, Fisher's holotype (21216), paratypes (21217). *T. zostericola*: MCZH, type (2181; this is a dried up bag of skin and of no value); SBNH (47662); USNM, Fisher's Baja material; many Californian specimens collected for us by Pacific Bio-Marine.

Discussion.—*Themiste hennahi* is an eastern Pacific taxon inhabiting intertidal gravely to silty sand (including mud flats, eel grass beds and between and under turnable boulders). Trunks are commonly 25–100 mm long (occasionally up to 200 mm, rarely larger) with a slender pyriform to cylindrical shape sometimes with a nipple-like posterior end. The introvert retractors commonly originate at 50–60% of the trunk length (Fig. 7) and the introvert is without a pigmented collar. The careful redescription by Rice and Stephen (1970) is well illustrated. Tarifeno (1975) gives detailed ecological and behavioral information. The tentacular crown is asymmetrical, with the dorsal pair being longer and splitting sooner than the ventral pair giving the appearance of six stems. The nephridiopores open 0–10% of the trunk length posterior to the anus, in larger worms this distance is usually less than 2%.

The 18 syntypes of Collins' *T. peruvianum* (reduced to junior synonym by Stephen 1964) all had pyriform trunks with the posterior end coming to a blunt point. The spindle muscle is very strong, and in a few this seems to be contracted along the rectum giving the latter an accordion pleated look. This population allegedly has protuberances on the esophagus. However, we see only a few bumps, which easily rub off and appear to be agglutinated gametes adhering to the esophageal wall.

Quatrefages' (1865) two species (*T. rapa* and *T. ramosum*) were considered incertae sedis until the reconsideration by Saiz-Salinas (1984) wherein he determined them to be synonyms of this species.

When Rice & Stephen (1970:56) redescribed this species, they made the following statement: "*Themiste hennahi* also shows many similarities to the species described as *Dendrostomum zostericolum* Chamberlin 1919 and *Dendrostomum schmitti* Fisher 1952. The possibility that these may all represent a single species remains to be determined by future studies." We are unable to find any truly meaningful characters that would serve to differentiate these species. Therefore, we reluctantly agree with their suggestion and place the familiar *T. zostericola* in synonomy. The apparent gap in distribution (Peru to Baja California) may be an artifact of undercollection in Central America, but we discarded the possibilty of subspecific rank. The small ones look different from the large ones, but, when one fills the gap with middle sized worms, the continuum becomes clear.

Fisher's *T. perimeces* was originally differentiated from *T. zostericola* by having more gut coils, fixing muscles usually absent, papillae of two or three sizes, and fewer contractile vessel villi. Our examination of Fisher's material (some not previously dissected) and other California specimens demonstrated that this dichotomy is artificial. At least one fixing muscle is present in almost every worm. There are usually 8–14 contractile vessel tubules, but one 9 mm worm has only four, so this, as well as both papillae size and number of gut coils, is somewhat age dependent. Variation exists and the worms bearing this name are simply large *T. hennahi.* Rice (1980) in the most recent general treatment of the California fauna did not include *T. perimeces.*

Themiste lissa is not well known (our total sample size is 19) and the putative differences from *T. hennahi* are subtle. Fisher (1952:422) comments on the close relationship between this taxon and his new *T. schmitti* (now considered a synonym of *T. hennahi*): ". . . possibly they represent the extremes of geographic variation of one species." We concur. In his key Fisher used the location of the gonads "on the surface of the retractors" vs. "on body wall just back of origins" to separate these two taxa. In our analysis of the *T. hennahi/peruvianum* and *T. lissa* material, we found the gonads to be located on the body wall, on the retractors, and on combinations of this in different worms but showing significant within-deme variation.

When Fisher asserted that *T. lissa* differed from the other Californian species (he did not mention *T. hennahi,* which had not been "rediscovered" at that time), he put considerable weight on the distance between the anus and the nephridiopores—he gave no measurements but stated that the distance was "conspicuous." In the holotype (with a 20 mm trunk) the distance is 10% of the trunk length, but in six of Fisher's paratypes (7–11 mm trunks) it varies from 4–7% (in one worm these are at the same level). In two recently collected specimens the distance was 12% in an 8 mm worm and 5% in an 11 mm worm. As noted in the introduction, this is not a species specific character.

Our present construct includes worms of

very different sizes from what may appear to be rather different habitats. The probability exists that some live in more optimal niches than others and that these can achieve a larger size. If a trend exists, it seems to be that the higher latitudes are better suited to this genotype. The smallest worms come from the Gulf of California, and this population may be isolated with restricted gene flow.

A reexamination of the two *T. lissa* from Durban (Cutler & Cutler, 1979a) showed them to be *Antillesoma antillarum.*

Distribution.—Chile and Peru, Gulf of California and California; unconsolidated intertidal or shallow subtidal sediments. Quatrefages' *T. ramosa* specimens are labeled, "Qf. du Bresil M. Pissis," but we are hesitant to accept this as a valid location as there have been no 20th century confirmations outside the eastern Pacific.

Those with hooks:

Themiste alutacea (Grube & Oersted, 1858)

Dendrostomum alutaceum Grube & Oersted, 1858:118.—Quatrefages, 1865:630.—Diesing, 1859:765.—Keferstein, 1865: 438.—Selenka et al., 1883:84–85.—Fischer, 1895:18; 1922:18.—Gerould, 1913:417–418.—Leroy, 1936:425.

Themiste alutacea.—Baird, 1868:98.—Stephen & Edmonds, 1972: 196–197.—Cutler, 1973:162–164.—Cutler & Cutler, 1979b:105–106.—Rice, 1975a:37–47, 1975b:147.

Sipunculus (*Phymosomum*) *orbiniensis* de Quatrefages, 1865:622.

Phascolosoma orbiniense.—Baird, 1868: 93.—Stephen & Edmonds, 1972:339 (in list of incertae sedis etc.).

Themiste (*Themiste*) *orbiniensis.*—Saiz-Salinas, 1984:124–132.

Themiste blandum [sic].—Murina, 1968: 423.

Dendrostomum petricolum Amor, 1964: 463–467, pl. 3, 5 figs.

Themiste petricola.—Stephen & Edmonds, 1972:209.—Amor, 1975:185–192.

Dendrostomum rosaceum Amor, 1964:459, pls. 1, 2 and 3.

Themiste rosacea.—Stephen & Edmonds, 1972:211–212.

Material examined.—MNHU, Grube's type (1033) plus some of Selenka's from Brazil; other material from North Carolina (Cutler, 1973) and M. Rice's Florida material. *T. orbiniensis*: MNHN, Quatrefages' material (V25). *T. rosacea* and *T. petricola*: USNM, paratypes (30995, 30996). *T. blanda*: ZIAS, Murina's Gulf of Mexico specimens.

Discussion.—This warm water, western Atlantic species inhabits hard substrates (spaces in coral, oyster beds or soft rock), is small (trunk rarely over 25 mm, commonly less than 15), and exhibits indirect development. As an early juvenile it has a single ring of introvert hooks, but these are soon lost and replaced by scattered adult hooks. We have sufficient data on this species (Rice 1975b) to assert that early in a worm's life four tentacular stems exist; two of these often subdivide near the base to give the appearance of six (sometimes five) in many adult worms. This is different than the four dividing into eight seen in *T. blanda.* The subsequent branching of these primary units is limited in the smaller worms, and the thin tentacules (with pigment spots) are located all along each branch. The hooks in this species can be numerous (over 100 in one 5 mm worm) but not as large as in other members of this subgenus (75–150 μm). This species has lecithotrophic pelagic larvae, i.e., indirect development (Rice 1975b).

Themiste rosacea and *T. petricola* were described from Argentina, and, while we have not been able to obtain additional material, our examination of the literature and the paratypes convinces us that these three putative taxa are not biologically distinct. The presumed differences are in the number of tentacles, the number of hooks, the size, shape and color of the trunk, and the position of the fixing muscles. As noted in the Introduction, these characters are too variable to be meaningful. While gene flow may be restricted and subspecific status might be appropriate, we cannot discern consistent and meaningful morphological differences.

Our examination of Murina's Gulf of Mexico worms convinced us that they belong to this taxon. The hooks in this population are larger, measuring up to 300 μm. Saiz-Salinas (1984) presented a detailed redescription of Quatrefages' *T. orbiniensis* and a comparison to others in this group. Towards the end of his discussion, he noted that a future comparative study of specimens may result in the synonymizing of Quatrefages' name. When Amor examined this material in 1969, she left a note in the bottle that she thought it was *T. alutacea,* and our analysis of all available information brings us to the same conclusion.

Distribution.—Western Atlantic Ocean from North Carolina (34°N) to Argentina (42°S) at depths less than 30 m.

Themiste blanda (Selenka, deMan, & Bulow 1883)

Dendrostomum blandum Selenka et al., 1883:85–86, pl. 1, fig. 9, pl. 11, figs. 159–162.—Selenka, 1885:14.—Ikeda, 1904: 53–55; 1924:30–31.—Ostroumov, 1909: 319–324.—(Not Fischer, 1922:18–19)—Sato, 1930:24–28; 1937:162; 1939:412.—Fisher, 1952:405.

Themiste blanda.—(Not Murina, 1968: 423)—Stephen & Edmonds, 1972:197.—Cutler, Cutler & Nishikawa, 1984:285.

Material examined.—MNHU, type and paratype (962, 1034); Our 1979 Japanese material.

Discussion.—In Cutler et al. (1984:285) we noted ". . . what has been called *T. blanda* may be simply small *T. hexadactyla.*" Our current studies cast some doubt on that hypothesis and we now consider *T. hexadactyla* to be a junior synonym of *T. pyroides.* While acknowledging the very similar nature of this taxon and the other two hooked members of this subgenus, we retain *T. blanda* as a distinct species for the present. It differs from *T. pyroides* in two ways: 1. Tentacular crown—this array is simpler with four tentacular stems, each dividing only once, and it has longer tentacules along each branch giving each branch a somewhat pinnate appearance. 2. The upper limit of trunk size seems to be about 25 mm (vs. 200 mm). The similarities are marked and some of the alleged differences referred to by earlier authors (such as fixing muscle arrangements) are not constant enough to be meaningful. The similarities to *T. alutacea* are also marked, but it differs by having four stems dividing symmetrically into eight, lacking pigment spots on its stouter tentacules, and by living in cool northern Pacific water vs. warmer western Atlantic water.

Distribution.—Intertidal in Honshu and Hokkaido, Japan.

Themiste pyroides (Chamberlin, 1920)

Dendrostoma pyroides Chamberlin, 1920: 31.—Fisher, 1952:406–409.

Themistse pyroides.—Stephen & Edmonds, 1972:210.—Rice, 1967:143–171; 1980: 492–493.—Frank, 1983:22.

Dendrostoma blandum.—Fischer, 1922:18–19.

Dendrostoma petraeum Fisher, 1928:195–196.

Dendrostoma hexadactylum Sato, 1930: 28–33, pl. 4, figs. 20–24, text-figs. 13–15; 1937:162–163; 1939:412.—Okuda, 1946: 224.

Dendrostomum hexadactylum.—Fisher, 1952:410–411, pl. 30, fig. 2.

Themiste hexadactyla.—Stephen & Edmonds, 1972:203–204.—Cutler & Cutler, 1981:75.—Cutler, Cutler & Nishikawa, 1984:285–286.

Material examined.—MCZH, Chamberlin's type (2.182) and paratype (2.183); USNM, several of Fisher's California specimens (21503, 21548), a few from Vancouver, B.C. identified by M. Rice (96094); our

1987 Carmel and Monterey, California specimens. *T. hexadactyla*: ZITU, type (G26) plus other Sato material (1–4, 1–5, 4–11, 5–11, 5–15; one now at USNM, 59994); USNM, Fisher's California specimens (21504, 27672).

Discussion.—This taxon is similar to the two previous species but does have a pyriform shape with a bluntly pointed posterior end regardless of size (Fig. 10). The morphological distinction we now affirm is; four primary tentacular stems divide close to their base into 2, 3, or 4 branches, each then subdividing, as the worm grows, into smaller branches giving off unpigmented tentacules mostly at the distal ends. In specimens the same size as a given *T. blanda* or *T. alutacea,* the crown of *T. pyroides* is much more voluminous with shorter terminal tentacules. Whereas many specimens from central California have trunks 20–40 mm long, some worms from the more northern latitudes (British Columbia and Hokkaido) may exceed 100 mm. The fixing muscle placement is not as constant as Fisher (1952) implies nor is the anastomosing network of contractile vessel branches as clearcut or consistent. In 12–14 mm worms only 8 or 10 long tubules are at the terminal end of the vessel, while in a 23 mm worm one sees branches off the main vessel adhering to the sides of the esophagus. In a 40 mm worm these branches are more elaborate and surround the esophagus. This network becomes much more complex in an 80 mm worm, much like that shown in Fisher's (1952) plate 29, fig. 3.

Distribution.—Honshu and Hokkaido, Japan and west coast of North America from southern Alaska to Baja California at intertidal depths.

Subgenus *Themiste* (*Lagenopsis*)
Edmonds, 1980

Diagnosis.—Contractile vessel villi many (more than 100), short and digitiform.

Two subsets exist in this taxon, those species with and without introvert hooks. Within the hookless triad is one common circum-subtropical inhabitant of hard substrates, *T. lageniformis,* which has a long list of junior synonyms. The other two species seem to be endemic to Australia living in soft substrates. The hooked subset also has two taxa endemic to Australia and one more widely spread subtropical taxon.

Fig. 10. *Themiste pyroides* of different sizes showing typical pointed pyriform trunks, hooks on introverts and voluminous tentacular crowns.

Those without hooks:

Themiste cymodoceae (Edmonds, 1956)

Dendrostomum cymodoceae Edmonds, 1956:299–301, pl. 2, fig. 1, text-figs. 15–16; 1957:55–63.—Åkesson, 1958:147–151.

Themiste cymodoceae.—Stephen & Edmonds, 1972:197–198.—Edmonds, 1980: 38–40.

Material examined.—Three specimens (79–85 mm trunks) from the type locality from collections of S. J. Edmonds.

Discussion.—This species is similar to *T. dehamata* in many ways (e.g., pigmented tentacules but unpigmented collar), and we have reservations about its distinct status. However, S. J. Edmonds (pers. comm.) has collected and observed these in the living state and feels strongly that they are different species. The differences we can agree on are not sharp or easily quantified. The trunk in *T. cymodoceae* is flask shaped or pyriform (length 50–90 mm but less than five times the width) whereas *T. dehamata* is slender and elongate (length at least 10 times width). The second morphological difference has to do with the tentacular crown. In *T. cymodoceae* the tentacular stems are shorter (2.5–4% of trunk length) and are of equal size (giving it a bushy appearance). In *T. dehamata* the stems are longer overall (4.5–7% of trunk length) and in each worm the dorsal stems are longer than the ventrals by 25–67% (Edmonds describes this as plumose). The niches of these two species *may* differ; however, they have both been collected from among the roots in intertidal eel grass beds (Edmonds, 1980).

Distribution.—South Australia; intertidal unconsolidated sediments.

Themiste dehamata (Kesteven, 1903)

Dendrostoma dehamatum Kesteven, 1903: 69–73, pl. 7, fig. 7.

Dendrostomum dehamatum.—Edmonds, 1956:296.

Themiste dehamata.—Stephen & Edmonds, 1972:198–199.—Edmonds, 1980: 34–36.

Dendrostoma ellipticum Sato, 1934:20–22, pl. 1, fig. 10, text-figs. 22–25; 1939:411.

Themiste elliptica.—Stephen & Edmonds, 1972:199–200.—Cutler & Cutler, 1981: 74–75; Cutler, Cutler & Nishikawa, 1984: 283.

Dendrostomum fisheri Amor, 1964:467–469, pl. 3 and 4.

Themiste fisheri.—Stephen & Edmonds, 1972:200.

Material examined.—Four specimens from near the type locality from the collections of S. J. Edmonds.

Discussion.—This taxon was recently redescribed by Edmonds (1980). Whereas the written description resembles *T. lageniformis* (see preceding section for comparison to *T. cymodoceae*), it is distinct in several ways. *Themiste dehamata* is more cylindrical, elongate, larger (commonly over 40 and up to 170 mm), and lives in sand or mud habitats.

Sato's (1934) *D. ellipticum* was based on a single 64 mm worm, which cannot now be located. Although Sato did not comment on the contractile vessel villi branching (and his drawing is not sufficiently detailed), Fisher (1952) asserted that they were unbranched, and, therefore, it was distinct from similar species. Sato differentiated it from others with short villi on the basis of papillae shape (elongate elliptical in this and roundish in others including *T. dehamata*). In Stephen & Edmonds' key (1972) they were unable to differentiate these two species. As suggested in Cutler & Cutler (1981) there now seems no justification for retaining this species name.

Edmonds (1980:35) first suggested that *T. fisheri* is very similar to this species. The only "significant" difference, according to him, is the absence of a rectal caecum in *T. fisheri*; however, Amor stressed the different number of tentacular stems. Amor's species rests on a single 100 mm specimen, which we have tried unsuccessfully to obtain for examination. Having only this one worm with only these minor differences, we hereby reduce it to a junior synonym.

Distribution.—New South Wales and South Australia; intertidal unconsolidated sediments. Because of our synonymies, one record is from Japan and one from Argentina. Since these latter specimens cannot be examined, we would caution against including them in zoogeographical analyses.

Themiste lageniformis Baird, 1868

Themiste lageniformis Baird, 1868:98–99, pl. 10, fig. 3.—Rice & Stephen, 1970:66–67.—Stephen & Edmonds, 1972:205–

206.—Cutler, 1977a:147.—Williams, 1977:1–206.—Cutler & Cutler, 1979a: 966.—Edmonds, 1980:41–42.—Pilger, 1982:143–156.—Cutler, Cutler, & Nishikawa, 1984:283–284.

Dendrostoma signifer Selenka et al., 1883: 86–87 (part).—Sluiter, 1886:515; 1891: 115; 1902:19.—Fischer, 1895:17; 1914a: 72–74; 1914b:10–11 (part); 1919:282–283 (part); 1922:19 (part); 1923:22.—Augener, 1903:300–301.—Ikeda, 1904:56–57.—Hammerstein, 1915:2–3.—Graveley, 1927:87.—Awati & Pradhan, 1935: 102–113; 1936:114–131.—Leroy, 1942: 41–43.

Dendrostomum signifer.—Edmonds, 1956: 297.—Wesenberg-Lund, 1959a:198–199; (Not 1959b:213; 1963:129–130).

Dendrostoma minor.—Chin, 1947:100.

Dendrostoma robertsoni Stephen & Robertson, 1952:438–439, pl. 1, figs. 3–4.

Dendrostomum robertsoni.—Wesenberg-Lund, 1963:130.

Themiste robertsoni.—Stephen & Edmonds, 1972:210–211.—Stephen & Cutler, 1969:116.—Cutler & Cutler, 1979a: 967–968.

Dendrostoma stephensoni Stephen, 1942: 252–253 (part).

NOT *Themiste stephensoni.*—Cutler, 1977b: 154.

Dendrostoma tropicum Sato, 1935:313–315, pl. 4, fig. 15, text-fig. 11; 1939:411.

Dendrostomum tropicum.—Wesenberg-Lund, 1963:131–132.

Themiste tropica.—Stephen & Edmonds, 1972:213.—Cutler, 1977b:154.—Cutler & Cutler, 1981:76–77.—Murina, 1981:16.

Phascolosoma glaucum Lanchester, 1905a: 32, pl.1, fig. 3.

Golfingia (*Thysanocardia*) *glauca.*—Stephen & Edmonds, 1972:123.—Cutler, 1977b:152.

Themiste glauca.—Gibbs, Cutler, & Cutler, 1983:302.

Phascolosoma pyriformis Lanchester, 1905b:39, pl. 2, fig. 5.—Sato, 1939:404–406.

Golfingia pyriformis.—Murina, 1964:261; 1967:43.

Golfingia (*Thysanocardia*) *lanchesteri* pro *Phascolosoma pyriformis* Lanchester, 1905b (pre-occupied by *Phascolosoma pyriforme* Danielssen in Théel 1875): Stephen & Edmonds, 1972:124.

Themiste pyriformis.—Gibbs, Cutler, & Cutler, 1983:302.

Material examined.—BMNH, syntypes (165.25.9/10); BPBM, Hawaiian collections (N101, 1973.205); Naval Oceans Systems Center, Kailua (at BPBM) and our 1984 Hawaiian worms plus Sta. 87 from Ft. Pierce, FL in the collections of M. Rice. *D. signifer*: ZMUH, Type (V2052); MNHU (384, 982). *T. robertsoni*: RSME, type (1958.23.74); UZMK, Wesenberg-Lund's; our own from Indian Ocean. *D. stephensoni*: RSME, type (1958.23.34) plus (1958.23.35, 37, 38; 1966.1.10). *T. tropicum*: Galathea Sta. 256 in our collections; the type cannot be located. *G. glauca*: UZMC, type; UZMK, Galathea Sta. 630, 631; *G. pyriformis*: UZMC, type material; ZITU, Sato's from Formosa (3–13).

Discussion.—This is the most common, most studied, and most widely distributed species in the genus. Baird's original description (1868) of this species was overlooked by Selenka and others for almost a century. Williams (1972, 1977) and Williams & Margolis (1974) have contributed to an understanding of its burrowing habits and its development (indirect with pelagic larvae). Pilger (1987) has demonstrated that this species may also be parthenogenic. The nature of this species has been fairly clear over the years with two exceptions. Several authors confused the issue by including some animals with introvert hooks. These are now considered to be *T. minor huttoni,* a taxon remarkably similar to this one except bearing hooks. Wesenberg-Lund (1963) reported the presence of two or three *rows* of hooks in two worms from Tristan de Cunha. We have not been able to locate these specimens and are reluctant to assign them to this genus because of the hook arrangement and her lack of comment on the tentacular crown. The alleged number of tentacular stems: 4, 5, 6 or 8 has also added to the confusion (see Morphological Characters).

When Stephen & Robertson (1952) described *T. robertsoni,* they differentiated it from this species on the basis of number of tentacular stems plus a few other points such as number of fixing muscles, length of retractors, number of contractile vessel villi, etc. That model was followed by a few other authors, but, as pointed out by Cutler & Cutler (1979a), the differences are subjective. Our current reexamination of this material indicates that these particular characters are within the range found in one *T. lageniformis* population.

While the holotype and some of Stephen's (1942) material of *T. stephensoni* are *Golfingia capensis* (Gibbs & Cutler 1987, Cutler & Cutler 1987), four specimens are *T. lageniformis.*

The original foundation for *T. tropica* was one 14 mm worm (Sato 1935). He did not compare it to this species since he incorrectly said it (*D. signifer* at that time) had long contractile vessel villi. Wesenberg-Lund (1959b) reported two worms from 90–110 m in the northern Gulf of Guinea. We could not find these in any museum collections, and, since these are the only records from this part of the Atlantic, we are skeptical. A careful reading of her description suggests that these are more probably two *Thysanocardia catharinae.* She later (1963) recorded three small (5–10 mm) worms from Capetown. There were a few puzzling aspects to her paper including rings of hooks and an apparent contradiction (key vs. text) about whether or not the villi were branched, a matter now known to be size dependent, not species specific. Without access to these worms we cannot reassign them with confidence, but they are in the *T. minor* group. Cutler's (1977b) and Murina's (1981) worms were all less than 20 mm long, and nothing would exclude them from our present concept of *T. lageniformis* (i.e., some unbranched contractile vessel villi in small specimens). Now it is clear that *T. tropica* should be considered a junior synonym.

The confusion created by Lanchester's (1905*a,b*) two species (*Phascolosoma glauca* and *P. pyriformis*) has been addressed in Gibbs et al. (1983) when they revised the golfingiid subgenus now genus) *Thysanocardia.* At that time it was recognized that these two taxa belong in *Themiste,* but they were not assigned to any different species in anticipation of the present work. All of Lanchester's specimens and some of Sato's (1939) *T. pyriformis* were highly contracted so that the anus and nephridiopores were withdrawn (both said "on the introvert"—a feature also noted by Murina (1964)). In some of our strongly retracted recently collected Hawaii material, the anus and nephridiopores were withdrawn, giving the false impression of being on the introvert (see section on Morphological Characters). Since we now find no significant differences, we submerge both names under *T. lageniformis.*

Themiste lageniformis is one of the smaller species (rarely more than 35 mm) which lacks hooks (after early juvenile stages), usually lives in soft rock, old coral or mussel beds, has a bluish band or collar on the introvert (sometimes very pale), and long tentacules.

Distribution.—Well established in the western Pacific (from Japan to Australia and Hawaii) and throughout the Indian Ocean. It has been recorded from South and Southwest Africa, Cuba, and Florida.

Species with hooks:

Themiste minor minor (Ikeda, 1904)

Dendrostoma minor Ikeda, 1904:57–59, text-figs. 16, 92–95.—Sato, 1939:411.—Stephen, 1942:252.—(Not Chin, 1947: 100).

Dendrostomum minor.—Wesenberg-Lund, 1963:128–129.

Themiste minor.—Stephen & Cutler, 1969: 116.—Stephen & Edmonds, 1972:207.—Cutler, 1977a:147.—Cutler & Cutler, 1979a:967; 1980:206; 1981:75–76.—Cutler, Cutler, & Nishikawa, 1984:284–285.

Dendrostoma signifer.—Fischer, 1914b:10–11 (part); 1919:282–283 (part); 1922:19 (part).

Dendrostomum fuscum Edmonds, 1960: 165–167, pl. 3, figs. 7–9.

Themiste fusca.—Stephen & Edmonds, 1972:200–201.—Edmonds, 1980:40–41.

Golfingia coriacea.—Murina, 1972:298.

Material examined.—ZMUT, Ikeda's type material was located but is completely dried out; RSME, Stephen and Cutler's South African worms (1966.1.9); our 1979 Japanese material from near the type locality (neotype named in Cutler and Cutler, 1981; part deposited at USNM). *T. fuscum*: two Australian worms from the collections of S. J. Edmonds.

Discussion.—Except for the presence of introvert hooks (generally 50–200 μm tall) and a more loosely wound gut coil, this taxon is ecologically and morphologically similar to *T. lageniformis.* The animals are small, i.e., trunk length usually less than 20 mm and we have seen 4 mm worms which are sexually mature.

Edmonds' (1960) differentiated *T. fusca* from *T. minor* on the basis of presumed but vague differences in hook and papillae structure, attachment of esophagus and the arrangement of the contractile vessel villi. In 1980 Edmonds did say that it was hard to distinguish it from some Japanese *T. minor* but that the contractile vessel and fixing muscles in the Japanese worms seem simpler. From our analysis of the literature and the animals, we conclude that the differences Edmonds reported probably result from Ikeda's narrowly constructed description but are not biologically meaningful, i.e., this amount of variation does exist within demes (see section on Morphological Characters above).

Murina's 1972 record of a single 7 mm worm which she named *Golfingia coriacea* was attributed to this species by Edmonds (1980:29), and we concur. Chin's 1947 record includes the statement that there were no hooks on his material; we herein move Chin's record to *T. lageniformis.*

Distribution.—Japan, China, South Australia, southern Africa, and one record from southern Argentina. The latter record (Cutler and Cutler, 1980) is a 4 mm worm of uncertain affinity. It seems clear that this is a cool temperate, intertidal, and shallow subtidal species. The few deep water records are based on few, very small specimens and may represent either anomalies or confusion in station data. The Cutler (1977*a*) record at 4510 m should, therefore, be ignored in zoogeographical analyses.

Themiste minor huttoni (Benham, 1904)

Phascolosoma huttoni Benham, 1903:177–184.

Dendrostoma huttoni Benham, 1904:306–307.

Dendrostomum huttoni.—Edmonds, 1960: 164–165.

Themiste huttoni.—Stephen & Edmonds, 1972:204.—Cutler, 1977a:146.—Edmonds, 1980:36–38.

Dendrostoma signifer Selenka et al., 1883: 86–87 (part).—Augener, 1903:337.—Fischer, 1919:282–283 (part); 1926:206.

Material Examined.—RSME, 1958.23. 124; two from the collections of S. J. Edmonds.

Discussion.—In the years 1903–1904 Benham published one faunal index and two publications in which the name "*huttoni*" appears. The formal new species description was in the 1904 paper. This name is presented in a confusing context along with *Sipunculus aeneus* Baird, 1868 and *S. lutulentus* Hutton, 1879. The former has been synonymized under *Siphonosoma australe* (Edmonds 1961; Rice and Stephen 1970) and the latter placed on the list of incertae sedis (Stephen & Edmonds 1972).

Themiste minor huttoni is here considered a subspecies of a more cosmopolitan taxon with restricted gene flow between the two populations. The similarities to the nominate form are substantial. The differences we can identify are: Larger (trunk length may reach 55 mm), more hooks, and the hook bearing region extends over more (55–75 vs. 25–35%) of the introvert. These are not clear distinctions and may represent only a more optimal set of conditions and less wave action, inducing or permitting a different expression of the genotype (e.g., larger size and more hooks produced or fewer rubbed off, like the situation seen in the Californian/Japanese *T. pyroides*). This hypothesis needs testing.

Distribution.—Australia, New Zealand and Chatham Is.; intertidal, hard substrates.

Themiste variospinosa Edmonds, 1980

Themiste variospinosa Edmonds, 1980:42–43, figs. 62, 68, 69.

Material examined.—A specimen from the collections of S. J. Edmonds from the type locality.

Discussion.—The six worms upon which this species is based have many ecological and morphological similarities to *T. minor huttoni*. The principal difference lies in the nature of the introvert hooks (Fig. 3). They exhibit much greater variation in size on any given worm (30–400 μm tall) and are pointing in all directions, not just posteriorly. While this may be only a localized variation of the surrounding population of *T. minor huttoni,* we propose no change in its status at this time. We hope that additional material will be collected to more firmly test the validity of this taxon.

Distribution.—Queensland, Australia, intertidal coral.

Zoogeographical Summary

The most striking feature is how nonoverlapping the two subgenera are. The five *Themiste* (*Themiste*) species live in the western Atlantic, eastern Pacific and Japanese waters. Three of the five *T.* (*Lagenopsis*) are endemic to Australia/New Zealand, the fourth lives in the western Pacific Ocean and South Africa while the fifth is circum-tropical/subtropical (but absent in the eastern Pacific). Overlap of subgenera exists on Honshu (central Japan) where *T.* (*T.*) *blanda* and *T.* (*T.*) *pyroides* are found along with *T.* (*L.*) *minor.* Another case is the Caribbean (and east coast of Florida) where *T.* (*L.*) *lageniformis* and *T.* (*T.*) *alutacea* coexist. Southern Argentina may be a third such place, but at this time the data base is not large enough to use with confidence.

Secondly, like in many other genera, there is one very widespread species (the circumtropical *T. lageniformis*) while most others have rather restricted distributions. Finally, this genus is absent from the North Atlantic above Cape Hatteras on one side and West Africa on the other.

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A NEW SPECIES OF POLYCHAETE, *SCOLELEPIS ANAKENAE* (POLYCHAETA: SPIONIDAE) FROM EASTER ISLAND, SOUTH PACIFIC OCEAN, WITH ECOLOGICAL COMMENTS

N. Rozbaczylo and J. C. Castilla

Abstract.—A new species of Spionidae, *Scolelepis anakenae* from Easter Island, is described. *Scolelepis anakenae,* which closely resembles *Scolelepis chilensis* (Hartmann-Schröder) from the coast of Chile was the only polychaete species found in sand at Anakena beach during a macrofaunistic study. Comments about its distribution and population density in the intertidal zone are included.

Easter Island, Rapa Nui in the native language, is one of the most isolated points in the southeast Pacific Ocean (27°07′S, 109°22′W) and the easternmost outpost of the Indo-Pacific Region. It lies 2230 miles from South America; the nearest land to the west is the uninhabited atoll Ducie Island, 1250 miles away, and Pitcairn Island of the Tuamotu Archipelago, 290 miles farther west. Its marine fauna is of the highest biogeographic and evolutionary interest because of the remarkable degree of endemism of its shore fauna at the specific level considering that the island is not only very young (2.5 million years), but rather small, with an area of approximately 118 km^2 (Newman & Foster 1983).

Recently, Castilla & Rozbaczylo (1987) prepared a bibliographic review on the littoral marine invertebrate fauna of Easter Island. The polychaete fauna is only partially known. The papers of Chamberlin (1919), Fauvel (1936), and Kohn & Lloyd (1973) include most of the records from the island. About 60 species of polychaetes are known to occur intertidally on Easter Island. Most of them inhabit rocky shores, since the coastline of the island is formed by volcanic rocks with just a few sandy beaches. Hitherto, no research has been done on the polychaete fauna of the island's sandy beaches. On Anakena, one of the two principal sandy beaches on the island, the macrofauna was sampled quantitatively along a perpendicular sea transect. Among the specimens collected, a new and undescribed species of spionid of the genus *Scolelepis* was found. This increases the known species of spionid polychaetes on Easter Island to three, since *Prionospio* (*Minuspio*) *cirrifera* (Wirén) and *Tripolydora spinosa* Woodwick, were the only species previously known (Rozbaczylo 1985). The new species is described and ecological comments on its distribution and population density are included.

Type specimens have been deposited in the Museo Nacional de Historia Natural, Santiago (MNHN); Sala de Sistemática, Laboratorio de Zoología, Pontificia Universidad Católica de Chile, Santiago (SSUC); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and in the personal reference collection of the first author (NR).

Materials and methods.—Samples were collected on 16 Oct 1982 at Anakena beach (27°04′S, 109°20′W) during an expedition sponsored by the Tinker Foundation and the Pontificia Universidad Católica de Chile through the Project "The Chilean Oceanic Islands: Our Knowledge and Future Needs"

(Las Islas Oceánicas Chilenas: Nuestro Conocimiento y Necesidades Futuras). Two transects perpendicular to the sea front were laid on the eastern portion of the beach, 22 and 28 m long, extending from the top part of the berm down to the lower intertidal limit at low tide. The profile of the beach was determined according to the method of Emery (1961) and its slope was 1:20 m. Low tide (0.23 cm) occurred at 10.30 AM. Sampling stations were set every 4 meters along the transects. The samples, 0.1 m^2, were taken at each station using a square iron sampler of 31.6 cm, open at both ends, and introduced to a depth of 20 cm in the sand. The sand was removed with a spade and sieved through a 1.5 mm mesh screen. Samples were washed in sea water and the macrofauna retained in the mesh was fixed in 10% formalin, then transferred to 70% alcohol; polychaetes were preserved in 70% ethanol with glycerine added. No analysis of the sand was made. The density of polychaetes at each level was expressed as numbers per square meter, by extrapolating from the data obtained with the sampler. Scanning Electron Microscope (SEM) observations were made with a JEOL-25 II. Photographs and drawings of the new species were executed by the first author. Figures were prepared by means of a drawing tube on a Wild M-5 microscope.

Scolelepis anakenae, new species
Figs. 1, 2

Material examined.—Easter Island, Anakena Bay, 27°04′S, 109°20′W, along a transect in the intertidal zone, 16 Oct 1982, J. C. Castilla, coll. (numerous specimens); 7 Mar 1984, J. C. Castilla, coll., holotype (MNHM 80009); paratype (MNHN 80010); 62 specimens (SSUC 6481); 41 specimens (USNM 104937).

Diagnosis.—Body wider anteriorly, flattened dorsoventrally, with short segments; posterior region subcylindrical, with longer segments. Prostomium pointed anteriorly, extending posteriorly as cephalic ridge to anterior margin of setiger one; 2 pairs of eyes. Peristomium with low lateral wings partially surrounding prostomium and forming ventral ruffled surface; palps extending posteriorly to setiger 20–30. Parapodia biramous throughout, with ciliated sensory organs between rami. Cirriform branchiae beginning on setiger 2, partially fused with notopodial lamellae, with subterminal enlargements forming knobbed tips. Anterior neuropodial lamellae entire and rounded up to setiger 34–40; in posterior segments completely divided into elongated, thickened interramal lamellae and conical ventral lobe. Anterior notosetae and neurosetae all winged capillaries; bidentate neuropodial hooded hooks from setiger 35–37 to end of body; without notopodial hooks. Pygidium forming thick cushionlike pad.

Description.—Color in alcohol light tan or pale brownish. One of largest specimens 36 mm long, 2 mm wide, with 120 setigers; one of smallest individuals 18 mm long, 1.2 mm wide, with 86 setigers; maximum body width reached approximately at setiger 20. Body distinctly divided into 2 regions: fusiform anterior region with segments rather flattened and rectangular in cross section; posterior region of numerous more or less rounded segments; segments from anterior region shorter than those from posterior region; change from one region to other marked by appearance of neuropodial hooded hooks and modifications in parapodial structure and setal distribution.

Prostomium pointed anteriorly, wider subterminally, and extending posteriorly as cephalic ridge to anterior margin of setiger 1 (Fig. 1a). Two pairs of dark eyes in nearly straight transverse row, located on each side of thickened part of prostomial ridge, just behind slight depression at beginning of ridge; dorsal pair more or less rounded, ventral pair oval.

Peristomium well developed, with low lateral wings, partially encompassing prostomium and forming ventral ruffled surface (Fig. 1b). Short, eversible, somewhat

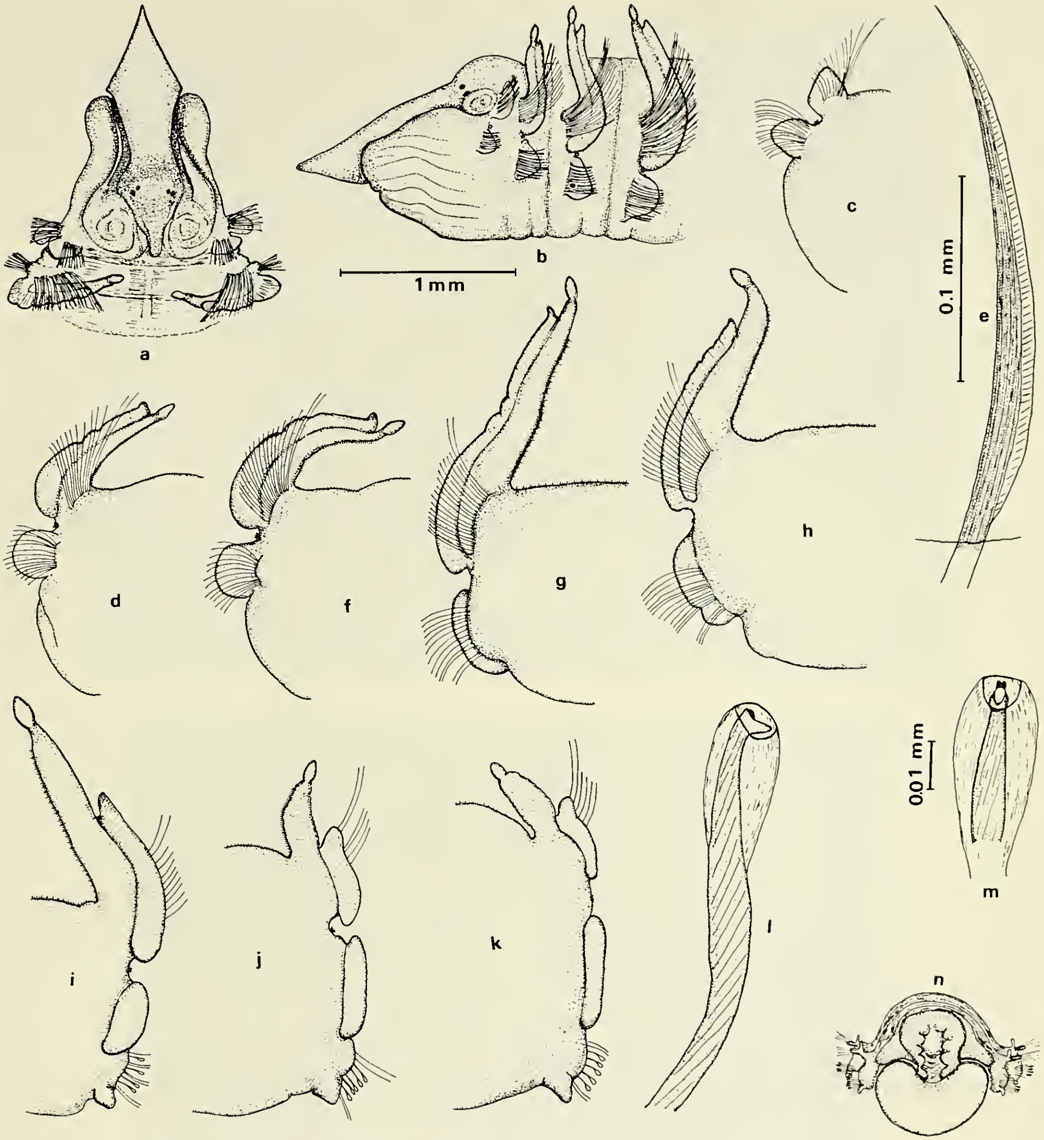

Fig. 1. *Scolelepis anakenae*: a, Anterior end, dorsal view, palps omitted; b, Same, lateral view; c, Setiger 1, anterior view; d, Setiger 2, anterior view; e, Capillary notoseta from anterior row of setiger 7 (third from top); f, Setiger 3, anterior view; g, Setiger 14, anterior view; h, Setiger 32, anterior view; i, Setiger 36, posterior view; j, Setiger 76, posterior view; k, Setiger 114, posterior view; l, Neuropodial hooded hook from posterior parapodium, lateral view; m, Same, frontal view; n, Posterior end of body, dorsal view. Scale under b applies to a–d, f–k, n.

lobulated proboscideal region. Palps thickened basally, tapering gradually, with conspicuous basal sheath or palpophore; when extended posteriorly palps reaching setiger 20–30.

Parapodia biramous throughout. First setiger smallest, although well developed, with lamellae of almost same size; notopodial lamellae more or less triangular while neuropodial more rounded (Fig. 1c). All para-

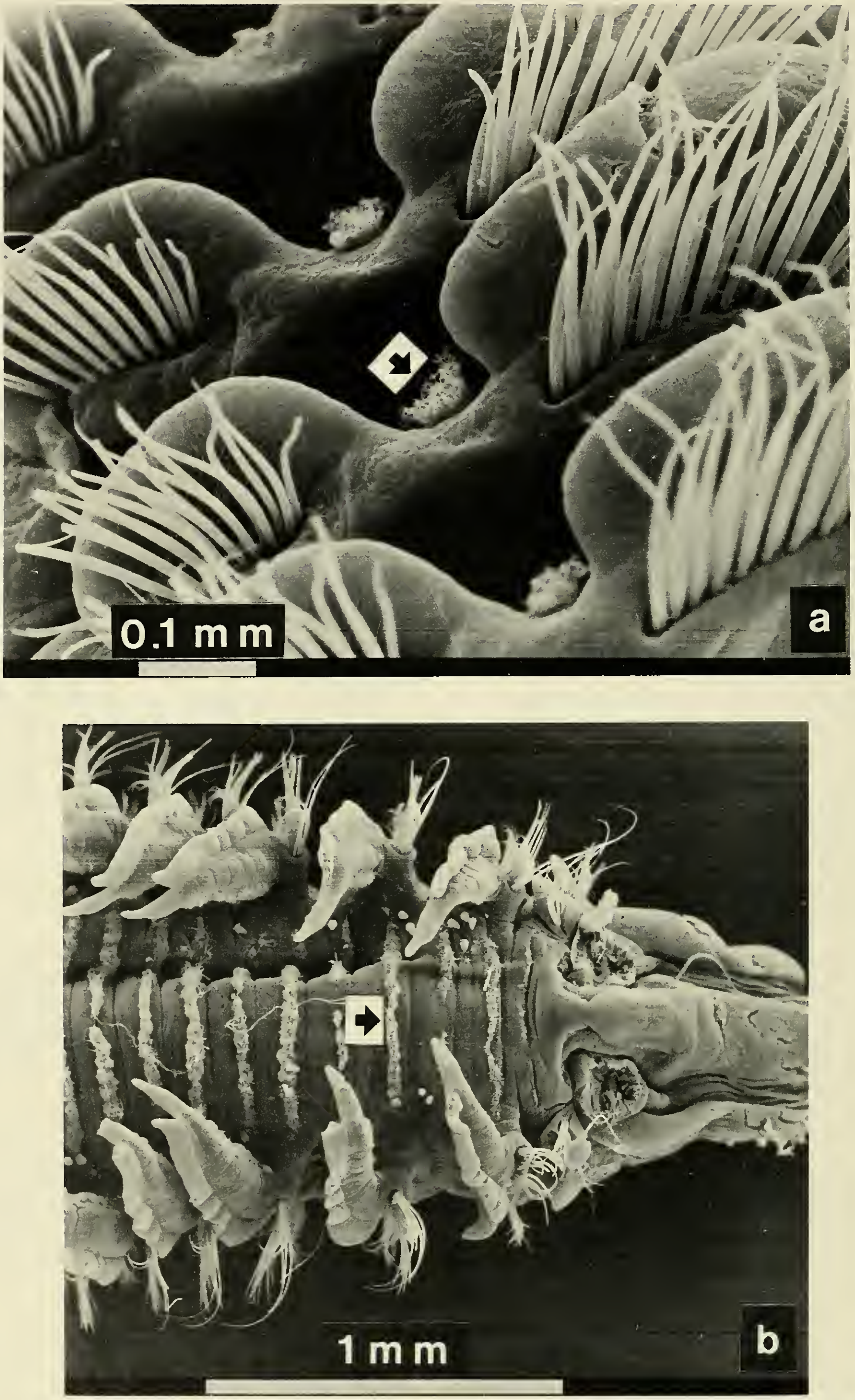

Fig. 2. *Scolelepis anakenae,* scanning electron micrographs: a, Anterior parapodium showing ciliated sensory organs between rami (arrow); b, Anterior end, dorsal view, showing ciliated bands across dorsum (arrow).

podia with ciliated sensory organs between rami, more conspicuous in specimens preserved in formalin than when transferred to alcohol (Fig. 2a, arrow).

Branchiae beginning on setiger 2, fused to notopodial lamellae, being free only at their tips, with distinct subterminal enlargements forming knobbed tips (Fig. 1d). Branchial pairs connected across dorsum by narrow ciliated ridge, rather difficult to see with light microscopy but evident with SEM (Fig. 2b, arrow). Notopodial lamellae fused to branchiae except distally in more anterior setigers, becoming more separated posteriorly and retaining only basal fusions in far posterior setigers (Fig. 1k); free margin of notopodial lamellae folded.

Anterior notosetae and neurosetae all winged capillaries, similar in structure, with shafts bearing fine granulations along internal striations and transparent sheaths with fine striations (Fig. 1e). Notosetae arranged in 2 rows in anterior setigers and single rows more posteriorly. Each row in anterior setigers forming fan-shaped fascicle of 13–15 setae per ramus, with 3–4 longer ones in superior position; setae of each row almost of same length, being shorter in anterior row than in posterior row. Median and posterior setigers with only 4–7 notosetae, with striated shafts but without granulations.

Postsetal neuropodial lamellae more or less rounded on first 5–6 setigers (Fig. 1c–f), being just slightly longer than wide, increasing in size and becoming broadly rounded in following setigers (Fig. 1g). Neuropodial lamellae entire up to setigers 31–40, then developing slight notch (Fig. 1h) and becoming deeper in following few setigers, and then becoming completely divided into rounded dorsal and conical ventral lobes (Fig. 1i). Neuropodial lobes becoming more prolonged vertically and further separated forming elongated thickened interramal lamellae and small conical ventral lobe (Fig. 1j, k). Neurosetae on anterior setigers all capillaries in 2 transverse rows, similar in arrangement and structure to notosetae, numbering about 12 setae per row with 3–4 slender setae, slightly separated from remainder, appearing like small ventral fascicle. Neuropodial hooded hooks beginning on setiger 35–37 and continuing up to end of body. Neuropodial fascicles in single rows, typically with 5–8 hooded hooks and 2–4 capillary setae in dorsal and ventral position, dorsal ones with striated shafts but without granulations, ventral ones with shafts coarsely granulated. Hooded hooks bidentate, with apical tooth formed by 2 incompletely separated teeth fused by ridge (Fig. 1l–m).

Pygidium with ventral cushion (Fig. 1n), with single achaetous preanal segment. Anus dorsal, surrounded by crenulate margin.

Distribution.—Known only from type locality, Anakena Bay (27°04′S, 109°20′W), north coast of Easter Island, intertidal zone, sandy beach.

Etymology.—The specific epithet is taken from the type locality, Anakena Bay where, according to tradition, King Hotu Matu'a and his followers from some region located in the east or northeast of Polynesia arrived as settlers on the island.

Remarks.—*Scolelepis anakenae* is closely related to *S. chilensis* (Hartmann-Schröder, 1962) from the coast of Chile in that the apical teeth of the hooded hooks are fused by a ridge, as clearly shown by Blake (1983, fig. 2K–L). It differs from *S. chilensis* in having conspicuous ciliated sensory organs between rami in all parapodia and by the total absence of notopodial hooded hooks. In *S. chilensis,* neuropodial hooded hooks begin on setiger 25–32, while in *S. anakenae* they begin more posteriorly, around setiger 35–37. Further, the SEM reveals significant differences in the ciliated bands across the dorsum between *S. anakenae,* which are narrow, and *S. chilensis* with wide and dense bands. In *S. anakenae,* the branchiae show conspicuous subterminal enlargements forming knobbed tips; this character has not been mentioned for *S. chilensis* either in Hartmann-Schröder's original description or by Blake (1983) in a recent revision of the species.

Ecological notes.—*Scolelepis anakenae* was the only polychaete found in the sandy beach transects at Anakena during this study. According to its macrofaunal components, the beach can be characterized by three fringes. The upper fringe, extending 8–10 m down from the berm, is very poor in macrofauna with only a single species of isopod and *S. anakenae* in very low densities, up to 10/m^2 towards the lower portion of the fringe. The middle fringe extends down for 8 m more and *S. anakenae* is the only species present, with maximum densities ranging between 460–180/m^2 at the lower border, and 260–70/m^2 at the upper border. The lower fringe encompasses the infralittoral sector of the beach, characterized by several species, including gastropods, sipunculans, and hippidean crustaceans; *S. anakenae* was found in low densities of about 20/m^2.

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DESCRIPTION OF *GUARANIDRILUS OREGONENSIS* (OLIGOCHAETA: ENCHYTRAEIDAE) FROM NORTH AMERICA, WITH ADDITIONAL COMMENTS ON THE GENUS

Kathryn A. Coates and Robert J. Diaz

Abstract.—Guaranidrilus oregonensis, n. sp., is described from specimens found in the Columbia River near Miller Sands, Oregon, and its relationships to other nominal species of *Guaranidrilus* are briefly considered. This is the first record of the genus from North America. Examination of type material of *G. glandulosus,* type species of the genus, and of *G. rarus,* showed that the former does not have esophageal appendages in VI, like *G. oregonensis,* and that the former two species are quite distinct. *Guaranidrilus sawayai* is a probable synonym of *G. rarus.* The new species is closely related to *G. glandulosus,* and two other species without esophageal appendages. A comparative table allows quick distinction of species of *Guaranidrilus* without oesophageal appendages.

The genus *Guaranidrilus* was erected by Cernosvitov (1937a, b) for three enchytraeid species from Argentina, *G. glandulosus, G. rarus* and *G. fridericoides,* the latter of which is a nomen nudum, and, provisionally, for *G. columbianus* (Michaelsen, 1913) from Colombia. Brinkhurst & Jamieson (1971) subsequently designated *G. glandulosus* as the type species. Some diagnostic characteristics of *Guaranidrilus* noted by Cernosvitov (1937a, b) were occurrence of two setae in each setal bundle, compact appendages on the dorsal side of the esophagus in VI, a large pair of intestinal diverticula originating at the transition from oesophagus to intestine, coiled vasa deferentia, and adiverticulate spermathecae not communicating with the intestine.

Guaranidrilus lamottei was described by Omodeo (1958) from Ivory Coast, but none of the nine specimens examined was mature. Omodeo expressed some ambivalence about whether the specimens should be attributed to *Guaranidrilus* or to a new genus. The systematic position of this species is still uncertain (Righi 1973, Healy 1979) and no type material is locatable.

Seven other species of *Guaranidrilus* have since been described from Brazil: *G. sawayai* Righi, 1973, *G. mboi* Righi, 1975, *G. athecatus* Christoffersen, 1977, *G. atlanticus* Christoffersen, 1977, *G. joanae* Christoffersen, 1977, *G. oiepe* Righi, 1974, and *G. finni* Christoffersen, 1977. The latter two species lack esophageal appendages in VI. In the most recent review of *Guaranidrilus,* Healy (1979) described *G. europeus,* the first species from Europe, which also is without esophageal appendages in VI. She also described *G. cernosvitovi* Healy, 1979, based on undescribed material collected by Cernosvitov (1937b) (see *G. fridericoides* nomen nudum). This review did not cover the recently described South American species.

Healy (1979) examined Cernosvitov's original material of *Guaranidrilus,* located at the British Museum (Natural History) (BMNH), and syntypes of *G. columbianus* in the Zoologisches Museum, Hamburg. After her examinations, Healy questioned the validity of *G. rarus,* suggesting that it could not be distinguished reliably from *G. glandulosus.* The quality of the syntype material of *G. columbianus* did not allow Healy to confirm all recorded anatomical details, but characteristics such as the presence of bilobed gut diverticula and form of the nephridia indicated to her that it belongs in *Guaranidrilus,* and, probably, is distinct from the other species, although presently not fully described.

In a phylogenetic study (Coates 1987a) it was found that both bisetate setal bundles and free adiverticulate spermathecae are plesiomorphies of Enchytraeidae. As well, coiled vasa deferentia is a synapomorphy of all or most of Enchytraeidae, although lost in more recent lineages (Coates 1987b, in press a). Within *Guaranidrilus,* gut diverticula have been lost one or more times and extra-lineal hybridization possibly complicates the genealogy of the lineage (Coates, in press b).

Recent collections made in the Columbia River near Miller Sands, Oregon, yielded the first specimens of *Guaranidrilus* for North America.

Material and Methods

Type specimens of *Guaranidrilus glandulosus, G. rarus, G. europeus,* and *G. cernosvitovi* were borrowed from the BMNH. Material of the new species was received from benthic collections made by the United States Army Corps of Engineers, from a field study to test the feasibility of developing marsh habitats on dredged material in the Columbia River estuary, Oregon (see Clairain et al. 1978 for details). All of the new material was stained in alcoholic borax carmine, dehydrated through an ethanol to xylene series then mounted whole in Canada balsam. Type material of the new species has been deposited at the National Museum of Natural History, Smithsonian Institution (USNM) and at the Royal Ontario Museum, Department of Invertebrate Zoology (ROMIZ).

Guaranidrilus Cernosvitov, 1937

Guaranidrilus Cernosvitov, 1937a:148–149.—1937b:282–283. Healy, 1979:7–8.

Type species.—*Guaranidrilus glandulosus* Cernosvitov, 1937.

Discussion.—Nominal species of *Guaranidrilus* are small to medium-sized terrestrial and freshwater enchytraeids with simple-pointed, anodulate, straight or slightly curved setae. These occur in 4 bisetate bundles per segment, except laterally in XII of mature specimens and rarely in some preclitellar segments. The head pore is anterior on the prostomium, and other coelomic pores are absent. Secondary pharyngeal gland lobes may be present. The species have compact nephridia with large anteseptal parts including some of the efferent canal. Their seminal vesicles are unpaired and dorsal, or apparently absent, and vasa deferentia are usually coiled. Vasa deferentia terminate in very small or no penial bulbs. Spermathecae, if present, are paired, free, with thick-walled ectal ducts and usually a sperm-containing dilation in V. The saccate ampulla may extend through several segments. The genus is primarily characterized by a pair of hollow, dorso-lateral gut diverticula originating near 7/8 or, rarely, originating in X. The diverticula sometimes are constricted, forming anterior and posterior lobes. These diverticula have been lost in some species.

Overall, the nominal species of *Guaranidrilus* are relatively underived within the lineage of Enchytraeidae. Only the presence of gut diverticula has been determined to be a synapomorphy of the genus (Coates, in press b). Gut diverticula at the esophago-intestinal transition (usually about VIII) also occur in the enchytraeid genera *Buchholzia, Enchylea, Punahenlea, Henlea,* and *Aspidodrilus.* The evolutionary origins of their diverticula are apparently all independent of those in nominal species of *Guaranidrilus* and, at least, some diverticular forms are reported to be distinguishable by their general appearances (Healy 1979). One group of *Guaranidrilus* is further characterized by esophageal appendages in VI. The species of this group also have relatively large seminal vesicles, whereas these are apparently absent or small in other nominal species of *Guaranidrilus*.

Specimens of several nominal species of *Guaranidrilus* with esophageal appendages, namely *G. atlanticus, G. athecatus, G. joanae,* and *G. mboi,* were not available (G. Righi & M. L. Christoffersen, pers. comm.) during the period of this research. Examination of specimens is required in order to complete a revision of the genus both because of taxonomic problems (see below) and descriptive inconsistencies. Each of these species does have some easily recognized specific characteristic: *G. atlanticus* has single esophageal diverticula in VI; *G. athecatus* lacks spermathecae; *G. joanae* has setae with very broad ental ends in anteriormost and posteriormost segments; and *G. mboi* has a pair of gut diverticula in X, rather than at 7/8 and is without pharyngeal glands at 6/7.

The summarized status of the nominal species of *Guaranidrilus* as a result of the conclusions drawn by Righi (1973), Christoffersen (1977), Healy (1979), Coates (1987a, in press a, b), and the taxonomic studies herein is:

- group 1: without esophageal appendages, with small or no seminal vesicles:
  - *G. glandulosus* Cernosvitov, 1937
  - *G. oiepe* Righi, 1974 (?=*G. glandulosus*)
  - *G. europeus* Healy, 1979
  - *G. oregonensis* new species;
- group 2: with esophageal appendages, in VI, rarely absent; seminal vesicles large, rarely absent:
  - *G. rarus* Cernosvitov, 1937 (*G. sawayai* Righi, 1973 = *G. rarus*) (see following)
  - *G. cernosvitovi* Healy, 1979
  - *G. mboi* Righi, 1975
  - *G. joanae* Christoffersen, 1977
  - *G. athecatus* Christoffersen, 1977
  - *G. atlanticus* Christoffersen, 1977, with several described forms
  - *G. finni* Christoffersen, 1977;
- other species:
  - *G. columbianus* (Michaelsen, 1913) sp. dubia, incompletely described
  - *G. lamottei* Omodeo, 1958 gen. dubia, incompletely described, based on immature specimens.

New Species Description and Remarks on Other Species

A. Species without esophageal appendages in VI

Guaranidrilus oregonensis, new species
Figs. 1, 2

Material examined.—Columbia River, Miller Sands, Oregon, about 46°15.00′N at 123°37.50′W. Collected VIII.1980 by E. J. Clairain and C. Newling. Holotype (USNM 118242) and 6 paratypes (USNM 118243–118245; and ROMIZ I1226–1228).

Etymology.—Named for the type locality.

Description.—Fixed, whole-mounted specimens 3.0 to 4.5 mm long, 0.19 to 0.24 mm [$\bar{x}$ = 0.22, s = 0.02, n = 5] wide at clitellum (specimens slightly compressed) (Fig. 1A); with 26 to 34 segments. Head pore dorsal on anterior third of prostomium. Setae 2 per bundle, absent entirely from XII, straight with ental hook. Preclitellar ventral setae 24 to 33 μm [$\bar{x}$ = 29, s = 4, n = 4] long (Fig. 1B, b); setae from clitellum to posterior 4 or 5 segments 28 to 41 μm [$\bar{x}$ = 35, s = 5, n = 5] long; posterior setae 52 to 78 μm [$\bar{x}$ = 62, s = 9, n = 6] long (Fig. 1B, a); more or less equal laterally and ventrally. Clitellum (Fig. 1A, c) extending over ½ XII to ½ XIII. Gland distribution: irregular dorsally, disrupted by large hyaline cells; in transverse rows ventro-laterally; reduced but complete ventrally between male pores. Cutaneous glands inconspicuous, in 1 to 4 regular transverse rows per segment, if only

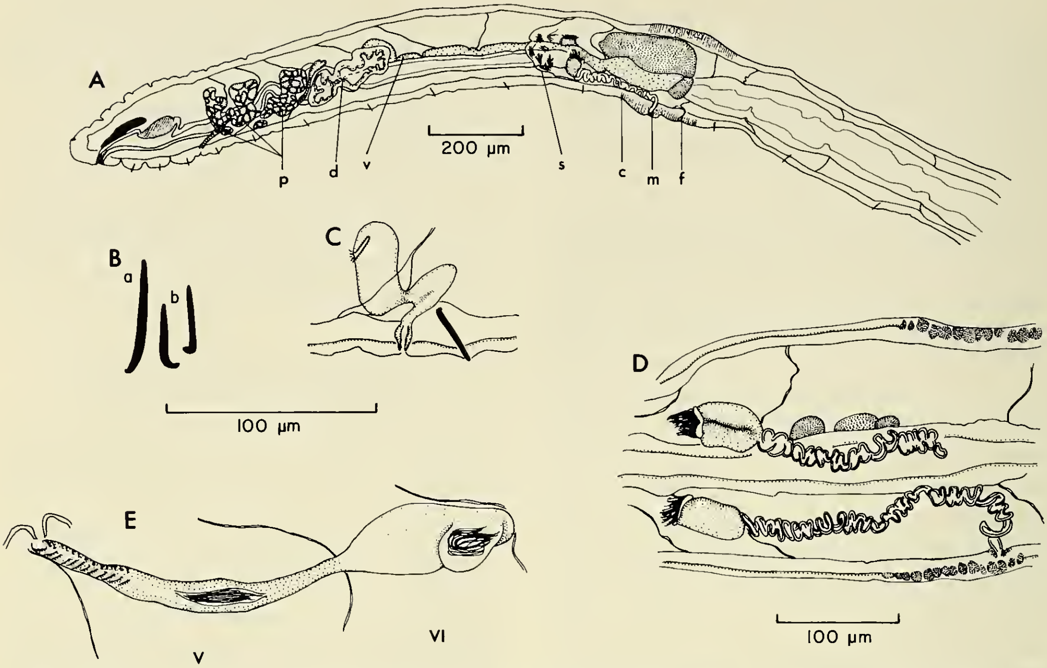


Fig. 1. A–E, *Guaranidrilus oregonensis,* n. sp., whole-mounted specimens. A, Lateral view of anterior segments through segment XVI; B, Setae from posterior segments, XXVIII or XXIX, and b. anterior segments III and IV; C, Nephridium at 7/8; D, Sperm funnels, vasa deferentia and male pore, ventro-lateral view; E, Spermatheca, dorso-lateral view; Abbreviations: c, clitellum; d, gut diverticulum; f, female pore; m, male pore; p, pharyngeal glands; s, seminal vesicle; v, dorsal blood vessel.

1 row, mid-segmental. Spermathecal pore small, in 4/5 in line with lateral setae; male pore small, in line with ventral setae, on a small papilla. With sensory or adhesive papillae on pygidium. *Internal.*—Posterior margin of brain deeply incised. Dorsal anterior blood vessel bifurcating in prostomium, originating in X to XII (Fig. 1A, v). Pharngeal glands (Fig. 1A, p) united dorsally at 4/5, 5/6 and 6/7; ventral lobes in V and VI; small, secondary glands antero-ventral in V and VI. Bilobed gut diverticula (Fig. 1A, d) communicating with gut in posterior half of VII, posterior lobes of diverticula extending into VIII; inner walls of diverticula ciliate. Without other gut diverticula or appendages. Chloragocytes golden-brown, most obvious in preclitellar segments. Lymphocytes nucleate, egg-shaped. Preclitellar nephridia on 6/7 through 8/9 (Fig. 1C); preseptal part half or more of entire nephridium; efferent duct terminal; interstitial tissue well-developed. Postclitellar nephridia of same shape as preclitellar, usually only 1 or 2 pairs. Seminal vesicle small (Fig. 1A, s) extending into X. Testes compact, paired on posterior of 10/11. Sperm funnels cylindrical, canal eccentric; granular; funnels about 61 μm [n = 3, s = 22] long and 42 μm [n = 3, s = 7] wide; collar subequal funnel width (Fig. 1D). Vasa deferentia long, narrow, coiled in XII (Fig. 1D); with very slight widening at penial pore. Male pore simple (Fig. 1A, m), without penial bulb, but with glandular, slightly enlarged, epidermal cells adjacent. Ovaries paired ventrally on posterior of 11/12. Female funnel (Fig. 1A, f) on 12/13, inconspicuous; pore in or just posterior to 12/13. Eggs extending posteriad into XV, in an egg sac, usually only 1 egg large. Spermathecal ectal ducts (Fig. 1E) thick-walled, without associated glands, with a small, sperm-containing widening in V; ampulla thin-walled,

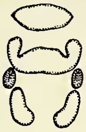
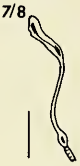
	oregonensis n. sp.	*glandulosus* Cernos.	*aiepe* Righi	*europeus* Healy	*finni* Christoffersen
body length (mm)	3.0-4.5	3-7	3.5-8.5	3-6	8-14
number of segments	26-34	-	31-34	23-29	41-56
setal length (μm) anterior	24-33	≈33	≈36	≈20	24-32
posterior	52-78	≈54	≈57	≈37	48-61
gut diverticula	bilobed	bilobed	unilobed	bilobed	bilobed
pharyngeal glands secondary lobes ●					
spermathecae scale equals 0.1 mm					
seminal vesicle	anterior	absent	absent	small/absent	anterior & posterior

Fig. 2. Tabular comparison of *Guaranidrilus oregonensis* n. sp. and the 4 other nominal species of *Guaranidrilus* without esophageal appendages.

irregular shaped, saclike, extending to VI or VII; sperm free in ampulla.

Habitat and distribution.—The Miller Sands area in the Columbia River, Oregon, is an active site for the disposal of dredged material. Snag Island, on which the oligochaetes were found, was a natural marsh used as a reference area. The tidal range in the freshwater marsh habitat of the worms was 1.9 m. *Guaranidrilus* specimens were collected in the high marsh where the sediments were a matrix of rhizomes and sandy mud (61% silt-clay) with 4.5% volatile solids. The dominant plants were spike-rush (*Eleocharis palustris*), Lyngby's sedge (*Carex lyngbei*), and tufted hairgrass (*Deschampsia caespiotosa*) (Clairain et al. 1978).

The benthos in this habitat was dominated numerically by oligochaetes, 93% of the total, with 84% of them being tubificids, 14% enchytraeids, and 2% lumbriculids. Other dominant taxa were the amphipod *Anisogammarus confervicolus,* sphaeriid clam, *Corbicula fluminea,* and chironomid and chrysomelid insect larvae (Clairain et al. 1978). In general the oligochaete fauna of the Miller Sands area is diverse with many unusual tubificid species (Brinkhurst & Diaz 1985).

Remarks.—A few characteristics distinguish *Guaranidrilus oregonensis* and *G. glandulosus.* Small differences exist between the species in location of the origin of the dorsal blood vessel, in distribution of clitellar gland cells, and in form of pharyngeal glands (Fig. 2). *Guaranidrilus glandulosus* also is reported to lack a seminal vesicle whereas one is present, although small, in *G. oregonensis.*

A further reason for recognition here of a distinct species is the apparent geographic separation of the respective populations of

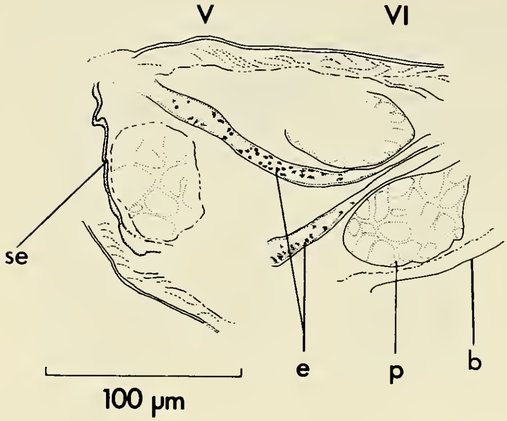


Fig. 3. *Guaranidrilus glandulosus,* BMNH 1949.3.1.951, dorsal sagittal section through V and VI showing ectal ducts of spermathecae. Abbreviations: b, body wall; e, spermathecal ectal ducts; p, pharyngeal glands (dorsal lobe at 5/6); se, septum.

Guaranidrilus glandulosus and *G. oregonensis.* Broad dispersion of some earthworm species by human activities are reported (Sims & Gerard 1985), but there is no existing evidence for this having occurred with *Guaranidrilus* species. There are few records of the genus outside of South America (Europe in Healy 1979; and Florida, Healy, pers. comm.) and few of the species are known to have large ranges of distribution. That of *G. rarus,* including Argentinian and Brazilian localities, is the broadest if the proposed synonymy of *G. sawayai* is valid.

It is of concern that descriptions of both *Guaranidrilus oregonensis* and *G. glandulosus* were based on small numbers of specimens and that both South and North America are poorly explored for enchytraeids. As well, there is no clear indication of the conditions required for speciation within enchytraeid lineages (Coates 1987b). Long periods of geographic separation need not guarantee the development of reproductive isolation mechanisms nor evolution in unique directions, unconstrained by earlier, shared historical events.

Guaranidrilus oregonensis is compared to *G. glandulosus* and the three other nominal species of *Guaranidrilus* without esophageal appendages, *G. europeus, G. oiepe,* and *G. finii,* in Figure 2.

Guaranidrilus glandulosus
Cernosvitov, 1937
Figs. 2, 3

Guaranidrilus glandulosus Cernosvitov, 1937a:149–151, figs. 1–9.—1937b:282.—Christoffersen, 1977:table 1.—Healy, 1979:8, table 1.

Material examined.—Syntypes, BMNH 1949.3.1.949–950, transverse and tangential sections; BMNH 1949.3.1.951–952, sagittal sections; BMNH 1949.3.1.953, whole-mounted specimens; collected at Loreto, Misiones, Argentina, 18.XI.1931.

Habitat and distribution.—In rich humic soil and in the detritus along a small stream. Loreto, near Santa Ana, Misiones, Argentina.

Remarks.—The specimens or parts of specimens catalogued as BMNH 1949.3.1.952 and 953 were not suitable for observations of internal structures.

In the complete description *Guaranidrilus glandulosus,* Cernosvitov (1937a, p. 151) stated that compact esophageal appendages "peptonéphridies" are located dorso-laterally in VI. Such structures were not found in any of BMNH 1949.3.1.949–951. Even though the ducts of the spermathecae follow a circuitous route into segment VI (Fig. 3, e) sections of these would not be confused with esophageal appendages as the cellular structures of these organs are distinctive (see Figs. 3, 4).

Cernosvitov (1937b) recognized two other species of *Guaranidrilus* in the material obtained from Argentina, but only *Guaranidrilus rarus* was described by him (Cernosvitov 1937a) at the same time as *G. glandulosus*; *G. cernosvitovi* was not described until some years later by Healy (1979). Both *G. rarus* and *G. cernosvitovi* are reported to have esophageal appendages, as did all the type specimens of them

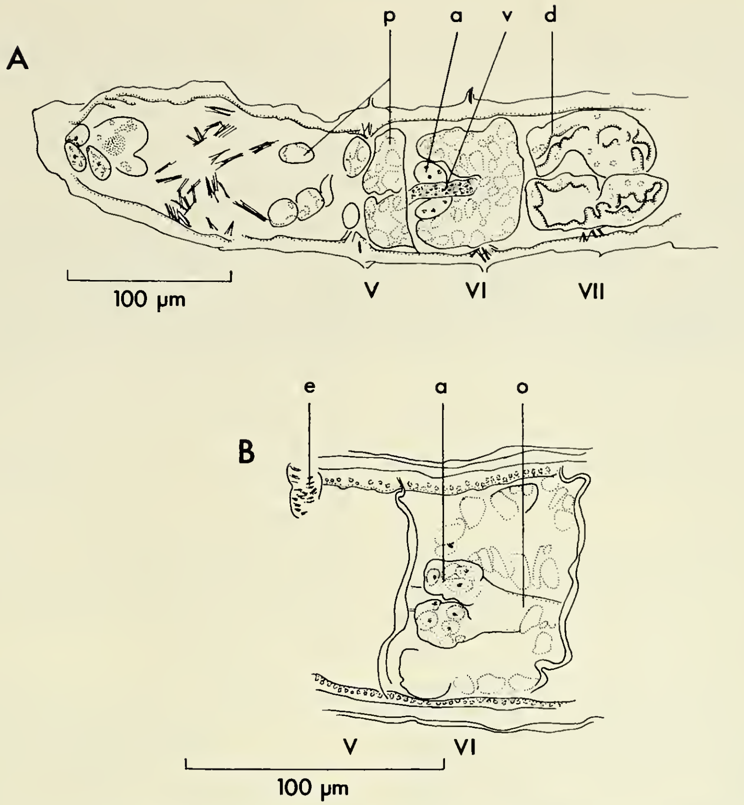


Fig. 4. A–B, *Guaranidrilus rarus,* BMNH 1949.3.1.955. A, Dorsal sagittal section of segments I through VII showing esophageal appendages; B, Enlargement of esophageal appendages, sagittal section ventral to dorsal blood vessel. Abbreviations: a, esophageal appendages; d, gut diverticulum; e, spermathecal ectal ducts; o, esophagus; p, pharyngeal glands; v, dorsal blood vessel.

examined here (see below). Cernosvitov (1937a, fig. 9, pt) clearly showed esophageal appendages in his illustration of *G. glandulosus* and it seems possible that he confused two species, but the type material that is still usable is of one species, without such appendages.

Guaranidrilus oiepe Righi, 1974
Fig. 2

Guaranidrilus oiepe Righi, 1974:140–141, figs. 32–40.—1975:144.—1981:427–428.—Christoffersen, 1977:table 1.

Habitat and distribution.—In decomposing wood covered with grasses, in a temporary pond. Mato Grosso, Rio de Janeiro, and Minas Gerais, Brazil.

Remarks.—Specimens of *Guaranidrilus oiepe* with sperm in the spermathecae have never been found, possibly indicating that the specimens seen were not mature or that the species is parthenogenetic. This species was distinguished from *G. glandulosus* by the shape and distribution of pharyngeal glands and by the shape of the intestinal diverticula (Righi 1974) (Fig. 2). Good records of intraspecific variation for either of these characters are not available. Re-examination of *G. oiepe* is required to further substantiate its specific distinction from *G. glandulosus.* Type and other material is not currently available for loan outside the country of its origin (Righi, pers. comm.).

Guaranidrilus europeus Healy, 1979
Fig. 2

Guaranidrilus europeus Healy, 1979:11–13, figs. 2a–i, 3a–d.

Material examined.—Paratype, BMNH 1978.39.2, whole-mounted; collected at le Corneau near Arcachon, France, 21.X.1977, by B. Healy.

Habitat and distribution.—Wet, marshy pasture at the edge of a small pond, pasture soil, and in moist sandy loam. Near Arcachon, southwest France and Roncesvalles, Spanish Pyrenees.

Remarks.—For the purpose of comparison with the South American species, some characteristics are noted from the type material in addition to the description made by Healy (1979). The setae of anterior segments were notably shorter than the setae of posteriormost segments (Fig. 2); nephridia were present from 6/7; and secondary pharyngeal glands were present in V and VI (Fig. 2). No scattered glands on the wall of the spermathecal ectal duct, as reported by Healy, were obvious in the fixed material but cells of the walls of the duct were coarsely granular. Gland cells of the clitellum were irregularly interspersed with hyaline cells in dorso-lateral regions. Penial bulbs were no more than glandular areas in the epidermis surrounding the male pores.

Guaranidrilus europeus was described as lacking a seminal vesicle but evidence of a very small seminal vesicle (Fig. 2) was found in the one specimen examined here. The form of the pharyngeal glands, spermatheca, and possibly the gut diverticula still distinguish it from the other species without esophageal appendages (Fig. 2).

Guaranidrilus finni Christoffersen, 1977
Fig. 2

Guaranidrilus finni Christoffersen, 1977: 188–190, figs. 1–12, table 1.

Habitat and distribution.—Banks of a small brook. Evangelista de Souza, Serra do Mar range, Sao Paulo, Brazil.

Remarks.—This species is distinctively larger than the other species without esophageal appendages (Fig. 2). The sperm funnels and spermathecae are correspondingly proportioned. *Guaranidrilus finni* is also unique in having encapsulated sperm bundles in the spermathecae (Fig. 2).

Phylogenetic analyses (Coates 198b, in press) indicate that *Guaranidrilus finni* is closely related to the larger species of *Guaranidrilus* with esophageal appendages rather than to other nominal species of *Guaranidrilus* lacking such appendages. In *G. finni* the absence of esophageal appendages is a derived character state. The opinion of Christoffersen (1977) that *G. finni* and *G. atlanticus,* in particular, had a close affinity also is supported.

B. Some species with esophageal appendages in VI

Guaranidrilus rarus Cernosvitov, 1937
Fig. 4

Guaranidrilus rarus Cernosvitov, 1937a: 151–153, figs. 10–15.—1937b:282.—Christoffersen, 1977:table 1.—Healy, 1979:14–15, table 1.

?*Guaranidrilus sawayai* Righi, 1973:470–472, figs. 1–9.—1975 [as *G. rarus*]:143–144.—1981:428, figs. 1–2.—Christoffersen, 1977:table 1.

Material examined.—Syntypes, BMNH 1949.3.1.955, tangentially sectioned, BMNH 1949.3.1.954, whole-mounted; collected at Loreto, Misiones, Argentina, 27.XII.1931, by L. Cernosvitov.

Habitat and distribution.—Under the bark of an old tree, in a tree-growing bromeliad; in a periodically flooded stream bed near Rio Parana; near Rio Capiroa. Loreto near Santa Ana, Misione, Argentina; Serra do Cipo, Minas Gerais, and Bataguassu, Mato Grosso, Brazil.

Remarks.—The whole-mounted type

Fig. 5. *Guaranidrilus cernosvitovi,* BMNH 1949.3.1.960.1A, sagittal lateral section showing prostomium to segment VII, with expansion of ectal duct of one spermatheca and one esophageal appendage. Abbreviations: a, esophageal appendages; e, spermathecal ectal ducts.

BMNH 1949.3.1.954 was unidentifiable and, if an oligochaete, immature.

The original description of *Guaranidrilus rarus* (Cernosvitov 1937a) indicated that the esophageal appendages in VI were ventral. Examination of the type material has shown this to be incorrect, and the esophageal appendages are dorso-lateral, as usual for the genus (Fig. 4A, B, a). Righi (1973, 1981) already may have recognized this error as he did not indicate any difference between *G. rarus* and *G. sawayai* for that character.

Righi (1973, 1975, 1981) has compared *Guaranidrilus rarus* to *G. sawayai* in detail. He most recently (1981) suggested that some of the characters he originally used to distinguish these, in particular the form of the brain and the form of the intestinal diverticula, were not good specific characters as presently determined. Righi (1973) described *G. sawayai* as possessing small, rounded penial bulbs. Bulbs were not apparent in his figures of the species, although a few small structures once were indicated around the male pore (Righi 1973, fig. 9). Penial gland development in sexually mature specimens may show enough variation in the species so that the state recorded for *G. sawayai* is not different from their absence as recorded for *G. rarus.* As Healy (1979) pointed out, the description of *G. rarus* was based on very few specimens.

Other characters that Righi (1981) identified as having states distinguishing *Guaranidrilus rarus* from *G. sawayai* were secondary pharyngeal glands and the position of the most anterior pair of nephridia. As *G. sawayai,* the sectioned type material of *G. rarus* has secondary glands in V and VI and the first pair of nephridia on 6/7. Righi also indicated that the intestinal diverticula in *G. sawayai* extended across the dorsal surface of the gut. Such a dorsal continuity could not be seen clearly in any available material of *G. rarus* (Fig. 4A, d) but this too could fall within the range of intraspecific variation recognized for other species of *Guaranidrilus* (Christoffersen 1977).

Observations of available material strongly suggest that *Guaranidrilus sawayai* is a junior synonym of *G. rarus.* Examination of type material of *G. sawayai* ultimately is required to decide the status of the synonymy.

Data available in the literature regarding the lengths of setae (Righi 1973) for *Guaranidrilus sawayai,* 3 μm anteriorly and 15 μm posteriorly, are very likely incorrect because the cuticle of the body wall is often thicker in an enchytraeid than the former measurement.

Guaranidrilus cernosvitovi Healy, 1979
Fig. 5

Guaranidrilus fridericoides Cernosvitov, 1937b:282, nomen nudum.

Guaranidrilus cernosvitovi Healy, 1979:10–11, fig. 1a–f, table 1.

Material examined.—Paratypes, BMNH 1949.3.1.960a–c, 2 sagitally sectioned specimens on three slides, BMNH 1949.3.1.957/8, whole-mounted specimen; collected at Loreto, Misiones, Argentina, 12.VI.1932.

Remarks.—The accession numbers for the holotype and other paratypes are, respectively, BMNH 1949.3.1.956 and 1949.3.1.959, 961a–b and 962–967 (E. G. Easton, pers. comm.). Accession numbers for this species were not correctly indicated in Healy (1979).

Guaranidrilus cernosvitovi is one of the larger nominal species of *Guaranidrilus,* belonging in a lineage with *G. finni* and *G. atlanticus* and several other South American species (Coates, in press *b*). It shares with these the character of ventral epidermal copulatory pads or papillae, occurring primarily in the clitellar region. As other nominal species of *Guaranidrilus* and "lower enchytraeids," *G. cernosvitovi* retains a sperm-containing expansion on each of the spermathecal ectal ducts just ental to the spermathecal pore (Fig. 5, e). These apparently were overlooked by Healy (1979). The esophageal appendages of this species are associated with large blood sinuses (Fig. 5, a).

Acknowledgments

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TAXONOMIC REVISION OF THE *PHALLODRILUS RECTISETOSUS* COMPLEX (OLIGOCHAETA: TUBIFICIDAE)

Christer Erséus

Abstract.—A complex of small marine tubificids previously regarded as one variable species is revised, partly on the basis of new material from Belize, Barbados, Florida, Hawaii, Great Barrier Reef (Australia), Fiji and Aldabra atoll (Indian Ocean). Four different species are recognized: *Phallodrilus rectisetosus* Erséus, 1979, s.s., *P. deminutius* Erséus, 1979, *P. molestus,* new species, and *P. heronensis* Erséus, 1981. They are distinguished from each other by differences in the number of (both somatic and penial) setae and in the morphology of the spermathecae. All four species exhibit wide geographical distribution in the warmer parts of the world; *P. rectisetosus* and *P. molestus,* at least, appear to be circumtropical.

A complex of closely related intertidal and subtidal tubificids, belonging to the marine genus *Phallodrilus* Pierantoni, 1902, was described by Erséus (1979) as a polytypic species, *P. rectisetosus.* The worms were characterized by their (1) small body size, (2) numerous, straight and sharply single-pointed penial setae arranged in tight bundles, (3) small, spindle-shaped atria, each with two compact prostate glands, and (4) pear-shaped, somewhat bipartite spermathecal ampullae. Material from Italy and France was regarded as the nominate subspecies, while specimens from Bermuda and Florida, having fewer setae in the somatic bundles than those from Europe, were assigned to a separate taxon, *P. rectisetosus deminutius* Erséus, 1979. Later, a third subspecies, *P. rectisetosus heronensis* Erséus, 1981, was established for material from Australia's Great Barrier Reef, separated from the other subspecies on dimensional differences in penial setae and atria. Peculiarities in the appearance of its spermathecae were, however, also noted (Erséus 1981: 16).

The distinction between the nominate *P. rectisetosus* and the subspecies *heronensis* appeared difficult to uphold, when somewhat intermediate specimens were found in Saudi Arabia, and it was therefore suggested (Erséus 1985) that the whole group should be regarded as one taxonomic entity (*P. rectisetosus*), until additional material from other parts of the world and non-morphological data become available. It was suspected (op. cit.) that more than one biological species may be involved, but it was found difficult to express the morphological variation observed in a further taxonomic division.

Subsequently, additional material of this complex has become available, and it is the basis for the present study. Firstly, material from Belize in Central America, consisting of two similar but distinguishable forms, led to a re-appraisal of the original material of *P. rectisetosus deminutius.* Upon re-examination the latter proved to contain the same two distinct forms, now concluded to be separate species. Secondly, specimens from Barbados, the Gulf of Mexico, Hawaii, Fiji, Australia, and Aldabra (Indian Ocean)—either collected by the author or received from other sources—further supported the view that more than one species is involved in the *rectisetosus* complex. The more than 300 individuals thus available (including the old material), could be separated into four groups, the members of each being slightly but consistently different morphologically from those of any other group, even over great geographical distances. The four forms are now regarded as different species, and they are diagnosed in the present paper.

Except when otherwise stated below, the new material was collected by the author while visiting: (1) the Carrie Bow Cay field station on the Barrier Reef off Belize (operated by the Smithsonian Institution) (1985), (2) the Bellairs Research Institute of McGill University in Barbados (1979), (3) the Lizard Island Research Station in the Great Barrier Reef (1982), and (4) the Mana Island Resort in Fiji (1982); or by Mr. D. Davis (University of Hawaii) and the author, during the latter's stay at (5) the Department of Zoology in Honolulu (1987). The live worms were sorted from sieved washings of sand samples, and then fixed in Bouin's fluid.

Material was also received from the Gulf of Mexico (courtesy M. R. Milligan), and the Aldabra Atoll (Seychelles) in the Indian Ocean (K. Fauchald, Smithsonian Institution). The type series and other material of *P. rectisetosus deminutius* were re-examined during a visit to the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

One worm from Fiji was sectioned and stained in Azan. The other specimens were stained in paracarmine and mounted whole in Canada balsam. Types and other reference material have been deposited in the USNM, the Australian Museum in Sydney (AMS), and the British Museum (Natural History) in London (BMNH).

The penial setae (in segment XI) were counted in all available specimens. Often the bundle on one side of the worm did not contain the same number of setae as that of the other side. For the statistics presented below, n thus refers to the total number of bundles studied, i.e., twice the number of specimens.

Systematics

General description of members of the P. rectisetosus *complex.*—Small, somewhat transparent tubificids, only a few mm long. Prostomium typically phallodriline: generally round, set off from peristomium. Clitellum extending over most posterior part of segment X, whole of XI and most of XII. Somatic setae bifid, with upper teeth thinner and often shorter than lower, and with subdental ligament. Bifids few per bundle, anteriorly up to four in *P. rectisetosus* s.s., but only two to three in other species, posteriorly one to two per bundle. Penial setae (ventral setae of XI) straight and short, sharply single-pointed, with tips often somewhat curved. In most species penials generally more than five per bundle (usually about three per bundle in *P. molestus,* n. sp.), arranged very tightly together, parallel or in somewhat fan-shaped formation within bundle. Bundles median to male pores; latter in line with ventral somatic setae in posterior part of XI. Spermathecal pores usually in line with ventral somatic setae anteriorly in X, near intersegmental furrow IX/X.

Pharyngeal glands well developed in IV–VI. Male genitalia (cf. Figs. 1D, 2C, F) paired. Vas deferens longer than atrium, entering apical end of latter. Atrium spindle-shaped, more or less erect, bearing two compact prostate glands, anterior one attached closer to entrance of vas deferens than posterior one. Outer lining of atrium very thin, inner epithelium ciliated and often granulated. Male pore inconspicuous; penis absent. Spermathecae with sperm in loose bundle or random mass.

Key to the Four Species within the Complex

1. Bifid setae fewer per bundle posteriorly than anteriorly (Penial setae generally more than 5 per bundle) 2

– Bifid setae almost invariably 2 per bundle throughout body (Penial setae generally 3–5, only occasionally more than 5 per bundle) ..... *molestus*

2. Spermathecal ampullae pear-shaped, gradually widening towards inner part and thus not clearly set off from duct (Figs. 2C, F), and with sperm in large bundle or mass (Atria at least about 45 μm long) 3

– Spermathecal ampulla small, somewhat spherical, clearly set off from long duct, and with a few loosely arranged spermatozoa (Fig. 3). (Atria at most about 40 μm long) .... *heronensis*

3. Bifid setae 2–3(4) per bundle anteriorly, 2 per bundle in postclitellar segments .... *rectisetosus*

– Bifid setae 2 (occasionally 3) per bundle anteriorly, 1 (2) per bundle in postclitellar segments ... *deminutius*

Phallodrilus rectisetosus
Erséus, 1979, *sensu stricto*
Fig. 1A

Phallodrilus rectisetosus rectisetosus Erséus, 1979:190–191, fig. 6.—Erséus 1981: table I.

Phallodrilus rectisetosus.—Erséus 1985:136–137, figs. 3–4.

Type material.—In Swedish Museum of Natural History (3086–3087): seven specimens from Ischia, Italy (see Erséus 1979).

Other material.—Re-examined: specimens from Italy, France and Saudi Arabia in author's collection (see Erséus 1979, 1985).—New material: USNM 104941, one specimen from Paiko Beach, Maunalua Bay, Oahu, Hawaii, barely subtidal mixed sand (2 Apr 1987).

Diagnosis.—Length 3.2–11.9 mm, 38–63 segments. Bifids 2–3(4) per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae 25–50 μm long, generally about 7–9 per bundle (total range 4–15, $\bar{x} = 7.9$, SD = 1.9, n = 68). Atria 45–90 μm long. Spermathecal ampullae pear-shaped, with sperm in large bundle or mass.

Description of specimen from Hawaii.—Length and segment number unknown (worm not complete). Width at XI 0.23 mm. Bifids 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae (Fig. 1A) 30–35 μm long, 8 per bundle. Atria about 60 μm long. Spermathecae about 75 μm long, with sperm in ampullae.

Variation in number of penial setae per bundle (Fig. 4).—Italy (n = 58): range 4–11, $\bar{x} = 7.7$, SD = 1.4.—France (n = 2): range 4–7, $\bar{x} = 5.5$, but worm not fully mature.—Saudi Arabia (n = 6): range 6–15, $\bar{x} = 10.3$, SD = 3.3.—Hawaii (n = 2): 8 (both bundles).

Distribution and habitat.—Hawaii (new record), Italy, Atlantic coast of France and Saudi Arabia (Fig. 5). Intertidal and barely subtidal sand.

Phallodrilus deminutius Erséus, 1979
Figs. 2A–C

Phallodrilus rectisetosus deminutius (part) Erséus, 1979:191–192, fig. 7.—Erséus 1981:table I.

Type material re-examined.—USNM 56200–56202, six specimens from Ferry Reach, Bermuda (see Erséus 1979).

Other material re-examined.—USNM 56223, two specimens from Blue Hole area, Bermuda, coll. by M. L. Jones (see Erséus 1979).—Author's collection: 12 specimens from Bermuda (11 from type locality; 1 from Whale Bone Bay, intertidal). Note that several other individuals from Bermuda, previously assigned to "*P. rectisetosus deminutius*" now are identified as *P. molestus*, n. sp., below.

New material.—USNM 104134, one specimen from N of inner end of dock at Carrie Bow Cay, Barrier Reef off Belize, 0.5 m, patch of poorly sorted medium to coarse sand (6 Nov 1985). USNM 104133, 104135, two specimens from N of dock, Carrie Bow Cay, 1 m, fine to medium sand and rubble (10 Nov 1985). USNM 104132, one specimen from Bellairs Reef, St. James, Barbados, 13–14 m, poorly sorted coarse sand (29 Oct 1979).—Author's collection: two specimens from 50 m N of Carrie Bow Cay, 0.7 m, rubble bed with coarse to medium sand beneath (8 and 24 Nov 1985); two specimens from immediately W of N tip of Carrie Bow Cay, 0.5 m, patch of medium sand amongst scattered rocks and *Thalassia* (8 Nov 1985); one specimen from SW of S tip of Carrie Bow Cay, edge of reef, near beginning of *Thalassia* bed, 2 m, poorly sorted sand (12 Nov 1985); and two specimens (coll. H. R. Baker) from near dock of Carrie Bow Cay, 1.5 m, poorly sorted coral sands with algal debris, roots and *Halimeda* flakes (25 Apr 1982).

Diagnosis.—Length 3.4–5.9 mm, 36–44 segments. Bifids 2(3) per bundle anteriorly, 1(2) per bundle in postclitellar segments. Penial setae 30–46 μm long, generally 5–8 per bundle (total range 4–11, $\bar{x}$ = 6.7, SD = 1.5, n = 60). Atria 60–85 μm long. Spermathecal ampullae pear-shaped, with sperm in large bundle or mass.

Description of material from Belize and Barbados.—Length 3.5–5.8 mm, 36–43 segments. Width at XI 0.14–0.27 mm. Bifids (Fig. 2A) 2(3) per bundle in II–VIII, 1 (very occasionally 2) per bundle thereafter, 28–37 μm long, about 2 μm thick. Penial setae (Figs. 2B, C, ps) 35–40 μm long, about 2 μm thick, 4–8 per bundle. Male genitalia shown in Fig. 2C. Vas deferens about 9 μm wide. Atrium 60–85 μm long, 23–35 μm wide. Spermathecae (Fig. 2C, s) 80–145 μm long, consisting of short ducts and pear-shaped, thin-walled ampullae; latter narrower ectally than entally, maximally 35–70 μm wide; sperm as thick bundle or large mass.

Variation in number of penial setae per bundle (Fig. 4).—Bermuda (n = 38): range 4–11, $\bar{x}$ = 7.0, SD = 1.7.—Belize (n = 20): range 4–8, $\bar{\chi}$ = 6.2, SD = 1.1.—Barbados (n = 2): range 7–8, $\bar{\chi}$ = 7.5.

Remarks.—The single individual from Fowey Rocks, Miami, Florida, that was identified as "*P. rectisetosus deminutius*" by Erséus (1979) is actually a specimen of *P. molestus*. However, although *P. deminutius* co-occurs with *P. molestus* in many places (even at the type locality of the former), the holotype and paratypes of it proved all, upon re-examination, to be the same species.

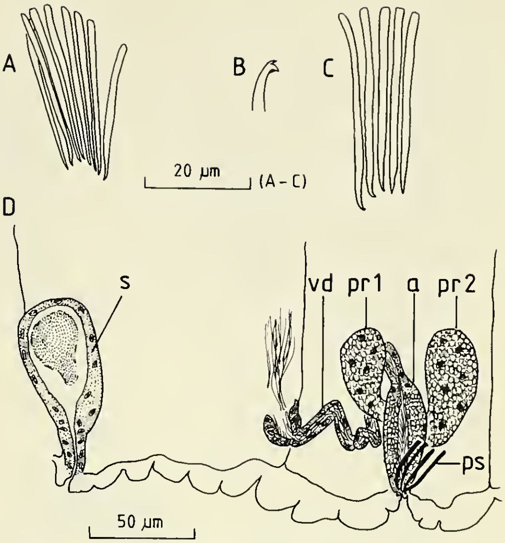

Fig. 1. A, *Phallodrilus rectisetosus*, from Hawaii, penial setae. B–D, *Phallodrilus molestus*, from Hawaii: B, Somatic seta; C, Penial setae; D, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations: a atrium, pr 1 anterior prostate gland, pr 2 posterior prostate gland, ps penial setae, s spermatheca, vd vas deferens.

The key characteristic separating this species from all the others within the complex is the low number of setae; with few exceptions the postclitellar bundles are unisetal. It is otherwise very similar to *P. rectisetosus*, both in terms of number of penial setae and in spermathecal morphology.

Distribution and habitat.—Belize, Barbados (both new records) and Bermuda (Fig. 5); apparently present throughout the Caribbean area. Intertidal and subtidal sand, down to at least about 14 m depth.

Phallodrilus molestus, new species
Figs. 1B–D, 2D–F

Phallodrilus rectisetosus deminutius (part) Erséus, 1979:191–192.—Erséus 1981:table I.

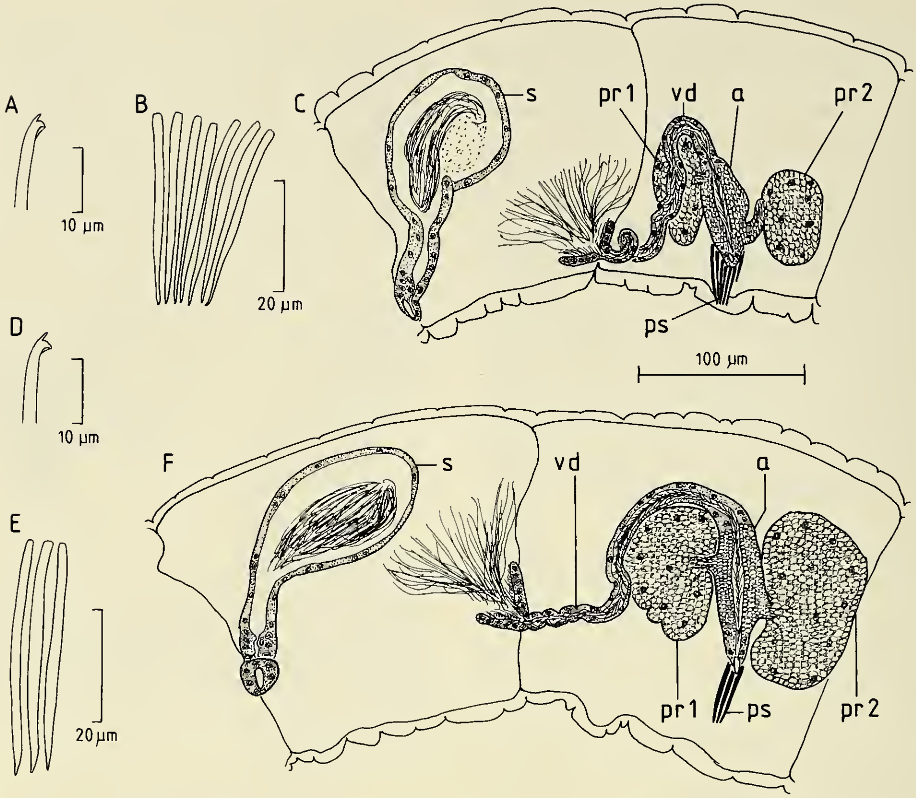

Fig. 2. A–C, *Phallodrilus deminutius,* from Belize: A, Somatic seta; B, Penial setae; C, Lateral view of spermathecae and male genitalia in segments X–XI. D–F, *Phallodrilus molestus,* from Belize: D, Somatic setae; E, Penial setae; F, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations: a atrium, pr 1 anterior prostate gland, pr 2 posterior prostate gland, ps penial setae, s spermatheca, vd vas deferens.

Holotype.—USNM 118352, whole-mounted specimen from outer end of dock at Carrie Bow Cay, Barrier Reef off Belize, 1.5 m, poorly sorted, somewhat muddy, medium to coarse sand (6 Nov 1985).

Paratypes.—USNM 118353–118356, four specimens from type locality.

Other material re-examined (author's collection).—Nine specimens from Bermuda (Erséus 1979:191): two from Ferry Reach (type locality of *P. deminutius*), three from North Rock, one from Tobacco Bay, one from Harrington Sound, and two from Bailey's Bay. One specimen from Fowey Rocks, Miami (Erséus 1979).

Other material.—USNM 118357, one specimen from inner end of bay at river mouth, River Bay, NE Barbados, low water mark, coarse sand (27 Oct 1979).—USNM 118358–118361, four specimens from Paiko Beach, Maunalua Bay, Oahu, Hawaii, barely subtidal mixed sand (2 Apr 1987).—AMS W202443, one specimen from beach at northern side of Palfrey Island, S of Lizard Island, Great Barrier Reef, Australia, lower intertidal, gravel with silt and fine sand (15 Nov 1982).—BMNH 1987.5.1/2, 1987.5.3, two specimens from Mana Island, off Lautoka, Viti Levu, Fiji (5 Dec 1982): one from flat W of Mana Island Resort, subtidal off beach rock, 0.5 m, fine coralline sand with lots of gravel and coral rubble; and one from rocks at W end of North Beach (Mana Island), tide pool in lower intertidal, stones and pebbles with some muddy sand beneath.—Author's collection: 20 specimens from type locality; 177 specimens from 32 other sampling stations in the reef areas near Carrie Bow Cay, Belize (Nov 1985); six specimens from Oahu, Hawaii, four from Paiko Beach (see above), one from off Keehi Lagoon, Honolulu, about 70 m, medium sand (Nov 1986; coll. D. Davis), and 1 from Kawaikui Beach Park, Maunalua Bay (9 Sep 1987; coll. D. Davis).—M. R. Milligan Collection: 1 specimen from about 4 km off mouth of Crystal River, W Florida (Gulf of Mexico), 28°58.7′N, 82°48.7′W, 4 m, coarse sand and shells (Nov 1984; coll. M. R. Milligan).

Etymology.—The species name *molestus* is Latin for "troublesome," referring to the previous difficulties in separating this form from *P. deminutius.*

Diagnosis.—Length 3.0–6.8 mm, 30–43 segments. Bifids almost invariably 2 per bundle, throughout body. Penial setae 28–47 μm long, generally 3–5 per bundle (total range 2–7, $\bar{x}$ = 3.1, SD = 0.7, n = 444). Atria 40–80 μm long. Spermathecal ampullae pear-shaped, with sperm in large bundle or mass.

Description of material from Belize (including type material) *and Barbados.*—Length 3.7–5.9 mm, 35–42 segments. Width at XI 0.19–0.24 mm. Bifids (Fig. 2D) 2 per bundle throughout (very occasionally 1 per 'bundle'), 26–42 μm long, 1.5–2.5 μm thick. Penial setae (Figs. 2E, F, ps) 35–46 μm long, about 2 μm thick, generally 3, but sometimes 2, 4 or even 5, per bundle. Male genitalia shown in Fig. 2F. Vas deferens 7–14 μm wide. Atrium 45–80 μm long, 20–30 μm wide. Spermathecae (Fig. 2F, s) 130–210 μm long, consisting of short ducts and pear-shaped, thin-walled ampullae; latter narrower ectally than entally, maximally 25–95 μm wide; sperm as thick bundle or large mass.

Description of material from Hawaii, Great Barrier Reef and Fiji.—Length 3.2–5.2 mm, 36–42 segments. Width at XI 0.20–0.35 mm. Bifids (Fig. 1B) 30–42 μm long, 1.5–2.5 μm thick, 2 (anteriorly sometimes only 1) per bundle throughout. Penial setae (Fig. 1C) 28–42 μm long, 1.5–2 μm thick, generally 4–5 (total range 3–6) per bundle. Male genitalia shown in Fig. 1D. Vas deferens 5–7 μm wide. Atrium 40–60 μm long, 15–23 μm wide. Spermathecae (Fig. 1D, s) 60–90 μm long, consisting of short ducts and pear-shaped, thin-walled ampullae; latter narrower ectally than entally, maximally 28–42 μm wide; sperm as large mass, or absent (lumen then filled with a round mass of secretion, as shown in Fig. 1D).

Variation in number of penial setae per bundle (Fig. 4).—Belize (n = 394): range 2–5, $\bar{x}$ = 3.0, SD = 0.6.—Bermuda (n = 18): range 2–5 (one bundle with 7), $\bar{x}$ = 4.1, SD = 1.1.—Miami (n = 2): range 4–5, $\bar{x}$ = 4.5.—Gulf of Mexico (n = 2): 2 (both bundles).—Barbados (n = 2): 3 (both bundles).—Hawaii (n = 20): range 3–6, $\bar{x}$ = 4.4, SD = 0.7.—Great Barrier Reef (n = 2), range 3–4, $\bar{x}$ = 3.5.—Fiji (n = 4): range 4–5, $\bar{x}$ = 4.3, SD = 0.4.

Remarks.—Some of the specimens from Bermuda and Florida were previously (Erséus 1979) identified as *P. rectisetosus deminutius,* but they have bisetal bundles of bifids throughout the body, and a low number of penial setae, the two features unique for the form now recognized as a separate species, *P. molestus.*

Distribution and habitat.—Belize, Barbados, Florida, Bermuda, Hawaii, Great Barrier Reef, Fiji (Fig. 5). Lower intertidal and subtidal sands, down to at least 70 m depth. *Phallodrilus molestus* is one of the most common tubificids on the Barrier Reef off Belize.

Phallodrilus heronensis Erséus, 1981
Fig. 3

Phallodrilus rectisetosus heronensis Erséus, 1981:15–17, figs. 1–3, table I.

Type material.—In Queensland Museum (G 12544–12551): eight specimens from Heron Island, Great Barrier Reef, Australia (see Erséus 1981).

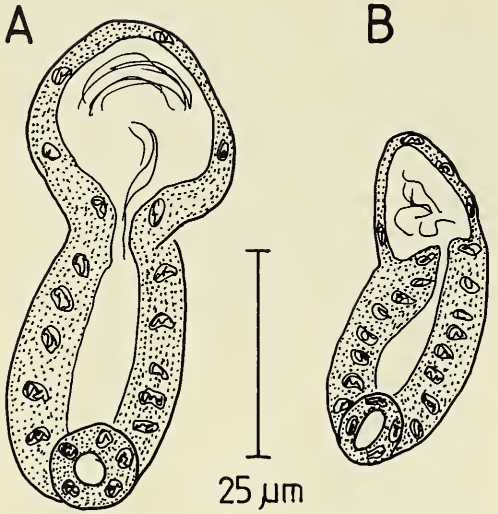

Fig. 3. *Phallodrilus heronensis,* spermathecae: A, Specimen from Fiji; B, Specimen from Aldabra.

New material.—BMNH 1987.5.4/5 and 1987.5.6, one sectioned and two whole-mounted specimens from reef flat off "Picnic Point," Mana Island, off Lautoka, Viti Levu, Fiji, 0.5 m, coarse gravelly sand (7 Dec 1982).—USNM 104129–104131, three specimens from Aldabra Atoll (Seychelles), coll. K. Fauchald: one from Basin Lebine, 0.5 m, from *Caulerpa* sp. clump (13 Mar 1985); and two from in front of laboratory, in *Thalassodendron* (Apr 1983).

Diagnosis.—Length 2.3–4.6 mm, 33–39 segments. Bifids 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae 20–35 µm long, 4–7 (occasionally up to 11) per bundle ($\bar{\chi}$ = 6.4, SD = 1.6, n = 30). Atria very small, only 25–40 µm long. Spermathecae club-shaped, with long ducts and small, somewhat spherical ampullae; latter containing a few loosely arranged spermatozoa.

Description of material from Fiji.—Length, 2.7–2.9 mm, 35–37 segments. Width at XI 0.26–0.27 mm. Bifids 30–35 µm long, 1.5–2 µm thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae about 25–30 µm long, 4–5(6) per bundle. Atrium about 30 µm long, about 10 µm wide. Spermathecae (Fig. 3A) 55–70 µm long, maximally 17–26 µm wide, with sperm as loose bundle in ampullae.

Description of material from Aldabra.—Length 2.3–3.5 mm, 33–37 segments. Width at XI 0.10–0.18 mm. Bifids 25–37 µm long, 1–2 µm thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae 20–25 µm long, 7(9) per bundle. Atrium about 25–30 µm long, 11–15 µm wide. Spermathecae (Fig. 3B) only 40–47 µm long, 10–20 µm wide, with a few spermatozoa in ampullae.

Variation in number of penial setae per bundle (Fig. 4).—Heron Island, Great Barrier Reef (n = 18): range 5–11, $\bar{\chi}$ = 6.7, SD = 1.6.—Fiji (n = 6): range 4–6, $\bar{\chi}$ = 4.8, SD = 0.7.—Aldabra (n = 6): range 7–9, $\bar{x}$ = 7.3, SD = 0.7.

Remarks.—The very small atria and spermathecal ampullae are diagnostic for *P. heronensis,* and separate it from the other species of the complex.

Distribution and habitat.—Aldabra, Fiji (new records) and Great Barrier Reef (Fig. 5). Intertidal and barely subtidal sand, down to at least 0.5 m depth.

Discussion

The species complex considered here is a homogeneous group of marine tubificids, with a few variable and somewhat confusing characters that made the original classification difficult (Erséus 1979, 1981, 1985). The new specimens from Florida, Belize, Barbados, Hawaii, Fiji, Australia and Aldabra, however, have revealed a pattern in the variation indicating the presence of four distinct species. Three characters have shown to be particularly useful.

First, the bifid (somatic) setae, which morphologically are more or less identical in the four forms (Figs. 1B, 2A, D), are up to 3(4) per bundle anteriorly, diminishing to 2 per bundle posteriorly, in *P. rectisetosus* and *P. heronensis,* whereas the bundles are (almost invariably) bisetal anteriorly and unisetal posteriorly in *P. deminutius.* Such a posterior decline in setal numbers does not characterize *P. molestus,* which has bisetal bundles throughout the body. Secondly, the latter species is also unique in its very low number of penial setae, in fact it is the only species in the group that in most cases can be separated solely on the basis of this number. The other three species have very wide, overlapping ranges for the numbers of penial setae (see Fig. 4), the means being very close to each other. Thirdly, although variable in shape, the spermathecal ampullae of *P. rectisetosus, P. deminutius* and *P. molestus* are large (relative to those of *P. heronensis*) and pear-shaped, sometimes with a tendency towards a bipartition (cf. Erséus 1979:fig. 6), and they are not always clearly set off from the ducts. In *P. heronensis,* however, the ampullae are very small, roundish and clearly set off from the (relatively long) ducts (Fig. 3).

Some of these differences may appear slight and not, per se, interspecific. For instance, a variation in the number of somatic setae between one and two, or two and three, per bundle may be considered intraspecific in other tubificid species. However, in the present study, which covers material from 13 different areas of the world (Fig. 5), each individual could rather easily be assigned to one of the four distinct forms; no intermediates were found. The forms are not even fully separated geographically, thus refuting the alternative of them being geographical races. As illustrated in Fig. 5, two forms are

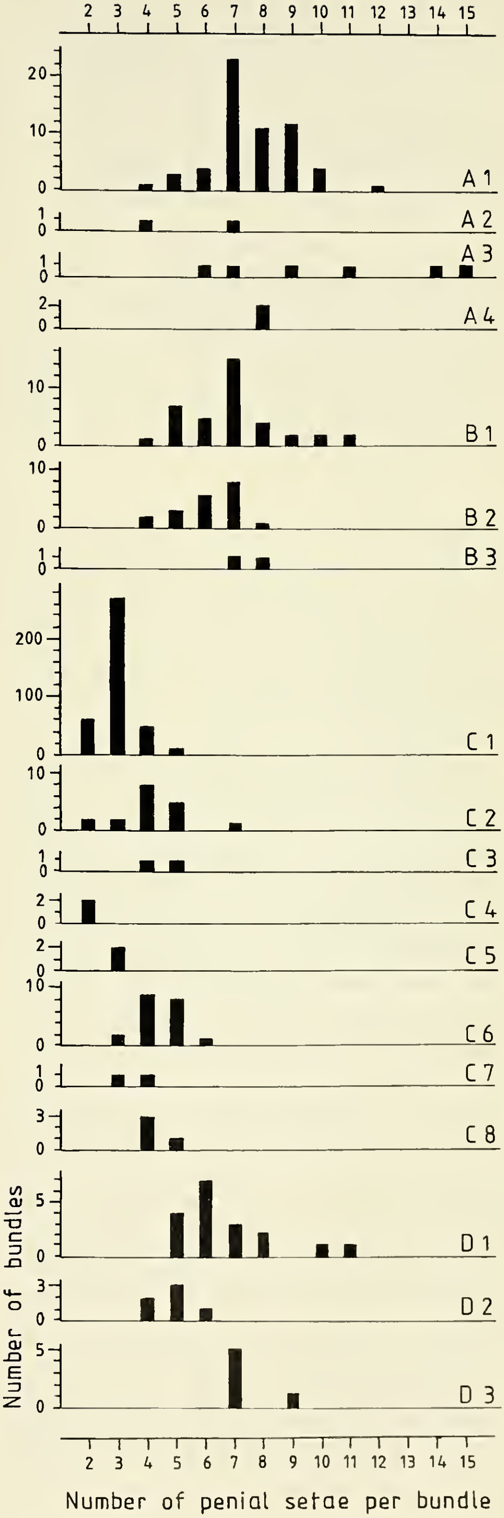

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Fig. 4. Variation in the number of penial setae per bundle, in various populations of the *Phallodrilus rectisetosus* complex. A, *P. rectisetosus* from Italy (A1), France (A2), Saudi Arabia (A3), and Hawaii (A4); B, *P. deminutius* from Bermuda (B1), Belize (B2), and Barbados (B3); C, *P. molestus,* from Belize (C1), Bermuda (C2), Miami (C3), Gulf of Mexico (C4), Barbados (C5), Hawaii (C6), Great Barrier Reef (C7), and Fiji (C8); D, *P. heronensis* from Great Barrier Reef (D1), Fiji (D2), and Aldabra (D3).

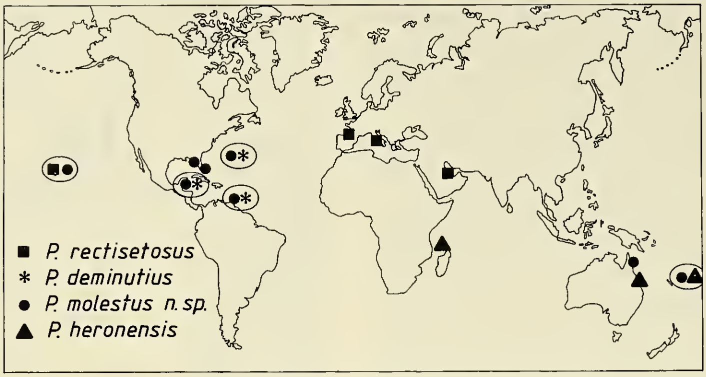

Fig. 5. Geographical distribution of the species within the *Phallodrilus rectisetosus* complex. Records of two species from the same area are encircled.

sympatric (in various combinations) in 5 of the 13 areas studied. The records suggest, however, that the Caribbean *P. deminutius* and the Indo-Pacific *P. heronensis* may be geographically more restricted than the apparently circumtropical *P. rectisetosus* and *P. molestus.*

Although these four species without doubt are closely related, they do not necessarily constitute a strictly monophyletic group. Their simple male ducts and penial setae do not appear to be apomorphic traits, but rather less derived structures possibly similar to those of an ancestral phallodriline; the male genitalia of most other members of the subfamily appear to be derived from the biprostate (i.e., unmodified) atria of *Phallodrilus.* This implies that the *rectisetosus* group, as well as the genus *Phallodrilus* as a whole, is likely to be paraphyletic. The recently described *P. duplex* Erséus, 1987, from the Mediterranean coast of Israel, most probably belongs to the same lineage. It has bisetal bundles throughout body, except for the penial ones which are trisetal, and it thus appears to be very closely related to *P. molestus*; it is distinguished from the latter by its somewhat more slender atria and the modified tips of its penial setae (see Erséus 1987). Particularly the latter feature makes it a slightly more derived species than the four taxa treated in the present paper.

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FOUR NEW SPECIES OF CAMBARINCOLIDS (CLITELLATA: BRANCHIOBDELLIDA) FROM THE SOUTHEASTERN UNITED STATES WITH A REDESCRIPTION OF *OEDIPODRILUS MACBAINI* (HOLT, 1955)

Perry C. Holt

Abstract.—Four new species of cambarincolid branchiobdellidans, *Cambarincola bobbi* from Virginia, *Ellisodrilus carronamus* and *Oedipodrilus anisognathus* from Tennessee, and *Sathodrilus rivigeae* from Arkansas are newly described. In addition, *Oedipodrilus macbaini* (Holt, 1955) is redescribed. Relationships and distributions are discussed.

When the branchiobdellidan collections belonging to the Virginia Polytechnic Institute and State University were given to the National Museum of Natural History of the Smithsonian Institution in the Spring of 1986, I retained in my possession as a loan certain collections from the southeastern United States, including all the material from Tennessee, which I knew to contain a number of new species. This opportunity is taken to describe four of these species and to more fully describe *Oedipodrilus macbaini* (Holt, 1955).

The region composed of the southern Appalachians and associated uplands (the Piedmont and the Interior Low Plateaus) and the Ozark Mountains contains the most diverse branchiobdellidan fauna known for any similarly sized region in the world and may include the original home of the order. An understanding of the relationships and history of the branchiobdellidans awaits a fuller description of this fauna.

Some discussion of generalities and generic and familial diagnoses may be found in Holt (1986). Herein, the intent is merely to describe new species with minimal emphasis placed on any other questions.

Cambarincola bobbi, new species
Fig. 1

Type specimens.—Holotype, USNM 101496, four paratypes, USNM 101497–101499, taken on *Cambarus bartonii bartonii* (Fabricius) from a medium-sized stream in Tom's Brook (a town) 5.7 miles south of Strasburg, Shenandoah County, Virginia, by Marvin L. Bobb and Perry C. Holt, 22 Jul 1948.

Diagnosis.—Small- to medium-sized worms (holotype 2.2 mm in length); lips obscurely lobed; no oral papillae; dorsal ridges weakly developed; jaws subequal in size, dorsal one slightly larger than ventral one, dark in color, dental formula 5/5; bursa about ½ to ⅗ body diameter in length, elongate ovoid, atrial fold thin, penial sheath about ½ total length, penis membraneous; spermiducal gland large, length about twice its diameter, no deferent lobes, flexed antero-ventrad at its mid-point; prostate about ½ length, ⅜ diameter of spermiducal gland, differentiated, with large clear ental bulb; spermatheca with prominent ectal duct, bulb ovoid to lanceolate (in optical section), length slightly less than diameter of body.

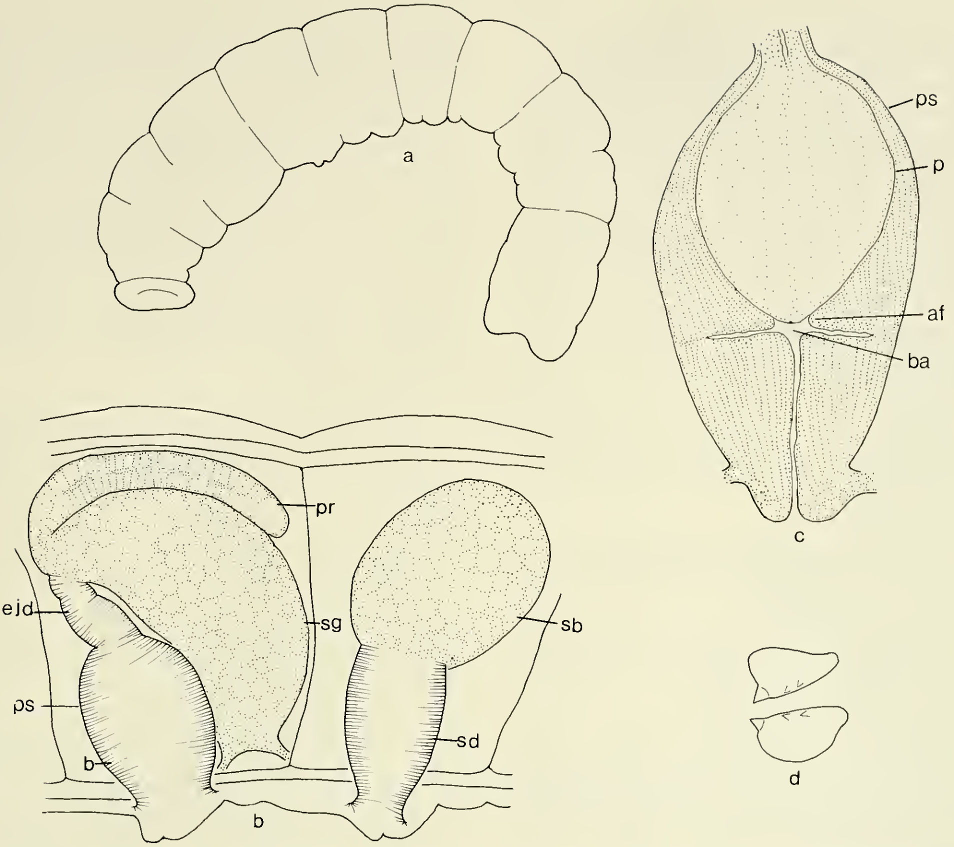

Fig. 1. *Cambarincola bobbi,* holotype. a, Lateral view of entire animal; b, Lateral view of reproductive systems; c, Optical section through bursa and penis; d, Lateral view of jaws. Abbreviations: af, atrial fold; b, bursa; ba, bursal atrium; ejd, ejaculatory duct; p, penis; pr, prostate; ps, penial sheath; sb, spermathecal bulb; sd, spermathecal duct; sg, spermiducal gland.

Etymology.—For Dr. Marvin L. Bobb, friend, fellow student, and for a season, field companion.

Description.—The five type specimens of *Cambarincola bobbi* have the following mean dimensions: total length, 2.0 mm; greatest diameter, 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.3 mm.

In external appearance, *C. bobbi* is unremarkable. The lips have four dorsal, two ventral, indistinct lobes. Oral papillae are not detectable, yet there are slight, low undulations of the inner margin of the mouth. The posterior fourth of the head is demarcated by a shallow external sulcus and a prominent pharyngeal one. Supernumerary muscles of the dorsal portions of the anterior prosomites of the body segments are poorly developed, thus in profile the body outline is smooth: there are no dorsal ridges. The sucker is prominent and slightly greater in diameter than segment I.

The length of the jaws is about $\frac{1}{18}$ that of the head; hence, of usual comparative size. The animals available for this study are all strongly bent ventrad. The exact distribution of the teeth, consequently, is difficult to ascertain in most specimens. There is a prominent apical tooth on each jaw with two small lateral ones flanking it on each side, producing a 5/5 dental formula.

The spermiducal gland is large and reflexed to some extent, often to a right angle, at its mid-length. It has no deferent lobes. The slender prostate is about ½ the length of the spermiducal gland and is "differentiated," that is, composed of cells less densely granular than those of the spermiducal gland. A large, clear ental bulb is present. The bursa is elongate ovoid in shape. The penis is distinctly less muscular than is usual among members of the genus, consisting of an ovoid sac, presumably protrusible, with a few strands (? muscular) traversing it. The ejaculatory duct is of the usual type, a short muscular tube.

The spermathecal duct is about ½ the body diameter in length; the bulb is ovoid without an ental process.

Variations.—No variations of note, except the extent of reflexion of the spermiducal gland, were detected.

Affinities.—*Cambarincola bobbi* clearly belongs to the group of species with a differentiated prostate with an ental bulb that Hoffman (1963:336–341) assigned to his "Philadelphica section" and "group" of the genus. The "Fallax subgroup" in this scheme is distinguished by an equal (and odd) number of teeth borne by each jaw. In this subgroup (consisting of *C. fallax* Hoffman, 1963, and *C. holostomus* Hoffman, 1963), *Cambarincola bobbi* most closely resembles *C. holostomus.*

Cambarincola holostomus is described by Hoffman (1963:361) as characterized by an entire peristomium; that is, there is no division of the peristomium into upper and lower lips, a 3/3 dental formula and a "slender elongate, fusiform" spermatheca. In addition to differing from *C. holostomus* in these respects, *C. bobbi* also is distinguished by a larger and more reflexed spermiducal gland and a shorter prostate (Hoffman 1963: 359, fig. 64). *Cambarincola bobbi* resembles *C. fallax* in these features and the 5/5 dental formula, but lacks the characteristic elongated peristomial tentacles of *C. fallax* and differs from both in its membranous penis. The structure of the penis of *C. bobbi* seems to reinforce the previously noted similarities between the bursal-penial complex of the genera *Cambarincola* and *Sathodrilus* Holt, 1968a (Holt 1982:254). However, in this case, it is most likely another example of convergence within the order, since the relatives of *C. bobbi* are presumably "advanced" members of the genus (Hoffman 1963:296–297).

Host.—*Cambarus bartonii bartonii.*

Distribution.—Known only from the type locality. Other similar streams of the Shenandoah River system should harbor this species.

Material examined.—The type series.

Note.—The tributaries of the New River in western Virginia and eastern West Virginia and the headwaters of the Holston, Roanoke, James, Shenandoah and Potomac rivers contain many similar species of the genus *Cambarincola.* Some specimens from this area are difficult to identify, but *C. bobbi* appears to be clearly distinct from any previously described species, and is another example of the diversity and the incipient speciation in these waters: waters undoubtedly linked by many stream captures in the recent past.

Ellisodrilus carronamus, new species

Fig. 2

Type specimens.—Holotype, USNM 119539 and two paratypes, USNM 119540–119541, taken on *Orconectes* sp., from Carr Creek, Overton County, Tennessee, about 3.0 miles south of Livingston, Tennessee, on State Highway 42, by Perry C. and Virgie F. Holt, 26 Jul 1961.

Diagnosis.—Small worms (holotype 1.95 mm in length); lips entire, no oral papillae; no dorsal ridges; upper jaw slightly longer than lower, dark brown in color, dental formula (?) 5/5; bursa slightly less than ½ body diameter in dorso-ventral length, antero-

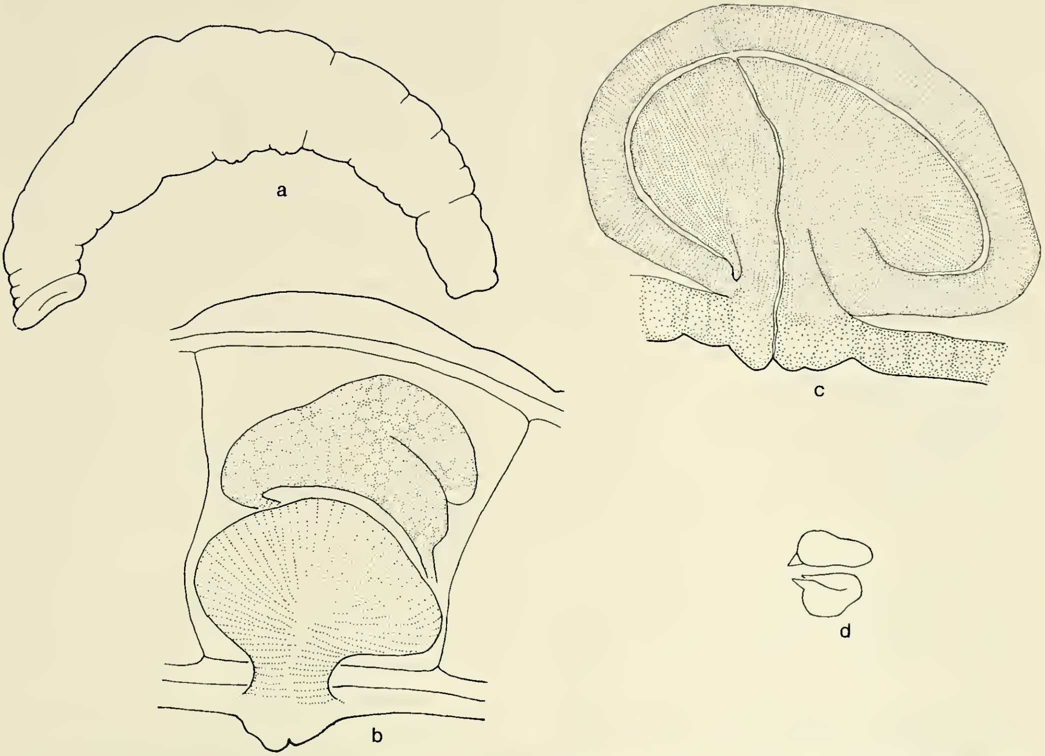

Fig. 2. *Ellisodrilus carronamus,* holotype. a, Lateral view of entire animal; b, Lateral view of male efferent apparatus; c, Optical section of bursa; d, Lateral view of jaws.

posterior dimension (diameter) slightly greater than dorso-ventral one; penis reduced to pore through ental portion of bursa, pseudo-penis formed by enlarged inner-directed atrial fold; ejaculatory duct short, thin; spermiducal gland oriented longitudinally in coelom, lying dorsad to gut, in length about twice its diameter; prostate arises entad to mid-point of spermiducal gland, less than ½ length, subequal in diameter to latter, non-differentiated, with small ental bulb; no spermatheca.

Etymology.—From Greek, *namos,* creek, hence Carr Creek for the type locality and a family that includes friends of my youth for whom the creek was named.

Description.—The holotype, which is comparable in size to the other specimens examined, has the following approximate dimensions: total length, 1.9 mm; greatest diameter, 0.4 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter segment I, 0.2 mm; diameter, sucker, 0.2 mm.

The lips lack lobes; there are no oral papillae. The one internal pharyngeal sulcus has no corresponding external one.

The jaws are brown and prominent, the upper about 1/14 the length of the head, the lower somewhat less. No lateral teeth are apparent in the holotype at a magnification of 500× but some of the paratypes appear to have two lateral teeth at the side of the large median tooth: the dental formula would be, then, 5/5, a point requiring further confirmation.

Dorsal ridges are absent from all segments, but the inter-segmental furrow between VI and VII is deeply incised and the clitellum of segment VII is prominent: this accounts for the greater diameter of segment

VII and gives to this segment a superficial appearance of a dorsal ridge, which, however, entirely lacks supernumerary muscles.

The spermiducal gland, though proportionately large, is unremarkable. There are no obvious deferent lobes and the organ tapers from its greatest diameter at the point of origin of the prostate to its ectal end.

The prostate arises from the spermiducal gland slightly more than ⅓ the length of the latter from its ental end and is almost as great in diameter. It is non-differentiated with a small, but distinct, ental bulb.

The bursa is large, filling the ventral half of its segment. Its ectal portion (atrium), which has an inner-directed circular fold (=atrial fold) whose lumen slants towards the postero-dorsal side of the bursa and opens into the bursal cavity opposite the opening of the ejaculatory duct into the atrium, is the most striking feature of the male reproductive system (Fig. 2c). In effect there is no structure which is homologous to the penis of other genera of the branchiobdellidans except the pore formed by the opening of the ejaculatory duct into the lumen of the bursa (atrium). The ejaculatory duct is thin, short and difficult to detect in available material. The atrial fold, a pseudopenis, would appear to be analogous to the penis of other branchiobdellidans.

There is no spermatheca, hence some form of hypodermic impregnation must occur, though no packets of spermatozoa have been observed on the dorsal surface of any specimen of any member of the genus. Such packets of spermatozoa have been reported by Holt (1949:549) in *Xironogiton instabilis* (Moore, 1894).

Variations.—In several of the specimens examined, the bursa lies along the dorsoventral axis of segment VI, presumably compressed by a contraction of the bodywall. No other variations were noted.

Affinities.—*Ellisodrilus durbini* (Ellis, 1919) and *E. clitellatus* Holt, 1960, have dorsal ridges on some segments: on segment VIII in *E. clitellatus* and segments II–V and VII, VIII in *E. durbini. Ellisodrilus carronamus* lacks these ridges produced by supernumerary muscles (Holt 1960:171–172). *Ellisodrilus carronamus* further differs from its two congeners in its apparently larger size and somewhat larger and darker jaws with a dental formula of (?)5/5. The absence of dorsal ridges distinguishes *E. carronamus.*

There appears to be a north-south gradient in the distributions of these species with *E. carronamus* the southern-most and *E. durbini* to the north, in part at least, in areas scoured by the Pleistocene glaciations (Holt 1960:171; 174).

Branchiobdellidan associates.—*Ellisodrilus carronamus* shares its type locality with four other branchiobdellidans: *Cambarincola philadelphicus* (Leidy, 1851), *Xironodrilus formosus* Ellis, 1918, *Pterodrilus cedrus* Holt, 1968b, and *Oedipodrilus anisognathus,* newly described herein.

Material examined.—The types; six specimens taken from Roaring River on *Cambarus tenebrosus* Hay, 4.7 miles north of Rickman, Overton County, Tennessee, by Perry C. and Virgie F. Holt, 4 Jul 1958.

Oedipodrilus anisognathus, new species
Fig. 3

Type specimens.—Holotype USNM 119534 and one paratype, USNM 119535 taken from a small stream on *Orconectes* sp. in Montgomery Bell State Park, Dickson County, Tennessee, by Perry C. and Virgie F. Holt, 4 Jul 1958; three paratypes, USNM 119536–119537 taken on *Orconectes* sp. from Carr Creek, about 3.0 miles south of Livingston, Overton County, Tennessee, by Perry C. and Virgie F. Holt, 26 Jul 1961.

Diagnosis.—Small worms (holotype 1.8 mm in length); lips entire; no oral papillae; no dorsal ridges; posterior segments markedly greater in diameter than anterior ones; jaws greatly dissimilar in size, upper one about ¼ to ⅓ that of lower in length, dental formula 2/1; bursa relatively small, ½ body diameter in length; penis with (?) hooks; spermiducal gland lies longitudinally in coelom, with obscure deferent lobes; prostate

Fig. 3. *Oedipodrilus anisognathus,* holotype. a, Lateral view of entire animal; b, Lateral view of male efferent apparatus; c, Optical section of bursa; d, Lateral view of jaws.

with ectal end arising at about ental third of spermiducal gland, about ⅓ length of latter, with ental bulb; spermatheca with ectal bursa, cylindrical bulb, narrow ental process.

Etymology.—Greek: *anisos,* unequal; *gnathos,* jaw.

Description.—The specimens of *Oedipodrilus anisognathus* that constitute the type series have the following mean dimensions: total length, 1.4 mm; greatest diameter, 0.4 mm; head length, 0.4 mm; head diameter, 0.2 mm; diameter, segment I, 0.3 mm; diameter, sucker, 0.4 mm.

The worms have a somewhat corpulent appearance with slender heads. There are no supernumerary muscles of the prosomites of the body segments: the outline of the body is smooth. There is a slight constriction delimiting the peristomium; an internal pharyngeal sulcus lies at the greatest diameter of the head, often marked by a slight, shallow external one. The lips are entire, the dorsal somewhat longer than the ventral one. No oral papillae are apparent.

The jaws are distinctive: unlike any others known for any member of the order. The upper jaw is small with two small, obscure teeth; the lower, three or four times the length of the upper, is massive, with flaring lateral flanges and a single, large, triangular tooth.

The spermiducal gland is proportionately small, as is the entire male reproductive system, and lies along the longitudinal axis of the body. Deferent lobes are not prominent. The prostate consists of a rather thick lobe of the spermiducal gland, about ⅓ the latter in length, with a clear ental bulb. It does not differ from the spermiducal gland in its histological appearance.

The bursa is an elongated ellipsoid with a shallow constriction separating its atrial and penial sheath portions. There is a somewhat irregular atrial fold. The penis is an elogated tube coiled inside the penial sheath, attached only at the ectal end of the lumen of the latter and to its ental continuation as the ejaculatory duct. In its everted position the penis would be lined by a thin layer of tissue, possibly muscular. Penial hooks are few in number and difficult to detect with customary methods: there appear to be two or three pairs.

The ejaculatory duct is a short, thick muscular tube, almost as great in diameter as in length.

The ectal duct of the spermatheca is a short, thick, muscular spermathecal bursa. About ½ the total length of the spermatheca is composed of the spermatozoa storing bulb. There is a narrowed ental process with a thick muscular wall.

Variations.—None were noted in the available material.

Affinities.—Three other species of *Oedipodrilus* have been described: *O. oedipus* Holt, 1967, the type species from Humphreys County, Tennessee; *O. macbaini* (Holt, 1955), from Tennessee northward to Illinois and Pennsylvania; *O. cuetzalanae* Holt, 1984, from the state of Puebla, Mexico. *Oedipodrilus oedipus* has dorsal ridges, jaws with a 5/4 dental formula, a much shorter penis with many penial hooks and lacks an ental process of the spermatheca, differing from *O. anisognathus* in all these features. *Oedipodrilus macbaini* principally differs from *O. anisognathus* in the 5/4 dental formula, the much longer penial sheath and remarkably longer penis with many prominent hooks and the very long ectal duct of the spermatheca and the absence of a spermathecal ental process. *Oedipodrilus cuetzalanae* has a 5/4 dental formula; a very small, often obscure, prostate; a long, coiled penis with many hooks; a slender spermatheca with a long ectal duct, a thick-walled bulb and no ental process: *O. anisognathus* is different in all these features. Holt (1984: 40) said that "[t]he three known species of the genus form a coherent group and it is futile at this stage to speculate about which is more closely related to the other." In general, this statement is still true, but perhaps the unusual (? gill-clipping) jaws of *O. anisognathus* separates it more widely from the other species of the genus. Notice should be taken here of some similarities of these species with some members of the genus *Sathodrilus,* all of which likewise have an eversible penis. In most species of *Sathodrilus* the penis is a straight tube attached by strands of tissue to the inner wall of the penial sheath and everts as a membranous cup-shaped structure. But the penis of *S. villalobosi* Holt, 1968a, is an elongated tube with shallow coils (Holt 1984:40, fig. 3a) that, however, lacks penial hooks. These penial hooks may be the only character that reliably separates the two genera.

Habitat.—*Oedipodrilus anisognathus* has, though, not to as marked degree as some such species, the appearance of parasitic, gill-inhabiting worms: a thinner than usual body-wall, expanded posterior body segments, elongated and tapering head and peristomium. The jaws, closer in shape than are those of any other species to those of *Bdellodrilus illuminatus* Moore, 1895, which is known to inhabit the gill chambers of its hosts and to be parasitic, seem well suited to piercing the thin cuticle of the host's gills. More to the point, the gut of all the specimens examined of *O. anisognathus* is filled with a homogeneous coagulum, most likely blood, without any of the usual components of the slime found on the outer surfaces of the host. These worms most likely inhabit the gill chambers of the host.

Hosts.—*Orconectes juvenilis* (Hagen).

Distribution.—*Oedipodrilus anisognathus* is known only from the two localities cited: the type locality is in the Central (Nashville) Basin; the other in the eastern Highland Rim, the uplands surrounding the Nashville Basin.

Oedipodrilus macbaini (Holt, 1955)

Figs. 4, 5

Cambarincola macbaini (Holt 1955:27–31).
Oedipodrilus macbaini (Holt 1969:205; 1984:39).

Type specimens.—Holotype, USNM 25952, six paratypes, PCH 134, taken from Charles Creek, eight miles west of Ashland on State Highway 5, Boyd County, Kentucky, on *Orconectes* sp. by Rodney MacBain, Jul 1948 (Holt 1955:29).

Diagnosis (emended).—Small- to medium-sized worms (average length of five specimens of type series and five specimens from Powell County, Kentucky, 1.8 mm); lips entire; no oral papillae; no dorsal ridges; jaws small, dental formula 5/4; bursa exceeds body diameter in length; penial sheath three to four times length of bursal atrium; penis long cuticular tube furnished with recurved hooks, coiled within lumen of penial sheath; ejaculatory duct proportionately short, thick, muscular; spermiducal gland about ⅔ body diameter in length, its diameter about ½ its length; prostate short, lying along ental third of spermiducal gland; non-differentiated, with ental bulb; spermatheca approximately equal to bursa and penial sheath in length, composed of long ectal duct, narrow median region, elongate bulb.

Etymology.—For the collector, Rodney G. MacBain.

Description.—Five specimens of the type series, collected in 70 percent ethanol have the following average dimensions: total length, 1.2 mm; greatest diameter, 0.3 mm; head length, 0.2 mm; head diameter, 0.1 mm; diameter, segment I, 0.1 mm; diameter, sucker, 0.2 mm (Holt 1955:27–28; modified to conform to current usage). In comparison, five specimens from Powell County, Kentucky, have the following average dimensions: total length, 2.4 mm; greatest diameter, 0.3 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter, segment I, 0.2 mm; diameter, sucker, 0.3 mm. The discrepancies in these measurements probably result from differences in the fluids used in collecting: material taken since 1958 by Holt has been fixed in a solution composed of five parts of formalin to 95 parts of 70 percent ethanol. The latter fluid is far superior to ethanol alone, in part because of a lesser degree of contraction of the animals.

The lips are entire; there are no oral papillae. There is one internal pharyngeal sulcus, but externally there is little indication (by an external sulcus) of its location. There are no supernumerary muscles of the dorsum of any body segments: the body outline is smooth.

The jaws present no distinctive features: they are small, delicate in appearance and light in color. The dental formula is 5/4. The gut is markedly narrowed in segments V and VI: most of the space in these segments is occupied by the spermatheca and male reproductive organs. Diatoms and detritus constitute the food found in the gut.

The anterior nephridiopore, undetectable in the entire specimens of the type series (Holt 1955:28) is, as determined by study of sectioned animals of the material from Powell County, Kentucky, a single minute opening on the dorsum of segment III.

The spermiducal gland is unremarkable, about twice its diameter in length and usually lying in a vertical position in the anterior portion of segment VI. The prostate, composed of cells similar to those of the spermiducal gland, is about ⅓ the diameter and length of the latter and arises entad to the junction of the spermiducal gland and ejaculatory duct (Fig. 4b). It has a small ental bulb in the Powell County animals which is not apparent in the paratypes. This discrepancy may be attributed to the contracted state of the latter.

The ejaculatory duct, as determined from sections (Fig. 5c) is a relatively short, thick and muscular tube distinctive only in the thickness of its inner layer of circular muscles.

The bursa is a very long, cylindrical tube that is variously bent as it courses dorsolaterad over the gut to its union with the ejaculatory duct. The bursal atrium is composed of a moderately thick inner layer of circular muscles and an outer thinner one of longitudinal (in reference to the organ) muscles and encloses what is actually the

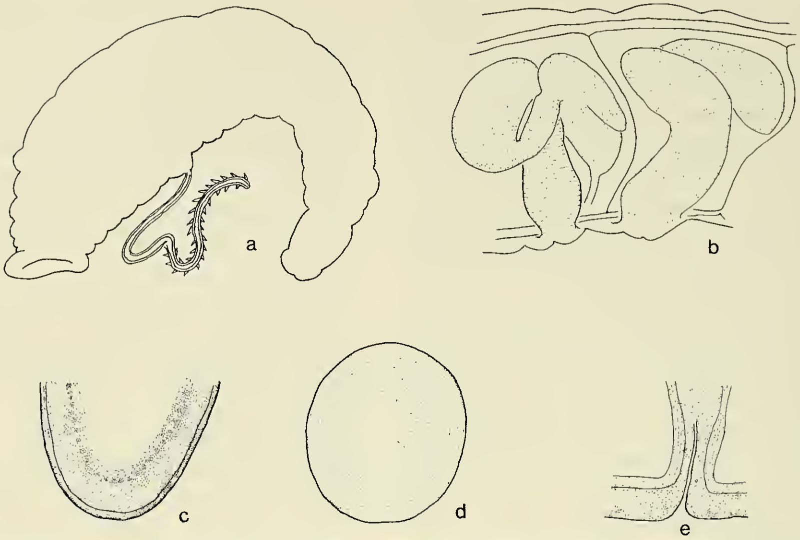

Fig. 4. *Oedipodrilus macbaini* (Holt, 1955), specimens from Powell County, Kentucky. a, Lateral view of entire animal with everted penis; b, Lateral view of reproductive systems (after Holt 1955); c, Section through ental end of spermathecal bulb; d, Cross section of ectal duct of spermatheca; e, Section through outlet pore of spermatheca.

portion of the penis that is not enclosed in the penial sheath in its retracted state (Fig. 5a). Most of the bursa consists of the penial sheath whose wall is apparently composed of the same, but much thinner layers as is the bursal atrium. Its capacious lumen contains the loops of the cuticular penis (Figs. 5b, c).

These dimensions of the bursa (atrium and penial sheath) accommodate the inordinately long cuticular penis. When completely everted the penis may actually be longer than the animal itself (Fig. 4a shows the penis much foreshortened). Retracted, the penis appears to consist of a thin layer of tissue with a cuticular lining. These layers are continuous with those composing the penial sheath and ejaculatory duct (Fig. 5a, b, d). When everted, the ectal portion of the penis is provided with recurved hooks (Figs. 4a, 5d, e) that lie within the lumen of the uneverted penis (Fig. 5d, e) which are absent from its ectal- and ental-most portions (Fig. 5a, b).

Such features of the penis, as might be expected, are matched by the structure which receives it in copulation: the spermatheca. There is a short ectal pore canal composed of the same layers as the body wall and the bursa (Fig. 4e) which passes shortly entad into the long and expanded ectal duct proper of the spermatheca (Fig. 4b, d, e). This duct courses dorsad, loops over the gut and is itself at least twice as long as the body diameter. The inner layer of the spermathecal duct is composed of cells with processes extending radially into the lumen of the duct (Fig. 4d). The spermatheca ends entally in a large, ventrally directed ovoid bulb.

Affinities.—See the discussion of the affinities of *O. anisognathus* above.

Variations.—The loops and bendings of the penial sheath and spermatheca take various positions within their segments. A careful comparison of paratypes with the other specimens herein assigned to the species lead to the conclusion that the differences in size and the apparent absence of

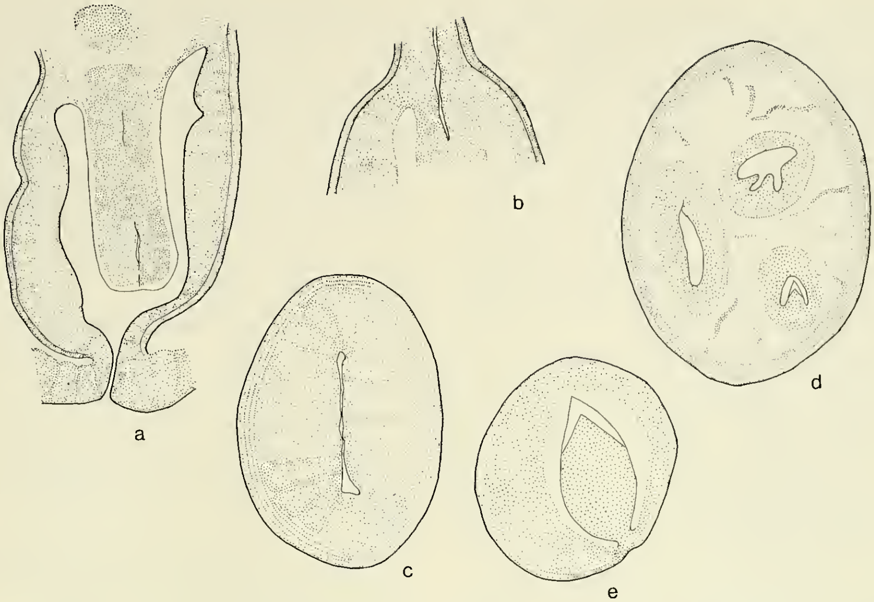

Fig. 5. *Oedipodrilus macbaini,* specimens from Powell County, Kentucky. a, Optical section through bursal atrium and ectal end of retracted penis; b, Optical section through ental end of penial sheath portion of bursa and penis; c, Optical cross section of ejaculatory duct; d, Optical cross section of penial sheath; e, Optical cross section of penis.

an ental bulb of the prostate in these type specimens is accounted for by the differences in fixation (see above).

Hosts.—See "Material Examined" below.

Distribution.—*Oedipodrilus macbaini* is widely dispersed throughout the Ohio River drainage in Tennessee, Kentucky, Ohio and Pennsylvania, and the Illinois River in Illinois. It is, therefore, a member of the diverse branchiobdellidan fauna that is derived from the pre-Pleistocene inhabitants of the Cumberland River and ultimately the ancient Teays drainages that has followed the retreating ice northward (Hobbs et al. 1967:69 et seq.; Holt 1968b:5, 1969:199).

Material examined.—(Unless otherwise noted all collections were taken by Perry C. and Virgie F. Holt). Illinois. Vermillion County, 9.2 miles north of Danville on U.S. Highway 136, on *Orconectes propinquus* (Girard), *O. virilis* (Hagen), *O. immunis* (Hagen), 25 Jul 1958. Indiana. Montgomery County, 6.4 miles north of junction of Indiana highways 47 and 234, 24 Jul 1958, on unknown host, PCH 802; Orange County, 8.3 miles north of Crawford County line on Indiana Highway 145, 26 Jul 1958, on *Cambarus laevis* Faxon, *O. virilis,* PCH 812; Parke County, 5.6 miles west of Bellmore on U.S. Highway 36, 26 Jul 1958, on *O. immunis, O. propinquus,* PCH 807; Parke County, 4.2 miles north of Rockville on U.S. Highway 41, on unknown host, 26 Jul 1958, PCH 806; White County, 2.6 miles north of junction of U.S. highways 421 and 24 at Reynolds, 24 Jul 1958, on *O. virilis, O. propinquus,* PCH 801. Kentucky. Boyd County, 8 miles west of Ashland from Charles Creek on Kentucky Highway 5, Jul 1948, on *Orconectes* sp., R. G. MacBain, PCH 134. [Type locality]; Carter County, 1.9 miles northeast of Carter-Rowan County line on U.S. Highway 60, on unknown host, 23 Apr 1961, S. E. Neff and P. C. Holt, PCH 1360; Clarke County, 4.6 miles south of Winchester from Howard Creek on U.S. Highway 227, 30 Jul 1958, on *O. rusticus* (Girard), PCH 840; Fleming County, 1.5 miles northeast of Cowan on Kentucky Highway 32, on unknown host, 20 Apr 1961, S. E. Neff and P. C. Holt, PCH 1357; Harrison County, 0.5 mile northwest of Renaker on Kentucky Highway 36 from South Fork of Raven Creek, on *O. rusticus, C. b. bartonii,* 27 Jun 1964, J. F. Fitzpatrick, PCH 1788; Jackson County 1.8 miles south of junction of Kentucky Highway 30 and 1190, 29 Jul 1958, on *O.* sp., PCH 831; Johnson County, 6 miles northeast of Paintsville on U.S. Highway 460, on *C. b. bartonii,* 6 Aug 1961, P. C. Holt, PCH 1454 (USNM 37799); Madison County, 9.3 miles north of Richmond on U.S. Highway 227, on unknown host, 30 Jul 1958, PCH 841 (USNM 37175); Nicholas County, at Meyers, on unknown host, 20 Apr 1961, S. E. Neff and P. C. Holt, PCH 1358; (USNM 37565); Powell County, 1.4 miles east of Slade on Kentucky Highway 11-15, on unknown host, 29 Jul 1958, PCH 836 (redescription based on this collection); Powell County, 4 miles northeast of Nada on Kentucky Highway 77, on unknown host, 30 Jul 1958, PCH 845. Ohio. Jefferson County, 4.2 miles northeast of Bloomingdale, on U.S. Highway 22, on *C. b. bartonii* and *O. obscurus* (Hagen), 7 Aug 1960, PCH 1226; Stark County, 3.8 miles west of Alliance on U.S. Highway 62, 3 Aug 1960, on *O. obscurus,* PCH 1205; Wayne County, 3.9 miles west of Riceland on U.S. Highway 30, on *O. propinquus,* 3 Aug 1960, PCH 1204; Williams County, 0.8 mile west of junction of U.S. highways 6 and 127, on *O. rusticus,* 3 Aug 1960, PCH 1201. Pennsylvania. Butler County, 4.6 miles northeast of crossing of Pennsylvania Highway 68 and Pennsylvania Turnpike near Zelienople, on *C. b. bartonii* and *O. obscurus,* 6 Aug 1960, PCH 1225; Butler County, Wolf Creek at crossing of Pennsylvania Highway 108, 4.9 miles northeast of Harlansburg, on *O. obscurus,* 6 Aug 1960, PCH 1224; Erie County, French Creek at junction of U.S. highways 6 and 19, on *O. obscurus,* 5 Aug 1960, PCH 1216; Erie County, 2.6 miles west of Union City on U.S. Highway 6, on *C. b. bartonii* and *O. obscurus,* 5 Aug 1960, PCH 1215. Tennessee. Putnam County on Tennessee Highway 56 at Baxter, on unknown host, 25 Jul 1961.

Notes.—The streams from which collections were taken by P. C. and V. F. Holt were all small- to medium-sized ones in which the hosts were taken by hand or with a dipnet. Most are in hilly, wooded country, but some (in Ohio) are in the plains on glacial silt.

The gut contents of *O. macbaini* include diatoms and the usual detritus that adheres to the exoskeleton of the hosts.

Sathodrilus rivigeae, new species
Fig. 6

Type specimens.—Holotype USNM 119545 and two paratypes, USNM 119546, [PCH 1089] taken from clear cool pools in a medium-sized stream in Ouachita National Forest, 3.2 miles east of Joplin, Montgomery County, Arkansas, at crossing of U.S. Highway 270, on *Orconectes palmeri longimanus* (Faxon) 23 Jun 1960, by Perry C. and Virgie F. Holt.

Diagnosis.—Medium-sized worms (holotype 2.8 mm in length); lips entire, peristomium demarcated by distinct sulcus; no oral papillae; no dorsal ridges of body segments; jaws small, delicate, in length $\frac{1}{18}$ head length, dental formula (indeterminant in types) (?)1/4; bursa about ½ body diameter in length, constriction at mid-length marks junctions of bursal atrium and penial sheath; penis eversible, membranous, equal (when retracted) to penial sheath in length, atrial fold present; spermiducal gland large, about $\frac{7}{11}$ body diameter in length, with large prominent deferent lobes; prostate subequal in diameter, ¾ in length of spermiducal

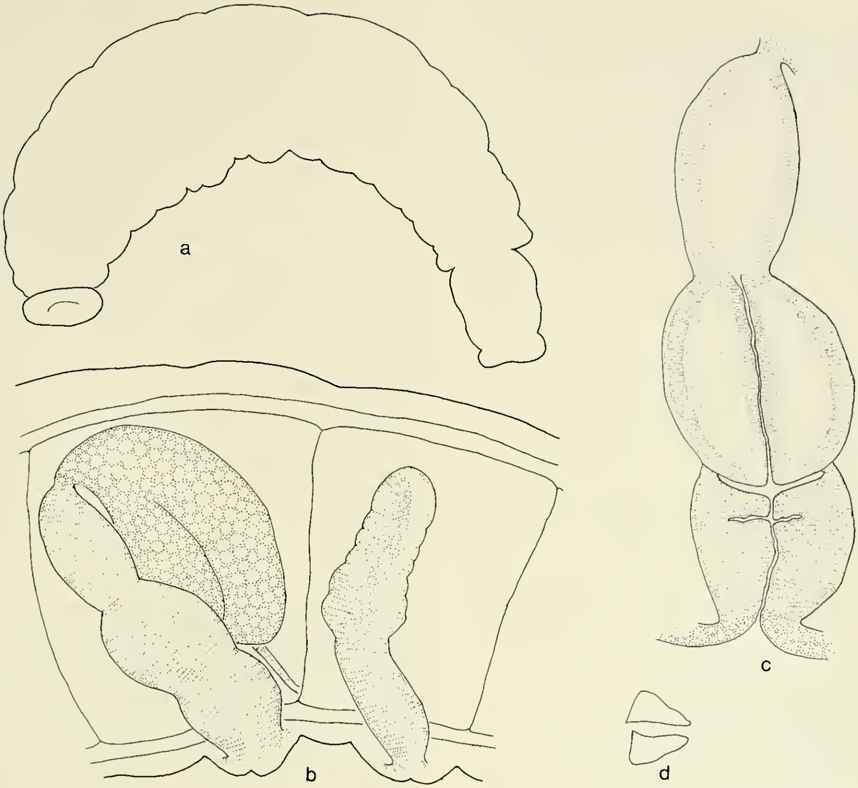

Fig. 6. *Sathodrilus rivigeae,* holotype. a, Lateral view of entire animal; b, Lateral view of reproductive systems; c, Optical section of bursal complex and ejaculatory duct; d, Lateral view of jaws.

gland, non-differentiated histologically; spermatheca with ectal duct, about ⅓ total length, bulb elongate ovate.

Etymology.—An anagram based on my co-collector's first name.

Description.—The paratypes are somewhat smaller than the holotype which has the following dimensions: total length, 2.8 mm; greatest diameter, 0.5 mm; head length, 0.4 mm; head diameter, 0.3 mm; diameter, segment I, 0.4 mm; diameter, sucker, 0.4 mm.

The lips lack lobes or tentacles, the peristomium is somewhat less in diameter than the greatest diameter of the head and a distinct annular sulcus separates it from the remainder of the head. The prominent internal pharyngeal sulcus is matched externally by a broad shallow one. Oral papillae are absent. There are no dorsal supernumerary segmental muscles: the body outline is smooth.

The jaws are difficult to interpret in the three available specimens: they are small and delicate in appearance, dark in color in the holotype, lighter in the paratypes and in one paratype the lower jaw appears to bear four teeth and the upper only one median tooth.

The spermiducal gland is of greatest diameter at the junction of the prominent deferent lobes and tapers gradually ectad to its union with the ejaculatory duct (the deferent lobes and ental portion of the gland are obscured in the illustration).

The prostate is unusually large among the members of the genus. It arises from the spermiducal gland about a third of the length of the latter from its ectal end and extends entally to the junction of the deferent lobes. It appears to be composed of the same granular epithelium as the spermiducal gland: it is non-differentiated. There is no obvious ental bulb; but one paratype appears to have a short clear space between the investing peritoneum and its ental-most glandular cells.

The bursa is elongate with a broad and deep constriction at its mid-length at the union of the penial sheath and bursal atrium. The atrium has thick muscular walls and the atrial fold is thin and irregular. The penial sheath is lined by an epithelium (? muscular) and encloses the penis in a commodious cavity. The latter is an almost straight cuticular tube with minute longitudinal folds and is likewise covered with a layer of presumably muscular tissue.

The diameter of the ejaculatory duct is more than half its total length and its lumen is greatly expanded. It has the structure of a bulb whose function is that of a pump.

The spermatheca has a long ectal duct. Its bulb in the holotype is a thickened muscular elongate sac with a narrow lumen. Spermatozoa may be absent. The spermathecal bulbs of the paratypes are of the more common obovate type without ental processes.

Variations.—Two were noted (an unusual number among branchiobdellidans): the differences in the spermathecal bulbs just noted and in the contents of the gut. In the holotype the middle sacculations of the gut contain dark brown particles of unidentifiable detritus; the guts of the smaller paratypes are filled with a homogeneous clear material similar in appearance to that found in gill-inhabiting species; but the jaws are ill-adapted for clipping the gill filaments or piercing the articular membranes of the host.

Affinities.—Seven species of *Sathodrilus* have distinct prostates (as opposed to "prostatic protuberances" or "bulbs"). In all of these species the prostate arises from the spermiducal gland entad to the junction of the latter with the ejaculatory duct. Of these, *S. dorfus* Holt 1977, *S. lobatus* Holt 1977, and *S. inversus* (Ellis, 1919) have ejaculatory ducts that are short and thickened ("bulb-like") and are the closest known relatives of *S. rivigeae. Sathodrilus lobatus* has an expanded peristomium furnished with 14 lobes, its spermiducal gland and prostate are proportionately lesser in diameter than those of *S. rivigeae* and the spermatheca has a prominent medial bulb and long ental process (Holt 1977:122–124, fig. 3). Peristomial lobes are absent in *S. inversus*; the spermiducal gland is noticeably narrowed at its ectal end; the spermatheca has a median bulb and a long spermatozoa storing bulb without a muscular wall or ental process (Holt 1977:128–131, fig. 6, 1981:855). The spermiducal gland and prostate of *S. dorfus* are short and thick; the spermatheca is composed of a long ectal duct, a median bulb and an ental process (Holt 1977:120–121, fig. 2). All three of these species are inhabitants of the Pacific versant of the northwestern United States. *Sathodrilus rivigeae* differs from them most noticeably in the muscular wall of its spermathecal bulb and is, at least superficially, closest to *S. inversus,* from which it further differs in the short lobes of the peristomium and the frequent divergence of the prostate from the spermiducal gland (Holt 1977, fig. 7) found in the latter.

Branchiobdellidan associates.—*Cambarincola vitreus* Ellis, 1918, a species of *Cambarincola* that appears to be *C. heterognathus* Hoffman, 1963, and a widespread undescribed Ozarkian species of *Xironodrilus* Ellis, 1918.

Host.—*Orconectes palmeri longimanus.*

Distribution.—Known only from the type locality.

Material examined.—The types.

Notes.—Branchiobdellidan associates of two species have been given herein because the data were readily available; it should always be borne in mind that rarely is only one species of branchiobdellidan found in any given locality.

The resemblances of *S. rivigeae* to its congeners of the Pacific northwest is another example of the homogeneity of the eastern and western branchiobdellidan faunas of North America, almost totally isolated now by the continental divide.

The expanded, bulb-like ejaculatory ducts of the species of *Sathodrilus* discussed herein should be further investigated. Function is difficult to infer from form alone, but it is probable that, in species with long, eversible penes and long spermathecal ectal ducts, that these expanded ejaculatory ducts aid in pumping spermatozoa into the spermathecal bulb.

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PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS V. A COLLECTION BY THE *KAKUYO MARU* FROM SAMOA

Koichiro Nakamura and C. Allan Child

Abstract.—A small shallow-water collection of Pycnogonida taken by the Japanese training vessel *Kakuyo Maru* in American Samoa and Western Samoa is described. The collection contains seven species, one of which is new: *Anoplodactylus crassus.* The species affiliations are discussed along with their limited known zoogeography. Little concerning zoogeographic affinities can be proposed due to lack of pycnogonid collections from most mid-Pacific localities.

Pycnogonids of the Samoan Islands have remained unknown until these first records of specimens taken from this locality. There were only seven species collected in two well known shallow-water genera, with six species known and one new to science: *Anoplodactylus crassus.* The six known species have mostly Indo-West Pacific distributions based on what little is known, but one species, *A. erectus,* has been collected many times in shallow waters along the west coasts of the Americas at least as far south as Colombia. This species is also known from the Tuamotus and from Korea, but its apparent main distributional locality of the American coasts makes it the only apparent emigrant from the east in the Samoa collection. One species, *A. perforatus,* has been taken only in Japanese waters, while *Ammothella stauromata* has been taken in the Marshall Islands and the northern and southern Philippines, *Anoplodactylus rimulus* only from the western Indian Ocean, and the other two species, *A. arescus* and *A. glandulifer,* have broader known distributions in the Atlantic and Indo-Pacific. The distributional knowledge of these species is undoubtedly fragmentary, as is that of most pycnogonids, and it will be extended for each species as more collecting is carried out in the vast areas still unsampled. None of the depths at which the six known species were taken extends the depth distribution for any of them.

Family Ammotheidae

Genus *Ammothella* Verrill, 1900

Ammothella stauromata Child

Ammothella stauromata Child, 1982:271–273, fig. 1; 1988a: 5, 7.

Material examined.—American Samoa: Tutuila; Pago Pago Harbor, 3 m, 23 Oct 1985, 2 ♂ with eggs, 1 ♂.

Distribution.—The type locality for this species is Enewetak Atoll, Marshall Islands, and it has also been taken in the Philippines in the south at Negros Island and in the north at Batan Island, Batanes Province. It is now known to inhabit American Samoa. All capture depths are shallow at 0–3 meters.

Remarks.—This is an easily recognized species in a genus with many similar species. The dorsal trunk tubercles almost match the ocular tubercle and the abdomen size and length, and make this species very distinctive. There are several *Ammothella* species with median trunk tubercles, but none of the others have this tall shape nor does any other species have a tall tubercle on the cephalic segment. Other recognition characters are the short first scape segment with small distal tubercles, anterolateral cephalic segment tubercles, and dorsodistal tubercles on the lateral processes. None of these characters is unique but their combination in this species makes it unique.

Family Phoxichilidiidae
Genus *Anoplodactylus* Wilson, 1878
Anoplodactylus arescus du Bois-Reymond Marcus

Anoplodactylus arescus du Bois-Reymond Marcus, 1959:105–107, pl. 21.—Stock, 1968:53 [text]; 1975:133, figs. 10–12.—Arnaud, 1973:954.—Child, 1988a:12.

Material examined.—Western Samoa: Apia; Upolu Island, 10 m, 25 Oct 1985, 1 ♂, 4 ♀.

Distribution.—This species was first taken in the Red Sea in sand and has had subsequent captures in Madagascar and Tanzania. It was recently found in the southern Philippines (Child 1988a), and is now also known from the mid-Pacific in Samoa, much farther east than previous records. This Samoan record marks the deepest capture for this species at 10 meters. The substrate at this locality is fine coral sand with small rubble bits. This species is one of the few pycnogonids known to prefer fine sand as a regular habitat. A few other *Anoplodactylus* species have been taken repeatedly from sand and most species of the genus *Rhynchothorax* are also known from this kind of substrate in at least one or more records.

Remarks.—These specimens have a slightly shorter neck, a second smaller heel spine proximal to the main spine, and the proboscis is more cylindrical than the swollen proboscis of the type. These specimens agree very well otherwise with the figures of the type. The integument is very papillose in all specimens examined. This is a very tiny species and is recognized by its distally extended tarsus, a round pad of integument at the heel base, a full propodal lamina, and a lack of any auxiliary claws, all characters shared by the 5 Samoan specimens.

Anoplodactylus crassus, new species
Fig. 1

Anoplodactylus viridintestinalis (Cole).—Kim, 1986:3–5, fig. 2.—Kim & Hong, 1986:44.—Hong & Kim, 1987:161.

Material examined.—American Samoa: Tutuila; Pago Pago Harbor, 3 m, 23 Oct 1985, holotype ♂ with eggs (USNM 234393), paratypes, 2 ♂ with eggs, 2 ♀, 1 juv (USNM 234394).

Description.—Size moderately small, leg span 8.3 mm. Trunk compact, circular in outline, unsegmented, lateral processes contiguous proximally, slightly separated distally, each armed with small conical dorsodistal tubercle bearing seta. Neck short, flanked by large bulges denoting palp rudiments. Ocular tubercle as tall as its diameter, capped by low anterodistal tubercle, eyes large, well pigmented. Proboscis short, with low midventral swelling. Abdomen broad in lateral view, only slightly longer than ocular tubercle, tapering distally, armed with 7–8 short distal setae.

Chelifore scape slender, 5 times longer than its diameter, armed with 3 low dorsal tubercles each bearing seta. Chela palm narrow, movable finger as long as palm, armed with several tiny serrate teeth and 3 ectal setae. Immovable finger shorter, more slender, armed with 2 tiny teeth. Fingers well curved, movable finger with greater curve, overlap at tips.

Oviger short, setose, second to fifth segments armed with lateral and distal setae,

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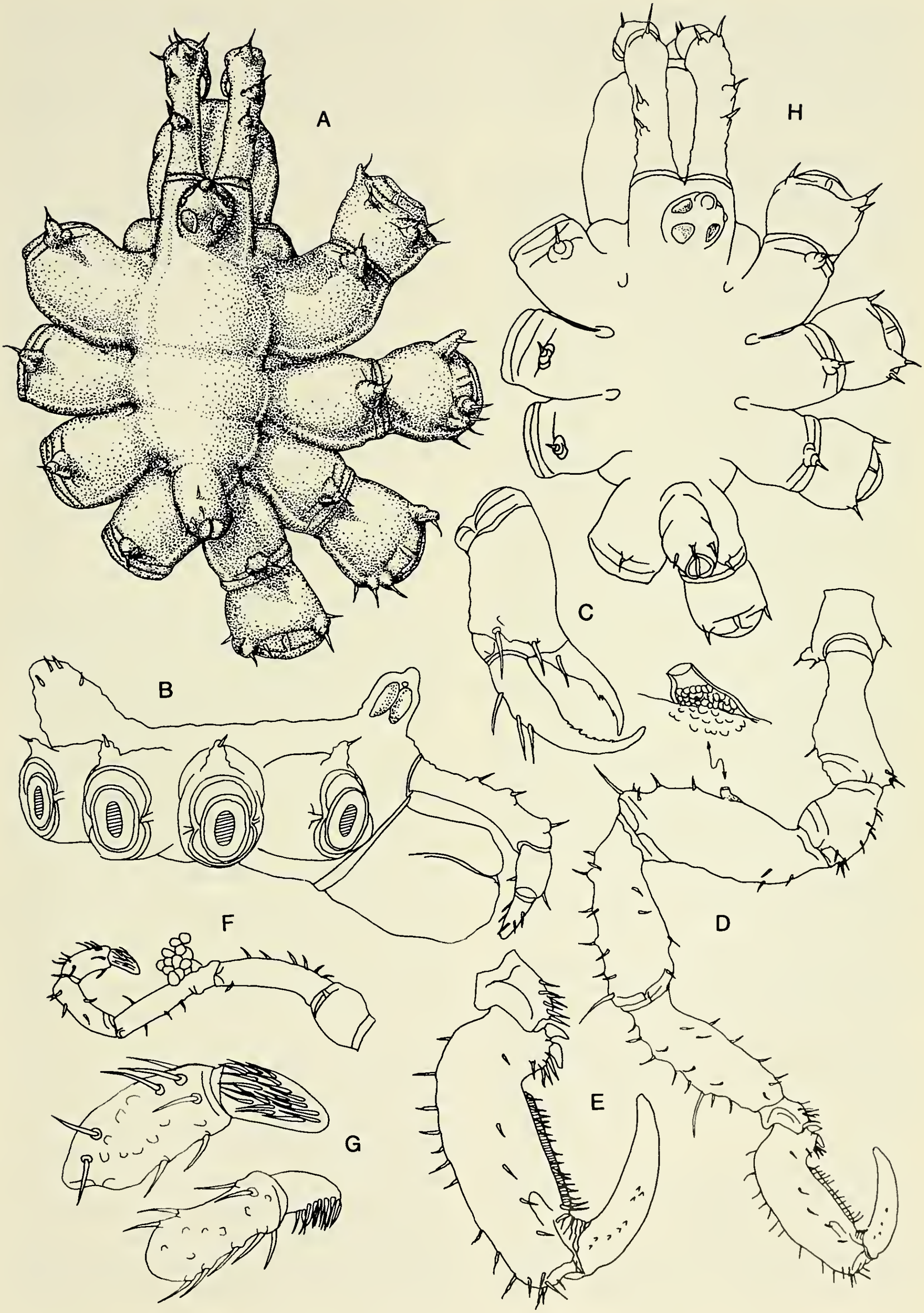
Fig. 1. *Anoplodactylus crassus*, holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Chela; D, Third leg with enlargement of cement gland tube; E, Leg terminal segments, enlarged; F, Oviger with several attached eggs; G, Oviger terminal segments, enlarged in lateral and ectal views. Paratype female: H, Trunk, dorsal view.


A
H
C
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G

sixth with dense field of short lateral setae on one side only. Second segment subequal to third which has proximal constriction, fourth slightly longer than fifth, sixth a short cone.

Legs moderately short, robust, lightly setose. First coxa almost length of third, first armed with 2–3 short dorsodistal tubercles bearing apical setae. Femur the longest segment, cement gland a single short truncate cone with broad tubular tip. First tibia longer than second, both armed with low dorsal bulges bearing setae. Tarsus triangular with many short endal setae. Propodus with strong heel armed with 2 short stout spines and 3 setae. Sole with many short setae flanking long lamina on entire sole length. Claw robust, well curved, about 0.6 propodal length, auxiliaries entirely lacking.

Female slightly larger than male, dimorphic in trunk shape. Posterior pair of lateral processes well separated from third pair imparting a more ovoid shape to trunk in dorsal outline. Lateral process tubercles and those of first coxae reduced or lacking with corresponding reduction of coxal setae.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 0.86; trunk width (across 2nd lateral processes), 0.8; proboscis length, 0.38; abdomen length, 0.29; third leg, coxa 1, 0.26; coxa 2, 0.37; coxa 3, 0.29; femur, 0.71; tibia 1, 0.6; tibia 2, 0.55; tarsus, 0.14; propodus, 0.51; claw, 0.34.

Distribution.—Known from the type-locality, Pago Pago, American Samoa, in 3 m, and from the Korean coast in littoral depths.

Etymology.—The species name *crassus* is Latin (thick, fat, or stout) and refers to the thick or stout appearance of these specimens.

Remarks.—This new species is very close to and forms a geminate pair with *Anoplodactylus viridintestinalis* (Cole, 1904). The two species are difficult to separate by superficial examination but close investigation of both sexes in each species shows many small differences between the eastern and the western Pacific species. Taken alone (as with Kim 1986), these differences could be attributable to variation in populations but examination of the cumulative effect of the many small differences suggests that isolation has produced speciation from what possibly was the original stock on the American west coast. A number of specimens of *A. viridintestinalis* from California (Fig. 2A–F), and the female holotype appendages were examined for comparison with the Samoan specimens. The trunk and its additional appendages in alcohol (not on slides made by Cole) were lost many years ago.

The mainland American specimens show almost no variation among themselves and are consistently different from *A. crassus* in the following characters. The proboscis of *A. crassus* is shorter in length and thicker in diameter than the mainland species. The trunk shape is always broader in dorsal view in males than in *A. viridintestinalis,* and the chelifore scape has 3 low setose tubercles in almost all specimens rather than one or none, the chelae are longer and more slender or rectangular in shape, the abdomen is broader, carried at less of an erect angle, and has more distal setae, the lateral process tubercles each bear a seta at the tip rather than anterolateral to the tubercle itself, the 3 laterodistal tubercles of the first coxae are larger while the mainland species may have only one or none, the ocular tubercle is more rounded distally with a small cap tubercle while Cole's species has a pointed conical ocular tubercle, and the ventrodistal sex pore tubercle on the second coxae is low and inconspicuous while it is as long as half the segment diameter in *A. viridintestinalis.* The cement gland tube, although it has the same bottle shape and location on the femur, is shorter in length than that of Cole's species. It is in the setation of the oviger terminal segment that the biggest difference is noticeable. In the new species, there is a field of many short setae, shorter than the maximum segment diameter, which occurs only on one side of the conical segment. On the terminal oviger segment of Cole's species, there are 6 to 8 setae, each longer than the maximum segment diameter, placed randomly on its endal and lateral surfaces.

Sexual dimorphism of the lateral process placement on the trunk is evident in both species but the female proboscis of mainland specimens invariably has a rather large proximoventral bulge which is not found in *A. crassus* females.

It would be rather difficult to separate these two species were specimens of both not at hand with which to compare the differences. The set of figures (Fig. 2A–F) of *A. viridintestinalis* from California is therefore provided so that these differences can be more readily seen.

Anoplodactylus erectus Cole

Anoplodactylus erectus Cole, 1904:289–291, pl. XIV, fig. 12, pl. XXVI, figs. 1–9.—Child, 1970:288–289 [early literature]; 1979:52.—Kim & Hong, 1986:41, fig. 5.—Hong & Kim, 1987:161.

Material examined.—American Samoa: Tutuila, Pago Pago Harbor, 3 m, 23 Oct 1985, 2 ♂ with eggs, 1 ♀.

Distribution.—This species has long been known to inhabit shallow waters from British Columbia, Canada, to Colombia, and it has also been taken in Hawaii, the Tuamotu Islands, and in Korea. This record extends its South Pacific distributional limits westward to Samoa, but adds nothing new to its shallow depth records.

Remarks.—Males of this species are easily recognized by the long subcutaneous cement gland tube extending almost to the proximal end of the femur, dorsodistal lateral process turbercles of varying lengths, the long third oviger segment, and the two short spines on the well formed heel of the propodus. The chelae are short and the overlapping fingers have no teeth. Female specimens, as with almost all females of this genus, need accompanying males which bear the critical characters essential for positive identification.

Anoplodactylus glandulifer Stock

Anoplodactylus glandulifer Stock, 1954:80–84, fig. 36.—Child, 1982:273–274 [literature]; 1988b:58–59.

Material examined.—American Samoa: Tutuila; Pago Pago Harbor, 2 m, 23 Oct 1985, 1 ♂ with eggs, 1 juv.

Distribution.—This species has been taken in a number of Indian Ocean localities from Kenya and the Red Sea to Singapore, and it has been found at Enewetak Atoll, Marshall Islands. This is the first South Pacific record, but it probably will be found to inhabit many other western Pacific localities. The Samoan capture depth contributes nothing new to the known depths of intertidal to 5 meters for the species.

Remarks.—The 3 small cement gland cups on each femur serve to distinguish this species from most others known, although it is not the only species to possess multiple cement gland outlets. It has no other outstanding characters except for the closely spaced lateral processes and a long propodal lamina, making isolated females difficult to impossible to distinguish without accompanying males. This species is little different from several other Pacific species except for the cement gland cups which may number from 2 to 4 per femur on the same specimen and for the very long propodal lamina which is another unusual character. The two characters serve to separate this species from any other small but similar species in the western Pacific.

Anoplodactylus perforatus Nakamura & Child

Anoplodactylus perforatus Nakamura & Child, 1982:289–291, fig. 3; 1983:49.

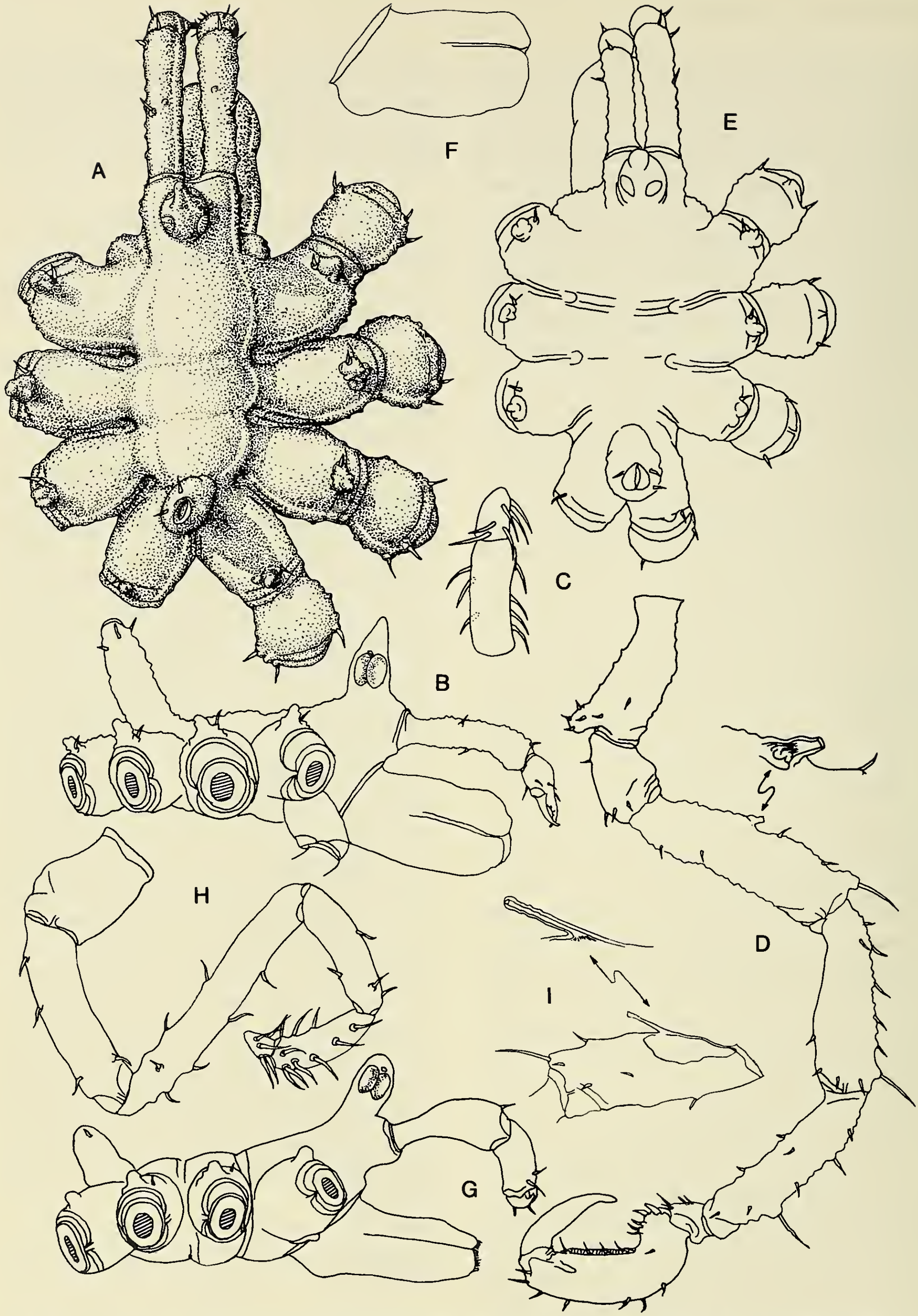

Fig. 2. *Anoplodactylus viridintestinalis,* California male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Oviger terminal segments, enlarged; D, Third leg, cement gland tube enlarged. California female: E, Trunk, dorsal view; F, Proboscis, lateral view. *Anoplodactylus rimulus,* Samoan male: G, Trunk, lateral view; H, Oviger, enlarged; I, Femur, cement gland tube enlarged.

Material examined.—American Samoa: Tutuila; Pago Pago Harbor, dredged in 15 m, 22 Oct 1985, 1 ♂. Western Samoa: Upolu Island; Apia, dredged in 10 m, 25 Oct 1985, 15 ♂ with eggs, 18 ♂, 44 ♀, 1 juv.

Distribution.—This species is very commonly found in large numbers in southern Sagami Bay, Japan (type locality), in depths of 7–15 and 113 meters. Its capture in 2 localities in the Samoa Islands greatly extends its known distribution eastward and to the South Pacific, without expanding its known depth range. The single capture of 78 specimens in Apia emphasizes its tendency to be found in large groups, the same as in many of the Sagami Bay captures. Nothing can be said concerning this gathering of specimens except that sufficient suitable food must be available for such an aggregation to remain grouped in a small restricted area.

Remarks.—This is another species in which males are made distinctive and easily identified by the cement gland openings which number from 17 to 25 pores on each femur, surpassing any other known species in number, and the very long oviger bearing only a tiny terminal segment. Similar species have a terminal segment half as long or longer in relation to the fifth segment, and always have far fewer cement gland openings. Other recognition characters are the very short propodal lamina, measuring less than 0.1 of the sole length, and the long chelae fingers without teeth.

Anoplodactylus rimulus Child
Fig. 2G–I

Anoplodactylus rimulus Child, 1988b, fig. 3.

Material examined.—American Samoa: Tutuila; Pago Pago Harbor, 3 m, 23 Oct 1985, 2 ♂ with eggs, 1 ♂, 2 ♀, 1 juv.

Supplemental description.—(Male) Proboscis tapering only from 0.77 length distally, with marked single proximoventral bulge lacking cleft. Femur less inflated, with cement gland from proximal rim to median dorsal point and cement gland tube, a long straight tube half femoral diameter situated just proximal to median point. Oviger fairly short, second, third and fourth segments with few short randomly placed setae, fifth with many setae equal to segment diameter placed in rows, sixth a tiny cone with 6–7 setae circling cone, setae as long as those on fifth segment.

Distribution.—The type locality for this species is Aldabra Atoll, Seychelles, Indian Ocean, in 3–6 meters. This is the second record for the species and it greatly extends the known distribution to the east in the mid-Pacific at Samoa. The depth of capture of the Samoan specimens is within that of the Aldabra records.

Remarks.—The elaborate proximoventral tubercles of the females in this species are not carried over to the male to as great an extent. This is true for the so called "alar processes" of many females in this genus, but the male of this species, now known from the Samoan material, does have a single proximoventral bulge on the proboscis. The female proboscis bulge of the Samoan specimens is not as large or elaborate as those of the Aldabra Atoll specimens. It consists of a bulge with a barely perceptible longitudinal cleft but lacks the lateral cleft of the type specimens. All other female characters appear to fall within acceptable bounds of variation as the differences are only slight between the two sets of specimens. The male was previously unknown, but aside from the male characters of oviger and cement gland, it is very similar to the female including length of propodal lamina, heel and sole spination, leg segment lengths, chelae characters, and lateral process tubercles. These tubercles are slightly smaller in the female, as would be expected. The grossly clubbed chelifore scape of this species is rare in the genus and affords a good recognition character along with the ventral proboscis bulges of this tiny species.

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The specimens are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the old United States National Museum (USNM).

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DARWINULOCOPINA (CRUSTACEA: PODOCOPA), A NEW SUBORDER PROPOSED FOR NONMARINE PALEOZOIC TO HOLOCENE OSTRACODA

I. G. Sohn

Abstract.—The new suborder Darwinulocopina is proposed in the order Podocopida Sars, 1865, superorder Podocopa Kesling, 1981 to include living and fossil ostracode genera. The new category is coordinate with the Cypridocopina Kozur, 1972 and the Cytherocopina Gründel, 1967. Diagnostic characters of the Darwinulocopina are a posterior process instead of furcae and furcal attachments, and a rosette adductor muscle attachment scar comprised of large stigmata. The geologic range of the Darwinulocopina is Paleozoic to Holocene.

The superfamily Darwinulacea Brady & Norman, 1889, contained, until after 1961, only one family, the Darwinulidae Brady & Norman, 1889, which in turn consisted of one genus: *Darwinula,* based on the type species *Darwinula stevensoni,* (Brady & Robertson 1870) (Swain 1961:Q253). Until 1972, the Darwinulacea Brady & Norman, 1889 have been classified in the suborder Podocopina Scott, 1961:Q86–Q88, in the order Podocopida Sars, 1865. Gründel (1967:324) discussed the classification of the Podocopida in the Treatise (Moore 1961), in which he included 3 suborders: Metacopina Sylvester-Bradley, 1961:358 (type genus *Quasillites* Coryell & Malkin, 1936, p. 18); Bairdiocopina new suborder (type genus *Bairdia* McCoy, 1844:164); and the Cytherocopina new suborder (type genus *Cythere* O. F. Müller, 1785, p. 49). The suborder Bairdiocopina Gründel, 1967, included the Bairdiacea Sars, 1885. Cypridacea Baird, 1845, and the ?Darwinulacea.

Kozur (1972:13–15) referred the Darwinulacea to his emended suborder Cypridocopina Jones, 1901 [*Nom. transl. ex* Cypridida Jones *in* Chapman, 1901:147, 154]. Kozur considered the suborder Metacopina Sylvester-Bradley, 1961, to be a junior synonym of the Cypridocopina (1972:13), to which he referred both the Darwinulacea and the Metacopina, and suggested that *Darwinula* Brady & Norman, 1889, developed from *Carbonita* because "The stem group [of *Darwinula*] is probably the genus *Carbonita,* that has hitherto been referred to the Cypridacea. According to Pollard (1966) *Carbonita claripunctata* has sometimes a rosette-like arrangement of the adductor muscle scars (similar to *Darwinula*). *Carbonita* is also very similar in outline to *Darwinula,* also in that the right valve is larger than the left in this genus. Therefore *Carbonita* should be referred to the Darwinulacea." [my translation]. Kesling (1981) also referred the Darwinulacea to the Cypridocopina, but recognized the Metacopina as an order in the superorder Podocopa. Kesling's (1981, p. 291, 300, 308) recommended classification of the Podocopida Sars, 1865, the superorder Podocopa is followed herein.

The Darwinulacea should be excluded from the Cypridocopina based on both shell morphology and soft parts; consequently, the new suborder Darwinulocopina (type genus *Darwinula* Brady & Robertson, in Jones 1885:346), is proposed for the living and fossil taxa that have been referred to the Darwinulacea (Sohn 1987:151).

Superorder Podocopa Sars, 1865

Kesling (1981:291) elevated the orders in Moore (1961) to superorder categories, and included the orders Podocopida Sars, 1865, p. 10, and the Metacopida Sylvester-Bradley, 1961, p. Q358 in the Podocopa.

Order Podocopida Sars, 1865

Kesling (1981:291) included in this order the suborders Bairdiocopina Gründel, 1967, Cypridocopina Jones (emend. Kozur, 1972) to include the superfamilies Cypridacea Baird, 1845, and Darwinulacea Brady & Norman, 1889, and the Cytherocopina Gründel, 1967. He described the Podocopida as follows: "Duplicature present except perhaps in earliest forms, typically large anteriorly and posteriorly and there set off from outer lamella by a vestibule. Contact groove not well developed if at all, at most a simple depression in inner lamella [infold]." (Kesling 1981:300).

The new suborder Darwinulocopina is proposed for the Darwinulacea to remove them from the Cypridocopina. The new suborder is coordinate with both the Cypridocopina and the Cytherocopina. The distinguishing characters among the Darwinulocopina, the Cypridocopina, and the Cytherocopina are listed in Table 1.

Darwinulocopina, new suborder

Diagnosis.—Small, smooth, elongate Podocopida; without any nodes, ridges, sulci; with very narrow normal and radial pore canals, without calcified inner lamella on infold. Hinge simple, overlap variable; outline of the adductor muscle-attachments scars (AMAS) pattern circular, consists of large individual scars (stigmata sensu Gramm 1982:201). Appendages of the type genus consist of pediform antennules and antennas; first thoracopod with respiratory plate; second and third thoracopods pediform: with posterior process; furcae lacking.

Discussion.—Howe, Kesling, & Scott (1961: Q112-Q14) described "furca" as follows: "Furcae (furcal rami of some authors) are appendage-like structures attached to the posterior end of the body .... In the Podocopina the furcae are extremely variable .... In the Darwinulidae (fig. 8a) they are lacking or represented by a reflex process at the end of the thorax . . ."

Rome (1969) described and illustrated the furcal attachments in different subfamilies in the Cypridae Baird, 1845. The Darwinulocopina differ from the Cypridocopina in having a unique AMAS, in absence of furcae and furcal attachments, in having a posterior process, and in lacking a wide calcified inner lamella on the infold.

Living darwinulids differ from living Cypridocopina in having pediform antennules and antennas without swimming setae (Sohn 1987:154, text fig. 1, pl. 1, figs. 2, 4, 16), in absence of furcae and furcal attachments, and in presence of a posterior process (Sohn 1987:105, fig. 1). The darwinulids differ from the Cytherocopina in having smooth instead of ornamented carapaces, in simple instead of complex hingement, in round AMAS outline, in stigmata symmetrically arranged (Sohn 1987: figs. 12, 17–19) instead of in a single vertical row.

Triebel (1941:219, fig. 48) illustrated with a photograph an AMAS of *D. stevensoni* with an accessory (frontal) scar in front and below the AMAS, and this scar was illustrated in Moore (Swain 1961:Q253, fig. 183, 2c). Sharapova (1947:215, fig. 53), illustrated with a drawing the frontal scars in *Darwinula,* and Starozhilova (in Lipatova & Starozhilova 1968:80, fig. 20a) published a drawing of two frontal scars of *Darwinula.* Frontal scars had not been recorded in other fossil and extant specimens of *D. stevensoni* until Swain (1986:pl. 4, fig. 14b) illustrated frontal scars on a Pliocene specimen from Idaho. However, I cannot explain why these scars have not been recorded in the numerous SEM micrographs of valves of living specimens of *Darwinula* (Keyser 1975; Sohn 1976, 1987).

Table 1.—Comparison of selected diagnostic morphological features among the Darwinulocopina, the Cypridocopina, and the Cytherocopina.

	Darwinulocopina	Cypridocopina	Cytherocopina
	Shell		
Shape	Elongate-ovate	variable	variable
Surface	smooth or with ventroposterior spine	ornamented or smooth	ornamented or smooth
Hinge	simple	simple	complex
Overlap	narrow	wide	narrow or wide
Vestibule	absent or present	present	present
Outline of AMAS	rosette	disorganised	vertical row
Number of spots	6–12	7 or less	4 or 5
Frontal & mandibular scars	absent or present	present	present
Eye tubercle	absent	absent	present or absent
	Appendages		
Antennules	pediform (Sohn 1987:pl. 2, figs. 1–6	natatory except candonids (Moore 1961: fig. 137, 1a)	pediform
Antenna, endopodite	pediform (Sohn 1987:pl. 2, figs. 7–13)	natatory except candonids (Moore 1961: fig. 137, 2a)	pediform with flagellum
Antenna, exopodite	vestigial	vestigial	flagellum with secreting duct (Moore, 1961: fig. 137, 3a)
Posterior process	Present	absent	absent
Furcal rami	absent	present or reduced	absent
Reproduction	asexual, ?sexual	sexual, rarely asexual	sexual

Stratigraphic range.—Carboniferous to Holocene.

Superfamily Darwinulacea Brady and Norman, 1889

Darwinulacea Swain, 1961:Q253.

Diagnosis.—A superfamily in Darwinulocopina with small (less than 1 mm), elongate, relatively thin shelled, smooth carapaces; gently convex dorsal margins; simple hinges; narrow overlap, AMAS outlines round, with large stigmata.

Family assigned.—Darwinulidae Brady & Norman, 1889.

Discussion.—Only the Darwinulidae Brady & Norman, 1889 and the Microdarwinulidae Kashevarova & Neustrueva, 1982 are based on living genera; the other families listed in Sohn (1987:151, table 1) are based on fossil taxa, and their referral to the Darwinulacea is based on published data and is subject to change. Except for *Whipplella* Holland, 1934 (type species (original designation) *W. cuneiformis* Holland, 1934:344, pl. 25, fig. 5. Permian), all the fossil genera in the list are based on European and Asiatic specimens that cannot be forwarded for study in the U.S. The only exception are two topotypes of *Panxiania subelliptica* Wang, 1978, the type species of the nominate genus of the family Panxianidae Wang, 1980, that Dr. Wang donated. The genus *Vymella* Kalis & Mischina *in* Mischina & Kalis 1975 (type species (original designation) *V. nazarovae* Kalis & Mischina: 77, pl. 9, figs. 1, 2. Late Triassic) contains species with an infold, which bears a wide calcified lamella, that excludes that genus from the Darwinulacea.

Stratigraphic range.—Carboniferous to Holocene.

Family Darwinulidae Brady and Norman, 1889

Darwinulidae Brady & Norman, 1889:121.
Darwinellidae Brady, Crosskey, & Robertson, 1874:140.
Microdarwinulidae Kashevarova & Neustrueva, 1982:148.
Suchonellininae Kukhtinov, 1985:68.

Diagnosis.—Same as the superfamily.

Genera assigned.—*Darwinula* Brady & Robertson in Jones, 1885; *Microdarwinula* Danielopol, 1968; *Paradarwinula* Kozur, 1970.

Discussion.—Kukhtinov (1985:68) included in the Darwinulidae the genera *Darwinula* (*Darwinula*), *Gerdalia* Belousova, 1961, and *Paradarwinula* Kozur, 1970, which he raised to generic rank, and he described the subfamily Suchonellininae in the family. Based on the illustrated darwinulid AMAS in the type species, *D.* (*P.*) *spinosa* (Kozur, 1970, fig. 1). *Paradarwinula* is confirmed in the Darwinulidae. Based on the original description, *Microdarwinula* does not require a separate suprageneric category. *Suchonellina* is considered herein to be a synonym of *Darwinula,* and, consequently, does not require a suprageneric category.

Stratigraphic range.—Carboniferous to Holocene.

Genus Darwinula Brady and Robertson in Jones, 1885

Darwinula Brady & Robertson in Jones, 1885: 346.
Polycheles Brady & Robertson, 1870:25.
Darwinella Brady & Robertson, 1872:50.
Suchonellina Spizharsky, 1937:156.
?*Cyprione* Jones, 1885: 343.
?*Gerdalia* Belousova, 1961:140.
Darwinula (*Neudarwinula*) Mischina, 1972: 49, 50.

Type species (monotypy).—*Polycheles stevensoni* Brady & Robertson, 1870:25.

Diagnosis.—Small, less than 1 mm in length, elongate, smooth darwinulids, with adont hinge, dorsal edge of one valve inserts into groove of other and ventral edge of groove of latter fits into groove of former valve, slight overlap of one valve over other along free margins. Apparently parthenogenetic; may or may not retain the eggs and brood the first two instars.

Discussion.—Reversal of overlap in *Darwinula* and the above synonyms has been recorded (Sohn & Chatterje 1979:584). Belousova described *Gerdalia* (type species (original designation) *Gerdalia polenovae* Belousova, 1961:141, pl. 1, figs. 1, 1a) from carapaces. Starozhilova (in Lipatova & Starozhilova, 1968:91) included species having a reversed overlap. Sharapova (1947:215) published a drawing showing the hinge of *Darwinula* having a ridge in the right valve that fits into a groove in the left valve. This hingement differs from the hinge of *Darwinula* illustrated by Sohn (1987: pl. 1) which has grooves in both valves. Sharapova's illustration of the hinge was published by Starozhilova (in Lipatova & Starozhilova 1968:80, fig. 20; 91, fig. 26; 97, fig. 31) for *Darwinula, Gerdalia,* and *Suchonellina* (type species (subsequent designation) *S. inornata* (McCoy, 1844) sensu Spizharsky 1939:194, pl. 46, fig. 7).

Mischina (1972) did not formally describe the subgenus *Neudarwinula;* she based her subgenus on measurements of *Darwinula parallela* (Spizharsky) without documentation. *Darwinula parallela* (Spizharsky) in Schneider 1948:24, pl. 1, figs. 5a, b, was a manuscript name of a Permian species described as *Suchonellina* Spizharsky, 1937 that was validated by Schneider (1948:24, pl. 1, figs. 5a, b). Kashevarova and Neustrueva (1982:143, 145) considered the subgenus *Darwinula* (*Neudarwinula*) to be a junior synonym of *Suchonellina.*

Although a male copulatory appendage was illustrated by Brady and Robertson in the original description of the type species (1870:pl. 10, fig. 13), and the antennule and the tip of the second foot of a male *D. improvisa* Turner, 1895 were illustrated (Turner 1895:263, pl. 81, figs. 1, 2), there are no other published records of males in *Darwinula* (Sohn, 1987:152). The presence of males in *Darwinula* and its suprageneric categories is considered dubious until such time that males are documented based on living material.

Jaanusson (1985:79–81) differentiated between the brood care of eggs in the platycopids and the podocopids. He named the platycopid egg care "*Cytherella* type," and the podocopid egg care, including *Darwinula,* "*Cyprideis* type." In *Cytherella abyssorum* Sars, 1865 the eggs are attached firmly to the inner epithelial layer inside the posterior part of the carapace where each egg leaves an impression in the inside of the valve; in the *Cyprideis* type the extruded eggs in the posterior part of the carapace are not attached and are freely movable. According to Jaanusson there is no evidence that *Cytherella* does or does not retain the early instars within the carapace. *Darwinula* retains the first two instars within the carapace where they can be observed with transmitted light or by video tape recordings opening their valves and/or extruding their appendages.

Ecology.—Mainly freshwater, rare in brackish water (salinity to 13‰ according to Keyser 1975:266), terrestrial (damp moss), and phreatic.

Geographic distribution.—Circumglobal.

Geologic range.—Mississippian to Holocene.

Genus Microdarwinula Danielopol, 1968

Microdarwinula Danielopol, 1968:154.

Type species (original designation).—(*Darwinula zimmeri* Menzel, 1916:487, figs. 16–21, and redescribed and reillustrated by Danielopol, 1968:figs. 1–28.

Diagnosis.—Differs from *Darwinula* in having smooth tripartite hinge that consists of terminal elongate smooth bars and smooth central groove in right valve and opposing structures in larger left valve; in having internal tubercles at both ends of ventral margins of left valve; and in not brooding the young.

Discussion.—Danielopol described, discussed and illustrated in detail females of the type species, but did not mention males.

Ecology.—Freshwater.

Geographic distribution.—Africa, Madagascar, and Europe.

Geologic range.—Oligocene to Holocene.

Genus Paradarwinula Kozur, 1970

Darwinula (*Paradarwinula*) Kozur, 1970: 434.

Type species (original designation).—*Darwinula dreyerae* Kozur, 1968:848, pl. 4, fig. 10.

Diagnosis.—Differs from *Darwinula* and *Microdarwinula* in having ventroposterior spine on left valve.

Discussion.—Based on the illustration of the AMAS by Kozur (1970:435, fig. 10) the genus belongs in the Darwinulidae. Because Kozur (1968; 1970) did not describe the inside of the valves, the inside morphology is unknown.

Ecology.—Brackish water.

Geographic distribution.—Europe.

Geologic range.—Late Triassic.

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HYALOPONTIUS BOXSHALLI, NEW SPECIES (COPEPODA: SIPHONOSTOMATOIDA), FROM A DEEP-SEA HYDROTHERMAL VENT AT THE GALAPAGOS RIFT

Arthur G. Humes

Abstract.—*Hyalopontius boxshalli,* a new species of megapontiid copepod (Siphonostomatoida) from a depth of 2451 m at the Galapagos Rift, is characterized in the male by the exopod of leg 1 having the armature I-1; O-1; II,2,3, the third segment of the exopod of leg 3 with II,I,5, and the distal seta on the lateral margin of the free segment of leg 5 being one-half the length of the segment.

Among many thousands of copepods recovered by deep-sea submersibles from depths of 2000 m or more in the eastern Pacific (see Humes 1987, in press) two large male siphonostomatoids were found, both belonging to a new species of the genus *Hyalopontius* Sars, 1909. Seven members of this genus have been described from plankton in the northeastern Atlantic (Sars 1909; Hulsemann 1965; Boxshall 1979). One species, *Hyalopontius pleurospinosus* (Heptner, 1968) is known from 3860–7100 m in the Kurile-Kamchatka Trench (Heptner 1968).

Siphonostomatoida Thorell, 1859
Megapontiidae Heptner, 1968
Hyalopontius Sars, 1909

Hyalopontius boxshalli, new species
Figs. 1–5

Type material.—2 ♂, in 2451 m at Galapagos Rift, 00°48.0′N, 86°13.0′W, 7 Dec 1979, DSRV *Alvin* dive no. 990 (Hollis, Jones, and Tuttle). Holotype (USNM 234119) and 1 paratype (dissected) (USNM 235272) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Male.—Body (Fig. 1a) elongate, 5.7 times longer than wide. Length (not including setae on caudal rami) 4.81 mm (4.75–4.86 mm) and greatest width 0.84 mm (0.84–0.85 mm), based on 2 specimens in lactic acid. Epimera of segments bearing legs 1–4 pointed (Fig. 1b). Ratio of length to width of prosome 3.05:1. Ratio of length of prosome to that of urosome 1.30:1.

Segment bearing leg 5 (Fig. 1c) 330 × 363 μm, a little wider than long. Genital segment 330 × 286 μm. Four postgenital segments from anterior to posterior 495 × 215, 363 × 203, 209 × 198, and 308 × 258 μm.

Caudal ramus (Fig. 1d) 330 × 110 μm, ratio 3:1, bearing 6 smooth setae, 2 lateral and subterminal (220 μm and 726 μm), 3 inner and slightly dorsal (from outer to inner 1000, 902, and 803 μm), and dorsal seta 638 μm.

Body surface mostly without ornamentation. Minute punctae over dorsal surface of rostrum (Fig. 1a). Anal segment with very small spinules over surface of anal operculum (Fig. 1c) and ventral transverse row of minute spinules near insertions of both caudal rami (Fig. 1d).

Rostrum (Fig. 1e) projecting in lateral view with slightly pointed apex. First antenna (Fig. 2a) 1650 μm long not including setae. Lengths of its 11 segments (measured along their posterior nonsetiferous mar-

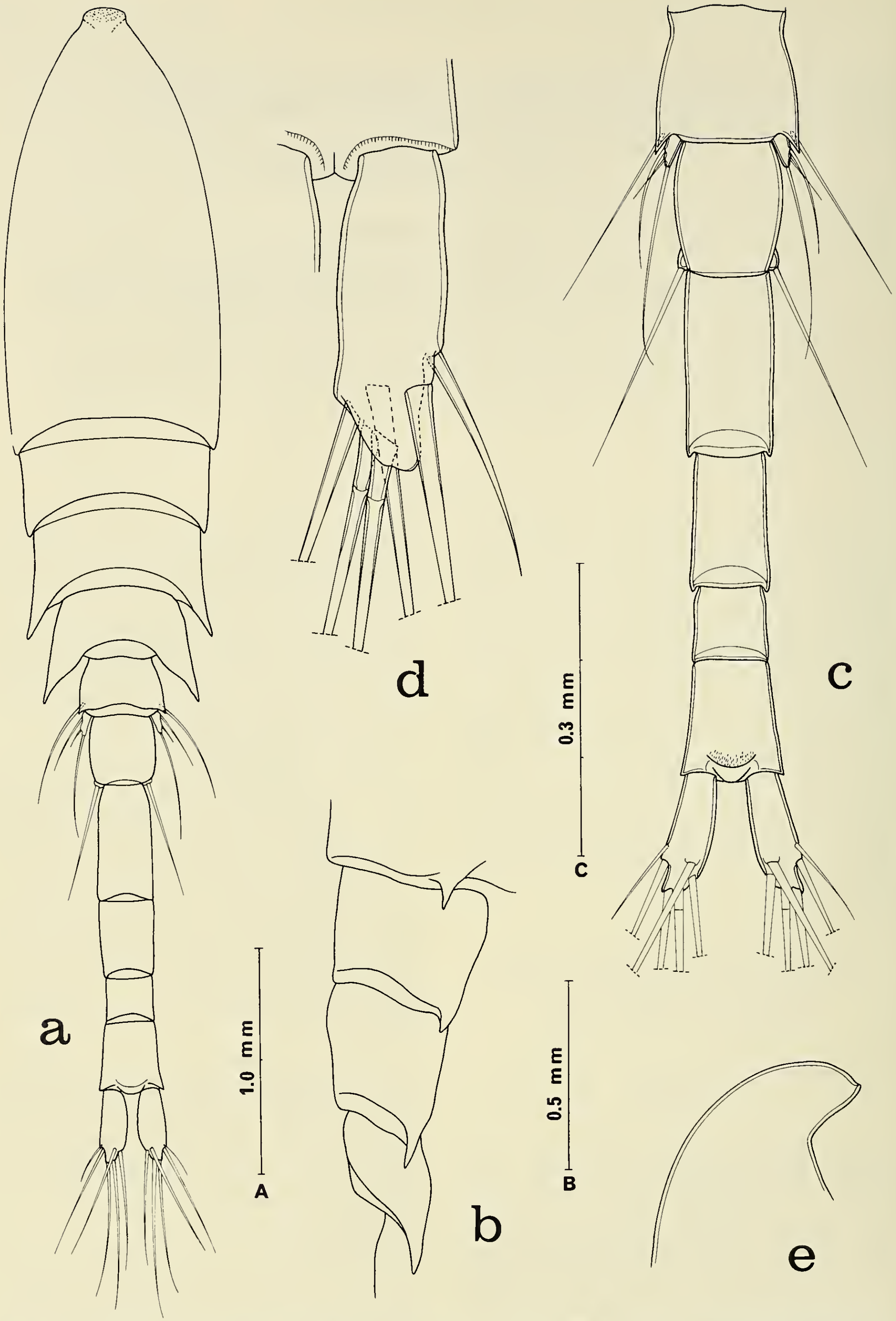

Fig. 1. *Hyalopontius boxshalli,* male: a, Dorsal (scale A); b, Outline of epimera of segments bearing legs 1–4, lateral (B); c, Urosome, dorsal (B); d, Caudal ramus, ventral (C); e, Rostrum, lateral (B).

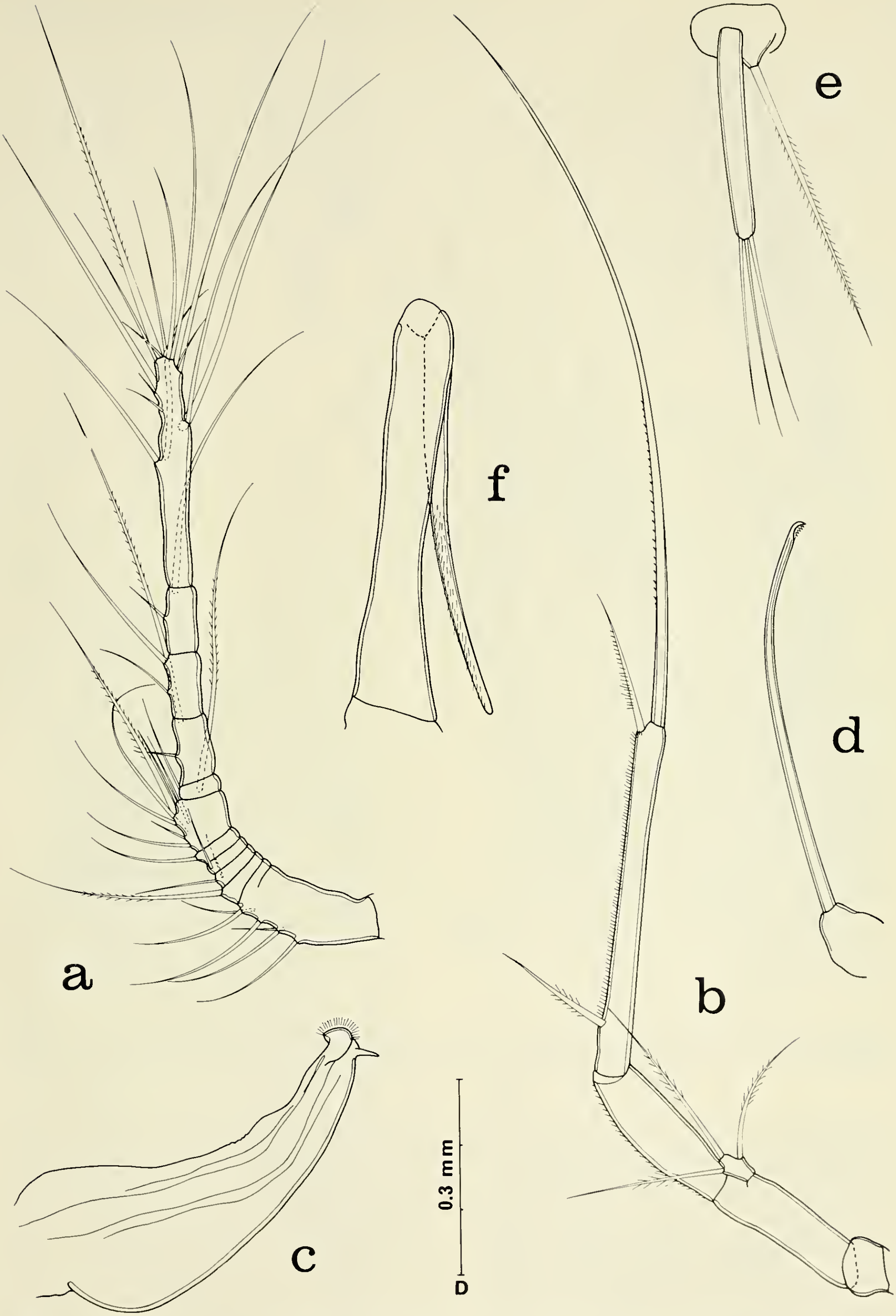

Fig. 2. *Hyalopontius boxshalli,* male: a, First antenna, anterodorsal (scale B); b, Second antenna, outer (D); c, Oral cone, lateral (D); d, Mandible, anterior (D); e, First maxilla, anterior (C); f, Second maxilla, anterior (C).

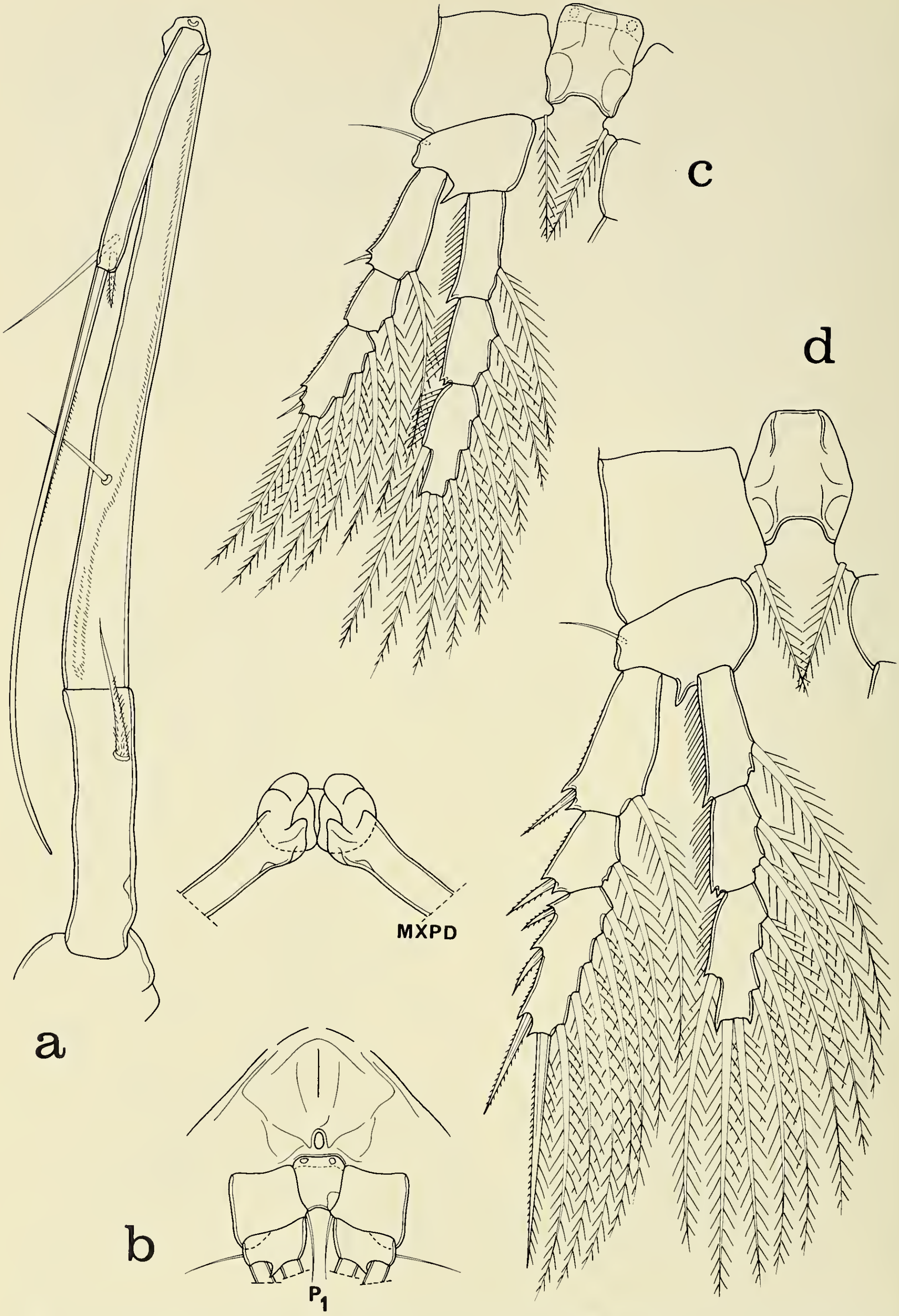

Fig. 3. *Hyalopontius boxshalli,* male: a, Maxilliped, anterior (scale D); b, Area between maxillipeds and first pair of legs, ventral (B); c, Leg 1 and intercoxal plate, anterior (D); d, Leg 2 and intercoxal plate, anterior (D).

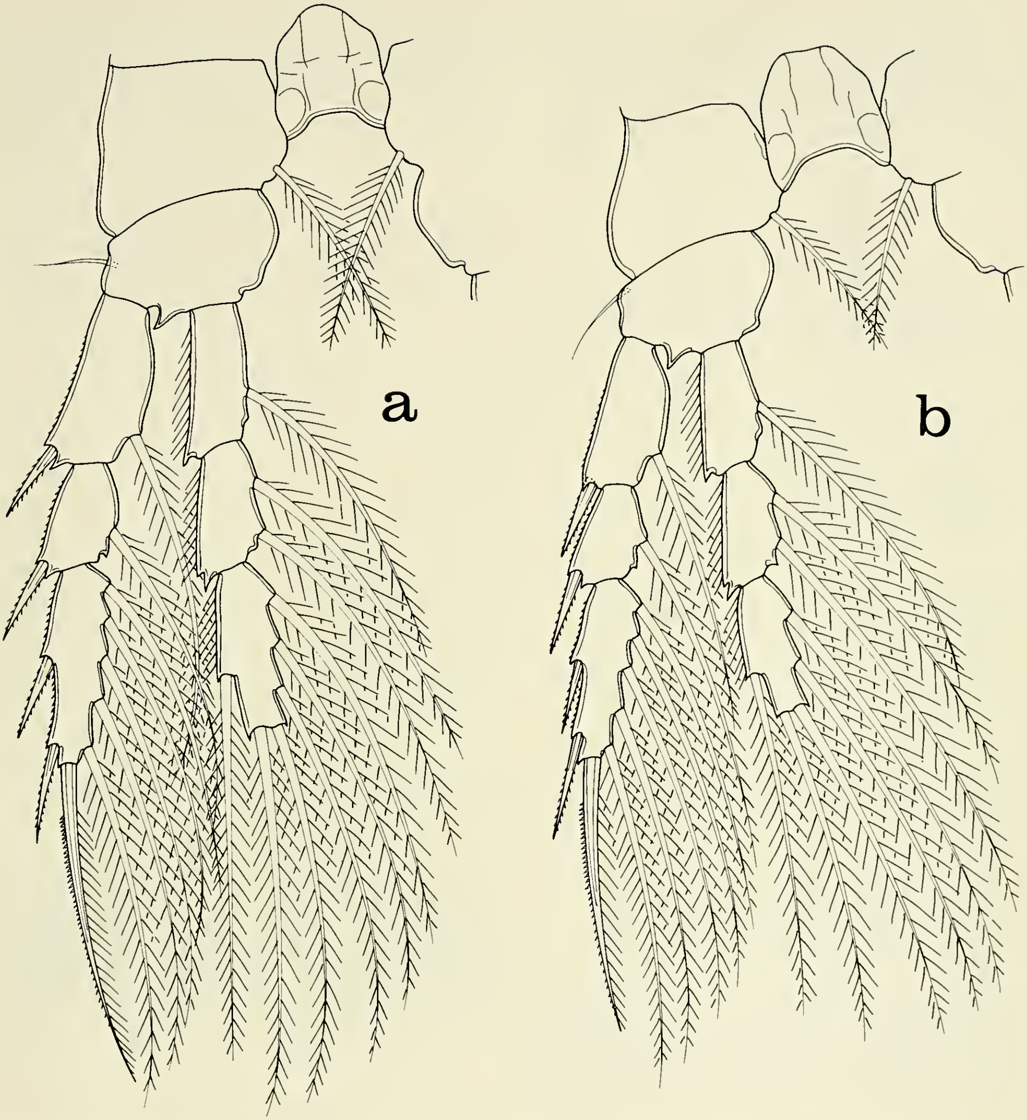

Fig. 4. *Hyalopontius boxshalli,* male: a, Leg 3 and intercoxal plate, anterior (scale D); b, Leg 4 and intercoxal plate, anterior (D).

gins): 319 μm (374 μm along its anterior margin) 26, 26, 29, 35, 100, 55, 143, 155, 165, and 505 μm, respectively. Setal formula: 6, 1, 2, 1, 1, 7, 2, 2, 2, 2, and 15. Most setae smooth but 1 seta on segments 2, 6, 7, 8, and 11 with small setules.

Second antenna (Fig. 2b) with small coxa and elongate basis bearing exopod 55 × 39 μm carrying 3 long minutely feathered setae. Endopod 2-segmented. First segment with minute spinules along inner edge. Second segment greatly elongated, 495 μm long, bearing proximal inner sparsely barbed seta located 67 μm from base of segment. Beyond this seta small spinules along edge of segment. Terminally very long outer seta 1,100 μm barbed on proximal inner half and shorter inner seta 200 μm with moderately long inner setules.

Oral cone (Fig. 2c) 575 μm long. Man-

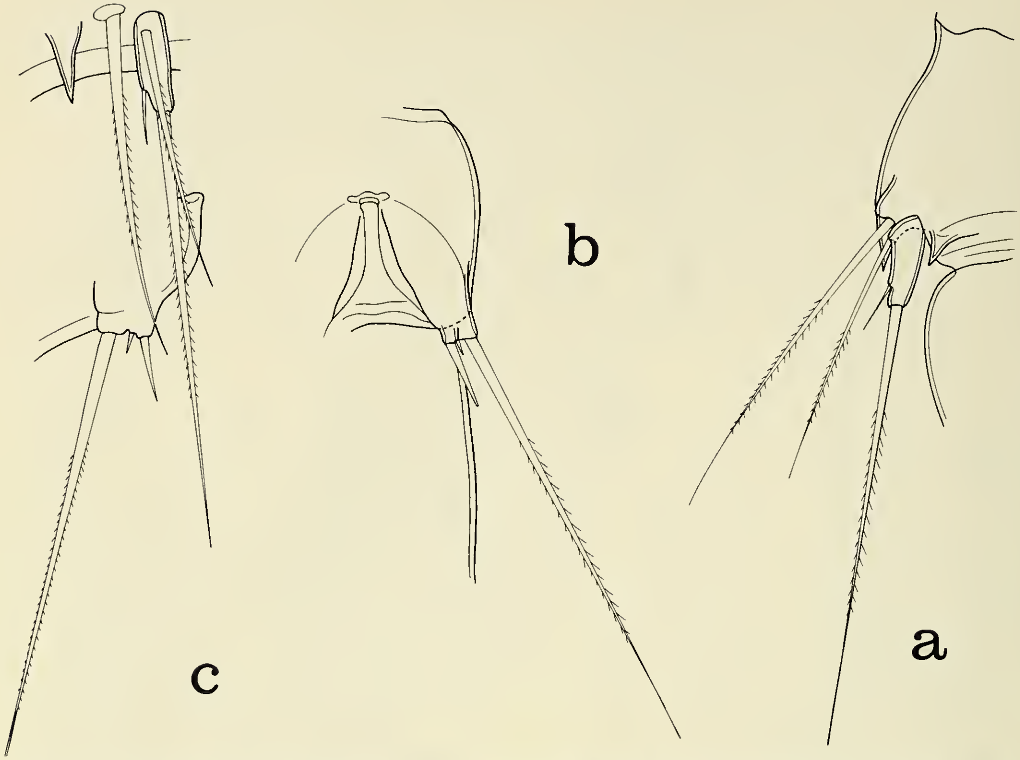

Fig. 5. *Hyalopontius boxshalli,* male: a, Leg 5, ventral (scale B); b, Leg 6, ventral (B); c, Leg 5 and leg 6, lateral (B).

dible (Fig. 2d) without palp, elongate, 573 μm, and very slender with few minute terminal teeth. First maxilla (Fig. 2e) bilobed; elongate inner lobe with 3 smooth apical setae, outer lobe small with 1 barbed seta. Second maxilla (Fig. 2f) 2-segmented, first segment smooth, second segment slender and spinulose with blunt tip. Maxilliped (Fig. 3a) elongate, 3-segmented. First segment 385 μm, with spinulose distal seta. Second segment 990 μm, with smooth inner seta and ornamented with 2 rows of small spinules along posterior surface. Third segment 374 μm, smooth, with 2 subterminal setae, longer seta smooth and shorter seta spinulose, and 1 long terminal claw 850 μm with inner row of small spinules proximally.

Ventral surface of body between maxillipeds and first pair of legs (Fig. 3b) slightly protuberant.

Legs 1–4 (Figs. 3c, d, 4a, b) with 3-segmented rami. Spine and setal formula as follows (Roman numerals representing spines, Arabic numerals indicating setae):

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

Leg 5 (Fig. 5a, c) situated ventrally, with free segment 117 × 52 μm, bearing 3 setae, proximal outer seta 385 μm and minutely barbed, distal lateral seta 60 μm and smooth, and apical seta 605 μm and minutely barbed. Seta on body adjacent to free segment 460 μm and minutely barbed.

Leg 6 (Fig. 5b, c) forming posteroventral flap on genital segment bearing 1 long barbed seta 605 μm, 1 shorter smooth seta 88 μm, and between them 1 very small seta 31 μm.

Color unknown.

Female.—Unknown.

Etymology.—The new species is named for Dr. Geoffrey A. Boxshall, who has contributed much to an understanding of the genus *Hyalopontius.*

Remarks.—*Hyalopontius boxshalli* may be distinguished from its eight congeners (shown in Boxshall's 1979 key to females) by a combination of characters. Unfortunately only the male of *H. boxshalli* is known. Congeners of the new species are known only from females, except for *H. typicus* Sars, 1909, where both sexes are known. Therefore, comparison of *H. boxshalli* with congeners must be made using characters not suspected of being sexually dimorphic. The formula for the armature of legs 1–5 seems to be constant in both sexes and thus is useful in making comparisons.

Hyalopontius boxshalli possesses the following distinctive characters that, used together, are regarded as supporting its status as a new species: (1) the exopod of leg 1 with the armature I-1; 0-1; II,2,3, (2) the third segment of the exopod of leg 3 with II,I,5, and (3) the distal seta on the lateral margin of the free segment of leg 5 being about one-half the length of the free segment.

Acknowledgments

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DESCRIPTION OF *MEMBRANOBALANUS ROBINAE,* A NEW SPECIES OF SPONGE BARNACLE (CIRRIPEDIA, ARCHEOBALANIDAE) FROM BAJA CALIFORNIA, WITH A KEY TO THE GENUS

Robert J. Van Syoc

Abstract.—The California Academy of Sciences, Department of Invertebrate Zoology and Geology has recently undertaken a joint research program with the Centro de Investigaciones de Ciencia y de Educacion Superior de Ensenada (CICESE). The present paper documents a new species of the sponge barnacle *Membranobalanus* Pilsbry from Bahía de los Angeles collected during two expeditions in 1984. A key to the genus *Membranobalanus* is included.

Systematic Account

Subclass Cirripedia Burmeister, 1834
Order Thoracica Darwin, 1854
Suborder Balanomorpha Pilsbry, 1916
Superfamily Balanoidea (Leach) Newman & Ross, 1976
Family Archaeobalanidae Newman & Ross, 1976
Subfamily Archaeobalaninae Newman & Ross, 1976
Genus *Membranobalanus* Pilsbry, 1916
Membranobalanus robinae, new species

Holotype.—Complete shell, opercular plates and body preserved in 75% EtOH, California Academy of Sciences (CAS), San Francisco, 061082.

Dimensions of holotype.—Height 4.6 mm; carinorostral diameter 4.0 mm; lateral diameter 3.7 mm.

Type locality.—Station BLA-11, 28°54′N, 113°30′W, Mexico, Baja California, Gulf of California, Bahía de los Angeles, ½ mile south of Casa Diaz, depth 10 feet, 6 Oct 1984.

Material examined.—CAS paratypes 061083, 061084, 061086, one specimen each, and CAS 056184, about 100 specimens, Mexico, Baja California, Gulf of California, Bahía de los Angeles, Punta Gringa, depth 10–15 feet. CAS paratype 061085, Mexico, Baja California, Gulf of California, Bahía de los Angeles, ½ mile south of Casa Diaz, depth 0–10 feet.

Paratype distribution.—Paratypes have been deposited at the National Museum of Natural History (USNM 211487), Scripps Institution of Oceanography (SIO C9559), the Santa Barbara Museum of Natural History (SBMNH 35076), the Los Angeles County Museum of Natural History (LACM 84-203.1), as well as the California Academy of Sciences (as listed above).

Diagnosis.—Shell thin, white, radii present, widening near orifice; orifice oval, summits of wall plates nearly level, not deeply toothed; rostrum same length as other compartmental plates or only slightly longer; base of wall plates rounded giving base a lobed appearance; opercular plates without chitinous lamellae; scutal adductor ridge incipient or lacking; tergal spur broad, extending about ⅔ of basal margin, and short, only about ⅕ of basal margin width; tergal articular ridge gently sloped to sharp crest, bending ½ way between apex and basal margin toward and descending to scutal margin then rising along margin to high point near basal margin; outer ramus of Cirrus IV with up to 6 recurved teeth per article; basal articles of Cirrus IV with several tooth-like spines at distal posterior margin.

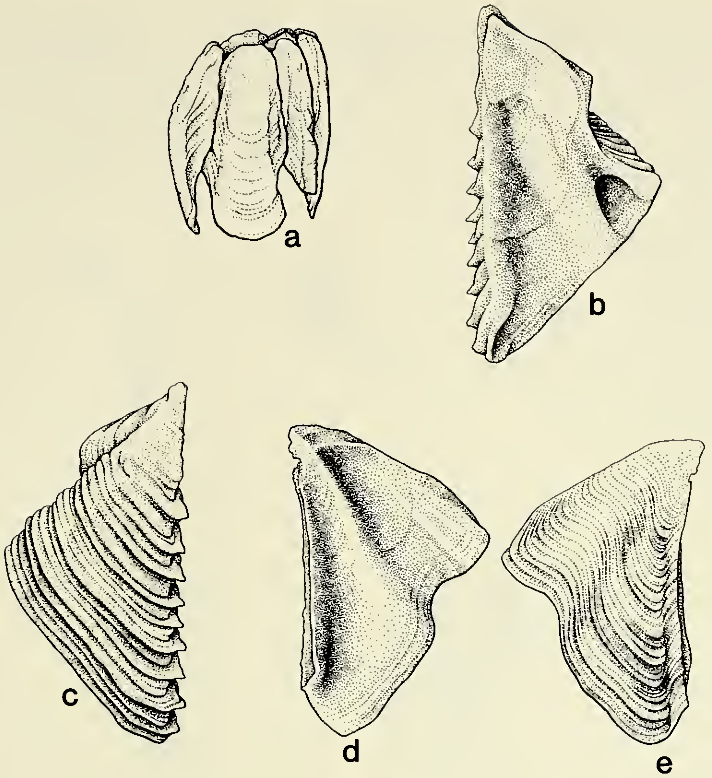

Fig. 1. *Membranobalanaus robinae*: a, Shell, holotype CAS 061082; b, Inner view of scutum, paratype CAS 061083; c, Outer view of scutum, paratype CAS 061083; d, Inner view of tergum, paratype CAS 061083; e, Outer view of tergum, paratype CAS 061083. Scale: a, ×10; b–e, ×50.

Description.—Shell (Fig. 1a) cylindrical to high-conic, white, opening oval with summits of plates even and flattened by wear; compartmental plates solid but very thin and fragile, easily disarticulated or broken; parietes with fine longitudinal striae perpendicular to growth lines; rostrum slightly longer than or equal to length of carina and laterals. Carinolaterals shorter and narrower than other plates; carina, rostrum and laterals very similar in length and width, all 4 with curved triangular shape on upper half with narrower semioval lower half. Carina very deeply curved laterally in comparison to other plates. Radii very broad, wider than paries of carinolaterals; alae broad, extending about ⅔ length of plates.

Scutum (Fig. 1b–c) thick, convex, white; basal margin slightly shorter than or equal to length of tergal margin; tergal margin inflexed; exterior with prominent growth ridges every second or third forming a tooth that extends onto occludent margin. Articular ridge triangular and as high as long, extending from apex to lower third of scutum; articular furrow moderately shallow and narrow. Adductor ridge absent or inconspicuous and rounded; triangular adductor pit shallow on its broad, rounded open basal end to deep and narrow on its apical end; depressor muscle pit large and deep, oval or triangular extending up from basal margin over ¾ distance to base of articular ridge.

Tergum (Fig. 1d–e) thin, white; about same width as scutum; basal margin slightly longer than scutal margin; growth ridges finer

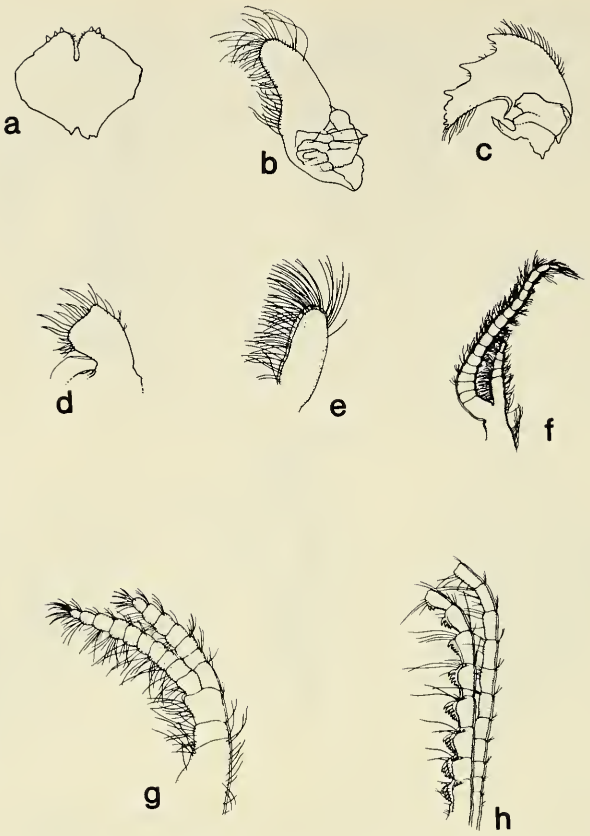

Fig. 2. *Membranobalanus robinae*: a, Labrum, paratype CAS 061084; b, Palp, paratype CAS 061084; c, Mandible, paratype CAS 061084; d, First maxilla, paratype CAS 061084; e, Second maxilla, paratype CAS 061085; f, Cirrus I, paratype CAS 061085; g, Cirrus II, paratype CAS 061085; h, Cirrus IV, paratype CAS 061085. Scale: a–e, g, ×100; f, ×50; h, ×75.

and shallower than those of scutum, spur fasciole broad and delimited only by shifts in orientation of growth lines with no abrupt changes in elevation; tergal spur ½ to ⅔ width of basal margin and about ⅓ as long as basal width of spur, basally truncate at angle to basal margin; articular ridge slightly concave, distinct, reflexed 90 degrees toward scutal margin about ½ way from apex to basal margin, height decreases from apex as ridge approaches scutal margin, then increases as ridge bends back along lower ½ of scutal margin; depressor crests may appear as 2 or 3 distinct ridges or incipient ridges without discernable depth or height, or may be absent.

Labrum (Fig. 2a) triangular, with deep notch at apex of crest; up to 3 teeth present on each side of notch.

Palp (Fig. 2b) kidney-shaped, upper margin concave, densely setose, setae slightly shorter than width of palp; tip of palp densely setose, setae pectinate and longer than those of upper margin; lower margin devoid of setae over proximal ⅔ of palp.

Mandible (Fig. 2c) with 3 large teeth and 2 smaller teeth; first tooth most robust, about same length as second tooth; second tooth not bifid, located near center of cutting edge; third tooth about ⅔ length of first and second teeth; fourth and fifth about ⅕ length of first and second teeth; inferior angle armed with 2 small denticles or spines; inferior and superior margins setose.

Maxilla I (Fig. 2d) with straight edge; upper spine largest but equaled in length by sixth spine; second spine about ⅓ length of first spine; third, fourth, fifth and seventh spines ⅔ to ⅞ length of first spine; inferior angle with several short spines; superior margin setose; inferior margin lacking setae.

Maxilla II (Fig. 2e) ovate, superior and posterior margins densely setose, hooked setae present on posterior margin.

Cirrus I (Fig. 2f) with unequal rami; anterior ramus about 3 times length of posterior ramus; articles of both rami slightly protuberant; both rami setose; hooked setae at apex of posterior rami; setae extremely pectinate near base, giving appearance of ferns or down feathers; short spines present near distal end of articles; Cirrus II (Fig. 2g) shorter than other cirri; inner ramus about ⅔ length of outer ramus; articles of both rami slightly protuberant; covered with pectinate setae; setae more fern-like near base; short spines present near distal end of articles; Cirrus III longer than Cirrus II; setae form and distribution similar to Cirri I and II; short spines present near distal end of articles; Cirrus IV (Fig. 2h) longer than Cirrus III; outer ramus bearing large, recurved teeth on medial protuberant articles; rami of equal length and diameter; setae pectinate; spines in rows along distal margins of articles, 3–6 most posterior of these spines much larger and tooth-like than spines on other cirri; pedicel about ½ length of rami; Cirrus V longer than Cirrus IV; setae as in other cirri; small spines present along distal anterior margin as in Cirri I–III; Cirrus VI longer than Cirrus V; pectinate setae as in other cirri; small spines on anterior distal margin as in other cirri.

Etymology.—The specific name *robinae* is in honor of Robin Ring.

Discussion.—*Membranobalanus robinae* is unique among species of *Membranobalanus* in possessing basally rounded compartmental plates of approximately equal length that give a lobed appearance to the whole barnacle when viewed from the side (Fig. 1a, Holotype). The new species bears recurved teeth on the outer ramus of Cirrus IV, indicating a relationship with Western Hemisphere *Membranobalanus* (Zullo & Standing 1983). Eastern Hemisphere membranobalanids have straight teeth or spines on the outer ramus of Cirrus IV.

The other Western Hemisphere membranobalanids are *M. declivis* (Darwin, 1854) (western Atlantic south of Cape Fear, N.C.), *M. costatus* Zullo & Standing, 1983 (Cape Fear, N.C.), *M. orcutti* (Pilsbry, 1907) (southern California and Mexico), and *M. nebrias* (Zullo & Beach, 1973) (Galapagos Islands).

Based on examination of approximately 50 specimens of *M. robinae,* the new species differs from *M. orcutti, M. nebrias* and *M. declivis* in the length of the rostrum. Both *M. orcutti* and *M. declivis* have rostra which are considerably longer than their other compartmental plates. The rostrum of *M. nebrias* while not as long as the rostra of *M. orcutti* or *M. declivis,* is decidedly longer than the other compartmental plates. There was very little variation in rostrum length relative to the length of other compartmental plates in the specimens of *M. robinae* examined. *M. robinae,* like *M. costatus,* has a rostrum whose length is nearly equal to that of its other compartmental plates. However, *M. robinae* differs consistently from *M. costatus* in many respects: (1) the rami of Cirrus IV are equal rather than unequal in length and diameter; (2) radii are present and well developed; (3) the parietes lack prominent costae; (4) the occludent margin of the scutum bears several teeth formed by extensions of prominent external growth ridges; (5) the bases of the parietes are rounded giving the base of the barnacle a lobed appearance when viewed from the side.

Species in the genus *Membranobalanus* Pilsbry are obligate symbionts of sponges. Although most species have been found in

Table 1.—Species of *Membranobalanus* and the species of sponge which they are known to inhabit. Authors of references used to compile this table are listed, complete citations may be found in Literature Cited.

Barnacle species	Sponge species	Author
M. declivis	*Spheciospongia vesparum*	Pearse 1932 Wells 1966 Zullo & Standing 1983
M. nebrias	"Clionid"	Zullo & Beach 1973
M. koreanus	*Cliona celata*	Kim & Kim 1983
M. cuneiformis	*Cliona* sp.	Hiro 1936 Utinomi 1968
M. longirostrum	*Spirastrella purpurea*	Rosell 1972 Utinomi 1968
M. longirostrum	*Suberites inconstans*	Utinomi 1968
M. costatus	*Anthosigmella varians*	Zullo & Standing 1983
M. orcutti	*Spheciospongia confoederata*	Jones 1978
	Cliona celata californiana	Jones 1978
	"red clionid"	Zullo & Beach 1973
	"calcareous"	Rosell 1973
M. brachialis	"probably *Cliona* sp."	Rosell 1972
M. basicupula	*Suberites inconstans*	Sukaimi 1966
M. robinae	*Delaubenfelsia raromicrosclera*	Van Syoc herein

only one species of sponge (Table 1), *M. longirostrum* in the western Pacific and Indo-Pacific inhabits at least two species of sponges (Utinomi 1968) as does *M. orcutti* (Jones 1978) in California and Baja California.

The question of host specificity in *Membranobalanus* has been considered only with regard to *M. orcutti* (Jones 1978) and *M. costatus* (Zullo & Standing 1983).

The other genus of sponge barnacle, *Acasta* Leach, has many species which inhabit more than one host sponge species. For example, *Acasta cyathus* inhabits *Verongula ardis* (de Laubenfels, 1950), *Ircinia campana* (Lamarck, 1813), *Erylus ministrongulus* Hectel, 1965, *Ircinia felix* (Duchasaing & Michelotti, 1864), *Spinosella* (=*Callyspongia*) *vaginalis* (Lamarck, 1814), and *Spongia tubulifera* Lamarck, 1814, and at least two other species of Demospongea in North Carolina (Wells 1966; Zullo & Standing 1983).

To date, *M. robinae* has been found in only one species of sponge, *Delaubenfelsia raromicrosclera* Dickinson, 1945, at one location, Bahía de los Angeles in the Gulf of California. If *M. robinae* lives in *D. raromicrosclera* throughout a greater part of the sponge's range, we might expect to find it elsewhere in the Gulf of California (Dickinson 1945, Hofknecht 1978).

Key to the Genus *Membranobalanaus*

1a. Rostrum much longer than other compartmental plates 2
b. Rostrum nearly as long, or as long as, other compartmental plates .. 6
2a. Fourth cirrus with recurved teeth or spines on proximal articles ... 3
b. Fourth cirrus with straight teeth or spines on proximal articles 4
3a. Radii present .. *M. declivis* (Darwin)
b. Radii lacking or very narrow ... . *M. orcutti* (Pilsbry)
4a. Radii present .... *M. koreanus* Kim and Kim
b. Radii lacking or very narrow ... 5
5a. Parietes with distinct horizontal growth lines .. *M. brachialis* (Rosell)

b. Parietes without distinct horizontal growth lines .... *M. longirostrum* (Hoek)

6a. Fourth cirrus with recurved teeth 7

b. Fourth cirrus with straight teeth . ... *M. cuneiformis* (Hiro)

7a. Base of barnacle having a lobed appearance in side view due to rounded ends of compartmental plates .... *M. robinae*, sp. nov.

b. Base not lobed in appearance when viewed from side 8

8a. Parietes costate .... *M. costatus* Zullo and Standing

b. Parietes not costate .... *M. nebrias* (Zullo and Beach)

Acknowledgments

I'd like to thank Welton L. Lee for giving me the initial opportunity to study barnacles. Special thanks to Victor A. Zullo for patiently training me in barnacle systematics and being very generous with his encouragement and continuing help and advice with this manuscript and other cirripedian projects. William A. Newman and Terrence M. Gosliner read the manuscript and offered helpful criticisms. Sarah Ward Klontz identified the sponges inhabited by *M. robinae*. Lynette Cook provided the illustrations of *M. robinae*.

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ELASMOPUS BALKOMANUS, A NEW SPECIES FROM THE FLORIDA KEYS (CRUSTACEA, AMPHIPODA)

James Darwin Thomas and J. L. Barnard

Abstract.—*Elasmopus balkomanus* is described from Looe Key Reef in the Florida Keys. The species is very close to the eastern Pacific *E. antennatus* but in the male has equally extending rami on uropod 3, only 2 (versus 4–6) spines on each lobe of the telson in adults, a lateral ridge on the propodus of male gnathopod 2 and very heavily armed flagella of antenna 2 in the male.

This species lives in a short-tufted algal turf community on coral rubble but apparently is rare because it has only been collected once in 10 years of sampling in the Florida Keys.

Elasmopus balkomanus, new species
Figs. 1–3

Etymology.—A.S. balko, ridge; L, manus, hand.

Diagnosis of male.—Eyes ordinary, brownish-purple in alcohol. Flagellum of male antenna 2 densely setose. Mandibular palp article 3 deeply falcate. Palm of male gnathopod 2 with weak, sparsely spinose hump near dactylar hinge, no marginal teeth, inner face with longitudinal, cuspidate ridge, setae all posterior ("below") ridge and not organized into rows perpendicular to ridge; dactyl overriding palm onto face of propodus. Article 2 of pereopods 5–7 with only tiny setules and tiny serrations posteriorly; locking spines of pereopods 3–7 thin and almost straight, smooth; main subapical spine-seta on dactyl of medium thickness, smooth, with 2 accessory thin setules. Epimera 1–2 with medium sharp posteroventral tooth, all ventral spines short, rarely paired. Uropod 3 with "long" rami (in generic context), inner almost as long as outer. Telson with sharply and deeply incised apices each bearing pair of spines, one spine elongate, other spine short.

Description of male.—Body generally as in other species of genus (for side views of body form in *Elasmopus* see Sars 1895, Barnard 1962, Bousfield 1973). Antenna 1 elongate, slender, article 1 with 3 ventral spines in tandem, accessory flagellum 3-articulate. Flagellum of antenna 2 densely armed with flags of setae. Upper lip rounded below, projecting slightly in front of epistome from side view. Incisors of right and left mandibles with 2 teeth, right lacinia mobilis bifid, proximal branch simple, distal branch with 7 teeth, left lacinia mobilis with 4 teeth; right rakers 3, left 4; molars moderately triturative, each with plumose seta; palp article 1 weakly elongate, article 2 with 2–3 short medial setae, 2–3 apicomedial long setae, article 3 with 1-1 A setae, many D setae forming comb on falcate invagination, 3 E setae. Lower lip, maxilla 2 and maxilliped like figure 35 of Barnard (1979) with following minor exceptions. Inner plate of maxilla 1 with 2 apical setae and 4 apicolateral setules, outer plate with 7 spines, palp article 2 with 2 sharp cusps, one apicolateral seta, 4 apicomedial marginal elements (2 thick, 2 thin) and 4 facial setae. Both lobes of maxilla 2 equally thin, inner plate with only single apicomedial seta no longer than apical setae, outer plates asymmetrical, no cusps, 3 facial 5 apicomedial, 3 apicolateral setae. Inner plate of maxilliped with weak apicomedial cusp, 8 apical setae, 6 medial setae, outer plate with 10 medial blades, 5 apicolateral setae, palp article 3 with scaly apicolateral irregular

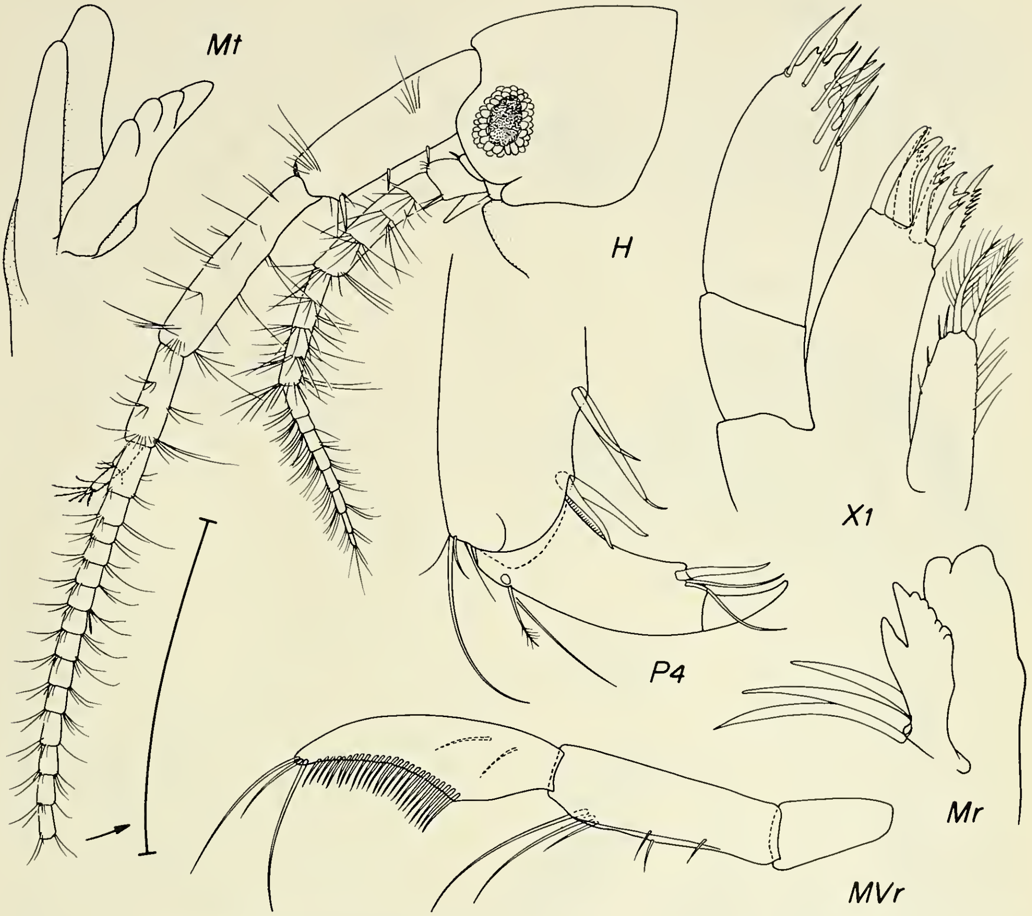

Fig. 1. *Elasmopus balkomanus,* male holotype "m" 7.13 mm. Capital letters refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as: C, coxa; G, gnathopod; H, head; M, mandible; O, outer pate or ramus; P, pereopod; R, uropod; T, telson; V, palp; W, pleon; X, maxilla; Z, gill; m, medial; r, right; s, setae removed; t, left.

lobe, dactyl with thick nail and 4 accessory setules.

Anterior margin of coxa 1 and posterior margin of coxa 4 weakly excavate, long setae on coxae 1–4 = 3-2-0-0. Gnathopod 1 ordinary, see illustrations. Article 2 of gnathopod 2 with weak lateral ridge and hollow. Pereopods 3–4 slender, 4 smaller than 3, article 6 with 6–7 posterior sets of spine pairs including locking spines.

Posterior margin of article 2 on pereopod 5 weakly excavate, posteroventral corner of weak lobe sharp; pereopods 5–7 relatively slender in generic context, serrations on article 2 tiny and numerous, dactyl relatively elongate. Broad gills present on coxae 2–6.

Dorsolateral margin of peduncle on uropod 2 with only 1 spine.

Female "f."—Like male but gnathopod 2 of female form, see illustration; merus with sharp tooth. Narrow oostegites present on coxae 2–5. Inner ramus of uropod 3 shortened.

Illustrations.—Telson magnified more

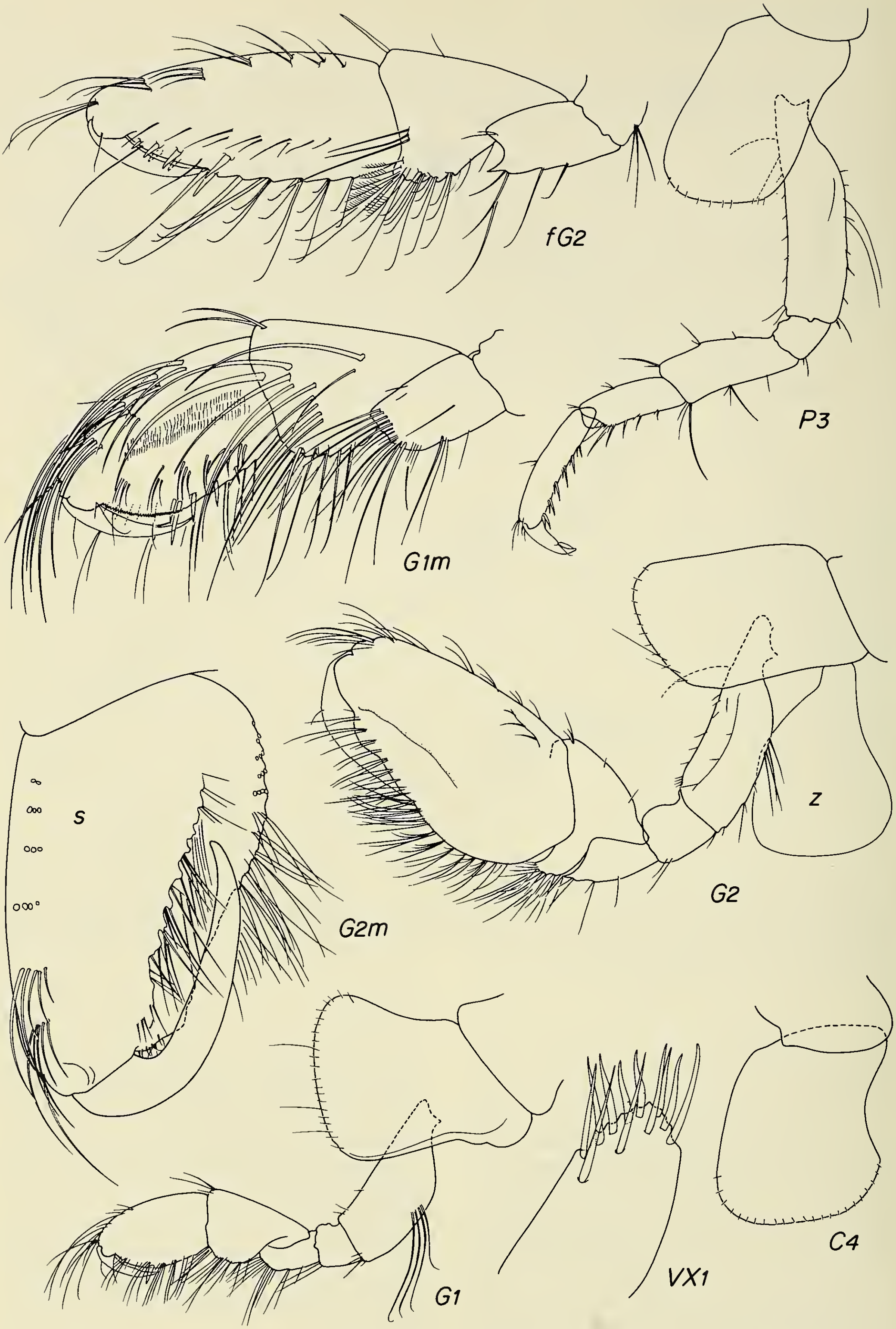

Fig. 2. *Elasmopus balkomanus,* unattributed figures = male holotype "m" 7.13 mm; f = female "f" 6.15 mm. Letter codes, see Fig. 1.

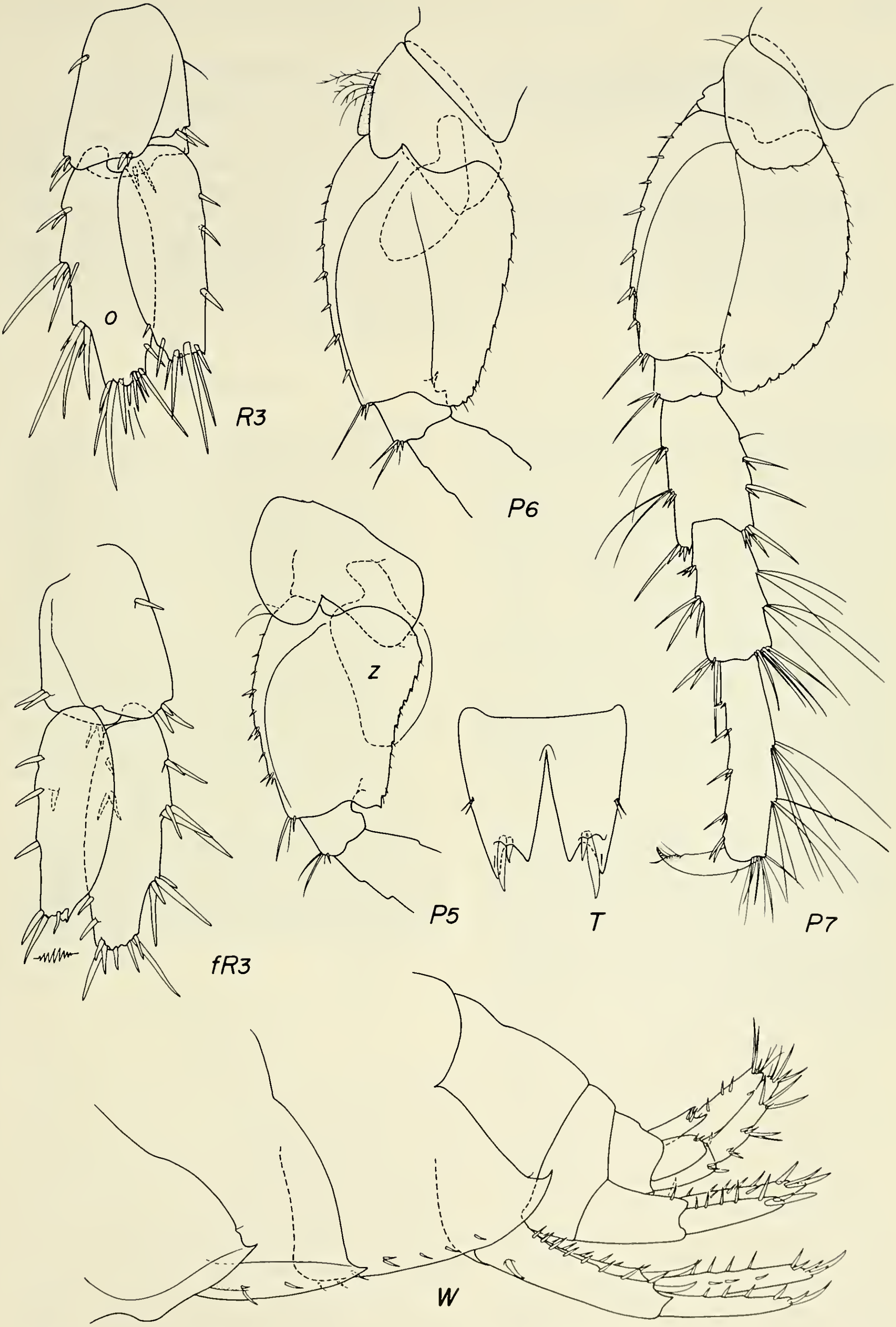

Fig. 3. *Elasmopus balkomanus,* unattributed figures = male holotype "m" 7.13 mm; f = female "f" 6.15 mm. Letter codes, see Fig. 1.

than uropod 3. Pereopod 4 not illustrated, like pereopod 3 but significantly smaller.

Holotype.—USNM No. 235007, male "m" 7.13 mm.

Type locality.—Florida: Florida Keys; Looe Key Reef, west end of rubble zone on backreef, formaldehyde wash of rubble in 2 m, 9 Oct 1983, coll. J. D. Thomas, associated amphipod genera, *Ceradocus, Maera, Spathiopus.*

Material.—Type locality, female "f" 6.15 mm, and 4 other specimens.

Relationship.—Differing from *E. antennatus* as in Abstract. Differing from *E. levis* Smith (Bousfield 1973) in the equal rami of uropod 3, lack of medial hollow and configuration on propodus of male gnathopod 2; the heavily armed flagellum of antenna 2 in male and presence of lateral ridge on propodus of male gnathopod 2.

Differing from *E. ecuadorensis* in the Galapagos Islands (Barnard 1979) by the subequal rami of uropod 3, presence of tooth on epimeron 3, the excavate telsonic lobes with weak spination (versus truncate lobes bearing numerous spines), and the distinctive locking spine formation on pereopods 3–7.

Differing from *E. hawaiensis* (as *E. ecuadorensis hawaiensis* in Barnard 1970) in the equal rami of uropod 3, presence of tooth on epimeron 3 and the ordinary locking spines of pereopods 3–7.

Distribution.—Florida: Florida Keys; Looe Key Reef, 2 m.

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SYNALPHEUS DORAE, A NEW COMMENSAL ALPHEID SHRIMP FROM THE AUSTRALIAN NORTHWEST SHELF

A. J. Bruce

Abstract.—A new species of alpheid shrimp, *Synalpheus dorae,* is described and illustrated. It occurs in association with sponges of the genus *Reniera* on the Australian Northwest Shelf at depths of 37–82 m. The species is unusual in having only four carpal segments on the second pereiopod and all 162 specimens collected appeared to be male.

A survey of the benthic fauna of the Australian Northwest Shelf carried out by the F.R.V. *Soela* of the Commonwealth Scientific and Industrial Research Organization's Fisheries Division in 1983–1984 provided abundant material of the family Alpheidae. The study of these shrimps was undertaken by Professor A. H. Banner and D. M. Banner and revealed numerous species new to the Australian fauna as well as many rare species and some undescribed species. On the death of Professor Banner the study was discontinued and the specimens returned to the Northern Territory Museum, Darwin. Amongst the material returned was one container with a note from Dora Banner enclosed, stating "This is definitely a new species. We had not had time to work on it." This material is now described below.

Synalpheus dorae, new species
Figs. 1–6

Material examined.—18 ♂, operation 7/12, 19°51.9′S, 117°0.78′E, 57–58 m, trawl, F.R.V. *Soela,* Cr. 0283, 10 Apr 1983, coll. P. Blyth, NTM. Cr. 005060.—136 ♂, sta NWS-22, 19°05.0′S, 118°57.8′E, 82 m, trawl, F.R.V. *Soela,* Cr. 0283, 24 Apr 1983, coll. A. J. Bruce, NTM. Cr. 005059.—1 ♂, locality D4, 19°29.6′S, 118°52.4′E, 37–38 m, trawl, F.R.V. *Soela,* Cr. 0583, 25 Oct 1983, coll. T. Ward, NTM. Cr. 005061.—7 ♂, locality D7, 19°29.7′S, 118°51.4′E, 40–41 m, epibenthic sledge, F.R.V. *Soela,* Cr. 0583, 25 Oct 1983, coll. T. Ward, NTM. Cr. 005062.

Description.—A small-sized, robust alpheid shrimp of subcylindrical body form. Carapace smooth, glabrous, slightly compressed; rostrum small, blunt, short, depressed, slightly upturned, slightly exceeding orbital teeth, with distal dorsolateral setae, about 1.4 times longer than proximal width, reaching to about middle of proximal segment of antennular peduncle, without orbitorostral process, orbitorostral notch broadly rounded, orbital teeth triangular, slightly upturned distally, with simple setae laterally, anterolateral margin unarmed, very obliquely angular, posterior margin broadly rounded, cardiac notch distinct.

Abdomen subcylindrical, glabrous, first 4 pleura small, rounded in female, similar in male, but first pleuron with acute posteroventral tooth, fifth pleuron with acute ventral tooth; sixth segment about subequal to length of fifth, about 1.5 times longer than deep, posterodorsal margin unarmed, posteroventral angle well developed, acute, posterolateral angle acute. Telson about 1.6 times sixth segment length, triangular, distally truncate, about 1.25 times longer than proximal width, lateral margins straight, convergent, posterior margin about 0.28 of anterior width, 2 pairs of large, erect dorsal spines at 0.35 and 0.82, posterior spines slightly longer than anterior, about 0.27 of

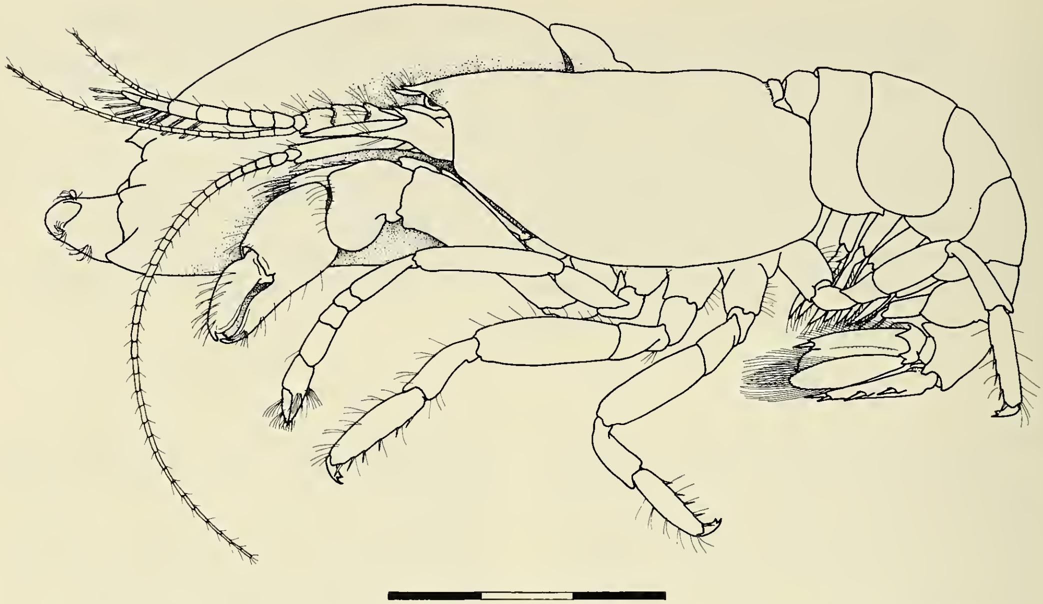

Fig. 1. *Synalpheus dorae* holotype male, Northwest Shelf, Western Australia. Scale bar in millimeters.

telson length; 2 pairs of posterior marginal spines, submedian slightly larger than lateral, about 0.21 of telson length, short median gap with 2 simple setae dorsally and 2 longer plumose setae ventrally; dorsal surface with sparse simple setae.

Antennule well developed; proximal segment of peduncle subcylindrical, with normal statocyst with granular statolith, stylocerite long, acute, reaching to about 0.8 of segment length, with short simple setae distolaterally; intermediate and distal segments subequal, cylindrical, together subequal to proximal segment length; upper flagellum biramous, rami fused for 5 segments, robust; short ramus with 2 stout segments, about 8 groups of aesthetascs; lower ramus with about 12 slender segments, length subequal to fused portion plus short ramus; lower flagellum short, slender, about 0.75 times carapace length, exceeding long ramus of upper flagellum.

Antenna with basicerite robust, with shorter acute dorsolateral and longer acute ventrolateral process, latter reaching or exceeding distal end of proximal segment of antennular peduncle, both with sparse simple setae distolaterally; merocerite and ischiocerite short; carpocerite subcylindrical, slightly flattened, about 4.5 times longer than wide, sparsely setose laterally; flagellum short, robust, about 1.3 times carapace length; scaphocerite with very robust lateral spine, slightly exceeding antennular peduncle, distinctly exceeding carpocerite, about 4.7 times longer than proximal width, lamella greatly reduced, reaching to about 0.5 of lateral margin, spine with several short simple setae distolaterally.

Eyes normal, completely covered dorsally by orbital hood, cornea well pigmented.

Epistome normal, without special features.

Mandible (left) with corpus moderately slender; palp 2-segmented, proximal segment subcylindrical, proximally tapered, non-setose, distal segment oval, flattened, about 1.8 times longer than broad, distal margin with numerous short, plumose setae; molar process robust, obliquely truncate distally, margin densely fringed with short setae, with strong blunt tooth poste-

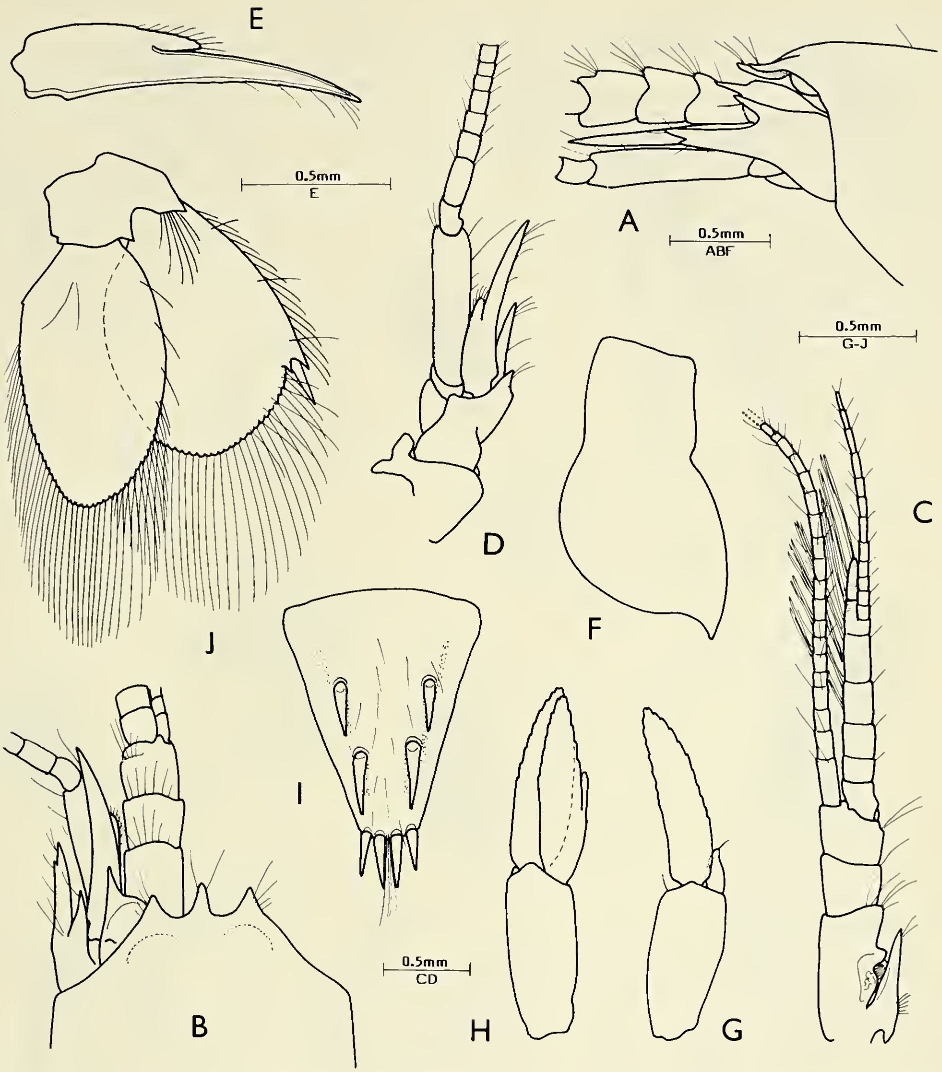

Fig. 2. *Synalpheus dorae* paratype male: A, Anterior carapace and antennal peduncles, lateral; B, Same, dorsal; C, Antennule; D, Antenna; E, Scaphocerite; F, First abdominal segment, lateral; G, First pleopod; H, Second pleopod; I, Telson; J, Uropod.

riorly; incisor process slightly expanded distally, truncate with 7 small irregular acute teeth, larger teeth laterally. Maxillula with bilobed palp, upper lobe long, acute, lower lobe short with distally setulose spine; upper lacinia broad with about 20 short simple acute marginal teeth, with numerous short denticulate setae submarginally; lower lacinia slender, curved, with several serrulate setae distally. Maxilla with short simple subcylindrical, distally tapering non-setose palp; basal endite broad, produced medially, partly bilobed, with dense setal fringe medially; coxal endite simple, reduced, small acute lobe with several long setae; scaphognathite 4.0 times longer than broad, anterior lobe distally narrow, medial margin concave, 1.8 times longer than wide, posterior

Fig. 3. *Synalpheus dorae* paratype male: A, Mandible; B, Same, incisor process; C, same, molar process; D, Same, palp; E, Maxillula; F, Same, palp; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Same, Lateral plate.

lobe about 0.35 of scaphognathite length. First maxilliped with 2-segmented palp, proximal segment about 2.2 times longer than broad, medial margin sparsely setose distally, distal segment about 0.8 of proximal segment length, 3.0 times longer than wide, tapering slightly, with single short simple distal seta; basal endite normal medial margin densely setose; coxal endite simple, sparsely setose, 4 long setae distomedially; exopod with well developed flagellum with numerous plumose setae dis-

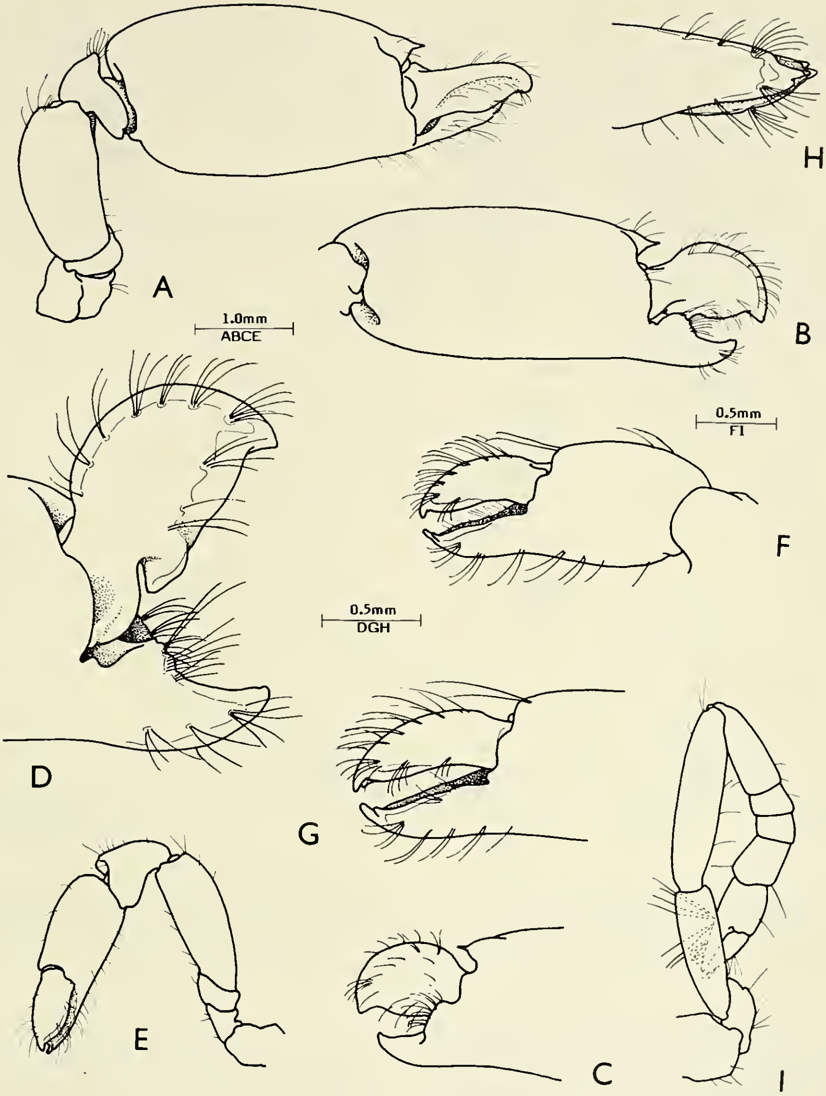

Fig. 4. *Synalpheus dorae* paratype male: A, Major first pereiopod; B, Same, chela, lateral; C, Same, fingers, medial; D, Same, fingers, lateral; E, Minor first pereiopod; F, Same, chela, lateral; G, Same, fingers; H, Same, ventral; I, Second pereiopod.

tally, caridean lobe small, feebly setose; epipod large, transversely oval, simple. Second maxilliped of normal form; dactylar segment narrow, about 4.6 times longer than broad, densely setose medially, propodal segment broad, distally rounded, sparsely setose, basis broad, medially excavate and setose, exopod flagellum well developed with numerous plumose setae distally; coxa broad, medially produced with long setae distally, small rounded epipod without podobranch laterally. Third maxilliped with endopod stout, exceeding carpocerite and antennular peduncle; isochiomeral segment 3.0 times longer than central depth, slightly tapered proximally, ventromedially excavate, margins feebly setose; carpal segment about 0.27 of ischiomeral segment length,

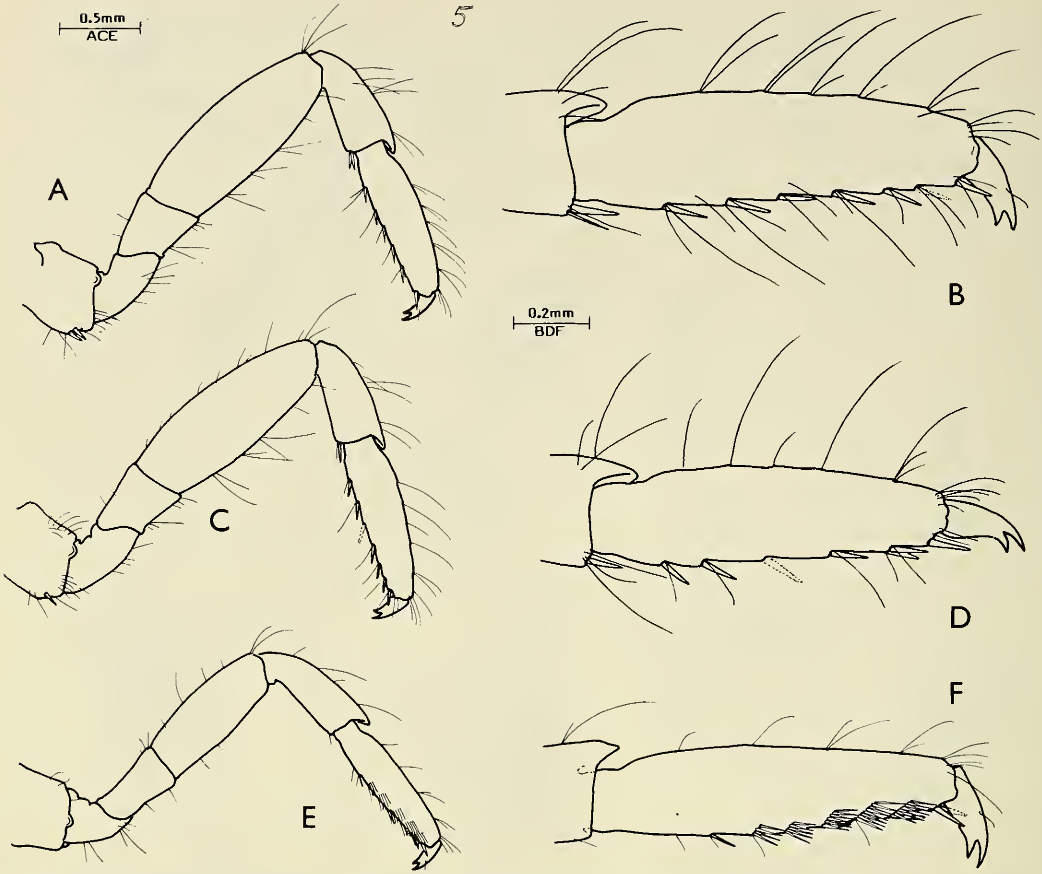

Fig. 5. *Synalpheus dorae* paratype male: A, Third pereiopod; B, Same, propod and dactyl; C, Fourth pereiopod; D, Same, propod and dactyl; E, Fifth pereiopod; F, Same, propod and dactyl.

as long as wide, subcylindrical, with 2 dorsolateral spines and several ventrolateral setae; distal segment about 0.3 times longer than proximal width, tapering distally, distal width 0.4 of proximal, length 0.83 of ischiomerus, with 7 transverse rows of serrulate spines medially and 8 stout, blunt, finely denticulate, distally; basis about 0.3 of ischiomeral length, sparsely setose, exopod with well developed flagellum reaching to about 0.85 of ischiomeral length, with numerous plumose setae distally; coxa stout, ventrally medially rounded, with long low dorsolateral plate with small recurved distal tooth, without epipod or arthrobranch.

Thoracic sternites narrow and unarmed, coxae of pereiopods in close apposition.

First pereiopods markedly unequal and dissimilar, apparently similar in males and females. Major chela enlarged, about 1.5 times carapace length, with palm subcylindrical, centrally moderately swollen, slightly dorsoventrally flattened, smooth, glabrous, about 1.8 times longer than greatest width, distodorsal angle produced, with slender acute tooth; dactylus strongly compressed, about 0.38 of palm length, semicircular, with stout acute distal tooth, molar process small, feebly produced, equal to 0.3 of cutting edge length, medial and lateral

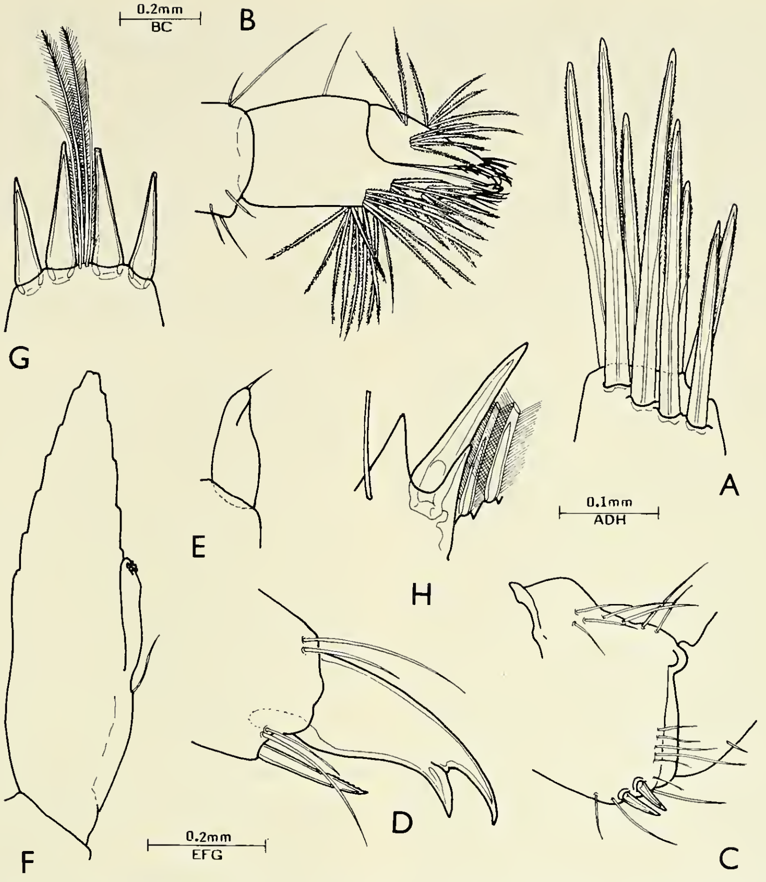

Fig. 6. *Synalpheus dorae* paratype male: A, Distal spines of terminal segment of third maxilliped endopod; B, Second pereiopod, chela; C, Third pereipod, coxa; D, Same, dactyl; E, First pleopod, endopod; F, Second pleopod, endopod; G, Posterior telson spines; H, Distolateral spine of exopod of uropod.

surfaces of dactyl with numerous submarginal groups of 2–3 simple setae; fixed finger short, curved, blunt distally, deeply excavate proximally for reception of dactylar molar process and cutting edge, with groups of simple setae; carpus very stout about 0.14 of palm length, expanded and excavate distally, unarmed; merus robust, 2.0 times longer than greatest width, about 0.57 of palm length, unarmed; ischium, basis and coxa, all short, robust, without special features, basis without exopod, coxa as in major chela, without epipod and setobranch. Minor second pereiopod with chela about 0.4 of major chela length, about 0.5 of carapace length; palm about 1.4 times longer than deep, smooth, slightly swollen centrally, compressed with scattered long simple setae; dactylus about 0.75 of palm length, about 2.5 times longer than proximal depth, broadly subspatulate with thickened edge laterally, strong blunt hooked tooth distally with smaller tooth medially, with numerous groups of long simple setae dorsally; fixed finger deeply excavate, with strong blunt tooth distally with smaller tooth laterally, with long setae medially and laterally; carpus about 0.6 of palm length, 0.9 times longer than wide, expanded distally deeply excavate, unarmed; merus about 0.8 of chela length, 2.8 times longer than greatest width; ischium, basis and coxa without special features.

Second pereipod moderately robust, exceeding carpocerite by chela and distal carpal segment, chela with palm compressed, about 1.2 times longer than deep, sparsely setose, fingers slender, tapering, with small hooked tips, cutting edges entire, with dense groups of coarsely serrulate setae proximally, shorter simple setae distally, dactylus about 2.8 times longer than proximal depth, subequal to palm length; carpus with 4 stout segments, 4:1:1:2, proximal segment longest; merus about 0.9 of carpus length, 4.0 times longer than wide; ischium 0.7 of merus length, 3.4 times longer than central width, tapering proximally; basis 0.6 of ischium length, without exopod; coxa robust, without epipod or setobranch.

Third pereiopod robust, exceeding carpocerite by about half propod length; dactyl with unguis not clearly demarcated from corpus, compressed, feebly curved, about 2.6 times longer than proximal depth, with well developed accessory tooth at 0.6 of dactyl length, shorter and stouter than terminal tooth; propod about 3.7 times longer than deep, compressed, 4.0 times longer than dactyl, with 2 robust distoventral spines and 6 ventral spines, with numerous long simple setae dorsally and ventrally, carpus about 0.6 of propod length, 2.2 times longer than distal width, slightly tapered proximally, with well developed distodorsal lobe, distoventral margin with 2 spines, one robust, one slender; merus 2.0 times length of carpus, 2.6 times longer than central width, unarmed; ischium about 0.33 of merus length as long as wide distally, tapered proximally, unarmed; basis 0.4 of merus length, unarmed; coxa robust with 2 submarginal ventral spines, without epipod or setobranch. Fourth pereiopod similar to third; propod 0.8 of third propod length, with single distoventral spine, 5 ventral spines; carpus with single distoventral spine; coxa with single distoventral spine. Fifth pereiopod generally as third; propod 0.8 of third propod length, 4.2 times longer than central depth with 2 distoventral spines and 3 ventral spines and 5 transverse rows short of serrulate setae ventrolaterally; coxa without distoventral spine.

Male first pleopod with basipodite 2.2 times longer than wide, exopod 1.15 times length of basipodite, 4.0 times longer than proximal width; endopod small, 0.25 of exopod length, 2.5 times longer than wide, tapering distally, with single short simple distal setae. Second pleopod with basipodite 2.5 times longer than wide; exopod about 3.6 times longer than proximal width, 1.1 times length of basipodite; endopod subequal to exopod length, without appendix masculina, appendix interna at 0.4 of endopod length, about 0.25 of endopod length, 5.5 times longer than central width with few (3–5) concinnuli.

Uropod with stout protopodite, with large acute dorsolateral tooth, with long simple setae medially, and smaller dorsal tooth; exopod broad, 1.4 times longer than wide, oval, lateral margin convex with acute distolateral tooth with long mobile spine and small acute tooth medially, without distinct diaeresis, lateral margin with submarginal row of setae ventrally; endopod subequal to exopod length, 1.8 times longer than wide.

Types.—An intact specimen from sta NWS-22 is selected as holotype and the other specimens from that station are designated as paratypes, catalog number NTM. Cr. 005059. Paratypes are deposited in the collections of the National Museum of Natural History, Washington, D.C., catalog number USNM 234305, the Bishop Museum, Honolulu, catalog number S10804 and the Rijksmuseum van Natuurlijke Historie, Leiden, catalog number RMNH 37179.

Measurements.—Holotype male, total length (approx.) 10.0 mm; carapace length, 4.0 mm, major chela, 5.5 mm; minor chela

2.0 mm. Paratype male, total length (approx.), 8.2 mm; carapace length, 3.5 mm; major chela, 4.15 mm; minor chela, 1.9 mm.

Host.—The specimens from T/12 and NWS/22 were obtained from sponges. The 136 specimens from NWS/22 were all obtained from a single sponge host, identified as *Reniera* sp. (Haliclonidae).

Parasites.—One specimen, sta NWS-22, was infected by an abdominal bopyrid parasite, *Eophryxus* sp. (Isopoda: Hemiarthrinae).

Etymology.—The species is named in honor of the late Dora May Banner, in recognition of her great contribution to alpheid taxonomy.

Systematic position.—Morphological features of special significance in the assessment of the relationships of *S. dorae* are (i) the lack of an orbitorostral process, (ii) the absence of a dense setal brush on the dactyl of the minor chela, (iii) absence of a strongly produced frontal region extending far beyond eyes, (iv) lack of a reduced accessory spine on ambulatory dactyls, and absence of spines on merus of third pereiopod, (v) lack of a rostrum markedly exceeding orbital teeth, and (vi) broad dentate fingers on minor chela. The first four items are characteristic of the "*Comatularum* Group" and the others of the "*Coutierei* Group," a species group largely characterized by its lack of consistent characters (Banner & Banner 1975). *Synalpheus dorae* appears most closely related to some of the species of the '*Coutierei* Group' and can be immediately distinguished from most of them by the presence of only four segments on the carpus of the second pereiopod, all other species except two having five segments. The two species with a 4-segmented carpus are *S. quadriarticulatus* Banner & Banner, 1975, and *S. redactocarpus* Banner, 1953. The first species lacks an orbitorostral process but its presence or absence in *S. redactodactylus* is not recorded.

Synalpheus dorae is most conveniently distinguished from *Synalpheus quadriarticulatus* by the telson, which bears two pairs of very large dorsal spines and two pairs of large subequal posterior spines, with the interspace between the submedian spines obsolete. In *S. quadriarticulatus* the dorsal spines are smaller, the posterior spines smaller, unequal, and the submedian spines well separated by a convex posterior margin. In addition the fingers of the minor chela are bidentate in *S. dorae,* simple in *S. quadriarticulatus.*

Synalpheus dorae is less closely related to *Synalpheus redactocarpus,* which has a well developed lamella on the scaphocerite and a telson lacking dorsal spines, with a well developed convex posterior margin with slender unequal posterior spines. In *S. redactocarpus* the orbital spines are longer, more acute and convergent, and the rostrum is longer and narrower. The palm of the major chela lacks a distodorsal spine and the fingers of the minor chela are less broadened and with simple finger tips.

In its general morphology *S. dorae* also shows a close resemblance to *Synalpheus pescadorensis* Coutière, 1905, from which it differs, in addition to the 4-segmented second pereiopod carpus, in having a much smaller lamella in the scaphocerite and lacking a very long posterolateral process on the protopodite of the uropod.

The thoracic sternites in *Synalpheus dorae* are narrow and the coxae of the pereiopods are medially flattened and apposed. The small spines on the coxa of the third and fourth pereiopods project posteriorly in this position, a feature that does not appear to have been noted in other species of *Synalpheus.*

Remarks.—Of the 162 specimens available, only a few are obvious juveniles on account of their small size. The rest are of adult size for a small *Synalpheus* species, yet no ovigerous females are present and all intact specimens are of the usual male form, with an angular posterior tooth on the first abdominal pleuron, and in the morphology of the first and second pleopods (Dardeau

1984). Similar populations have been reported in other sponge-inhabiting *Synalpheus* species: *S. neptunus germanus* (Banner & Banner, 1975, 44 specimens), *S. paradoxus* (Banner & Banner, 1981, 241 ♂, 4 ♀), *S. crosnieri* (Banner & Banner, 1983, 144 ♂, 3 ♀). The condition was first noted in Atlantic species by Coutière (1909) in *S. pectiniger* Coutière, and Chace (1972) has also reported on a paucity of ovigerous females in some West Indian populations of *S. paraneptunus* Coutière, so the phenomenon is clearly of widespread distribution. Banner & Banner (1981) have suggested that toxic or pheromone-like metabolites produced by sponges may be the cause of abnormal *Synalpheus* populations. Progress in the study of these peculiar populations is clearly handicapped by the lack of any detailed knowledge of the sponge hosts of many species of *Synalpheus* and of the degree of host specificity in most of the sponge-associated species.

Acknowledgments

I am particularly grateful to the late Dora May Banner for drawing my attention to these new shrimps, to J. N. A. Hooper for the identification of the sponge host, and to Dr. J. C. Markham for the identification of the bopyrid parasite.

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REDESCRIPTIONS OF *TETRALIA CAVIMANA* HELLER, 1861 AND *TRAPEZIA CYMODOCE* (HERBST, 1799) FIRST STAGE ZOEAS WITH IMPLICATIONS FOR CLASSIFICATION WITHIN THE SUPERFAMILY XANTHOIDEA (CRUSTACEA: BRACHYURA)

Paul F. Clark and Bella S. Galil

Abstract.—The first stage zoea of *Tetralia glaberrima* (Herbst, 1790) (now *T. cavimana* Heller, 1861) and *Trapezia cymodoce* (Herbst, 1799) of Gurney (1938) are redescribed and compared both with the original description and with the description of *Tetralia glaberrima* by Al-Kholy (1963). Differences between the two larvae are tabulated and larval characters that appear to support the separation of the families Platyxanthidae and Trapeziidae, as proposed in a classification of adult xanthoids by Guinot (1977 and 1978), are identified.

Guinot (1978) proposed a new classification of adult Brachyura based primarily on the position of female and male genital openings. Eight families were recognized within the superfamily Xanthoidea, and she supported Ortmann (1897) in giving the rank of family to the Trapeziinae as defined by Miers (1886). But for a few minor changes, Guinot indicated that the family contained all the genera listed by Balss (1957) in his subfamily Trapeziinae. Guinot did not use any larval characters to corroborate her classification.

Rice (1980) and Martin (1984) related larval groupings, based on chaetotaxy, to various classifications of adult xanthoids. Both found that many existing descriptions of xanthoid larvae were inadequate or unreliable, and each attempted to use larval evidence to resolve incongruences between different schemes of adult classification. Rice found that his larval groupings did not correspond to the simple divisions of the Xanthidae by Balss (1957), while Martin (1984) endorsed the scheme proposed by Glaessner (1969) because it was based on fossil and recent forms. But later, Martin et al. (1985) stated that evidence appeared partly to support Balss, as their group I corresponded to the subfamily Xanthinae. Rice (1980) and Martin et al. (1985) agreed that the genus *Homalaspis* warranted separation from the remainder of the Xanthinae of Balss and thereby corroborated the Platyxanthidae of Guinot. Rice therefore tended to support the more complex divisions suggested by Guinot.

The larval descriptions of *Tetralia glaberrima* (Herbst, 1790) (now *T. cavimana* Heller, 1861; see synonomy of Galil, 1988) and *Trapezia cymodoce* (Herbst, 1799) by Gurney (1938) and of *Tetralia glaberrima* by Al-Kholy (1963) are incomplete. Therefore, the aim of this paper is to redescribe these larvae and use this information to reexamine the classification of the xanthoids.

Materials and Methods

Material collected and hatched at the Biological Station, Ghardaqa, Egypt, by Gurney (1938) was fixed originally in formalin and recently transferred to 70% ethanol. The female and the first zoea of *Trapezia cy-*

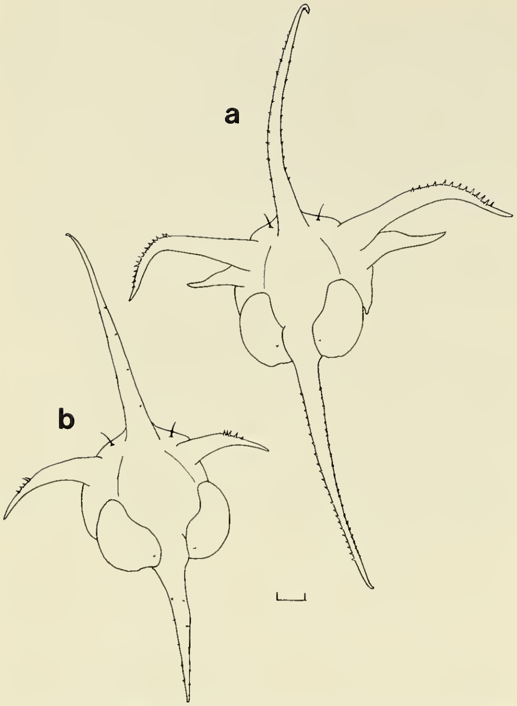

Fig. 1. Carapace of a, *Tetralia cavimana*; b, *Trapezia cymodoce*. Scale bar = 0.1 mm.

modoce (Herbst) are stored in the British Museum (Natural History), registration number 1986:915, and those of *Tetralia cavimana* Heller, were registered as 1986: 53. Dissected appendages were mounted in polyvinyl lactophenol and examined using an Olympus BH-2 microscope with Nomarski interference contrast. Drawings were made with the aid of a camera lucida. When comparing the first stage zoea of the two species, the setal arrangement on many appendages was similar and it was only necessary to figure fully the chaetotaxy of one species, *Tetralia cavimana,* and illustrate the differences in *Trapezia cymodoce.*

Tetralia cavimana Heller, 1861
Figs. 1a, 2a–d, 3a, b, 4c, d

Tetralia glaberrima (Herbst, 1790).—Gurney, 1938:77, pl. III, figs. 29–33.—Al-Kholy, 1963:138, pl. I, figs. 1–7.—Williamson, 1970:37.

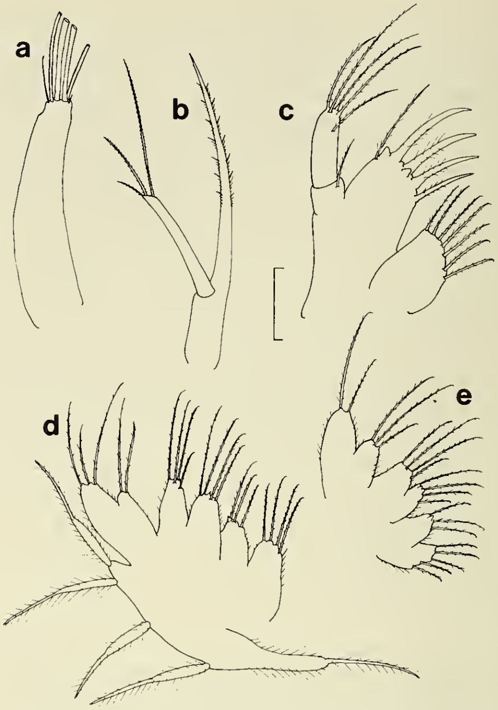

Fig. 2. *Tetralia cavimana*: a, Antennule; b, Antenna; c, Maxillule; d, Maxilla. *Trapezia cymodoce*: e, Setation of maxilla coxal, basial and endopod lobes. Scale bar = 0.1 mm.

non *Tetralia glaberrima* (Herbst, 1790).—Al-Kholy 1963:139–140, pl. I, figs. 8–21, pl. II, figs. 22–33.

First zoea.—Carapace (Fig. 1a): Long dorsal and rostral spines spinulate; 2 pairs of lateral spines, dorsal pair j-shaped and spinulate on dorsal margin, ventral pair smaller than dorsal pair, unarmed; one pair of posterodorsal setae; ventral margin of carapace with minute denticles, marginal setae absent; one pair of posterodorsal carapace setae; eyes sessile with small setule on each eye.

Antennule (Fig. 2a): Endopod absent; exopod unsegmented with 4 terminal esthetascs, 1 terminal seta and 1 minute terminal spine.

Antenna (Fig. 2b): Spinous process distally spinulate; endopod absent; exopod with unequal terminal setae.

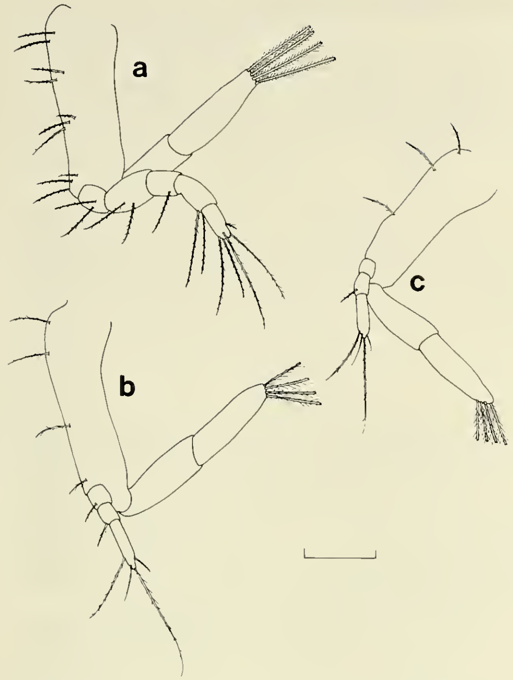

Fig. 3. *Tetralia cavimana*: a, First maxilliped; b, Second maxilliped. *Trapezia cymodoce*: c, Second maxilliped. Scale bar = 0.1 mm.

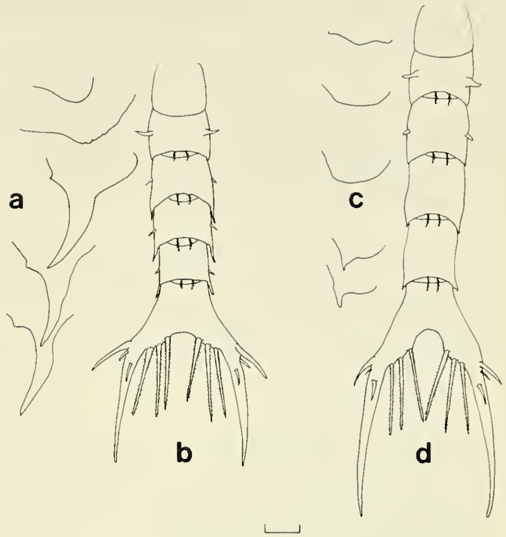

Fig. 4. *Trapezia cymodoce*: a, Dorsolateral spines of somites 1–5; b, Abdomen from dorsal aspect. *Tetralia cavimana*: c, Dorsolateral spines of somites 1–5; d, Abdomen from dorsal aspect. Scale bar = 0.1 mm.

Mandible: Endopod (palp) absent.

Maxillule (Fig. 2c): Coxal endite with 7 setae; basial endite with 5 processes on inner margin plus 2 minute teeth, single seta absent from outer margin; endopod 2-segmented, proximal segment with 1 seta, distal segment with 1 subterminal and 4 terminal setae.

Maxilla (Fig. 2d): Coxal endite bilobed with 4+3(+1 minute tooth) setae; basial endite bilobed with 4(+1 minute tooth)+4 setae; endopod bilobed with 2+3 setae; scaphognathite (exopod) with 4 marginal setae plus 1 long stout posterior seta.

First maxilliped (Fig. 3a): Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 2,2,1,2,5 setae respectively; exopod 2-segmented, distal segment with 4 terminal natatory setae.

Second maxilliped (Fig. 3b): Basis with 4 setae; endopod 3-segmented with 1,1,4 setae respectively; exopod 2-segmented, distal segment with 4 terminal natatory setae.

Third maxilliped: Undeveloped.

Pereiopods: Undeveloped.

Abdomen (Fig. 4c, d): 5 somites; somites 2 and 3 each bearing 1 pair of dorsolateral processes; somites 1–3 with rounded posterolateral margins; somites 4 and 5 with small posterolateral spines; somites 2–5 with pair of posterodorsal setae; pleopods absent.

Telson (Fig. 4d): Each long fork with 1 prominent and 1 small lateral spine plus 1 prominent dorsal spine; posterior margin with 3 pairs of setae.

Trapezia cymodoce (Herbst, 1799)
Figs. 1b, 2e, 3c, 4a, b

Trapezia cymodoce (Herbst, 1799).—Gurney, 1938:76, pl. II, figs. 23–28.

First zoea.—Carapace (Fig. 1b): long dorsal and shorter rostral spine lightly spinulate; single pair of curved, lightly spinulate lateral spines; one pair of posterodorsal se-

Table 1.—Differences in first stage zoea of *Tetralia cavimana* Heller as described by Gurney (1938) and as described in this study.

Character	Gurney (as *T. glaberrima*) (p. 77 & pl. 3, figs. 30, 31)	This study (Figs. 3d & 4c, d)
Dorsolateral process on abdominal somite 3	absent	present
Posteriolateral spines on abdominal somites	*3–5	4 & 5
Number of spines on telson fork	**2 (1 lateral, 1 dorsal)	3 (2 lateral, 1 dorsal)

* Gurney (p. 77), lists somites 3–5 with small lateral spines, but figures a first stage (pl. 3, fig. 30) with small lateral spines on somites 4 and 5 only.

** Gurney figures (pl. 3, figs. 29, 30 & 31) the telson without the minute third spine, but states (p. 77) that a specimen caught in the plankton had this spine.

tae; ventral margin of carapace with minute denticles, marginal setae absent; one pair of posterodorsal carapace setae; eyes sessile with small setule on each eye.

Antennule: Endopod absent; exopod unsegmented with 4 terminal esthetascs, 1 terminal seta and 1 minute terminal spine.

Antenna: Spinous process distally spinulate; endopod absent; exopod with unequal terminal setae.

Mandible: Endopod (palp) absent.

Maxillule: Coxal endite with 7 setae; basial endite with 5 processes on inner margin plus 2 minute teeth, single seta absent from outer margin; endopod 2-segmented, proximal segment with 1 seta, distal segment with 1 subterminal and 4 terminal setae.

Maxilla (Fig. 2e): Coxal endite bilobed with 5+3(+1 minute tooth) setae; basial endite bilobed with 4(+1 minute tooth)+4 setae; endopod bilobed with 3+2 setae; scaphognathite (exopod) with 4 marginal setae plus 1 long stout posterior seta.

First maxilliped: Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 2,2,1,2,5 setae respectively; exopod 2-segmented, distal segment with 4 terminal natatory setae.

Second maxilliped (Fig. 3c): Basis with 3 setae; endopod 3-segmented with 0,1,4 setae respectively; exopod 2-segmented, distal segment with 4 terminal natatory setae.

Third maxilliped: Undeveloped.

Pereiopods: Undeveloped.

Abdomen (Fig. 4a, b): 5 somites; somites 2–5 each bearing a pair of dorsolateral processes; somites 1–3 with rounded posterolateral margins; somites 3–5 with long posterolateral spines; somites 2–5 with pair of posterodorsal setae; pleopods absent.

Telson: Each long fork with 1 prominent and 1 small lateral spine plus 1 prominent dorsal spine; posterior margin with 3 pairs of setae.

Discussion

The differences between the descriptions by Gurney (1938) and Al-Kholy (1963) of *Tetralia cavimana* Heller (as *T. glaberrima* Herbst) and the present study are listed in Tables 1 and 2. In his description of *Trapezia cymodoce* Gurney (1938) figured only abdominal somites 2 and 3 with dorsolateral processes, but on re-examination of this material they were found additionally on somites 4 and 5 (Fig. 4b). Although the first stage zoeas of *Trapezia guttata* Rüppell, 1830 and *Trapezia maculata* (MacLeay, 1838) have been described by Gurney (1938) and Al-Kholy (1963) respectively, these descriptions are inadequate for comparison. Differences in appendage chaetotaxy between *Trapezia cymodoce* (Herbst) and *Tetralia cavimana* Heller first stage zoeas are listed in Table 3.

Rice (1980), from larval descriptions, divided the Xanthidae into 4 groups. He com-

Table 2.—Differences in first stage zoea of *Tetralia cavimana* Heller as described by Al-Kholy (1963) and as described in this study.

Character	Al-Kholy (as *T. glaberrima*) (p. 138 & pl. 1, figs. 2–7)	This study (figs. 2–4)
Terminal armature of antennule	2 esthetascs	4 esthetascs 1 seta & 1 minute spine
Terminal setae on exopod of antenna	*4	3
Setae on coxa of maxillule	5	7
Terminal setae on endopod of maxillule	3	4
Setae on bilobed coxa of maxilla	4+5	4+3
Setae on bilobed basis of maxilla	2+3	4+4
Total no. of setae on scaphognathite	4	5
Endopod setal formula of 1st maxilliped	1,3,0,0,3	2,2,1,2,5
Basial setal formula of 1st maxilliped	5(2,3)	10(2,2,3,3)
No. of endopod segments of 2nd maxilliped	2	3
Setal formula of 2nd maxilliped endopod	2,3	1,1,4
No. of basial setae of 2nd maxilliped	1	4
Dorsolateral processes on 3rd abdominal somite	absent	present
Armature of telson fork	1 prominent lateral spine	1 prominent & 1 small lateral spine + 1 prominent dorsal spine

* Al-Kholy figures 3 terminal setae on antenna exopod (pl. 1, fig. 2), but scores an exopod with 4 terminal setae in his description on page 138.

pared these groupings with several adult classifications, and concluded that they gave some support to the divisions proposed by Guinot (1978). Martin (1984) recognized six groups (I–VI) within the Xanthidae, based on zoeal characters, but gave his groupings no formal taxonomic status. He adopted the classification of xanthoids proposed by Glaessner (1969), because his larval groups did not correspond to the eight families of Guinot.

Rice (1980) and Martin (1984) agree on the suite of characters that defines their xanthoid group III. The genera that they assigned to their respective groups III differs. *Eriphia, Homalaspis, Ozius* and *Tetralia* form the group III of Rice. The group III of Martin contains *Baptozius, Carpilius, Epixanthus, Paramedaeus, Pilumnoides, Platyxanthus* and *Trapezia* in addition to those of Rice. Both include ASM 26 in group III. However, the present redescription of *Trapezia cymodoce* (Herbst) and *Tetralia cavimana* Heller first stage zoeas indicates that the group III of both workers can be divided into two subgroups A and B, the characters of which are defined in Table 4.

Group A includes the first stages zoeas of *Tetralia cavimana* Heller and *Trapezia cymodoce* (Herbst) and corresponds to the Trapeziidae of Guinot (1978). Group B comprises her Platyxanthidae and contains the zoeas of *Homalaspis plana* (A. Milne Edwards) (Fagetti 1970), *Platyxanthus*

Table 3.—Differences in chaetotaxy of appendages between first zoea stages of *Trapezia cymodoce* (Herbst) and *Tetralia cavimana* Heller.

Character	*Trapezia cymodoce*	*Tetralia cavimana*
No. of lateral carapace spines	1	2
Setation of maxilla endopod	3+2	2+3
Setation of maxilla coxa	5+3	3+4
Setal formula of endopod of 2nd maxilliped	0,1,4	1,1,4
Basial setae of 2nd maxilliped	3	4
Abdominal somites with dorsolateral processes	2–5	2 & 3
Abdominal somites with dorsolateral spines	3–5 (long)	4 & 5 (short)

Table 4.—Proposed characters that subdivide the xanthid group III of Martin (1984) and Rice (1980).

Character	Group A	Group B
Setation of distal endopod segment of maxillule	1 subterminal + 4 terminal	2 subterminal + 4 terminal
Setation of maxilla endopod	subterminal setae absent (2 or 3 terminal setae only)	subterminal setae present (2 subterminal + 3 terminal setae)
Setation of basal endopod segment of 1st maxilliped	2	*3
Setation of distal endopod segment of 2nd maxilliped	4	**6

* Lumare & Gozzo (1972) figure the zoeal stages of *Eriphia verrucosa* as variously having 2 or 3 setae on this segment. Examination of *E. verrucosa* 1st stage zoeas from Ischia, Italy (plankton caught material by Galil) revealed 3 setae in this position. Hashmi (1970) described and figured the 1st zoeal stage of *Eriphia laevimana smithii* (MacLeay) with 2 setae, but re-examination of his material, BM(NH) registration number 1986:908, also revealed 3 setae. Wear (1968) illustrated the 1st maxilliped of *Ozius truncatus* H. Milne Edwards stage I zoea with only 1 seta on the basal endopod segment. Other zoeas in this group have 3 setae.

** The following 1st stage zoea all have 6 setae present on the distal segment of second maxilliped endopod; *Baptozius vinosus* (H. Milne Edwards), *Eriphia laevimanus smithii* MacLeay, *Eriphia verrucosa* (Forskal), *Homalaspis plana* (A. Milne Edwards), *Monodeus couchii* (Couch) & *Platyxanthus patagonicus* A. Milne Edwards.

crenulatus (A. Milne Edwards) (Menu-Marque 1970) and *P. patagonicus* A. Milne Edwards (Iorio & Boschi 1986). Guinot (1978) also lists the genera *Homalaspis* and *Platyxanthus* in her Platyxanthidae. Other larvae that fit in group B include the menippids *Baptozius vinosus* (H. Milne Edwards) (Saba et al. 1978a), *Epixanthus dentatus* (White) (Saba et al. 1978b), *Eriphia laevimana smithii* MacLeay (Hashmi 1970), *E. spinifrons* (Herbst) (Bourdillon-Casanova 1960; Hyman 1925; Paolucci 1910), *E. verrucosa* (Forskål) (Lumare and Gozzo 1972), *Ozius rugulosus* Stimpson (Kakati and Nayak 1977), *O. truncatus* H. Milne Edwards (Wear 1968) and the pilumnid *Pilumnoides perlatus* (Poeppig) (Fagetti & Campodonico 1973). None of these are listed in Guinot's classification, but on the basis of larval characters these genera appear to have affinities with the Platyxanthidae. The xanthids *Monodaeus couchi* (Couch) (Ingle 1983) and *Paramedaeus noelensis* (Ward) (Suzuki 1979) are also grouped in the Platyxanthidae. In her classification of adult Xanthidae, Guinot (1978) placed *Monodaeus* and *Paramedaeus* in the sub-family Euxanthinae Alcock, 1898. Apart from this anomaly, the larval evidence presented here appears to correspond to the classification of adult Platyxanthidae and Trapeziidae as proposed by Guinot (1978).

The status of the third stage zoea of "ASM 26 (Menippinae or Trapeziinae)," as described by Rice and Williamson (1977:52–54, fig. 27) remains uncertain; it does not have a menippid type antenna, maxillule or maxilla endopod. Martin (1984) believed that "ASM 26" was more likely to be in the Trapeziinae, but from evidence presented here it does not appear to share the characters defining group A (see Table 4).

Carpilius was placed by Martin et al. (1985) in xanthid group III. Laughlin et al. (1983) described the zoeal stages of the coral crab *Carpilius corallinus* (Herbst) and noted a number of diagnostic characters: 5 zoeal stages, the separation of the 6th abdominal somite from the telson in stage II zoea, appearance of pleopod buds in stage II, the large size of the zoea, the increased numbers of natatory setae in the maxillipeds in later stages (i.e., zoea IV with 15–16 and zoea V with 20–22 natatory setae), and the large size of the mandibles. In combination, these larval characters are interpreted by Laughlin et al. (1983) as evidence supporting the establishment of the family Carpiliidae by Guinot (1978).

Careful re-examination of other xanthoidean larval descriptions may further substantiate the classification proposed by Guinot (1978).

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ALLOPOTAMON, A NEW GENUS FOR THE FRESHWATER CRAB *POTAMON* (*POTAMONAUTES*) *TAMBELANENSIS* RATHBUN, 1905 (CRUSTACEA: DECAPODA: POTAMIDAE) FROM THE TAMBELAN ISLANDS

Peter K. L. Ng

Abstract.—The types of the poorly known potamid crab, *Potamon* (*Potamonautes*) *tambelanensis* Rathbun, 1905, are reexamined, and its systematic position clarified. The male first pleopod structure is unusually twisted, unlike any other potamid known from Southeast Asia, and warrants the establishment of a new genus, *Allopotamon*, for the species. Its affinities with allied Asiatic genera are also discussed.

Potamon (*Potamonautes*) *tambelanensis* was described from the Tambelan Islands in the Straits of Kalimantan, between Sumatra and Borneo, by Rathbun in her important revision of the world freshwater crabs in 1905. Although she provided a detailed description with figures, the drawings, especially of the male first pleopods, were too diagrammatic. In Bott's (1970b) revision of the Asian and Australian freshwater crabs, the species was mentioned only very briefly together with *Isolapotamon chaseni* (Roux, 1934). He implied that *Potamon tambelanensis* should be placed in the genus *Isolapotamon* Bott, 1968, in the family Isolapotamidae Bott, 1970a.

A reexamination of the pair of types showed, however, that Rathbun's species should be placed in a separate genus. In this paper I describe a new genus, *Allopotamon*, for *Potamon tambelanensis*. Detailed illustrations of its gonopods are provided and its affinities with related taxa are discussed. Types are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. The abbreviations G1 and G2 are used for the male first and second pleopods, respectively. Measurements are of the carapace breadth and length, respectively.

Allopotamon, new genus

Diagnosis.—Carapace quadrilateral, gastric and branchial regions distinctly inflated, dorsal surface strongly convex. Exopod of third maxilliped with long flagellum. G1 relatively stout, strongly twisted, terminal segment distinctly demarcated from subterminal, tip pectinated, slightly truncate, pointing towards sternum, dorsal fold dilated. G2 with long flagellum, about half length of basal segment.

Type species.—*Potamon* (*Potamonautes*) *tambelanensis* Rathbun, 1905.

Etymology.—The name is derived from the Greek "allos" for 'the other,' and "Potamon," the type genus of the family. The gender is neuter.

Allopotamon tambelanense
(Rathbun, 1905), new combination
Figs. 1, 2

Potamon (*Potamonautes*) *tambelanensis* Rathbun, 1905:182–183, pl. 15 fig. 4, fig. 46.

Potamon (*Potamon*) *tambelanensis* Bott, 1970b:191.

Diagnosis.—As for the genus.

Description.—Only a few points need to

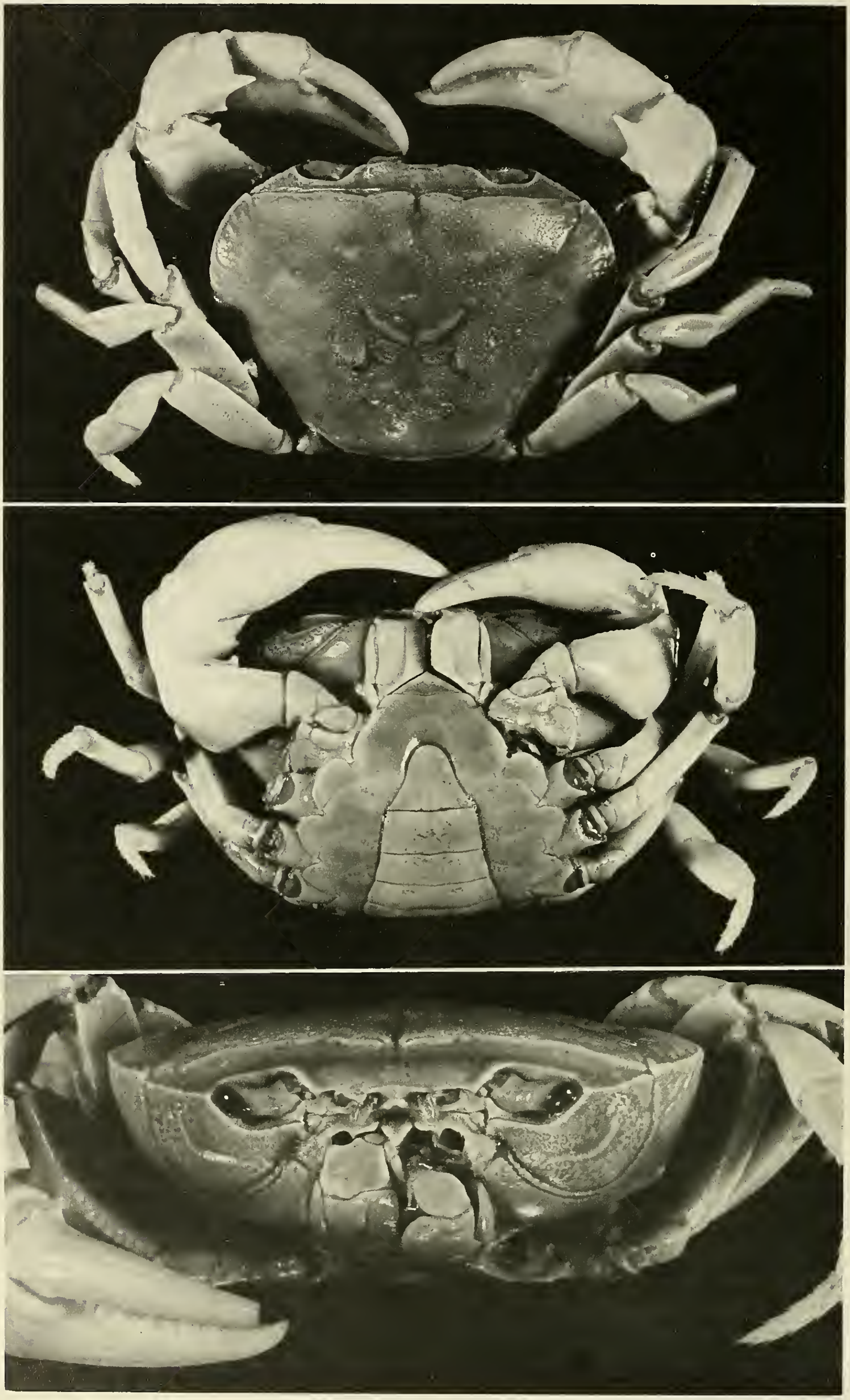

Fig. 1. *Allopotamon tambelanense,* holotype male.

be added to supplement Rathbun's (1905) excellent description of the species. The posterior margin of the epistome is produced in three lobes; the median one is triangular, and delimited from the others by well developed sutures; the openings for the efferent branchial channels are concave. The G1 is relatively stout and appears twisted. The terminal segment is distinctly demarcated from the subterminal; the dorsal lobe is dilated laterally, appearing swollen, ventrolateral margin distal to the swollen area bears numerous short hairs, the distal part is slender, tapered, and the slightly truncate tip, pectinate. The subterminal segment appears to be 2-segmented because of severe twisting, with the midlateral margin cleft, the proximal region of the distal part is strongly depressed. The flagellum of the G2 is long, about half the length of the basal segment, the latter is relatively straight, the tip of which is expanded into a cup-like structure, the proximal part of the basal segment is broadly dilated.

Material.—Holotype male (35.5 by 26.7 mm), paratype female (40.6 by 30.4 mm), USNM 23369, Big Tambelan Island (Pulau Tambelan Besar), South China Sea, Straits of Kalimantan, ca. 1°00′00″N, 107°33′26″E, leg. W. S. Abbott, 8–11 Aug 1899.

Remarks.—*Allopotamon tambelanense* can be distinguished easily from all other potamids by its swollen carapace and characteristically twisted G1. The G1 structure of *A. tambelanense* is like no other presently known potamid from Southeast Asia, and warrants the establishment of a new genus for the species. The severity of the twisting, especially in the median region, resembles that in the genus *Candidiopotamon* Bott, 1967, especially that of *C. rathbunae* (De Man, 1914) from the Republic of China (Formosa, Taiwan) and *C. okinawaense* Minei, 1973, from Okinawa, Japan. Direct comparisons of the G1s of *C. rathbuni* and *A. tambelanense* show however, that the terminal segment of *A. tambelanense* is very different, being more conical, and the tip dilated. The carapace of *Candidiopotamon* is flatter, more nearly square, and the male abdomen is much more quadrate than are their respective structures in *A. tambelanense*.

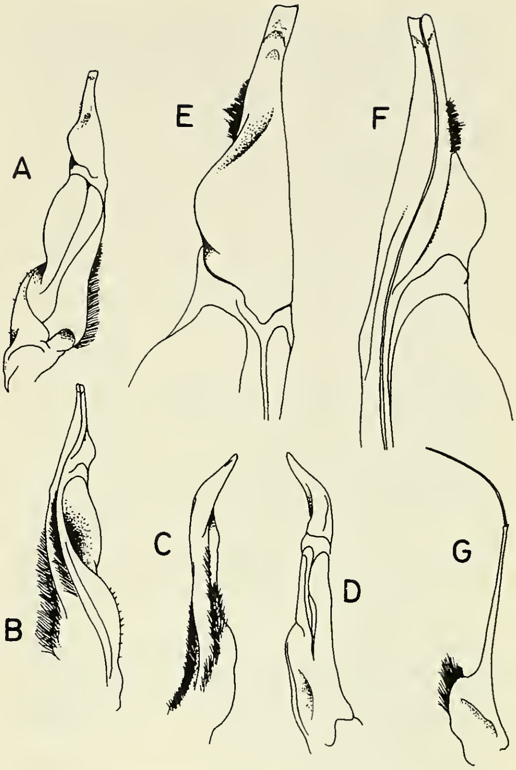

Fig. 2. *Allopotamon tambelanense,* holotype male. A–F, Left G1; G, Left G2; A, Dorsal view; B, Ventral view; C, Mesial (upper marginal) view; D, Mantel (lower marginal) view; E, Terminal segment (dorsal view); F, Terminal segment (ventral view).

Bott (1970b), in transferring *Potamon* (*Potamiscus*) *chaseni* Roux, 1934, to the genus *Isolapotamon* and family Isolapotamidae, commented that "... In diese Verwandtschaft gehort vermutlich auch *Potamon* (*Potamon*) *tambelanensis* Rathbun 1904 ... von der Insel Tambelan zwischen Boreno und Singapore" (p. 191). Although he implied a relationship with the genus *Isolapotamon,* he did not formally classify Rathbun's species with any known genus. In the general structure of the carapace, shape of the male abdomen, and presence of a distinct flagellum on the exopod of the third maxillipeds *Allopotamon* resembles *Isolapotamon,* but their G1s argue for the separation of the two taxa. The G1s of *Isolapotamon,* in sharp contrast to those of *Allopotamon,* are very long and slender, the terminal segment very elongate, being almost as long as the subterminal. Most of the *Isolapotamon* species also have flatter carapaces. Possessing a very different G1 and lacking a flagellum on the exopod of the third maxilliped, *Potamon chaseni* also cannot be retained in the genus *Isolapotamon* as currently defined (Ng 1986a, 1987b), but should instead be transferred to the genus *Stoliczia* Bott, 1966, s.s. (Ng, 1988). Although Bott (1970b) established a new family for the genus *Isolapotamon* and its kin, Ng & Yang (1985, 1986) and Ng (1986a, 1987b) regarded the differences between the Isolapotamidae and Potamidae s.s. as too minor to justify two separate families. They synonymized the two families, with the Potamidae having seniority, and this classification is adopted herein.

Bott (1970b) gave the date of Rathbun's species as 1904, but it should be 1905. Rathbun's classic monograph on the freshwater crabs was originally intended for publication as one volume, but eventually came out in three consecutive volumes, each with the same title but different dates of publication (1904 to 1906). They should thus be treated as separate publications (Schmitt 1973). *Potamon tambelanensis* was described in the second volume (7), published in 1905.

Although Bott (1970b) dismissed the value of the exopod flagellum of the third maxilliped in the classification of freshwater crabs, there has been some revival in its use (Rodriguez 1982, Ng & Yang 1985, Ng 1985, 1987a). With regards to the Southeast Asian potamid freshwater crab fauna, only the genera *Isolapotamon, Ranguna* Bott, 1968 s.s., *Johora* Bott, 1968, sensu Ng, 1987a, and *Terrapotamon* Ng, 1986b) (partim), have a distinct flagellum. The genus *Ranguna,* as defined by Bott (1970b), contained taxa from peninsular Malaysia, but Ng (1987a, 1988) revised it, restricting *Ranguna* to species found north of the Kra of Isthmus (ca. 8°N). The G1s of these genera however, are very different from those of *Allopotamon.* The G1 terminal segment of *Allopotamon* resembles that of many *Ranguna* species, but in *Allopotamon,* it is stouter, and the subterminal segment is stout and twisted. The general shape of the G1 resembles that of *Terrapotamon,* but in this genus, neither the terminal nor the subterminal segments are as complex. The carapace of *Allopotamon* is quite close to that of *Terrapotamon,* being inflated, probably associated with their semiterrestrial habits. The male abdomen of *Terrapotamon* however, is more distinctly triangular, and the flagellum on the exopod of the third maxillipeds is either short as in *T. aipooae* Ng, 1986b, or vestigial as in *T. abbotti* (Rathbun, 1898) (fide Ng 1986b, 1988).

The Tambelan Islands are 140 km west of Borneo and 280 km east of the Riau Archipelago, and in all likelihood, the prolonged isolation of these islands accounts for the unusual G1 structure of *A. tambelanense.* The montane habitat of the crab (preferred by most potamids) would probably also serve to isolate the taxon further (Ng 1985, 1987a).

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THE STATUS OF *CRYPTOCHIRUS HONGKONGENSIS* SHEN, 1936 (BRACHYURA: CRYPTOCHIRIDAE)

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Abstract.—Morphological differences in the extent of the inner orbital angle, the length of the dactylus of the claw, and the shape of the abdomen are presented which support the removal of *Pseudocryptochirus viridis* Hiro from the synonymy of *Cryptochirus hongkongensis* Shen. This evidence also indicates that *C. hongkongensis* should be transferred to *Neotroglocarcinus* and considered a subjective senior synonym of *N. monodi* Fize and Serène.

In a short paper, Shen (1936) described two new species of the coral gall crab genus *Cryptochirus*. One of these, *C. granulatus*, was synonymized with *C. crescentus* Edmondson, 1925 [now *Opecarcinus crescentus*, see Kropp & Manning (1987)] by Utinomi (= Hiro, 1944), an action followed by all subsequent authors. The status of *C. granulatus* is under review and will be discussed in a subsequent manuscript on the genus *Opecarcinus* in the Indo-Pacific.

The second species described by Shen was *C. hongkongensis*. Utinomi (1944) transferred it to his genus *Pseudocryptochirus* as a subjective senior synonym of *P. viridis* Hiro, 1938, but erred by continuing to use the latter as the valid name for the taxon. This mistake was followed by Fize & Serène (1957), but corrected by Takeda & Tamura (1981). Both of the major works on Indo-West Pacific gall crabs published since Utinomi have upheld the synonymy (Fize & Serène 1957, Takeda & Tamura 1981). Both noted apparent discrepancies between Shen's account and the morphology of *P. viridis*, but neither disputed the synonymy of the two.

Here, I discuss the discrepancies mentioned by Fize and Serène and Takeda and Tamura and present additional evidence supporting the dissolution of the synonymy between *P. viridis* and *C. hongkongensis*. Furthermore, I argue that *C. hongkongensis* is a subjective senior synonym of *Troglocarcinus monodi* Fize & Serène (1955), the type species of *Neotroglocarcinus* Fize & Serène (1957).

Types

I have not been able to locate the holotype of *Cryptochirus hongkongensis* Shen, 1936. Contrary to the assertion of Fize & Serène (1957:59), it is probably not in the British Museum (Natural History), London (BMNH). Dr. Raymond B. Manning (Smithsonian Institution, Washington, D.C.), in 1984 and 1987, examined the gall crab collection in the British Museum and did not see any types for the species although he did find the holotype of *C. granulatus*. Shen (1936) did not report the disposition of the holotype of *C. hongkongensis*. Although relatively crude, his figures and description do provide enough information by which comparisons to other species can be made. The types for *Neotroglocarcinus monodi* (Fize & Serène, 1955) are also not available, however material identified by Serène is available from the BMNH and the Muséum National d'Histoire Naturelle, Paris (MNHN). Additional material examined was collected by the author in Micronesia (HAP and PHAP denote my collection numbers) and is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

A series of morphological features that were easily interpreted was selected from the figures and description of *C. hongkongensis* published by Shen (1936). This series was compared among the species in question. As the description of Shen's species is based on a male, only males were used in the comparisons. The results are presented below in the form of brief comparative diagnoses, based on males only, for each species. I have reproduced Shen's figures of *C. hongkongensis* and provided comparative figures of *P. viridis* and *N. monodi.* Abbreviations used in the text are: km, kilometers; m, meters; ov, ovigerous; P, pereopod. Size ranges of material examined are given in millimeters as carapace length (cl) × width.

At the first occurrence in the text of collection localities in the Caroline Islands, locality names are given as the new orthographic spelling (Motteler 1986) followed parenthetically by the former spelling.

Pseudocryptochirus viridis Hiro, 1938
Figs. 1a–c, 2a–d

Material.—Viet Nam: Nhatrang (12°14′N, 109°12′E), Rocher Noir, Rte. 1643, on *Turbinaria* sp., 1 ♀ (ov), 1 ♂, BMNH. Guam: Toguan Bay (13°17′N, 144°39′E), reef front south of river channel, 6 m, 27 May 1984, HAP 229, on *T. stellulata* (Lamarck, 1816), 1 ♀ (ov), 1 ♂; USNM; Cocos Lagoon (13°14′N, 144°39′E), southwest corner of lagoon just inside barrier reef, 1 m, 6 Mar, 3 Oct 1984, HAP 155, 272, on *Turbinaria stellulata,* 3 ♀ (2 ov), 1 ♂, USNM. Belau (Palau): Ngeruktabel (Urukthapel) Is. (07°15′N, 134°24′E), north shore, west end of rock islands, 2 m, 22 Jul 1984, PHAP 166, on *T. reniformis* Bernard, 1896, 2 ♀ (ov), USNM. Same locality: 2 m, 23 Jul 1984, PHAP 193, 199, on *T.* cf. *patula* (Dana, 1846), *T. reniformis,* 3 ♀ (2 ov), USNM. Pohnpei (Ponape): Main lagoon, inside barrier reef about 1.6 km north of Main Passage (07°00′N, 158°13′E), 2 m, 14 Nov 1984, PHAP 244, on *T.* cf. *mesenterina* (Lamarck, 1816), 1 ♀ (ov), 2 ♂, USNM. Ant Atoll (06°47′N, 147°58′E), reef front off Imwinyap Is., 100 m west of pass, 8 m, 17 Nov 1984, PHAP 284, on *T. reniformis,* 1 ♀, 1 ♂, USNM.

Size ranges.—Females, 1.8 × 1.6 to 3.3 × 2.8; smallest ovigerous female, 1.8 × 1.6; males, 1.6 × 1.3 to 2.1 × 1.8.

Diagnosis.—Anterior third of carapace slightly depressed, not sharply set off from posterior carapace, latter lacking grooves or depressions; internal orbital angle greatly exceeding anterolateral angle of carapace. Basal segment of antennule with mesial margin straight, dorsal surface with longitudinal row of spines near mesial margin. Width of abdominal somite 6 about ½ that of somite 3. Dactylus of cheliped (P-1) longer than dorsal margin of palm, latter with spines along entire length. Propodus of P-3 about 1.4 times longer than high, dorsal margin with tubercles. Gonopod tapering sharply, mesial and lateral margins with plumose setae originating just proximal to midlength.

Neotroglocarcinus monodi (Fize & Serène, 1955)
Figs. 1g–i, 2i–l

Material.—Viet Nam: Nhatrang, Rte. 1590, on *T. peltata* (Esper, 1797), 1 ♀ (ov), 1 ♂, MNHN. Bai Miew, 11 Apr 1956, Rte. 1637, on *T. peltata,* 1 ♂, BMNH. Rocher Noir, 8 May 1956, Rte. 1643, on *T. peltata,* 1 ♀ (ov), BMNH.

Size ranges.—Females, 3.2 × 2.7 to 4.6 × 4.1; smallest ovigerous female, 3.2 × 2.7; males, 3.2 × 2.9 to 3.8 × 3.4.

Diagnosis.—Anterior third of carapace markedly depressed, sharply set off from posterior carapace, latter with series of shallow, longitudinal depressions; internal orbital angle slightly exceeding anterolateral angle of carapace. Basal segment of antennule with mesial margin convex, dorsal surface with scattered tubercles, lacking longitudinal row of spines near mesial margin. Width of abdominal somite 6 about ¾ that of somite 3. Dactylus of P-1 shorter than dorsal margin of palm, latter with few tubercles proximally. Propodus of P-3 about 1.8 times longer than high, dorsal margin entire. Gonopod not tapering sharply, mesial and lateral margins with plumose setae originating at about midlength.

Cryptochirus hongkongensis Shen (1936)
Figs. 1d–f, 2e–h

From Shen (1936).

Size.—Male, 2.3 × 2.0.

Diagnosis.—Anterior third of carapace markedly depressed, sharply set off from posterior carapace, surface of latter uncertain; internal orbital angle slightly exceeding anterolateral angle of carapace. Basal segment of antennule with mesial margin convex, dorsal surface with scattered tubercles, lacking longitudinal row of spines near mesial margin. Width of abdominal somite 6 about ¾ that of somite 3. Dactylus of P-1 shorter than dorsal margin of palm, latter with few tubercles proximally. Propodus of P-3 about 1.7 times longer than high, dorsal margin entire. Gonopod tapering sharply, mesial and lateral margins with simple setae originating near or distal to midlength.

Discussion

From the above comparisons and the figures provided, it is clear that *C. hongkongensis* is quite different from *P. viridis,* and further, that *C. hongkongensis* strongly resembles *N. monodi.* These relationships are most strongly supported by features such as the relative extent of the internal orbital angle compared to the anterolateral angle of the carapace, the relative demarcation between the anterior and posterior parts of the carapace, the relative length of the dactylus of the P-1, and the shape of the abdomen as indicated by the relative widths of somite 3 and 6.

Some evidence is equivocal. Setation on the dorsal margins of the walking legs (Fig. 2) allies *C. hongkongensis* more closely to *P. viridis* than to *T. monodi.* However, I have noticed that setation can be variable within gall crab species. Also, setules on walking leg setae are often difficult to see and may have been missed by Shen. The gonopod figured by Shen is problematic. It tapers, as does the gonopod of *P. viridis.* Yet, the setation differs between the two, both in type (plumose in *P. viridis,* simple in *C. hongkongensis*) and position of origin (proximal to midlength in *P. viridis,* midlength or just distal in *C. hongkongensis*). Shen may have erred in figuring the gonopod. Shen's figures and descriptions of the mouthparts and antenna of *C. hongkongensis* are too general to be of use in resolving the affinities of each taxon.

The evidence presented by Utinomi (1944) for synonymizing *P. viridis* with *C. hongkongensis* is weak. He noted (p. 702) the antennule of "*hongkongensis* seems akin to *viridis*" and (p. 703) the third maxilliped of *hongkongensis* "shows close similarity to that of *viridis.*" He further argued (p. 725) that the probable identity of the two was supported by "distributional evidences that both forms have been recorded together from neighboring seas."

Fize & Serène (1957:142) noted in particular the differences in the relative extent of the internal orbital angle and the relative length of the dactylus of the P-1 among the three taxa that I have mentioned. However, they did not ally *C. hongkongensis* with *T. monodi,* stating that Shen described the carapace as having "petites épines," a feature they attribute to *P. viridis,* not *T. monodi.* This is not true. Shen (p. 23) describes the carapace as "finely granulate," not as having spinules.

Takeda & Tamura (1981:16) noted the same two discrepancies mentioned above and the relative demarcation between the

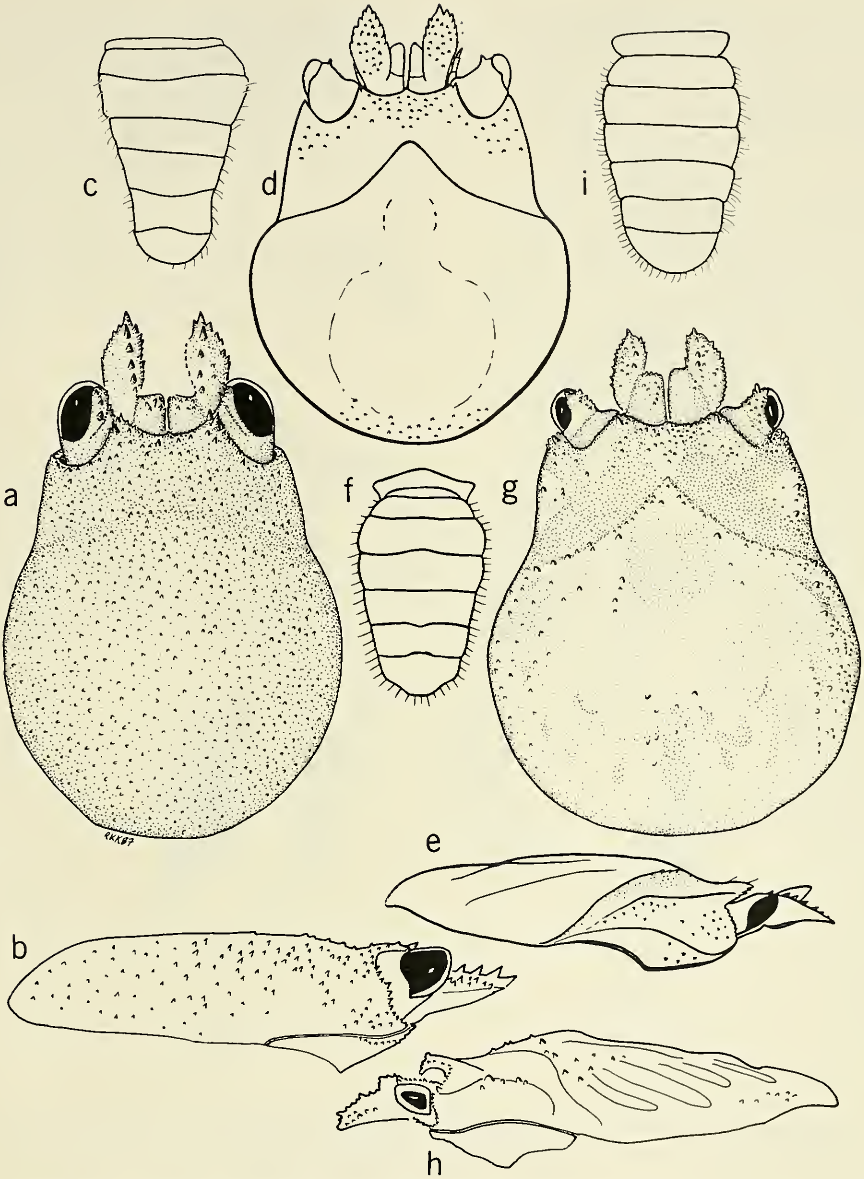

Fig. 1. Dorsal, lateral views of carapace, and abdomen: a–c, *Pseudocryptochirus viridis*, Pohnpei, USNM, cl = 1.9 mm; d–f, *Cryptochirus hongkongensis*, from Shen (1936), cl = 2.3 mm; g–i, *Neotroglocarcinus monodi*, Viet Nam, MNHN B-18762, cl = 3.8 mm. All males. Not to scale.

anterior and posterior carapace regions. They declared that these differences are "too small" to warrant separation of the two species; I disagree. Differences of the magnitude presented here are enough to separate species of gall crabs.

The evidence presented here supports the restoration of *Pseudocryptochirus viridis* Hiro to valid status. This evidence further indicates that *Cryptochirus hongkongensis* Shen is a subjective senior syyonym of *Troglocarcinus monodi* Fize & Serène, the

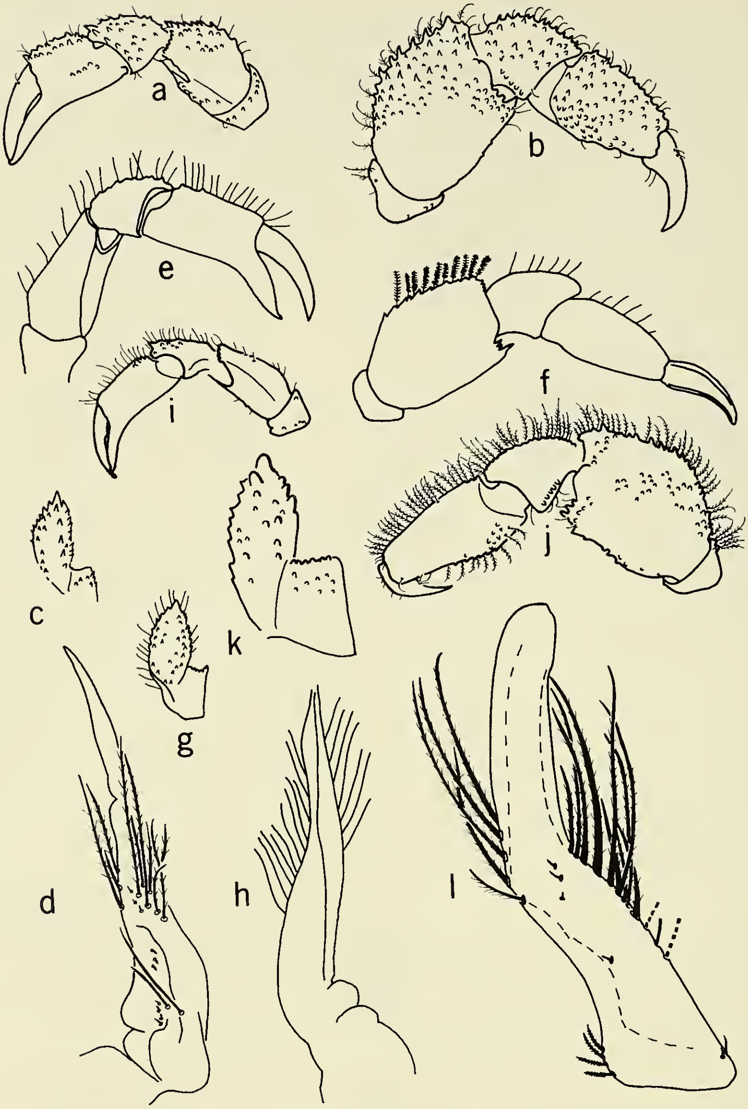

Fig. 2. Pereopods 1 and 3, antennule, and gonpod: a–d, *Pseudocryptochirus viridis,* USNM; e–h, *Cryptochirus hongkongensis,* from Shen (1936); i–l, *Neotroglocarcinus monodi,* MNHN B-18762. All males. Not to scale.

type species of *Neotroglocarcinus* Fize & Serène. Shen's species should now be known as *Neotroglocarcinus hongkongensis* (Shen).

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THE STATUS OF *CRYPTOCHIRUS CORALLIODYTES* HELLER AND *LITHOSCAPTUS PARADOXUS* MILNE EDWARDS (BRACHYURA: CRYPTOCHIRIDAE)

Roy K. Kropp

Abstract.—The types of *Cryptochirus coralliodytes* Heller and *Lithoscaptus paradoxus* Milne Edwards were examined and found to differ in sculpture of the carapace, the epistome, and relative lengths of the carpus and merus of the fifth pereopod among other features. Therefore, the latter is removed from the synonymy of the former. The type of *Cryptochirus rugosus* Edmondson was examined and found to be indistinguishable from *C. coralliodytes*; thus, *C. rugosus* is placed in synonymy with *C. coralliodytes*. The available data suggest that *Cryptochirus bani* Fize & Serène is synonymous with *L. paradoxus*. Lectotypes are designated for *C. coralliodytes* and *L. paradoxus* and are described and figured.

Two years after the description of the first known coral gall crab, *Hapalocarcinus marsupialis* Stimpson, 1859, the second recorded species, *Cryptochirus coralliodytes,* was described by Heller (1861a:19). Milne Edwards (1862:F10) followed this with the description of a third species, *Lithoscaptus paradoxus.* All three species were rather incompletely described, probably because they were reasonably different from most other brachyurans known at the time. Although this inadequacy has not been a problem for the first species it has resulted in some misunderstanding regarding the latter two species.

The problem regarding the identities of *C. coralliodytes* and *L. paradoxus* can be traced to the failure of authors to examine type specimens or to carefully consider information provided in the original descriptions that should have been useful in separating the two species. Paulson (1875) was the first to place the two in synonymy, but did so by erroneously considering *L. paradoxus* a senior synonym of *C. coralliodytes.* He did not justify his action. Richters (1880) agreed, but did correct the order of synonymy. Rathbun (1897) also noted Paulson's error. After Calman (1900) followed Paulson's action, all authors up until the review of the family of Fize & Serène (1957) attributed the synonymy of the two species to Paulson and/or Calman without question or examination of the types (e.g., Edmondson 1933, Shen 1936, Utinomi 1944). Fize & Serène (1957) discussed *Cryptochirus* in detail and examined the syntypes of *Lithoscaptus* and *Cryptochirus* that are in the collection of the Muséum National d'Histoire Naturelle, Paris. In spite of doing so, they upheld the synonymy of the two species. More recently, Takeda & Tamura (1980) reviewed *Cryptochirus,* but did not alter the status of the two species.

I examined the syntypes of *C. coralliodytes* and *L. paradoxus* and determined that they are not synonymous. Herein I designate lectotypes for each species and conclude that Heller's species is a subjective senior synonym of *Cryptochirus rugosus* Edmondson, 1933. Because *C. rugosus* is the type species of the genus *Favicola* Fize &

Serène, 1957, the latter should now be considered a subjective junior synonym of *Cryptochirus* Heller, 1861.

Materials and Methods

I examined the male and female syntypes of *Cryptochirus coralliodytes* Heller housed in the Muséum National d'Histoire Naturelle, Paris (MNHN) and Naturhistorisches Museum, Vienna (NMW), respectively; the syntypes of *Lithoscaptus paradoxus* Milne Edwards in the MNHN; and the holotype of *Cryptochirus rugosus* Edmondson held in the B. P. Bishop Museum, Honolulu (BPBM). Additional material examined came from the BPBM and my own collections (denoted as HAP and PHAP) made in Micronesia in 1984. The Micronesian material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Place names for collection sites in the Caroline Islands are from Bryan (1971). At the first occurrence in the text of each locality, the new orthographic spelling (Motteler 1986) is given followed parenthetically by the former spelling. Subsequently, only the new spelling is used.

Some of the Micronesian material was used in the preparation of the figures and for study by Scanning Electron Microscopy (SEM). In preparation for SEM, specimens were dissected and cleaned by gentle mechanical agitation, and brushing with a fine paint brush. Specimens were then transferred to 100% ethanol via a graded series and air-dried overnight. Dried specimens were mounted on stubs and sputter-coated with gold-palladium and viewed with a Cambridge Stereoscan-100 microscope at an accelerating voltage of 10 kv.

Drawings were made with a camera lucida mounted on a Wild M-5 microscope. The cheliped was drawn so that the outer surface of the manus is in the plane of the printed page. This distorts the relative proportions of the other segments, particularly the merus. Male pleopods were prepared for illustration by lactic acid digestion and staining using methods described in Kropp & Manning (1987), except acid fuchsin was substituted for fast green.

The carapace length and width of each specimen were measured to the nearest 0.1 mm with an ocular micrometer on a Wild M-5 microscope and are reported in mm as length × width. Abbreviations used in the text are: m, meters; MXP, maxilliped; ov, ovigerous; P, pereopod; PLP, pleopod; and TL, type locality.

In the systematic account, I have restricted the generic synonymies to the original usage of a name for each taxon. For each nominal species the type locality and the location of the type specimen are included.

Systematic Account

Cryptochirus Heller, 1861

Cryptochirus Heller, 1861a:19 [type species: *Cryptochirus coralliodytes* Heller, 1861a: 19 by monotypy; gender masculine].

Favicola Fize & Serène, 1957:84 [type species: *Cryptochirus rugosus* Edmondson, 1933:6; subsequent designation by Serène (1966:396); gender masculine (see Remarks)].

Remarks.—The International Code of Zoological Nomenclature (ICZN, 1985) specifies that a genus-group name ending in a noun of variable gender, such as *-icola,* should be treated as masculine unless its author specifies that it is feminine or treats it as feminine by the use of feminine species-group names [Article 30 (a) (i)]. Serène (1966) was the first to use *Favicola* as a distinct generic name and did so with masculine species-group names. Therefore, the gender of *Favicola* is masculine.

Cryptochirus coralliodytes Heller

Figs. 1–3

Cryptochirus coralliodytes Heller, 1861a:19 [TL: Red Sea; lectotype NMW, paralectotype MNHN]; 1861b:370, pl. IV, figs. 33–39.

Cryptochirus corralliodytes Heller, 1861a:19 [incorrect original spelling].

Cryptochirus rugosus Edmondson, 1933:6, fig. 1, pl. 1 [TL: Line Islands, Teraina [= Washington Island]; holotype BPBM S3668].

Types.—Two syntypes of *C. coralliodytes* are extant. The female syntype is ovigerous, 6.6 × 4.5 mm, in NMW. It is herein designated the lectotype. The specimen is disarticulated, with the carapace being detached from the thorax which is missing. The right P-3 to P-5, mouthparts, antennae, and antennules are missing. The abdomen is detached, in poor condition, some pleopods are present. The male syntype, 5.0 × 3.0 mm, is in good condition having all pereopods, mouthparts, and pleopods present. It is in MNHN and is herein designated the paralectotype. I examined the holotype of *C. rugosus* at the BPBM in 1984, but have not been able to re-examine it as it is now missing (B. Burch, pers. comm. to R. B. Manning, 1987). It is a female and agrees with the lectotype of *C. coralliodytes.*

Material examined.—Red Sea [no specific locality]: lectotype, ♀, 6.6 × 4.5, (NMW); paralectotype, ♂, 5.0 × 3.0, (MNHN 198-63). Caroline Islands: Belau (Palau): Ngerekebesang (Arakabesan) Is. [07°21′N, 134°27′E], north side of cove on west side of island, PHAP 078, 4 m, 7 Jul 1984, on *Platygyra lamellina* (Ehrenberg, 1834), 2 ♀ (1 ov), 1 ♂. Pohnpei (Ponape): Sokehs Passage [07°00′N, 158°11′E], patch reef bordering west side of reef, PHAP 270, 2 m, 16 Nov 1984, on *P. daedalea* Ellis & Solander, 1786, 2 ♀. Mariana Islands: Guam: Double Reef [13°36′N, 144°50′E]; shoreward side of main patch reef, HAP 125, 9 m, 24 Feb 1984, on *Platygyra* sp., 1 ♀, 1 ♂. Line Islands: Teraina (=Washington Is.) [04°43′N, 160°24′W], 1 ♀ (BPBM S3668, holotype of *Cryptochirus rugosus* Edmondson).

Description.—Lectotype female (Figs. 1, 2), except mouthparts, antenna, antennule, and epistome (based on material from Micronesia). Carapace about 1.5 times longer than broad, widest near midlength. Anterior carapace with inverted V-shaped depression, anterior gastric region slightly inflated; midcarapace with clusters of prominent, rounded tubercles on posterior gastric, anterior and posterior epigastric regions; posterior surface with scattered pointed and rounded tubercles. Regions of posterior half of carapace set off by series of well-formed grooves, epigastric region divided into anterior, posterior parts by distinct groove. Anterolateral margin of carapace spinous.

Anterolateral angle of carapace with single tubercle, apex exceeding inner orbital angle, latter swollen, with tubercle. Front concave, with few tubercules just behind margin; width about ½ that at anterolateral angles, latter about 2/5 greatest carapace width. Orbit deeply V-shaped.

Epistome with subparallel longitudinal ridges laterally, median area produced anteriorly into longitudinal ridge subequal in thickness to lateral ridges; anterior margin with few tubercles, slightly sinuous, with scant median indentation.

Basal segment of antennular peduncle with elliptical projection extending beyond length of eyestalk, apex spine-tipped, no angled lateral lobe. Dorsal surface flat, with few pointed tubercles. Mesial margin spinous. Ventral surface of second antennal segment with scattered granules, distal margin toroidal (Fig. 2c).

Eye directed anterolaterally, extending beyond anterolateral angle; cornea subterminal, occupying distal third of stalk in dorsal view. Stalk mostly exposed, broadening proximally; ventral surface with few granules.

MXP-3 with exopod, mesial margin of ischium convex; outer surface with distally-raised granules. Merus longer than broad, width less than half that of ischium. Carpus shorter than length of propodus and dactylus combined.

Endopod of MXP-1 triangular, mesial

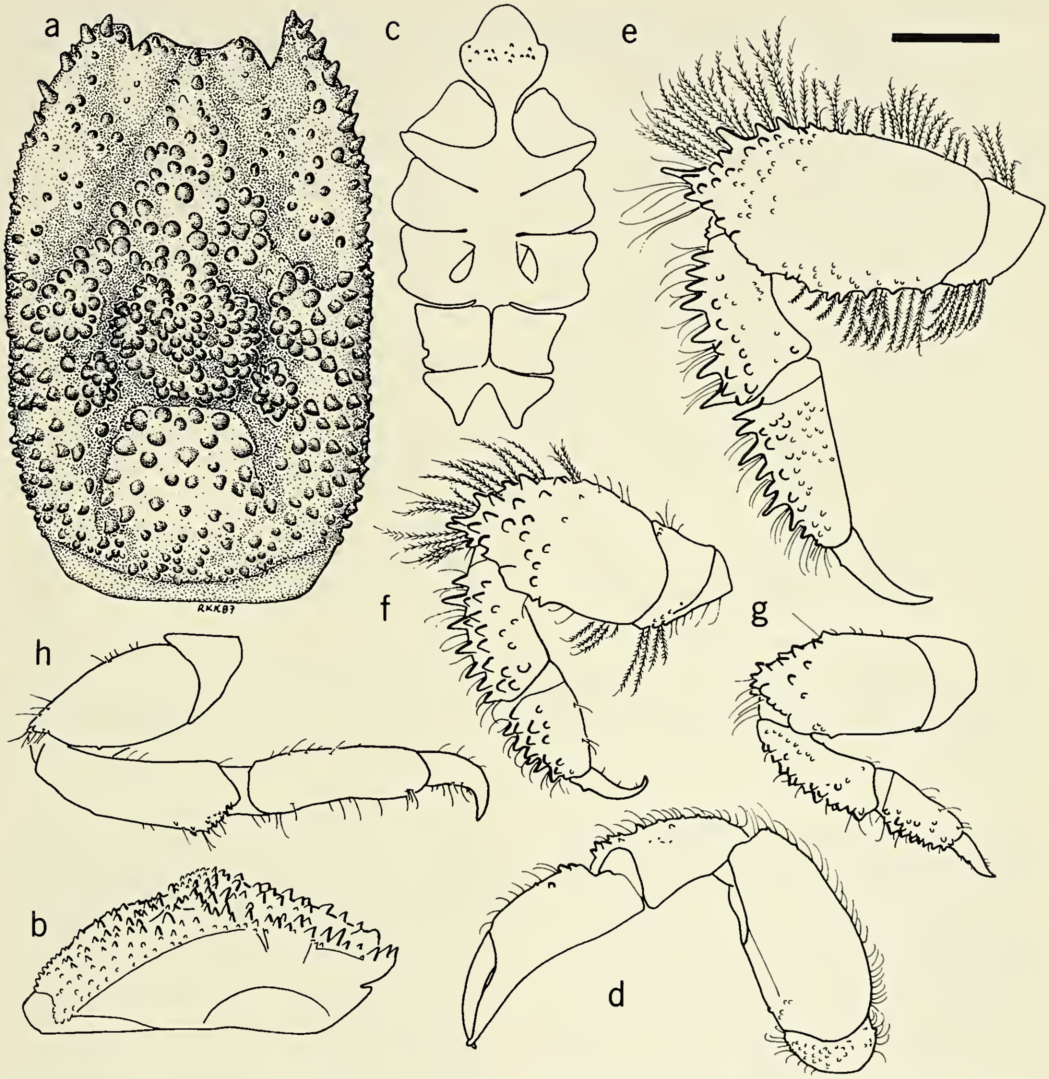

Fig. 1. *Cryptochirus coralliodytes,* ♀ (a, b, d–h from lectotype, c from Guam ♀, USNM): a, Carapace (dorsal view); b, Carapace (lateral view); c, Thoracic sternites; d–h, P-1 to P-5. Scale: a = 0.8 mm; b = 2.1 mm; c–h = 1 mm. [Setae on surface of carapace and pereopods not shown.]

margin about ⅔ length of lateral margin, anterior margin with sharp curve occurring mesially, lined with stout simple setae.

Chelipeds (P-1) with few scattered simple, pappose setae on upper margins. Dactylus longer than dorsal margin of palm, cutting edges of fingers entire. Dorsal margin of palm entire, outer and upper surfaces with few granules proximally. Manus slightly smaller than merus.

Dorsal margin of merus of P-2 with spines distally, fringed with pappose setae of length >2 times that of spines; outer surface flat, with granules dorsodistally, ventrally; ventral margin relatively straight, with few tubercles, fringed with pappose setae; ven-

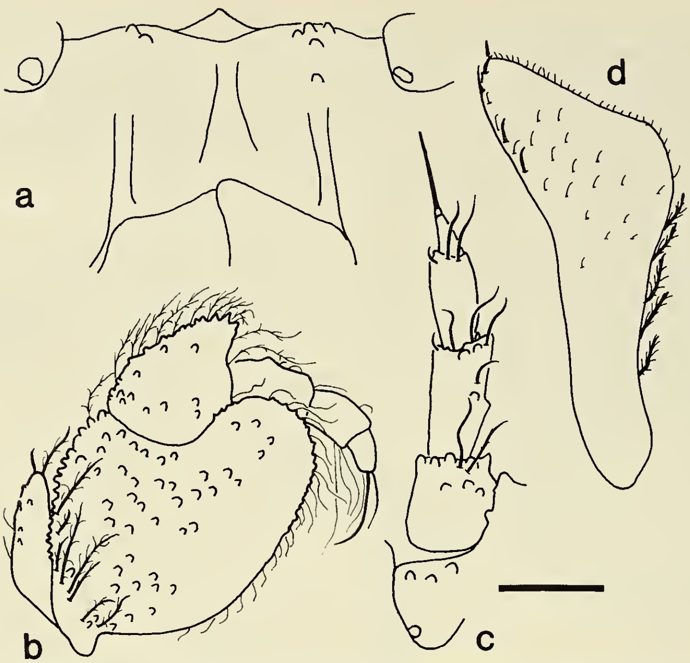

Fig. 2. *Cryptochirus coralliodytes,* ♀ (Guam, from SEM micrographs): a, Epistome; b, MXP-3 (outer view); c, Antenna (ventral view); d, Endopod of MXP-1 (outer view). Scale: a = 0.3 mm; b = 0.5 mm; c, d = 0.2 mm.

trodistal angle with prominent tubercles (tubercles worn on lectotype). Merus height <2 times that of carpus. Dorsal margins of carpus and propodus with robust spines, simple setae; outer surfaces with tubercles dorsally, ventrally; carpus subequal in length to propodus. Dactylus with proximal tooth dorsally; tip with subterminal pore. P-3, P-4 similar in form to P-2, stockier, P-4 less setose. P-5 elongate, smooth; carpus longer than other segments; propodus, dactylus directed anteriorly.

Sternite of P-1 with few granules, that of P-4 with median suture. Female opening longitudinal, oval, with hood; PLP-2 biramous, PLP-3 uniramous.

Variations.—May have spines instead of tubercles at inner orbital angles, anterolateral angles, and on anterior surface of carapace. Spines vary as to number and sharpness. The width and depth of the grooves on the carapace varies considerably. The dactylus of P-2 may be missing. Smaller females may have a deeper depression on the anterior carapace, may be less spiny, and have a more elongate projection of the antennule base than larger females. The carapace length : width ratio ranged from 1.2 to 1.7 with most crabs within 1.4 to 1.6.

Paralectotype male (Fig. 3).—Similar to, smaller than female. Carapace regions distinctly marked as female, spines, rounded tubercles less pronounced. Projection of antennule base more elongate, pointed. P-1 robust, palm inflated, with tubercles; dactylus slightly longer than dorsal margin of palm. Abdominal somites 5–7 narrower than somites 3–4; telson broadly rounded. PLP-1 reaching middle of sternite of P-1; slightly curved, apex sharply pointed, directed slightly laterally; lateral margin with stout setae.

Variations.—P-1 much less robust in proximal tooth on the dorsal surface of the smaller males, with the dactylus relatively longer than paralectotype. Regions of carapace may have fewer tubercles.

Lithoscaptus Milne Edwards, 1862

Lithoscaptus Milne Edwards, 1862:F10 [type species: *Lithoscaptus paradoxus* Milne Edwards, 1862:F10, by monotypy; gender masculine.]

Lithoscaptus paradoxus Milne Edwards
Figs. 4–6

Lithoscaptus paradoxus Milne Edwards, 1862:F10 [TL: Reunion; lectotype, MNHN].

Cryptochirus coralliodytes var. *rubrolineata* Fize & Serène, 1957:40, fig. 5D, pl. 14, figs. E–H [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus coralliodytes var. *cubrolineata*.—Fize and Serène, 1957:201 [erroneous spelling].

Cryptochirus coralliodytes var. *fusca* Fize and Serène, 1957:40, fig. 5B [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus coralliodytes var. *parvulus* Fize and Serène, 1957:40, fig. 5C [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus bani Fize and Serène, 1957: 44, figs. 5F, 6, pl. 1, fig. 7 [TL: Nhatrang, Viet-Nam; location of type unknown].

Type.—Two specimens are in the vial from the MNHN labelled *Lithoscaptus paradoxus* "TYPE." One is a nonovigerous female that is herein designated the lectotype. The carapace of this female is somewhat misshapen, but still recognizable. Both P-2 are missing, but the remaining pereopods are present as are all mouthparts. The pleopods are present and are uniramous. The second specimen is *Cryptochirus coralliodytes* Heller. Milne Edwards indicated which specimen on which he based his description by his reference to uniramous female pleopods (1862:F12). For this reason the larger female is selected as the lectotype.

Material examined.—Indian Ocean: Reunion Island [20°18′S, 57°29′E], lectotype, 1 ♀ 6.4 × 5.3 (MNHN). Pacific Ocean: Caroline Islands: Belau: Ngeruktabel Is., patch reef among rock islands on northeast shore, PHAP 045, 2 m, 2 Jul 1984, on *Goniastrea pectinata* (Ehrenberg, 1834), 2 ♀ (1 ov), 1 ♂; Mariana Islands: Guam: Luminao Reef [13°28′N, 144°39′E], reef flat toward Magundas, HAP 315, 1 m, 13 Oct 1984, on *P. daedalea*, 2 ♀ (ov), 1 ♂; Cook Islands: Rarotonga [21°14′S, 159°46′W], Ararua, Wilder and Parks, Jun-Jul 1929, [no host], 13 ♀ (ov) (BPBM S3221).

Description.—Female, based on lectotype in conjunction with a Guam female (Fig. 4, 5, USNM). Carapace about 1.2 times longer than broad, widest just posterior to midlength. Anterior carapace with broadly W-shaped depression having scattered spines; anterior gastric region slightly inflated; median gastric with 2 depressions; mid to posterior carapace with many rounded tubercles, regions of carapace not well defined; cardio-intestinal region rimmed anteriorly, laterally with depression. Anterolateral margin of carapace spinous.

Anterolateral angle of carapace with single spine, apex exceeding inner orbital angle, latter swollen, with subterminal spine. Front concave, entire, width about ½ that at anterolateral angle, latter 2/5 greatest carapace width. Orbit V-shaped.

Epistome with subparallel longitudinal ridges laterally; median area swollen, lacking ridge; anterior margin entire, straight, with scant median indentation.

Basal segment of antennular peduncle with suboval projection extending slightly beyond eyestalk, rounded distally, no angled lateral lobe; dorsal surface flat, without tubercles; entire margin with subequal spines. Ventral surface of second antennal segment with few granules, distal margin with few raised granules.

Eye directed anterolaterally, extending just

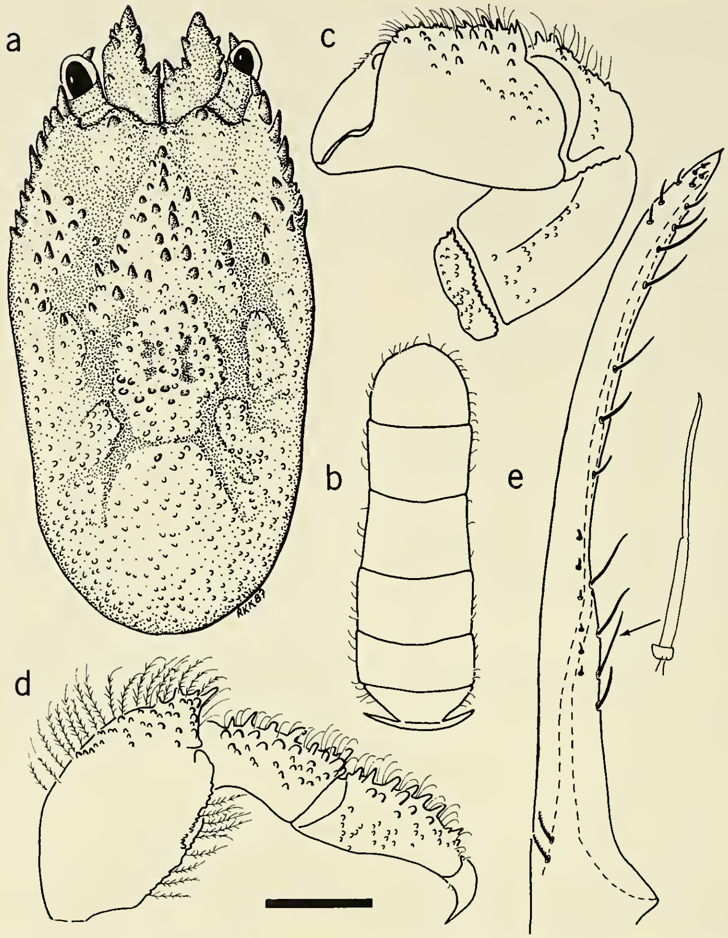

Fig. 3. *Cryptochirus coralliodytes*, ♂, (a–d from paralectotype, e from Guam ♂, USNM): a, Carapace (dorsal view); b, Abdomen; c, Left P-1; d, Right P-2; e, PLP-1 (outer view). Scale: a = 0.9 mm; b–d = 1 mm; e = 0.1 mm.

beyond anterolateral angle; cornea subterminal, occupying distal quarter of stalk dorsally. Stalk mostly exposed, not broadening proximally; ventral surface smooth.

MXP-3 with exopod, mesial margin of ischium slightly convex, outer surface with many distally-raised granules. Merus longer than broad, width less than half that of ischium. Carpus shorter than length of propodus and dactylus combined.

Endopod of MXP-1 subquadrate, mesial margin about 3/5 length of lateral margin; anterior margin with sharp median curve, lined with stout simple setae.

Chelipeds (P-1) with many scattered simple setae on upper margins. Dactylus longer than dorsal margin of palm; cutting edge with low tooth proximally. Dorsal margin of palm with few tubercles proximally, outer surface smooth. Manus much smaller than merus.

Dorsal margin of merus of P-2 with spines distally, fringed with pappose setae of length >2 times that of spines; outer surface flat, with tubercles distally; ventral margin convex, with few tubercles, fringed with pappose setae. Merus height >2 times that of carpus. Dorsal margins of carpus, propodus

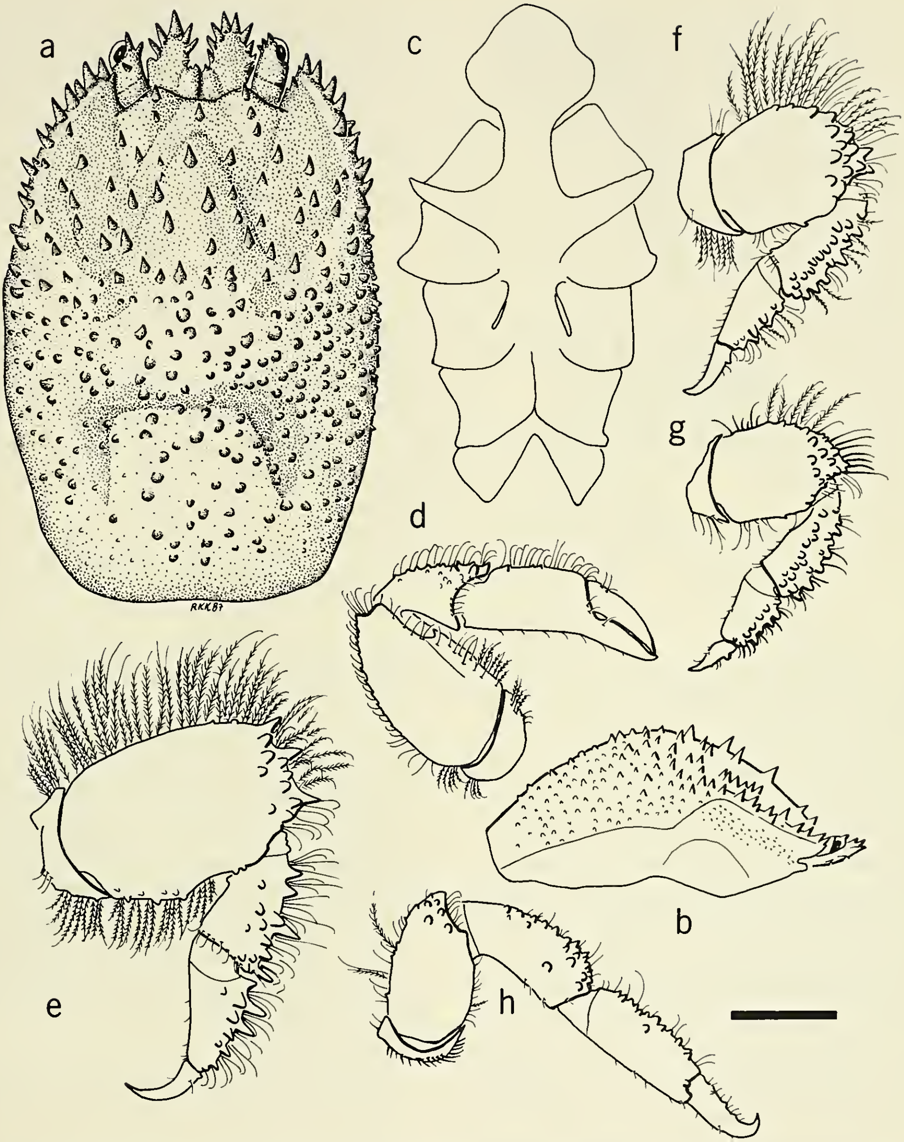

Fig. 4. *Lithoscaptus paradoxus,* ♀ (Guam, USNM): a, Carapace (dorsal view); b, Carapace (lateral view); c, Thoracic sternites; d–h, P-1 to P-5. Scale: a = 0.8 mm; b = 2.1 mm; c–h = 1 mm.

with spines, simple setae; outer surfaces with few tubercles; carpus longer than propodus. Dactylus lacking proximal tooth dorsally, tip with subterminal pore. P-3, P-4 similar in form to P-2; outer surfaces of carpi, propodi with longitudinal row of rounded tubercles near upper margins, upper margins with simple, pappose setae. P-5 elongate, with tubercles dorsally on proximal 3 segments; merus and carpus subequal in length, each longer than propodus; propodus, dactylus directed anteriorly.

Sternite of P-1 smooth, that of P-4 with median suture. Female opening longitudinal, oval, with anterior hood; PLP-2, PLP-3 uniramous.

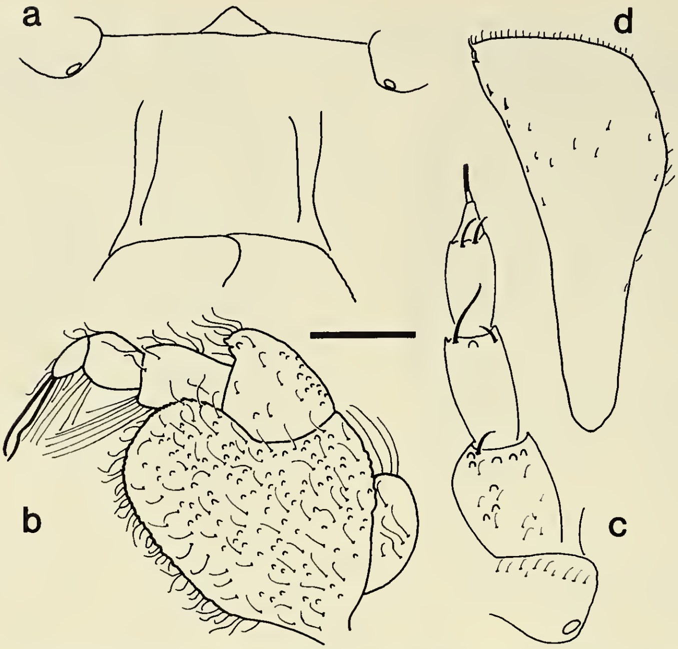

Fig. 5. *Lithoscaptus paradoxus,* ♀ (Guam, from SEM micrographs): a, Epistome; b, MXP-3 (outer view); c, Antenna (ventral view); d, Endopod of MXP-1 (outer view). Scale: a, c, d = 0.2 mm; b = 0.4 mm.

Variations.—Relative sculpture of the carapace variable, particularly the median gastric area which may have depressions from two to four in number which may vary from obvious to faintly detectable. The extent of the depression on the anterior carapace varies from occupying the entire surface between the anterolateral margins to somewhat less. The size and number of spines and/or tubercles is highly variable. The carapace length : width ratio ranged from 1.2 to 1.5 with most crabs within 1.3 to 1.4. In some specimens the lateral projection of the antennule base is more elongate than described. Also, the anterolateral angles of the carapace may extend only slightly beyond the inner orbital angles.

Male.—Based on specimens from Micronesia. Similar to, smaller than female. Carapace detail similar to females, spines proportionally smaller. Projection of antennule base elongate, with apical spine. P-1 robust, palm inflated, with few tubercles; dactylus longer than dorsal margin of palm. Abdominal somites 3–7 similar in width, telson broadly rounded. PLP-1 slightly curved, apex sharply pointed, directed slightly laterally; reaching posterior of sternite of P-1; lateral margin with stout setae.

Variations.—Smaller males have a relatively smooth carapace, with the anterior depressions more distinct. The inner orbital angle may equal or exceed anterolateral angle of the carapace.

Remarks.—The original description of *Cryptochirus bani* by Fize & Serène (1957) did not provide information necessary to distinguish it from *Lithoscaptus paradoxus.* Serène (1962), in a discussion of some material from Rarotonga sent to him by Edmondson, alluded that *C. bani* might be synonymous with *C. coralliodytes.* Serène thought that this material was very similar to *C. bani.* I have examined material from the same collection (BPBM S3221) and found them to be *L. paradoxus.* Without examination of the type of *C. bani,* there is some uncertainty, but it is likely that *C. bani* is a subjective junior synonym of *L. paradoxus.* Fize & Serène (1957) named three varieties of *C. coralliodytes* based primarily on color differences, giving no substantial morphological data by which to distinguish them. The varieties, *rubolineata, fusca,* and *parvulus* are therefore considered subjective junior synonyms of *L. paradoxus.*

Discussion

Paulson (1875) felt that many taxonomists of the period were not making useful contributions to systematics as a science, and that their research "provides only a useless ballast." He was particularly critical of Heller and A. Milne Edwards. Yet careful consideration of the original species descriptions by Heller and Milne Edwards and comparisons of those with material at hand might have prevented Paulson's confusion of *C. coralliodytes* with *L. paradoxus.* Heller's original species account (1861a:19) was scanty, but the generic description included a characterization of the endopod of the first maxilliped that is useful. This was supported by his later (1861b), more detailed, account which included an accurate figure of the appendage (1861b, pl. IV, fig. 39). The endopod of the first maxilliped is quite different in *L. paradoxus* (triangular in *coralliodytes* versus subquadrate in *paradoxus,* compare Fig. 2d and 5d herein). Heller's figure of the female type (1861b: pl. IV, fig. 33) shows enough carapace detail, despite Edmondson's (1933:4) complaint, to distinguish the two species.

Milne Edwards also gave information sufficient to separate the two species by referring to the uniramous condition of the female pleopods (1862:F12). Although female PLP-2 form is often not a reliable character (McCain & Coles 1979; Kropp & Manning 1987), in this case it is applicable because among the specimens of either species that I have examined, the PLP-2 is consistently uniramous in *L. paradoxus* and consistently biramous in *C. coralliodytes.*

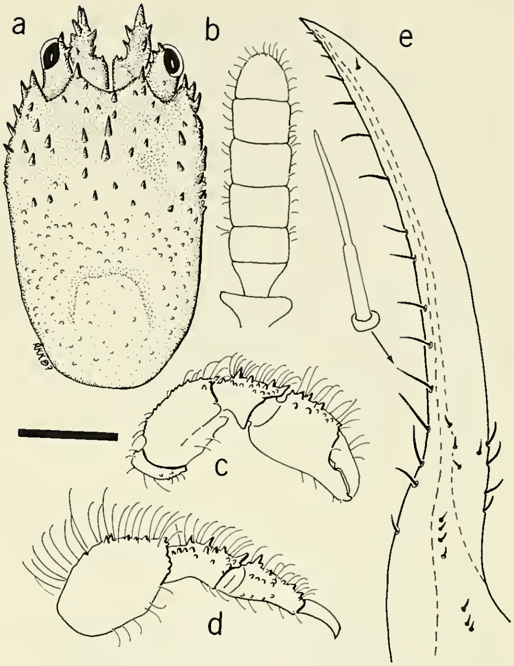

Fig. 6. *Lithoscaptus paradoxus,* ♂ (Guam, USNM): a, Carapace (dorsal view; b, Abdomen; c–d, Right P-1, P-2; e, PLP-1 (outer view). Scale: a–d = 1 mm; e = 0.1 mm.

Several features other than the above information from the original literature allow separation of the two species. The most obvious difference is that the regions of the carapace of *C. coralliodytes* are well defined whereas those of *L. paradoxus* are not. Additionally, in the former, the epistome has a median ridge, and leg P-5 is smooth, with the carpus longer than the other segments whereas there is no median epistomal ridge and leg P-5 is tuberculate dorsally, with the carpus and merus subequal in length in *L. paradoxus.* Leg P-2 permits the two species to be distinguished because the merus is larger relative to the carpus in *Lithoscaptus* than in *Cryptochirus.*

The changes made here have a bearing on the other species presently included in *Cryptochirus* and *Favicola.* I am reviewing these species and will clarify their status as a part of a revision of the genera of cryptochirids.

Acknowledgments

I am grateful to the University of Guam Marine Laboratory and the Marine Mariculture Demonstration Center for supporting my field work in Micronesia, to the Division of Crustacea (USNM) for providing support for my systematic studies, and to the SEM lab (USNM) personnel for assistance with the SEM work. Specimens used in this study were kindly provided by V. Stagl (NMW), A. Crosnier (MNHN), B. Burch (BPBM), and R. Ingle (BMNH). The corals I collected in Micronesia were identified by R. H. Randall. R. B. Manning and G. J. Vermeij reviewed the manuscript and provided encouragement. Financial support was provided in part by the University of Maryland's Department of Zoology and Graduate School and a grant to G. J. Vermeij by the Biological Oceanography Section of the National Science Foundation. This is from a dissertation to be submitted to the Graduate School, University of Maryland, in partial fulfillment of the requirements for the Ph.D. degree in Zoology and is Contribution No. 250 of the University of Guam Marine Laboratory.

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THE STATUS OF *CALLIANASSA HARTMEYERI* SCHMITT, 1935, WITH THE DESCRIPTION OF *CORALLIANASSA XUTHA* FROM THE WEST COAST OF AMERICA (CRUSTACEA, DECAPODA, THALASSINIDEA)

Raymond B. Manning

Abstract.—*Callianassa hartmeyeri* Schmitt, 1935, a species of uncertain identity, is redescribed. It proves to be a member of *Corallianassa* Manning, 1987. Specimens from the Eastern Pacific previously identified with *Callianassa hartmeyeri* or *Callianassa placida* De Man are described as a new species, *Corallianassa xutha.*

In 1924, Balss identified a callianassid from Kingston, Jamaica, with *Callianassa grandimana* (Gibbes, 1850) (as *Glypturus grandimanus*), a species then unknown since its original description. Balss' poor figures (Fig. 1) distinctly showed a species with a three-spined front, a large terminal cornea, and a major cheliped with ventral spines on the ischium and merus. Schmitt (1935:2, 3, 4), in his review of the North American callianassids, recognized that Balss's species differed from *C. grandimanus* in having ventral spines on the ischium and merus of the cheliped, and proposed the name *Callianassa hartmeyeri* for *Glypturus grandimanus* sensu Balss, 1924. *Callianassa hartmeyeri* has remained "incertae sedis" since Schmitt's account was published (see remarks in Biffar 1971:640–641, 649).

In 1938, Hult reported a specimen of *Callianassa hartmeyeri* from the Galapagos Islands, and in 1939 Schmitt reported additional material from Clipperton Island in the East Pacific. Chace (1962) studied material from Clipperton Island, identified it with *Callianassa placida* De Man, 1905, and synonymized *Glypturus grandimanus* sensu Balss, 1924, and *Callianassa hartmeyeri* Schmitt, 1935, with *C. placida.*

No additional material from the Americas identified with either *C. hartmeyeri* or *C. placida* has been reported.

In 1987 I showed that *Callianassa grandimana* Gibbes, 1850, was conspecific with the species then known as *Callianassa branneri* (Rathbun, 1900), and that *Glypturus* Stimpson, 1866, was distinct enough from *Callianassa* Leach, 1814, sensu stricto, to be recognized as a distinct genus. I also recognized a new genus *Corallianassa* for *Callianassa longiventris* A. Milne Edwards, 1870, from the Caribbean, and *C. borradalei* (De Man, 1928), from the Indo-West Pacific, and noted (p. 388) that "The identity of *Callianassa hartmeyeri* Schmitt is still uncertain."

Collection of a pair of chelipeds of a *Corallianassa* at Lake Worth Inlet, Florida, in March 1987, prompted me to try to determine the identity of *Callianassa hartmeyeri* and to determine whether it was congeneric with or conspecific with *Corallianassa longiventris* (A. Milne Edwards, 1870). The chelipeds taken at Lake Worth Inlet proved to be those of *C. longiventris.*

Through the kindness of H.-E. Gruner, Zoological Museum, Berlin, I was able to examine the type of *Callianassa hartmeyeri.* It proves to be a species of *Corallianassa* distinct from *C. longiventris* and *C. borra-*

dalei, the two species originally assigned to *Corallianassa,* from the Eastern Pacific population previously identified with *P. hartmeyeri,* and from *C. placida,* a species herein transferred to *Corallianassa,* as well. Roy Oleröd, Swedish Museum of Natural History, Stockholm, allowed me to examine Hult's specimen of *Callianassa hartmeyeri* from the Galapagos Islands; it proved to belong to the new species described below.

All measurements are in millimeters (mm). Carapace length (cl) is the postorbital carapace length; total length (tl) is measured on the midline. Specimens have been deposited in the collection of the National Museum of Natural History, Smithsonian Institution, Washington (USNM), the Swedish Museum of Natural History, Stockholm (SMNH), and the Zoological Museum, Berlin (ZMB).

Corallianassa hartmeyeri (Schmitt, 1935)

Figs. 1, 2

Glypturus grandimanus.—Balss, 1924:179, figs. 3, 4.—Schmitt, 1935:4 [footnote].—Biffar, 1971:640.—Manning, 1987:399. [Not *Callianassa grandimana* Gibbes, 1850.]

Callianassa hartmeyeri Schmitt, 1935:3, 4; 1939:15.—Biffar, 1971:640, 641, 649, 651, 653.—Manning, 1987:388, 399.

Material.—Jamaica: Kingston [Kingston Harbor = 17°57′N, 76°47′W]; Kükenthal and Hartmeyer leg., 1907, 1 ovigerous female (holotype, ZMB 20284).

Description.—Carapace trispinous, with long rostral spine overreaching base of cornea. Anterolateral spines strong, separated from front by non-calcified membrane. Dorsal oval 0.8 carapace length. Eyes extending to end of first segment of antennular peduncle, cornea large, terminal; eye with distinct ventromesial projection extending beyond cornea. Antennular and antennal peduncles incomplete; third maxilliped missing in holotype.

Major cheliped large, distance from proximal end of merus to end of cheliped 1.6 times carapace length. Ischium lined ventrally with tubercles and spines increasing in size distally. Merus longer than high, ventral margin convex, armed with small spines and tubercles decreasing in size distally. Carpus shorter than merus, about half palm length, much higher than long, cristate dorsally and ventrally, inner side of ventral margin with few low serrations, appearing smooth in outer view, distal margin produced into spine. Palm longer than high, longer than dactylus, with distinct proximal crest dorsally, cristate ventrally. Dactylus stout, hooked, shorter than palm, cutting edge with 2 low, obtuse teeth in proximal third. Fixed finger indistinctly toothed, with proximal notch in opposable margin. Fingers crossing when closed.

Minor cheliped broken in type. Ischium spined ventrally, spines increasing in size distally. Merus longer than high, cristate dorsally and ventrally, with 4 low tubercles ventrally, only proximal (largest) visible in outer view. Carpus shorter than merus, slightly longer than high, cristate dorsally and ventrally, with ventrodistal spine.

Second abdominal somite as long as sixth. Latter inflated, more than twice as long as telson. Telson trapezoidal, much shorter than uropods, lateral margins convergent posteriorly, posterior margin with rounded median projection.

Size.—Ovigerous female holotype, broken, cl 8 mm (tl, from Balss 1924, ca. 35 mm).

Remarks.—*Corallianassa hartmeyeri* can be distinguished immediately from the only other Western Atlantic species of the genus, *Corallianassa longiventris* A. Milne Edwards, 1870, in that the carpus of the major cheliped is about half as long as the palm, whereas in *C. longiventris* it is longer than half the palm. This was one of the characters used by Schmitt (1935:4) to differentiate *C. longiventris* and *C. hartmeyeri* in his key. As both Chace (1962:619) and Biffar (1971: 649) pointed out, Schmitt inadvertently transposed the names in the couplet of his key differentiating *C. hartmeyeri* and *C. longiventris.*

Corallianassa hartmeyeri differs from *C. longiventris* and resembles the species from the Eastern Pacific, named below, and differs from *C. placida* (De Man), as well, in having a ventrodistal spine on the carpus of both first pereopods.

The type of *Corallianassa hartmeyeri* could be compared with more than a dozen specimens of *C. longiventris* from Caribbean localities in the collections of the National Museum of Natural History, as follows: Bermuda (1 male, USNM 122449), Lake Worth, Florida (2 chelipeds, USNM 205698), Jamaica (1 male, 1 female, USNM 70799), Barbados (1 female, USNM 68939), Antigua (1 male, USNM 122448), and Carrie Bow Cay, Belize (4 males, 1 ovigerous female, USNM 221700; 1 female and 2 chelipeds, USNM 221701; 2 females (1 ovigerous), USNM 205699; and 3 males, 1 female, USNM 205700). No specimen of the latter species was found to have the ventrodistal spine on the carpus of the chelipeds, and in all specimens of *C. longiventris* at all sizes, the carpus of the major cheliped is longer than half the dorsal length of the palm.

The habitat of the type is unknown.

The color pattern, distinctive in *C. borradalei, C. longiventris,* and *C. xutha,* new species, is unknown in *C. hartmeyeri.*

Distribution.—Caribbean Sea, from Kingston, Jamaica. It is known only from the type locality.

Corallianassa xutha, new species
Fig. 3

Callianassa hartmeyeri.—Hult, 1938:7, figs. 1–4, pl. 1—Schmitt, 1939:15.

Callianassa (*Callichirus*) *placida.*—Chace, 1962:617. [Part, not reference to Edmondson (1944). Not *Callianassa placida* De Man, 1905].

Callianassa placida.—Hernández Aguilera et al., 1986:206.

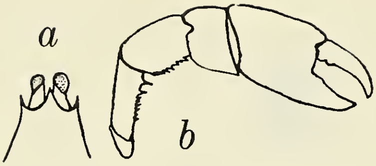

Fig. 1. *Corallianassa hartmeyeri* (Schmitt). Holotype. a, Anterior margin of carapace; b, Major cheliped. (From Balss, 1924.)

Material.—Mexico: María Madre Island, Baja California [21°35′N, 106°33′W], 4–10 fm (= 7–18 m), California Academy of Sciences, 1 female (USNM 142539).

Clipperton Island [10°18′N, 109°13′W]: Shore collecting on rocks to south of landing place, Presidential Cruise sta 9, W. L. Schmitt leg., 21 Jul 1938, 1 male (holotype, USNM 77861); same data, 1 ovigerous female (USNM 205906); Northeast side, low tide, reef flat, 0–1 ft (= to 18 cm), collected with Endrin, Limbaugh, Chess, and Hambly leg., 13 Sep 1958, 1 male (USNM 110974); East end, coral reef, Reese, Baldwin, and Wintersteen leg., sta W58-289, 15 Aug 1958, 1 ovigerous female (USNM 110978); South shore, coral reef, Reese, Baldwin, and Limbaugh leg., sta W58-295, 1 ovigerous female (USNM 110979).

Colombia: Port Utria [Ensenada Utria = 6°00′N, 77°21′W], mainland shore, first beach, intertidal, *Velero III* sta 418-35, 24 Jan 1935, 1 male (USNM 142538).

Galapagos Islands: Academy Bay [0°45′S, 90°17′W], Indefatigable Island, lagoon, in sand at low tide, Rolf Blomberg leg., 9 Aug 1934, 1 male (SMNH 13883).

All specimens other than the holotype are paratypes.

Description.—Carapace trispinous, with long rostral spine overreaching base of cornea. Anterolateral spines strong, separated from front by non-calcified membrane. Dorsal oval 0.8 carapace length. Eyes extending to end of first segment of antennular peduncle, cornea large, terminal; eye with distinct ventromesial projection extending beyond cornea. Antennal peduncle longer

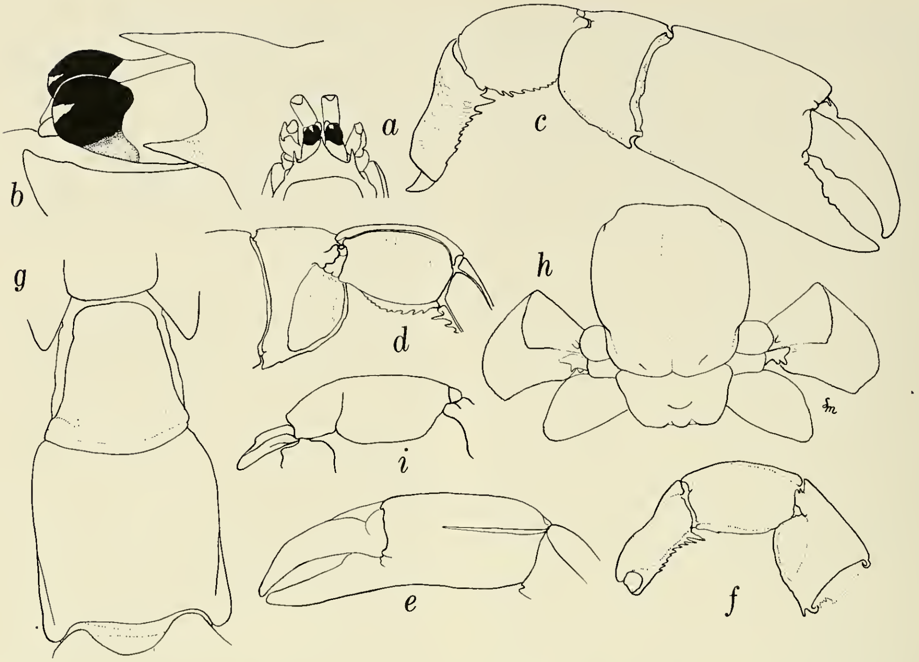

Fig. 2. *Corallianassa hartmeyeri* (Schmitt). Holotype. a, Front; b, Front, in oblique lateral view; c, Major cheliped; d, Inner face of merus and carpus of major cheliped; e, Major chela, dorsal view; f, Minor cheliped (broken); g, Second abdominal somite; h, Sixth abdominal somite, telson, and uropods; i, Sixth abdominal somite and telson, lateral view.

than antennular peduncle. Ischium and merus of third maxilliped not greatly expanded, ischium with spinous crest on inner surface, merus broader than long, dactylus simple, slender, slightly shorter and much narrower than propodus.

Major cheliped very large, distance from proximal edge of merus to end of chela more than twice carapace length. Ischium lined ventrally with tubercles and spines, increasing in size distally. Merus slightly longer than high, ventral margin semicircular, distinctly flared, with small spines and tubercles, decreasing in size distally. Carpus shorter than merus, more than half palm length, much higher than long, cristate dorsally and ventrally, inner side of ventral margin with a few large tubercles, distal margin produced into spine. Palm slightly longer than high, about as long as dactylus, with distinct proximal crest dorsally, cristate ventrally. Dactylus stout, hooked, shorter than palm, cutting edge with 2 triangular teeth in proximal third, distal tooth more acute than proximal. Fixed finger indistinctly toothed, with proximal notch on opposable margin. Fingers crossing when closed.

Minor cheliped extending about to dactylus of major. Ischium spined ventrally, spines increasing in size distally. Merus longer than high, cristate dorsally and ventrally, unarmed ventrally. Carpus shorter than merus, slightly longer than high, cristate dorsally and ventrally, with ventrodistal spine. Propodus longer than high, longer than carpus, cristate ventrally, cristate on proximal half dorsally. Movable finger longer than palm, stout, with obtuse basal tooth. Fixed finger indistinctly toothed, fingers crossing when closed.

Second abdominal somite as long as sixth. Latter inflated, twice as long as telson. Telson trapezoidal, much shorter than uro-

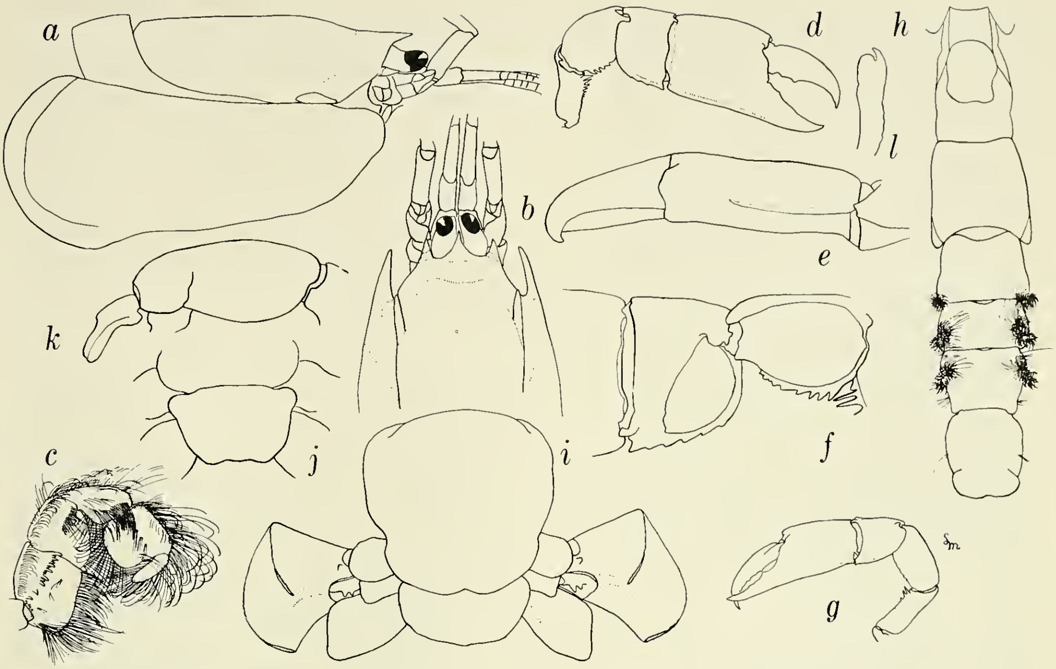

Fig. 3. *Corallianassa xutha,* new species (USNM 77861). a, Carapace, lateral view; b, Front, dorsal view; c, Third maxilliped; d, Major cheliped; e, Major chela, dorsal view; f, Merus and carpus of major cheliped, inner face; g, Minor cheliped; h, Abdomen; i, Sixth abdominal somite, telson, and uropods; j, Sixth abdominal somite, lateral view; k, Sixth abdominal somite and telson, lateral view; l, Endopod of first pleopod. a–g, i, Female; h, j, k, Male.

pods, lateral margins convergent posteriorly, posterior margin with indistinct rounded median prominence.

Size.—Males, cl 6.0 to 8.5 mm; non-ovigerous females cl 3.8 and 4.1 mm; ovigerous females cl 6.1 to 9.8 mm. Largest male, tl 48 mm; largest female, ovigerous, tl 55 mm. Hult's specimen, a male, is 37 mm long.

Name.—The specific name is from the Greek, xouthos, yellowish brown, alluding to the color of the chelipeds reported in this species.

Remarks.—This species is very similar to *C. hartmeyeri* in basic facies, agreeing with it and differing from all other species of *Corallianassa* in having a distinct distal spine on the ventral margin of the carpus of both first pereopods. The ventral border of the carpus is unarmed in *C. borradalei, C. longiventris,* and *C. placida,* the other species now assigned to *Corallianassa. Corallianassa xutha* differs from *C. hartmeyeri* in several features: the carpus of the major cheliped is more than half as long as the palm, and is distinctly serrate, almost spined, on its inner, ventral margin (these serrations are scarcely or not at all visible in external view); in *C. hartmeyeri* the carpus is no more than half the length of the palm, and the ventral serrations on the carpus are scarcely distinguishable. The movable finger of the major chela is armed with an obtuse and an acute tooth, separated by a gap; in *C. hartmeyeri* the two teeth are obtuse and are adjacent. The merus of the minor cheliped is twice as long as high and unarmed below; in *C. hartmeyeri* it is less than twice as long as high, armed below with a single denticle.

Hult reported that the anterolateral spines of the carapace were not articulated in his specimen; in all of the material reported here, including the specimen studied by Hult, these spines are distinctly separated from the anterior margin of the carapace by a non-calcified membrane.

Little is known about the habitat of this species. Hult's (1938) specimen from the Galapagos was taken in sand at low tide. The two specimens reported by Schmitt (1939) from Clipperton Island were taken while shore collecting. The material studied by Chace (1962) was taken on reef, coral cobble beach; coral reef; and on a reef flat, 0–1 foot at low tide. Hernández Aguilera et al. (1986) reported it from under rocks of dead coral. Apparently most specimens taken so far were found in shallow water; the specimen from María Madre Island was taken in 7–18 meters.

As is the case with *C. longiventris,* this appears to be a brightly colored species. Schmitt (1939:15) reported that "On the chelae of these specimens there were bright ochraceous to orange ochraceous (Ridgway) irregular color markings; both fingers toward their distal china-white tips were of this golden yellowish brown, the palm showed an irregular pattern of color and the upper surface of carpus and merus were likewise suffused with it, the color being more concentrated and stronger on the merus and on the carpus." Schmitt further commented that such a distinctive color pattern was unusual in the callianassids, and Manning (1987:397) suggested that the bright color patterns might be characteristic of the genus *Corallianassa.*

Distribution.—Eastern Pacific, from María Madre Island, Mexico; Bahía Azufre [18°21'N, 114°44'W], Isla Clarión, Mexico (Hernández Aguilera et al. 1986); Clipperton Island (Schmitt 1939, Chace 1962); Port Utria, Colombia; and Indefatigable Island, Galapagos Islands (Hult 1938).

Discussion

The genus *Corallianassa* Manning (1987: 393) was established for two species, the type species *Corallianassa longiventris* (A. Milne Edwards) from the Caribbean and *C. borradalei* (De Man) from the Indo-West Pacific. In the original account of *Corallianassa,* I noted that *Callianassa placida* De Man, 1905, differed from the two species placed in *Corallianassa* in that the second abdominal somite was not longer than the sixth. In the two species reported above, the second somite is subequal in length with the sixth, as is the case in *C. placida* (in contrast, in *C. borradalei* and *C. longiventris* the second somite is much longer than the sixth, being almost as long as the sixth and telson together). Inasmuch as *C. hartmeyeri, C. xutha,* and *C. placida* otherwise share several distinctive features with *C. borradalei* and *C. longiventris,* including the large, well-formed cornea, the anterior ventral projection on the eye, and the anterolateral spines of the carapace which are separated from the carapace by a non-calcified membrane, all of these species are placed in *Corallianassa.*

Other characters that may prove to be diagnostic for the genus are the low, rounded median prominence on the posterior margin of the telson, and the inflated sixth abdominal somite.

Members of the genus can be distinguished by the following key:

1. Second abdominal somite longer than sixth, almost as long as sixth and telson combined 2
– Second abdominal somite subequal in length to sixth 3
2. Dorsal carina on palm of major cheliped extending over entire length of palm, ending in distinct flange ... . *C. borradalei* (De Man)
– Dorsal carina on palm short, not extending to distal end, not ending in distinct flange .... *C. longiventris* (A. Milne Edwards)
3. Ventral margin of carpus of both chelipeds terminating in spine ... 4
– Ventral margin of carpus of both

chelipeds unarmed distally .... *C. placida* (De Man)

4\. Carpus of major cheliped more than half as long as palm, inner ventral margin distinctly serrate .... *C. xutha,* n. sp.

– Carpus of major cheliped half as long as palm, inner ventral margin with low, indistinct tubercles .... *C. hartmeyeri* (Schmitt)

Acknowledgments

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LABRAL MORPHOLOGY IN HEART URCHINS OF THE GENUS *BRISSOPSIS* (ECHINODERMATA: SPATANGOIDA), WITH AN ILLUSTRATED REVISED KEY TO WESTERN ATLANTIC SPECIES

Richard L. Turner and Cathleen M. Norlund

Abstract.—Existing keys to *Brissopsis* rely partly on the morphology of the labrum, an unpaired post-oral plate. As documented here, the unreliability of labral morphology has frequently resulted in misidentification of *B. atlantica* Mortensen, 1907 as *B. elongata* Mortensen, 1907. A revised key to western Atlantic species, using the number and shapes of plates below the periproct as substitutes for labral morphology, is provided.

The current authority on systematics of the spatangoid genus *Brissopsis* in the Atlantic Ocean is Chesher's (1968) revision based on analysis of 41 morphometric and meristic characters. His work includes a key that relies on only a few characters. The first couplet of this key separates *B. elongata* Mortensen, 1907 from other *Brissopsis* by the degree to which a post-oral plate, the labrum, extends posteriorly compared to adjoining plates. The basic format of Chesher's key was incorporated by Serafy (1979) into his key to spatangoids of the Gulf of Mexico and vicinity.

Labral extension is a convenient character to examine: a specimen need not be denuded of spines or dried, and damaged specimens often have the oral region intact. *Brissopsis* recently collected and examined by us included several specimens that were not *B. elongata* but had the labral condition of that species (Mortensen 1907). Subsequent examination of hundreds of museum specimens revealed many that were misidentified as *B. elongata*; nearly all of these had the labral condition of *B. elongata.* The purposes of this paper are to document the unreliability of labral extension as a taxonomic character in the genus and to provide for western Atlantic species a revised key that uses new characters of greater reliability.

The Labrum

The labrum is a tee-shaped, unpaired, interambulacral plate (plate 5.1, Lovén's system) located just posterior to the peristome of spatangoids (Fig. 1). Its anterior margin forms the broad posterior lip of the peristome, giving the ventrum the appearance of a carpenter's plane. Projecting posteriorly from the lip, the narrowed stem of the labrum abuts the first paired plates (sternal plates a.2 and b.2) of interambulacrum 5, which, along with the second pair (episternal plates 5.a.3 and 5.b.3), forms the broad plastron of the animal's ventrum. The labrum, plastron, and rest of interambulacrum 5 are bordered right and left by columns I.a and V.b, respectively, of the posterior paired ambulacra.

The length of the labral stem varies interspecifically. In most *Brissopsis* it is short and does not reach the suture between plates 1 and 2 of the adjoining ambulacra (viz., I.a.1 and I.a.2 or V.b.1 and V.b.2) (Mortensen 1951, Chesher 1968, Serafy 1979). In *B. elongata* and *B. obliqua* Mortensen, 1948, the labrum typically extends beyond ambulacral plates I.a.1 and V.b.1 and abuts plates I.a.2 and V.b.2. [Mortensen's (1907) statement that the labrum of *B. pacifica* (A. Agassiz, 1898) extends beyond the first ambulacral plates is in error (Mortensen 1951).]

Both Mortensen (1951:373, 377–378) and Chesher (1968:15) considered labral extension to be a stable and useful character in the genus *Brissopsis.* Variability in labral extension has been known to occur in some species, but the specimens have been considered abnormal. Mortensen (1907, 1951) found a few *B. lyrifera* (Forbes, 1841) in which the labrum extended beyond the first ambulacral plate on one (unilateral extension) or both sides (bilateral extension) or at least reached the suture between the first and second plates (Fig. 2). Mortensen (1951) pointed out that the holotype of *B. pacifica* is "abnormal" in having an extended labrum, and he included an appropriate cautionary note in his key (p. 379, footnote 3; see also p. 424 regarding a second specimen). One specimen of *B. columbaris* A. Agassiz, 1898 was reported to have an extended labrum (Mortensen 1951). Mortensen (1951:416) examined few specimens of *B. atlantica* Mortensen, 1907 and did not report any cases of abnormal labra. Chesher (1968) reported 2 of 105 *B. atlantica* with labra extended unilaterally; he also described and illustrated a case of bilateral extension in an apparent hybrid from the Caribbean coast of Colombia, where *B. atlantica* and *B. elongata* are sympatric.

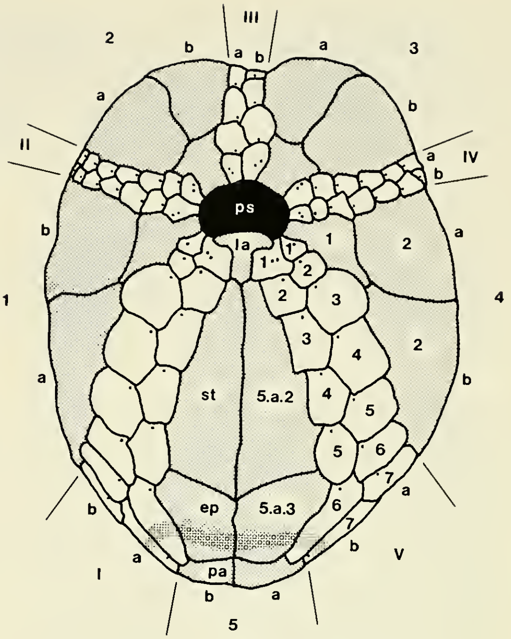

Fig. 1. Generalized ventral view of the test of a heart urchin, illustrating the alphanumeric designation of plates in the Lovénian system. Numbers of individual plates are given for interambulacrum 4 and ambulacrum V, and full designations are given for the sternal and episternal plates in column 5a. The schematic style follows David (1987). Abbreviations and conventions: ep, episternal plate; la, labrum; pa, preanal plate; ps, peristome; st, sternal plate; light stipple, interambulacra; dense stipple, subanal fasciole; ambulacra are not stippled.

Variation in *Brissopsis atlantica*

The problem of variability of labral extension in *Brissopsis atlantica* first came to the attention of one of us (RLT) in 1983 while examining uncatalogued material at the Indian River Coastal Zone Museum (IRCZM), Harbor Branch Oceanographic Institution, Florida. The material, from the east coast of Florida, was tentatively labelled *B. elongata* and consisted of 32 *B. atlantica* (IRCZM 72:346) with the labral conditions given in Table 1. Most recently, material collected specifically for this study in 1986 from the Gulf of Mexico included 24 *B. atlantica,* of which 19 had extended labra (6 lots; IRCZM 72:486–491). Thirty lots of *B. elongata* housed at the National Museum of Natural History (USNM), Smithsonian Institution, have been examined. The following misidentifications were found among them: (E10771), 2 *B. atlantica* with bilaterally extended labra; (E14283), 4 *B. atlantica,* 3 with bilaterally and 1 with unilaterally extended labra; (E14365), 1 *B. atlantica* with unilaterally extended labrum, redesignated E30961; 5 *B. elongata* remain in this lot; (E14373), 5 *B. atlantica,* 3 with bilaterally and 2 with unilaterally extended labra; (E14374), 2 *B. atlantica* with bilaterally extended labra, redesignated E30962; 56 *B. elongata* remain in this lot; (E14377), 5 *B. atlantica,* 4 with bilaterally and 1 with unilaterally extended labra, redesignated E30960; 41 *B. elongata* remain in this lot;

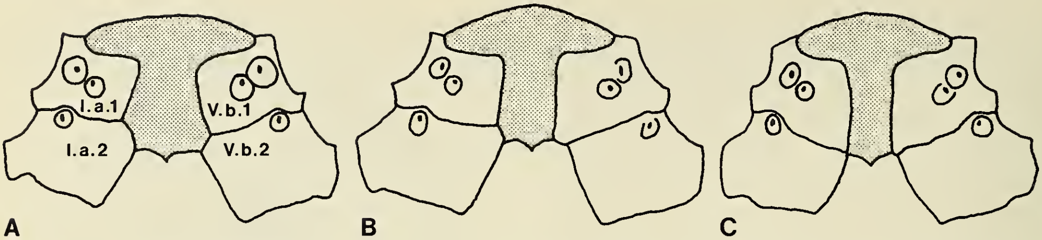

Fig. 2. Examples of variation in extension and symmetry of the labrum (stippled). A, Labrum bilaterally extended between ambulacral plates I.a.2 and V.b.2. B, Labrum unilaterally extended to plate I.a.2. C, Labrum unilaterally extended to suture between I.a.1 and I.a.2. All *B. atlantica,* IRCZM 72:346.

(E14389), 3 *B. atlantica,* 2 with bilaterally extended labra, 1 with unextended labrum; (E15552), 6 *B. atlantica,* 5 with bilaterally extended labra, 1 with unextended labrum; (E15560), 4 *B. atlantica,* 3 with bilaterally and 1 with unilaterally extended labra; (E15572), (E15573), and (E15574), each with 1 *B. atlantica* with a bilaterally extended labrum; (E15587) and (E15588), each with 2 *B. atlantica* with bilaterally extended labra; (E15589), 5 *B. atlantica,* 2 with bilaterally and 3 with unilaterally extended labra; (E15599), 1 *B. atlantica* with a bilaterally extended labrum.

The incidence of an extended labrum in some populations of *B. atlantica* is high, and misidentification of *B. atlantica* as *B. elongata* is frequent. It appears that the initial taxonomic assignment of USNM specimens was based only on the labral condition, for the course of the peripetalous fasciole over interambulacrum 3 and the ordinal number of ambulacral plates within the subanal fasciole in the specimens were typical of *B. atlantica.* Because existing keys separate *B. elongata* and *B. obliqua* from other *Brissopsis* spp. by labral morphology (Mortensen 1951, Chesher 1968, Serafy 1979), the potential exists for continued misidentification.

Pre-anal and Anal Plates

Having eliminated labral extension as a useful character for Atlantic species of *Brissopsis,* we propose two replacement characters: the number of pre-anal plates and the shape of the first anal plates. The arrangement of the labrum, sternal plates, and episternal plates of interambulacrum 5 is described above. Following these plates in columns 5a and 5b is a variable number of pre-anal and anal plates (Fig. 3). Members of the pair(s) of pre-anal plates abut each other along their interradial margins, and none touches the periproct. Beyond the pre-anal plates, the two columns of interambulacral plates diverge around the periproct; where they border the periproct, members of these columns are called anal plates, and only members of the first and last pairs are partly in contact interradially. Each anal plate has by definition a margin along the periproct.

In each column (a or b) of interambulacrum 5, *Brissopsis alta* Mortensen, 1907 has two pre-anal plates (5.4 and 5.5; Fig. 3C).

Table 1.—Labral condition of 32 atypical *Brissopsis atlantica* in IRCZM 72:346. Symmetry of extension refers to extension on one (unilateral) or both sides (bilateral) of interambulacrum 5 (see Fig. 2). Degree of extension refers to the plate number in ambulacral column I.a or V.b to which the stem of the labrum extends.

	Symmetry of extension	
Degree of extension	Unilateral	Bilateral
Suture between ambulacrals 1 and 2	3	0
Beyond ambulacral plate 1	6	22
Mixed condition	—	1

The first anal plate is, therefore, 5.6. All other western Atlantic *Brissopsis* spp. have one pre-anal plate (5.4), and plate 5.5 is the first anal plate. The shape of the first anal plate differs among species. Plate 5.5 of *B. atlantica* (Fig. 3A) is elongate and tapered, with a short periproctal margin and a much longer adradial margin, at which it abuts the adjoining ambulacral column. The interradial suture shared with the opposing member of the pair is long. The ratio of the adradial to periproctal margins is highly variable but always exceeds 2.4 (Fig. 4). In *B. elongata* (Fig. 3B), the periproctal margin is long, and the ratio is less than 2.4 (Fig. 4). The interradial margin shared with the opposing member of the pair is short. It is easy to distinguish *B. atlantica* and *B. elongata* by the shape of plate 5.5. The adradial-periproctal margin ratio for the lectotype of *B. atlantica* (USNM E10703) is 5.8. A photograph of a type specimen of *B. elongata* (Mortensen 1907; pl. IV, fig. 18) gives a ratio of 1.4. Additionally, the ratio is 1.7 for a specimen of *B. elongata* (USNM 7117, *ALBATROSS* sta 2145) mentioned by Mortensen (1907:163, 426) to be conspecific with his type material, which we have not examined. The first anal plate of *B. mediterranea* Mortensen, 1913 is of variable shape in the few nominal western Atlantic specimens available to us.

The number and shapes of the pre-anal and first anal plates are partly correlated with overall body form in Atlantic *Brissopsis* (Fig. 3). In contrast to the low profile of *B. atlantica* and *B. elongata*, the presence of a second pair of pre-anal plates gives the

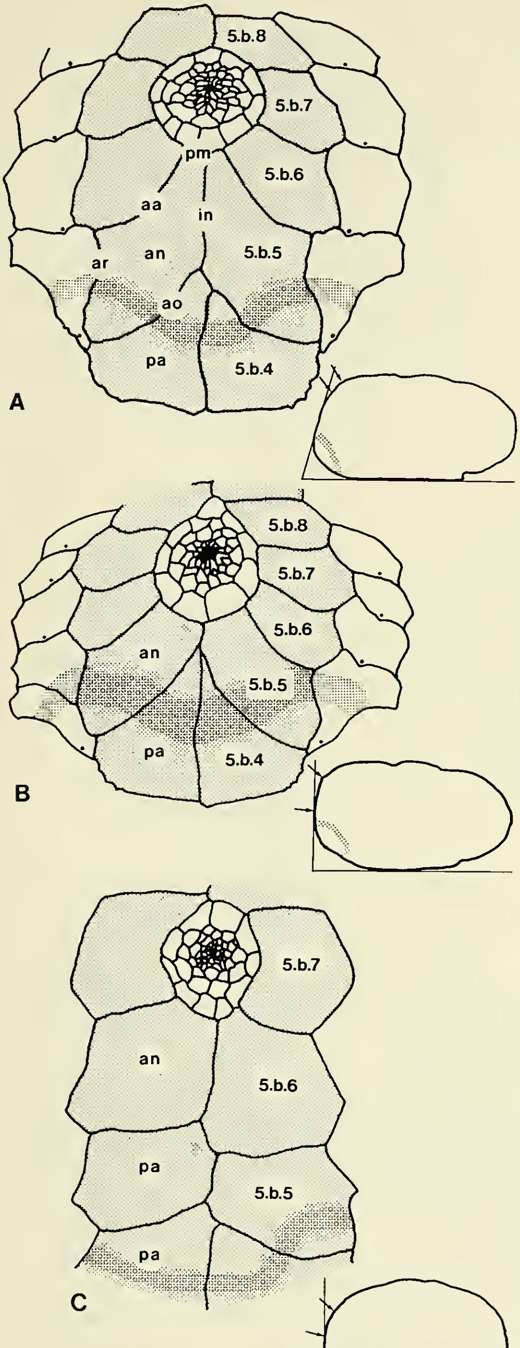

Fig. 3. Pre-anal and anal plates. A, *B. atlantica*, lectotype (USNM E10703, test length [TL] = 54 mm). B, *B. elongata*, (USNM 7117, TL = 30 mm). C, *B. alta*, lectotype (USNM E10704, TL = 67 mm). Outlined profiles give general shape of test, location of subanal fasciole, position of periproct (arrows), and angle of posterior margin of test for each species. Abbreviations and conventions: aa, adapical suture; an, first anal plate; ao, adoral suture; ar, adradial suture; in, interradial suture; pa, pre-anal plate; pm, periproctal margin; light stipple, interambulacrum 5; dense stipple, subanal fasciole; periproct and ambulacra I and V are not stippled.

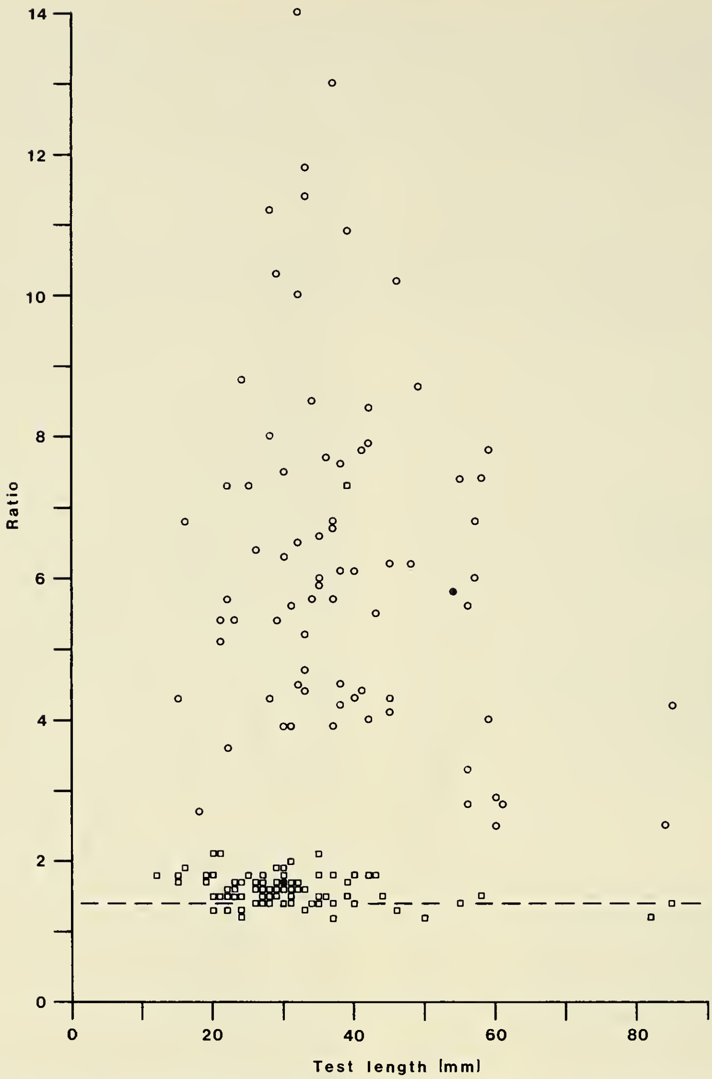

Fig. 4. Ratio of lengths of the adradial suture and periproctal margin of the first anal plates (5.a,b.5) of 78 *B. atlantica* and 94 *B. elongata.* Conventions: open circle, *B. atlantica*; closed circle, *B. atlantica,* lectotype; open square, *B. elongata*; closed square, *B. elongata* (USNM 7117); broken line, *B. elongata* from Mortensen (1907, pl. IV, fig. 18, test length unknown); overlapping plots not indicated.

posterior of *B. alta* a high profile. The inclined posterior of *B. atlantica* results from the tapered adapical extension and lengthened interradial suture of the first anal plates. On the other hand, the vertical posterior of *B. alta* is produced by the squareness of the first anal plates; and that of *B. elongata* by the strap-like first anal plates with a shortened interradial suture. Judging from illustrations of other species of *Brissopsis* (Mortensen 1951), the number and shapes of these plates should be examined further for their taxonomic utility.

Key to Western Atlantic Species of *Brissopsis*

The key presented below is a revision of keys given in Chesher (1968) and Serafy

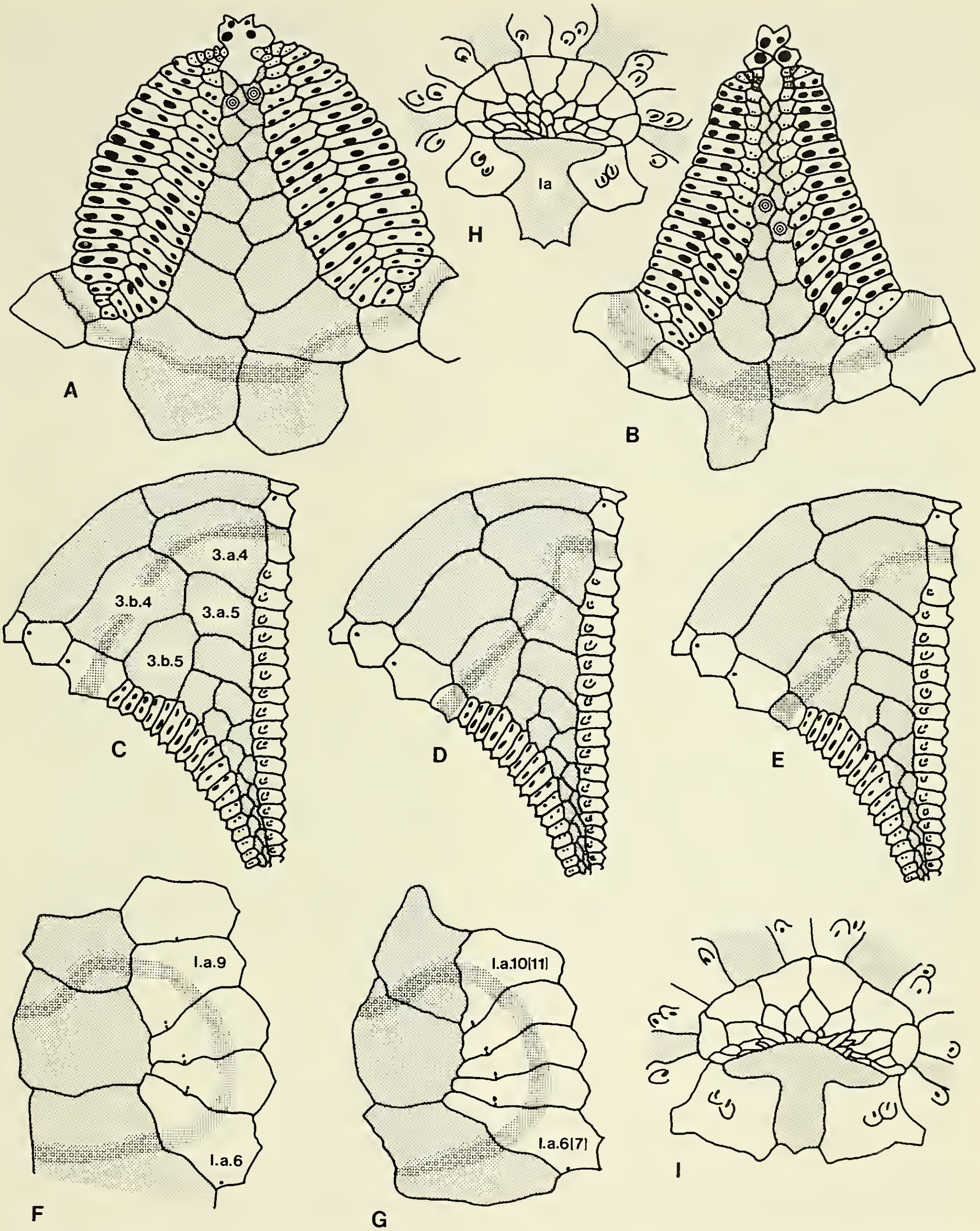

Fig. 5. Diagrams of *Brissopsis* showing features used in key. A, Divergent posterior paired petals; adapical primary tubercle of each column in interambulacrum 5 is indicated. B, Confluent posterior paired petals; adapical primary tubercles as in A. C, Peripetalous fasciole without re-entrant angle on plate 3.a.4. D, E, Peripetalous fasciole with re-entrant angle on plate 3.a.4. F, Subanal fasciole crossing 4 plates of ambulacrum I. G, Subanal fasciole crossing 5 plates of ambulacrum I. H, Lip of labrum straight. I, Lip of labrum produced. Abbreviations and conventions: la, labrum; light stipple, interambulacra; dense stipple, fascioles; ambulacra, apical system, and peristome are not stippled.

(1979). It resolves an apparently recurring problem of distinguishing *B. atlantica* and *B. elongata* by eliminating reference to labral morphology. Neither we nor Chesher had the opportunity to examine type material of *B. mediterranea,* for which published illustrations of interambulacrum 5 do not exist; our inclusion of this species in the key is tentative. Reference to globiferous pedicellariae is omitted because their scarcity on museum material [as noted also by Mortensen (1951:378)] makes their use impractical. *Brissopsis elongata* with TL < 20 mm often do not have features described below and cannot be identified by using the key; e.g., the cardinal and ordinal numbers of plates crossed by the subanal fasciole in small specimens are not consistent, indicating a prolonged period of allometric growth in this species (McNamara 1987). Finally, we caution that most larger *B. elongata* (TL > 20 mm) we have examined from the western Atlantic have the peripetalous fasciole crossing ambulacrum III on plate 7 [contrary to Chesher (1968)], but smaller specimens (TL < 20 mm) often have it crossing III.6. Therefore, this character is omitted from the key. Characters used in the key but not illustrated in Figs. 1–4 are depicted in Fig. 5. Examination of specimens is aided by brushing spines from interambulacra 3 and 5 and from ambulacra I and V; sutures between plates can be made visible by streaking with a cotton swab moistened with xylene.

1\. Posterior paired petals divergent, first primary tubercles of interambulacral columns 5.a, 5.b occurring 1–2 plates behind apical system (Fig. 5A); peripetalous fasciole without re-entrant angle in interambulacral column 3.a, crossing plates 3.a.4, 3.b.4 (Fig. 5C); 2 pairs of pre-anal plates (Fig. 3C); first anal plates are 5.a.6, 5.b.6; subanal fasciole crossing 4 ambulacral plates on each side (I.a.6–9, V.b.6–9) (Fig. 5F) .... *B. alta* Mortensen, 1907

– Posterior paired petals confluent, first primary tubercles occurring 3–7 plates behind apical system (Fig. 5B); peripetalous fasciole with re-entrant angle in interambulacral column 3.a, crossing at least plates 3.a.4, 3.a.5 (Fig. 5D, E); 1 pair of pre-anal plates (Fig. 3A, B); first anal plates are 5.a.5, 5.b.5; subanal fasciole crossing 4 or 5 ambulacral plates (Fig. 5F, G) 2

2\. Subanal fasciole crossing 4 ambulacral plates on each side (I.a.6–9, V.b.6–9) (Fig. 5F), *and* peripetalous fasciole in interambulacral column 3.b crossing only plate 5 (Fig. 5D) *B. mediterranea* Mortensen, 1913

– Subanal fasciole usually crossing 5 ambulacral plates on each side (Fig. 5G); path of peripetalous fasciole in 3.b various 3

3\. First ambulacral plates to enter subanal fasciole are I.a.7, V.b.7 (Fig. 5G); adradial suture of first anal plate less than 2.4 times the length of periproctal margin (Fig. 4), interradial suture short, adapical and adoral sutures parallel, plate strap-like (Fig. 3B); lip of labrum straight (Fig. 5H); peripetalous fasciole crossing only plate 5 in interambulacral column 3.b (Fig. 5D) .... *B. elongata* Mortensen, 1907

– First ambulacral plates to enter subanal fasciole are I.a.6, V.b.6 (Fig. 5G); adradial suture of first anal plate more than 2.4 times the length of periproctal margin (Fig. 4), interradial suture long, adapical and adoral sutures distinctly not parallel, plate adapically elongate and tapered (Fig. 3A); lip of labrum produced (Fig. 5I); peripetalous fasciole crossing plates 3.b.4, 3.b.5 (Fig. 5E) .... *B. atlantica* Mortensen, 1907

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PATTERNS OF GEOGRAPHIC VARIATION IN THE ARABIAN WARBLER *SYLVIA LEUCOMELAENA* (AVES: SYLVIIDAE)

Steven M. Goodman

Abstract.—The distribution and relationships of *Sylvia leucomelaena,* a species generally found in *Acacia* parkland, are reviewed. Analysis of seven morphological and two plumage characters results in the recognition of three subspecies: *S. l. leucomelaena* (Hemprich & Ehrenberg) from western Saudi Arabia, the Yemens, and the Dhofar region of Oman; *S. l. somaliensis* (Sclater & Mackworth-Praed) from Somalia and Eritrea; and *S. l. blanfordi* Seebohm from southeastern Egypt and eastern Sudan. Birds inhabiting the Arava of southern Israel are closest to nominate *leucomelaena* but differ in several characters. A phytogeographical analysis is presented of the origin, dispersal, and modern distribution of this habitat, and how it relates to the present patterns of geographic variation in *S. leucomelaena.*

Of the 15 species in the Palearctic genus *Sylvia* Scopoli, the Arabian or Blanford's Warbler, *S. leucomelaena,* is the only one breeding south of the Sahara (Watson et al. 1986). Its nesting range includes portions of southern Israel, the Arabian Peninsula, and the African Red Sea mountains and coastal plain, generally in relatively dense *Acacia* parkland. This habitat consists of widely dispersed clusters of trees, often in remote and relatively undisturbed country. Except for a recent study in southern Israel virtually nothing is known about the Arabian Warbler's natural history and ecology. To date, no published study has examined patterns of geographic variation in this species.

In the course of a 1985 biological survey of Gebel Elba in the Red Sea Mountains of southern Egypt, just north of the Sudanese border, a population of *S. leucomelaena* was discovered and a small series collected. Before a subspecific designation could be placed on this material it was necessary to review patterns of geographic variation in this species. The purpose of this paper is to describe these patterns and to present a phytogeographical analysis that may account for them. Information is also given on distribution, sexual dimorphism, several aspects of natural history, and taxonomic conclusions.

Materials and Methods

Seven measurements were taken from museum specimens (all in mm): Wing—measured from the bend of flattened wing at carpal joint to longest primary tip. Tail—measured between the insertion of central tail rectrices to distal tip. Exposed culmen—measured from base of feathering on the forehead to maxilla tip. Bill from nostril—measured from anterior edge of nostril to maxilla tip. Bill width—measured across upper mandible at anterior edge of nostril. Gonys—measured from junction of rami to maxilla tip. Tarsus—measured from the junction of tibiotarsal-tarsometatarsal joint to distal edge of distal most undivided scute overlying the toes (little variation was found in the scale pattern of the feet). A rule was used to the nearest 1.0 mm for the wing and tail measurements and a dial calipers to the nearest 0.1 mm for the other measurements.

Since virtually no information is available in the literature on the weight or food habits of *S. leucomelaena* this information, based on field and museum studies, is summarized herein. Weights of the Egyptian specimens were taken to the nearest 0.1 gm. All other weight data are from museum specimens and the unpublished field notes of Mr. G. Nikolaus or Mr. M. C. Jennings. All references to altitude are presumed to be m above sea-level.

Four specimens were selected as standards for comparison of crown-color. These are (darkest to lightest): BMNH 1925.11.20.26, male, Sogsode, Somalia; BMNH 1919.12.17.702, male, Erkowit, Sudan; BMNH 1915.12.24.720, female, Erkowit, Sudan; and BMNH 1919.12.17.686, female, Sinkat, Sudan. The contrast between the crown and back did not enter into the selection of these standards. Four standards were used to quantify the amount of white on the outer pair of rectrices (Fig. 1). Individual specimens were compared to these standards and scored accordingly.

Statistical tests used MIDAS programs, written by the University of Michigan Statistical Research Laboratory. Differences among means and variances were tested by Student's t-test or analysis of variance (ANOVA), as appropriate. Scheffé tests were also used in pairwise combinations to test differences in means between geographical regions. Probabilities of 0.05 or less are considered statistically significant and sufficient to reject the null hypothesis that the means are equal.

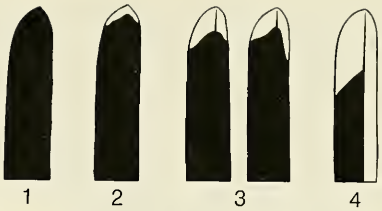

Fig. 1. Four standards used to quantify the amount of white on the outer pair of rectrices.

Review of *Sylvia leucomelaena* Taxonomy

The original description of *S. leucomelaena* by Hemprich & Ehrenberg (1833) was based on material taken in Arabia. They placed the bird in genus *Curruca*. In a review of Hemprich and Ehrenberg specimens in the Berlin Museum, Dresser & Blanford (1874) described the type of *S. leucomelaena*, gave measurements and noted this species resemblance in details to *Sylvia rueppelli*. In 1878 Seebohm described *Sylvia blanfordi* based on a single specimen taken at Rairo, Habab, Abyssinia (=Eritrea). Although he cited the paper of Dresser and Blanford, Seebohm believed that the Rairo specimen represented a new species, with some similarity to *S. curruca, S. melanocephala* and *S. rubescens* (=*S. mystacea*).

In a review of birds collected in the Yemens, Hartert (1917) named a subspecies, *Parisoma blanfordi distincta*. His placement of this form in *Parisoma* was unexplained but may have been due to the notion of his time that the Palearctic and the Afrotropical (=Ethiopian) biogeographic realms were completely distinct. It would thus have been difficult to explain a *Sylvia* breeding in sub-Saharan Africa.

Sclater & Mackworth-Praed (1918) described the new form *somaliensis* from material collected at Mundara, Somalia, and retained this species in *Parisoma*. Their diagnosis noted that *somaliensis* was distinguishable from *blanfordi* and *distincta* by its smaller size and differences in back coloration and tail pattern. Meinertzhagen (1949) reviewed this situation and considered *Curruca leucomelaena* and *Sylvia blanfordi* conspecific. Further, he presented evidence that the species should be shifted from *Parisoma* to *Sylvia*.

Afik & Pinshow (1984) questioned the allocation of this species to *Sylvia*, primarily on several aspects of natural history, and suggested a reexamination of its generic position. As pointed out by Dowsett-Lemaire

& Dowsett (1985), however, little comparative natural history information is currently available on most Afrotropical Sylviidae. Furthermore, the genus *Sylvia* shows a remarkable degree of plasticity in aspects of life history, and such characters probably provide little information on the naturalness of the group.

General Distribution of *Sylvia leucomelaena* by Country

ISRAEL—In April 1972 this species was found nesting in the Arava (Rift Valley), 10 km south of the southern end of the Dead Sea (Zahavi and Dupai 1974) (Fig. 2). In more recent years it has been observed in relatively dense *Acacia tortilis* and *A. raddiana* stands from the southern end of the Dead Sea south to within 40 km of Eilat (Afik & Pinshow 1984; H. Shirihai, pers. comm.).

SAUDI ARABIA—The Arabian Warbler is a breeding resident of southwestern and western Saudi Arabia, often in areas with thick vegetation such as along the Tihama (Stagg 1985). Hutchinson (1975) reported several observations from central Saudi Arabia near Riyadh; these records were rejected by Jennings (1981). Meinertzhagen (1954) designated the type locality of *Curruca leucomelaena* Hemprich & Ehrenberg as Midian (perhaps Maidn Salah, 26°45′N, 37°55′E; Jennings 1981), a northern area of the country for which there are no modern records (M. C. Jennings, pers. comm.).

THE YEMENS—During a trip to North Yemen from 7–29 Apr 1979 Cornwallis & Porter (1982) recorded this species on nine occasions in the Western Ramparts and Highland Plateau between 500 and 1700 m, invariably in *Acacia* groves. This species is a fairly common but local resident of the Tihama foothills, particularly in *Acacia/Commiphora* bushland (Brooks et al. 1987).

SULTANATE OF OMAN—The Arabian Warbler is known from Dhofar, in the southwestern corner of the Sultanate, where it tends to occur "on hillsides and in mountain wadis" (Gallagher & Woodcock 1980: 252). In this region it has been recorded in every month of the year and is considered a breeding resident (Gallagher 1986). The Oman distribution of the Arabian Warbler is exceptional. In some regions it inhabits areas of mixed woodland, without extensive tracts of *Acacia* spp. (M. D. Gallagher, pers. comm.).

SOMALIA TO ERITREA—Archer and Godman (1961) noted that this species occurs in Somalia along the coastal plain and plateau between sea-level and up to about 1800 m, and as far south as Galoli and Burao. More recently it has been presumed to be a "fairly common" resident in the northern portion of Somalia above 8°30′N in acacias along the coastal plain and up to the plateau beyond the coastal mountains (Ash & Miskell 1983:59). This species has been noted throughout portions of Djibouti, particularly in *Acacia* scrubland (G. Welch, pers. comm.). Smith (1957) noted that the Arabian Warbler was found in the Red Sea coastal hills of Eritrea, at least between Massawa and Dankalia, generally in deep wadis below 320 m and with acacia cover.

SUDAN—Cave & Macdonald (1955:255) listed this species as a "rather uncommon resident of the old Red Sea Province."

EGYPT—In early 1985 this species was discovered in the immediate vicinity of Gebel Elba (22°11′N, 36°21′E), Sudan Government Administration Area (Goodman & Meininger in press a). Although no nests were found, numerous singing males were observed in the dense *Acacia* groves and clear territorial interactions noted. Five adult specimens were collected, all of which had enlarged gonads. This species is presumed to be a local breeding resident in the Gebel Elba area. There are no specimen records from elsewhere in the country (Goodman and Meininger in press b); although it is plausible it occurs in extreme eastern Sinai just across the border from known Israeli populations.

Fig. 2. Distributional map of *Sylvia leucomelaena* across its complete range. Open triangles represent specimens examined and open squares sight records from the literature or unpublished information.

Notes on the Recently Discovered Egyptian Population

The Egyptian population of *S. leucomelaena* appears to be limited to the slopes and valleys of Gebel Elba in the extreme southeastern corner of the country. This mountain, which rises to 1428 m, is unique for Egypt in that a significant portion of the plants and animals are of Afrotropical rather than Palearctic origin. The Gebel Elba area has relatively heavy vegetation and contains dense *Acacia* parkland (Kassas & Zahran 1971). *Acacia tortilis* is common along the coastal plain, foothills and lower slopes of Gebel Elba, and *A. raddiana* on the north slopes and in valleys bisecting the southern slope (Kassas & Zahran 1971).

The Arabian Warbler was observed at various sites around the mountain but was more common on the northern side, where the *Acacia* parkland is most extensive. Generally they were observed singly or in pairs. The first territorial aggression was noted on 13 Apr 1985, although songs were heard soon after our arrival in February. Interspecific encounters were recorded on several occasions. On 13 April one adult *S. leucomelaena* was noted flying in a mixed flock of three *Cercomela melanura* and six *Sylvia melanocephala*. Later that same day one adult *S. leucomelaena* was observed chasing a male *S. melanocephala.* On 14 April four adult *S. leucomelaena* were noted foraging in a mixed flock with *S. curruca* and *Cercomela melanura.* In the Gebel Elba area *Cercomela* is a local breeding resident and *Sylvia curruca* and *melanocephala* migrants and winter visitors.

Results

Sexual dimorphism in measurements.—No single geographically constant pattern of sexual dimorphism was found in this species (Table 1). Morphological differences were not detected between the sexes in the Arava or in the combined Somalian and Eritrean samples. Only a single female was available from the Gebel Elba, Egypt, population and no statistical comparison was made; however, for all seven measurements the value of the female fell within the range of males from this locality. In both the Saudi Arabian and Yemen samples, males have statistically longer wings and tails than females. Sudanese males have longer wings than females.

Sexual dimorphism in plumage coloration within geographic regions.—In the Saudi Arabian, Somalian/Eritrean and Sudanese samples, adult males have darker crowns than adult females (Table 2); the contrast was most notable for Sudanese birds. These sexual differences are statistically significant. No sexual variation was found in this character for the Yemen, Arava or Egyptian populations, although in the latter two cases the sample size was limited. Within the various geographical regions sexual difference was found in tail pattern only in the Saudi Arabian sample (Table 3), in which males tend to have more white on the outer rectrices than females ($P = 0.018$).

Geographic variation in plumage coloration.—No statistically significant difference between regions was found in the head coloration of adults, whether partitioned by sex or lumped together. For the tail pattern the situation is more complex. Since no sexual variation was found in this character for any population inhabiting the western side of the Red Sea, the sexes were combined in this analysis. In this region there is clinal variation in the tail pattern. Adult birds from Egypt have less white on the outer rectrices (n = 5, mean = 2.0) than Sudanese (n = 21, mean = 2.9, $P = 0.0001$), and Sudanese birds have less white than Somalian/Eritrean (n = 27, mean = 3.9, $P = 0.0001$). The pattern on the eastern side of the Red Sea is similar with an increasing amount of white on the tail from north to south, but the range of variation is not as great, perhaps in part due to small samples from some areas. Scores were only available from the Arava population for adult females. These birds have less white on the outer rectrices (n = 2, mean = 2.0) than Saudi Arabian females (n = 10, mean = 2.2) and Yemeni females (n = 7, mean = 2.4). None of these comparisons showed statistical significance. Males from Saudi Arabia had slightly more white (n = 15, mean = 2.7) than those from Yemen (n = 8, mean = 2.6). The single male from Oman has a tail score of 2. No difference was found between the Arava and Egyptian populations.

Geographic variation in morphology.—Since the wing and tail measurements of adult males and females are dimorphic in two populations they were partitioned within each sample (Table 4). No differences were found between birds from Saudi Arabia and Yemen, and these populations are combined in subsequent analyses. The wing lengths of both male and female populations living on the west side of the Red Sea are similar to one another; the only exception is that males from the Sudan have slightly longer wings than males from the Somalia/Eritrea sample ($F = 5.98$, $P = 0.017$).

There is considerable variation in tail length among the five geographic areas. Within either sex class no significant variation was found between the Egyptian and Sudanese samples; however, when these samples were compared to birds from Somalia/Eritrea differences were found in both cases (Table 4). Males from Arava have longer tails than those from the Arabian Peninsula ($F = 4.05$, $P = 0.048$), while females are similar to one another. Within each sex class there is a cline in tail length on both sides of the Red Sea, decreasing in size from north to south.

Sylvia leucomelaena from Arava have substantially wider bills than the other four samples (Table 5). There appears to be clinal variation in bill width on the western side of the Red Sea, decreasing in size from north to south.

Analysis of the exposed culmen measurement showed a unique pattern of variation (Table 5). Significant differences were found in the Sudanese birds relative to those from the Arabian Peninsula ($F = 21.60$, $P = 0.0000$), Somalia/Eritrea ($F = 33.54$, $P = 0.0000$), and Egypt ($F = 15.15$, $P = 0.0002$). This variation shows no clear clinal pattern. The bill length from nostril also revealed an unusual pattern of variation (Table 5); the statistically significant differences were between the Arabian Peninsula and Somalia/Eritrea samples ($F = 7.97$, $P = 0.005$), the Arabian Peninsula and Sudan samples ($F = 4.28$, $P = 0.04$), and Somalia/Eritrea and Sudan samples ($F = 19.28$, $P = 0.0000$).

The gonys length of Sudanese birds was the smallest of any of the samples and statistically different from all others, except the Egyptian birds (Table 5). A comparison of F-statistics for tarsus length was not included in Table 5. The only statistically significant difference was between the Somalia/Eritrea and Egyptian samples ($F = 5.50$, $P = 0.03$), which most likely reflects two extremes of a cline.

Weight.—Weights from three adults handled by Mr. Michael C. Jennings at Hejaz, Saudi Arabia, in mid-May 1976 are 14.8, 15.3, and 16.3 g. For 29 unsexed autumn birds weighed by Mr. Gerhardt Nikolaus during ringing operations near Erkowit, Sudan, the mean weight was 13.9 g and range 12.5–16 g, excluding one bird which weighed 9 g. Four weights are available for wild birds from the Arava population, two adult males at 15 and 13.5 g, and two adult females at 16 (with "full grown egg") and 15 g (UTM). Weights of Egyptian birds include: five males—mean 12.3 g and range 11.2–13.2 g, and one female—12.5 g (UMMZ).

Food.—Meinertzhagen (1954) considered the Arabian Warbler an insectivore. Afik & Pinshow (1984) reported that it searched acacia bark for larvae, hawked flying insects, and dug for small insects on the ground under acacia. They further noted that this species frequently eats ripe fruits of three perennial shrubs: *Nitraria retusa, Lycium shawii* and *Ochradenus baccutus.*

Of the five specimens taken at Gebel Elba, Egypt (UMMZ), three had empty stomachs and two contained unidentified fruits. Two birds collected at Sinkat, Sudan (BMNH), had seeds in their stomachs and no insects, while a third contained berries. One bird from Somalia (LSUM) had Coleoptera remains in the gizzard.

Discussion

The East African Rift Valley, the Red Sea, Gulf of Aqaba, and the Arava are portions of a single tectonic system, often referred to as the Afro-Arabian Rift Valley. The shearing of the Red Sea apparently commenced in the early Miocene (Ross & Schlee 1973), as the Arabian plate drifted away from the African plate. This rifting activity continued with varying intensity through the upper-most Miocene or lowest Pliocene, at which time the southern Red Sea opened into the Indian Ocean (Hötzl 1984). Presently, the Red Sea is a little under 2000 km long. The southern strait at Djibouti, Bab el Mandab, is about 30 km wide. In the north the average width varies from 150 to 180 km and between 15° and 18°N the sea widens to 350 km. The Gulf of Aqaba is about 170 kms long and varies between 15 and 30 km in width.

Table 1.—Sexual differences in seven morphological characters in adult *Sylvia leucomelaena*.[1]

	Wadi Arava		Saudi Arabia		Yemen		Somalia and Eritrea		Sudan		Egypt	
Measurement	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Wing												
n	2	3	15	9	10	7	22	10	18	8	4	1
Range	73–74	67–72	68–77	67–72	68–72	66–71	63–72	65–68	65–70	65–67	65–68	65
Mean	73.5	70.0	71.5	69.2*	70.2	68.1*	66.0	66.3	67.6	65.9**	66.3	
SD	0.71	2.65	2.69	1.64	1.39	2.04	1.88	1.06	1.42	0.83	1.50	
Tail												
n	2	3	13	7	10	7	21	10	17	8	4	1
Range	69–71	62–68	64–71	60–68	63–68	60–65	56–67	56–63	59–65	60–63	61–65	63
Mean	70.0	64.7	67.4	65.0**	65.5	62.4**	59.0	59.5	62.4	61.4	62.5	
SD	1.41	3.06	2.53	2.58	1.58	2.37	2.65	2.37	2.06	0.92	1.91	
Exposed culmen												
n	2	3	15	9	10	7	20	9	18	8	4	1
Range	11.4–12.0	10.7–11.2	10.6–12.7	9.6–12.4	10.5–12.2	11.8–12.0	10.9–12.8	10.9–12.7	10.1–11.7	10.0–11.8	11.5–12.4	11.6
Mean	11.70	11.03	11.52	11.48	11.37	11.87	11.71	11.71	10.89	10.89	12.03	
SD	0.42	0.29	0.55	0.76	0.51	0.09	0.55	0.56	0.58	0.54	0.41	
Bill width												
n	2	3	15	9	10	7	20	9	18	8	4	1
Range	3.2–4.3	3.8–4.5	2.8–3.4	2.8–3.2	2.5–3.5	3.1–3.6	2.8–3.5	2.9–3.2	2.7–4.4	2.7–3.1	3.1–3.4	3.2
Mean	3.75	4.06	3.09	3.04	2.96	3.28	3.09	3.09	3.28	2.94	3.23	
SD	0.78	0.38	0.18	0.10	0.30	0.19	0.18	0.13	0.53	0.12	0.15	
Gonys												
n	2	3	15	9	10	7	22	10	18	8	4	1
Range	7.1–8.2	6.8–8.8	7.2–8.9	6.6–8.3	7.0–8.2	7.2–8.7	6.9–8.7	7.3–8.7	6.4–8.0	6.7–7.9	7.0–8.0	7.0
Mean	7.65	7.87	7.79	7.61	7.59	7.72	7.71	7.92	7.38	7.30	7.53	
SD	0.78	1.01	0.42	0.47	0.44	0.59	0.44	0.47	0.43	0.35	0.41	
Bill from nostril												
n	1	2	15	9	10	7	20	9	14	8	4	1
Range	8.5	8.3–9.4	8.0–9.8	7.2–9.2	7.8–9.3	7.8–9.1	8.0–9.4	8.3–9.3	7.5–8.8	7.8–8.8	8.2–9.0	8.4
Mean		8.85	8.54	8.69	8.43	8.29	8.75	8.90	8.16	8.36	8.60	
SD		0.78	0.45	0.66	0.48	0.42	0.42	0.36	0.38	0.35	0.34	

Table 1.—Continued.

Measurement	Wadi Arava		Saudi Arabia		Yemen		Somalia and Eritrea		Sudan		Egypt	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Tarsus												
n	1	2	15	9	10	7	22	9	14	8	4	1
Range	22.2	22.0–22.6	21.2–23.0	20.8–24.5	20.8–24.0	20.5–22.8	20.1–23.6	20.8–22.7	21.0–23.1	21.5–22.8	21.7–24.4	22.0
Mean		22.30	22.07	22.36	22.14	21.96	21.87	21.59	22.05	22.19	22.88	
SD		0.42	0.58	1.18	0.98	0.89	0.91	0.60	0.68	0.38	1.26	

[1] Sexual differences between the means were tested with Student's *t*-test, one asterisk $P < 0.05$, two asterisks $P < 0.01$.

Table 2.—Percentages of adult *Sylvia leucomelaena* within a geographic region scored for different head color standards.[1]

Region	Standard (dark to light)				
	1	2	3	4	Mean
Arava					
Male (n = 1)	0.0	100.0	0.0	0.0	2.0
Female (n = 1)	0.0	100.0	0.0	0.0	2.0
Saudi Arabia*					
Male (n = 15)	6.7	80.0	13.3	0.0	2.1
Female (n = 10)	0.0	70.0	30.0	0.0	2.3
Yemen					
Male (n = 8)	0.0	90.0	10.0	0.0	2.1
Female (n = 7)	0.0	57.1	28.6	14.3	2.6
Somalia and Eritrea*					
Male (n = 20)	15.0	80.0	5.0	0.0	1.9
Female (n = 8)	0.0	62.5	37.5	0.0	2.4
Sudan***					
Male (n = 14)	7.1	92.9	0.0	0.0	1.9
Female (n = 8)	0.0	25.0	62.5	12.5	2.9
Egypt					
Male (n = 4)	25.0	75.0	0.0	0.0	1.8
Female (n = 1)	0.0	0.0	100.0	0.0	3.0

[1] Within a geographical region sexual differences between the means of the two sexes were tested with Student's *t*-test, one asterisk $P < 0.05$, three asterisks $P < 0.001$.

As mentioned earlier, *Sylvia leucomelaena* is generally confined to relatively dense *Acacia* groves, and its distribution seems to partially coincide with that of *A. tortilis* and *raddiana*. Both of these trees often occur sympatrically and their local distribution is adjusted to the local micro-climate. *A. tortilis* is adapted to higher temperatures and dryer conditions than *raddiana*; while *raddiana* is more tolerant of a wider range of temperature and moisture (Halevy and Orshan 1972). The exception to this apparent habitat requirement is in Oman, where the bird occurs in mixed open woodland areas of the Dhofar region.

Zohary (1962) hypothesized that before the Miocene *A. tortilis* and *raddiana* migrated from Africa along the eastern coast of the Red Sea across to and north along

Table 3.—Percentages of adult *Sylvia leucomelaena* within a geographic region scored for different tail pattern standards.[1]

Region	Standard 1	2	3	4	Mean
Arava					
Female (n = 2)	0.0	100.0	0.0	0.0	2.0
Saudi Arabia*					
Male (n = 15)	0.0	26.7	73.3	0.0	2.7
Female (n = 10)	0.0	80.0	20.0	0.0	2.2
Yemen					
Male (n = 8)	0.0	37.5	62.5	0.0	2.6
Female (n = 7)	0.0	57.1	42.9	0.0	2.4
Somalia and Eritrea					
Male (n = 19)	0.0	0.0	5.9	94.1	3.9
Female (n = 8)	0.0	0.0	12.5	87.5	3.9
Sudan					
Male (n = 14)	0.0	0.0	100.0	0.0	3.0
Female (n = 7)	0.0	14.3	85.7	0.0	2.9
Egypt					
Male (n = 4)	0.0	100.0	0.0	0.0	2.0
Female (n = 1)	0.0	100.0	0.0	0.0	2.0

[1] Within a geographical region sexual differences between the means of the two sexes were tested with Student's t-test, one asterisk $P < 0.05$.

western Arabia, to the Gulf of Aqaba, into the Arava and other portions of the Levant. Given our present knowledge of plate tectonics of this area, these two land masses would have been at least partially connected at that time. Shmida & Or (1986) presented a strong case that the invasion of these plants into the Arava, although along the same route suggested by Zohary, has been since the end of the Pleistocene, long after the shearing took place. Their argument is primarily based on the low degree of local endemism in these Afrotropical elements, their wide distributional disjunctions, and adaptations to arid conditions and long-distance dispersal. In either case, the modern range of *Acacia* spp. in the mountains and along the coastal plains bordering the Red Sea is evidence to support this dispersal route, whether it took place before or after rifting, and most importantly how this distribution is relevant to that of *Sylvia leucomelaena.*

Several species of *Acacia* are common along the western Red Sea coastal plain from the East African Rift Valley (Beals 1970), north through Eritrea (Hemming 1961), to the Red Sea Mountains of Sudan (Kassas 1956, 1957). Just north of the Egyptian/Sudanese political border, near Gebel Elba, nine *Acacia* spp. are known to occur; these are dominated by *tortilis* and *raddiana* (Kassas & Zahran 1971, Täckholm & Boulos 1972, Täckholm 1974). North of Gebel Elba, in the Egyptian Eastern Desert, there

Table 4.—Comparison of F-statistics by geographic region for two sexually dimorphic characters in adult *Sylvia leucomelaena,* wing length (upper right corner) and tail length (lower left corner).[1]

Region	1	2	3	4	5
1		3.09 1.57	26.12*** 10.64**	16.16*** 14.78***	18.14*** 7.46**
2	4.05* 0.42		68.02*** 10.75**	29.82*** 17.55***	19.67*** 5.27*
3	43.29*** 13.76***	118.18*** 22.41***		5.98* 0.62	0.03 0.79
4	19.37*** 4.44*	31.20*** 5.24*	23.00*** 4.69*		1.56 0.27
5	13.88*** 0.39	10.25** 0.09	9.15** 2.84	0.13 0.44	

[1] For each matrix the numbers on top within a geographic region comparison are males and below females. 1 = Arava, 2 = Arabian Peninsula (combined Saudi Arabia, Yemen, and Oman), 3 = Somalia and Eritrea; 4 = Sudan, 5 = Egypt. One asterisk $P < 0.05$, two asterisks $P < 0.01$, three asterisks $P < 0.001$.

Table 5.—Matrices of *F*-statistics by geographic region for non-sexually dimorphic characters in adult *Sylvia leucomelaena.*[1]

Geographic area	Bill width/exposed culmen					Bill from nostril/gonys				
	1	2	3	4	5	1	2	3	4	5
1		0.75	2.91	2.12	3.47		0.16	0.85	3.99*	1.60
2	37.04***		2.96	21.60***	2.64	0.69		1.91	10.51**	1.67
3	33.77***	0.07		33.54***	0.52	0.09	7.97**		18.10***	3.79
4	27.40***	2.01	1.13		15.15**	2.78	4.28*	19.28***		0.12
5	13.64**	1.31	0.98	0.17		0.28	0.05	1.38	1.65	

[1] Character to left of slash is on bottom half of matrix, character to right of slash is on top half of matrix. 1 = Arava, 2 = Arabian Peninsula (combined Saudi Arabia, Yemen, and Oman), 3 = Somalia and Eritrea, 4 = Sudan, 5 = Egypt. One asterisk $P < 0.05$, two asterisks $P < 0.01$, three asterisks $P < 0.001$.

are only small patches of *Acacia raddiana* and most of the other species fall out (Kassas & Imam 1959; Kassas & Zahran 1962, 1965; Boulos & Hobbs 1986). This is compared to the eastern side of the Red Sea, where relatively dense *Acacia* parkland occurs along the Arabian Peninsula coastal plain and above the Tihama in the Asir and Hejaz Mountains (M. C. Jennings, pers. comm.); forming a more or less continuous band from East Africa across to and along the eastern edge of the Arabian Peninsula (Vesey-Fitzgerald 1955, 1957). Based on the present distribution of *Acacia* along the western side of the Red Sea (including the Gulf of Suez), it appears that contiguous tracts have not existed in this region in the recent geological past; precluding the possibility that these trees migrated through this pathway into the Levant. Clearly, this is based on the assumption that the modern distribution of *Acacia* in this area parallels that since the end of the Pleistocene, and that changes in climatic patterns and human land-use have not resulted in the extinction of areas of *Acacia* parkland. The main point of this phytogeographical analysis is that evidence exists that *Acacia* spp. spread from East Africa into the Levant via the Arabian Peninsula, and that a habitat corridor existed along this pathway for dispersal from the northern Afro-Arabian Rift Valley into East Africa.

Seventeen species of *Sylvia* are known to occur in Africa (Vaurie 1959, Etchécopar & Hüe 1967, Moreau 1972, Watson et al. 1986). Of these, eleven have breeding populations on the continent. (This figure includes *S. sarda,* but see Thomsen & Jacobsen 1979.) For the most part the breeding ranges of the other ten species are restricted to the Mediterranean Sea coastal zone, in areas receiving about 100 mm of precipitation per year and basically with a Palearctic flora; a few species also occur south into coastal Mauritania. The exceptions are *S. nana deserti* and *S. deserticola* which penetrate into portions of the western Sahara; the latter species is endemic, as is the subspecies *S. melanocephala norrisae* known from the Faiyum of Egypt. Excluding *leucomelaena,* none of these *Sylvia* occur in areas with Afrotropical biota and the habitat of their African breeding range is basically an extension of what they use in Eurasia.

Several workers have speculated that *hortensis* and *leucomelaena* form a superspecies, are part of the same subgenus, or each others closest relatives (Hall & Moreau 1970, Wolters 1980, Watson et al. 1986). Four subspecies of *hortensis* are currently recognized (Vaurie 1959, Watson et al. 1986), three of which are important for this review: nominate *hortensis* breeds in portions of central Europe and North Africa from Morocco to Tripolitania (western Libya), and winters in portions of the Sahara and northern sub-Saharan Africa; *crassirostris* breeds in eastern and southeastern Europe, the Middle East and Cyrenaica (eastern Libya), and winters in east Africa; and *balchanica* breeds in Transcaspia and Iran and winters in Arabia. Given the variety of ecotypes used by *hortensis,* ranging from temperate forest and high mountain country during the breeding season to desert scrub during the winter, and its close relationship with *leucomelaena,* it seems plausible for the latter form to have adapted to one of these habitats, namely *Acacia* parkland. Throughout much of the Arabian and east African wintering grounds *hortensis* occurs in scrubland, often sympatrically with *leucomelaena*; for example, in the *Acacia* plains of coastal Eritrea (Moreau 1972).

Remembering that the genus *Sylvia* is of Palearctic origin, and that *leucomelaena* is the only *Sylvia* breeding in sub-Saharan Africa, it is presumed that *leucomelaena* speciated in the northern portion of the Afro-Arabian Rift Valley, then spread along the *Acacia* corridor of the western Arabian Peninsula, and then crossed over the Red Sea (presumably at the narrows in the south) into east Africa. Once in Africa it spread north through the Red Sea Mountains and coastal plain until it reached the northern limit of dense *Acacia* groves. The modern sympatric occurrence of *leucomelaena* and *hortensis* during the winter months in portions of Arabia and eastern Africa is presumably secondary contact after the events of speciation and dispersal. The possibility that a population of the proto-modern *hortensis/leucomelaena* group wintering in east Africa became resident, speciated and spread northwards on both coasts of the Red Sea cannot be eliminated. However, this seems unlikely since no parallel exists for any other *Sylvia* species, the majority of which winter at least in part in Africa.

Taxonomic Conclusions

Sylvia l. leucomelaena.—Meinertzhagen (1949) noted that the head and mantle colors of nominate *leucomelaena* were paler than African birds. This conclusion is generally supported by the present study. Since several populations are sexually dimorphic in head coloration it is important to analyze this character only within a sex class. Some of Meinertzhagen's other color comparisons were confounded by not taking this factor into account. Birds from the Arabian Peninsula, including Yemen and Oman, tend to have less white on the outer pair of rectrices than African birds, particularly those from Somalia/Eritrea.

Specimens from the Arava differ from Arabian Peninsular birds in several ways: less white on the outer pair of rectrices (although the Arava sample consisted of only two birds); males have longer tails; and both sexes have substantially wider bills. These differences seem to warrant subspecific separation of the Arava population. However, the naming of a new form is suspended until further data are available.[1]

Sylvia l. distincta.—No consistent difference was found between birds from the Yemens and the balance of the Arabian Peninsula. *S. l. distincta* is a synonym of *S. l. leucomelaena.*

Sylvia l. somaliensis.—Populations from Somalia and Eritrea are easily recognizable from all others by the large amount of white on the outer pair of rectrices. No consistent difference was found in head coloration between these populations and other African populations or those from the Arabian Peninsula (cf. Meinertzhagen 1949).

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[1] Shirihai, H. 1988. A new subspecies of Arabian Warbler *Sylvia leucomelaena* from Israel.—Bulletin of the British Ornithologists' Club 108:64–68, has recently proposed the name *Sylvia leucomelaena negevensis* for the Arava population. A copy of the current paper was sent to Mr. Shirihai on 26 June 1987 for his comments. In subsequent correspondence he made no mention that a manuscript describing this subspecies was in preparation and never provided the reciprocal courtesy of reviewing it. His paper was received by the Bulletin of the British Ornithologists' Club on 10 August 1987.

Sylvia l. blanfordi.—Morphologically the Gebel Elba, Egypt, and Sudanese populations seem similar to one another, or differences are part of a north-south cline. The only exception is that Gebel Elba birds have distinctly longer exposed culmens than Sudanese birds; however, the degree of difference may be partially an artifact of the small number of Egyptian birds available for comparison. Egyptian and Sudanese birds tend to have a shorter gonys. Both of these populations have significantly less white on the outer pair of rectrices than those Somalian/Eritrean. No important difference was found in head coloration among any of the African populations.

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Appendix 1

Material of *Sylvia leucomelaena* Examined

Museum codes: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), Tring; HH, Private collection of Haim Hovel, Haifa; LSUM, Louisiana State University Museum, Baton Rouge; SGM, Sudan Government Museum, Khartoum; UMMZ, The University of Michigan Museum of Zoology, Ann Arbor; UTM, Zoological Museum, University of Tel Aviv, Tel Aviv; YPM, Yale Peabody Museum, New Haven; ZFMK, Zoologisches Forschungsinstitut und Museum Koenig, Bonn.

Israel.—Km 20 on Arava Road, UTM 8088, 8089; Yotvata, HH 82110, 82112, ZFMK 8416; Hatzeva, UTM 8153.

Saudi Arabia.—Al Jurf, BMNH 1936.6.29.20–23 (4); Ashaira (Asheira, Ushayeah), BMNH 1935.1.5.81–82 (2); Bir Askar, Taif Plateau, BMNH 1935.1.5.78–79 (2); Bir Braman (Burayman), 15 km NE Jidda, BMNH 1940.4.1.24; Birka, BMNH 1950.58.2; Farha, BMNH 1935.1.5.80; Hadda, Wadi Fatima, BMNH 1936.6.29.18–19 (2); Hamdha, upper Wadi Tathlith, BMNH 1937.4.17.275; Hejaz (al Hijaz), BMNH 1946.69.76–77 (2); Jidda (Jedda), 10 miles E., BMNH 1934.9.20.140–142 (3), 1937.12.26.15; Khadra, Najran, BMNH 1937.4.17.273, 1937.4.17.277; Madriga (Madrakah), nr. Jidda, BMNH 1965.M.13775; Wadi Hafra, 80 km NE Jidda, BMNH 1940.4.1.25; Wadi Harjab, Wadi Bisha, BMNH 1937.4.17.276, 1948.58.29; Wadi Hijla, BMNH 1946.69.78; Wadi Jaura, Tihama, Jizan, BMNH 1937.4.17.22; Wadi Krarrar, near Taif, BMNH 1949.5.33.

The Yemens.—Al Kubar (el Kebir), Amiri Dist., South Yemen, BMNH 1903.8.12.25, AMNH 608810; Dhala (Dthala), Amiri Dist., South Yemen, BMNH 1903.8.12.26, 1965.M.13777; Gerba, Amiri Dist., South Yemen, BMNH 03.8.12.21–24 (4), AMNH 608806 (type of *distincta*), 608807–809 (3); Habil, South Yemen, BMNH 1965.M.13776; Jajeilha, Yemen, AMNH 608811; Jebel Manif, north of Lahej, South Yemen, BMNH 1900.8.5.193; Lodar (Lawdar), South Yemen, BMNH 1965.M.13778; Ma'ir, Abian, South Yemen, BMNH 1900.8.5.194; Tullah, Hadhramaut, South Yamen, BMNH 1932.4.20.5; Wadi Awa, Hadhramaut, South Yemen, BMNH 1933.6.26.6; Wadi Khabb (Khubb), southeast Najran, Yemen, BMNH 1937.4.17.274; Wadi Thibi, South Yemen, BMNH 1937.6.5.81.

Oman.—Khadrafi, Jebel Qamr, Dhofar, BMNH 1977.1.10.

Somalia.—Berbera Plain, BMNH 98.7.27.80; Bihendula (Bikendula), AMNH 608789–90 (2); Burao (Buraa), BMNH 1923.8.7.3038; Dubar, AMNH 608803–805 (3), BMNH 1905.11.27.164–165 (2); Erigavo, BMNH 1965.M.13773, LSUM uncataloged (2); Galoli, BMNH 1923.8.7.3036; Gardo, BMNH 1945.10.11; Gidial (Gidil) Valley, Golis, AMNH 608800, BMNH 1923.8.7.3035; Las Khorai (Khoreh), AMNH 608791–792 (2); Mush Haled (Mush Aled, Musha Aled, Mash Caleed), Warsangli, 200 miles E. Berbera, AMNH 608793–794 (2), YPM 32258; Mundara (Mandara), BMNH 98.6.13.76 (type of *somaliensis*); Sogsode (Sogsoda, Suksodi, Sugsade), BMNH 1923.8.7.3037, 1925.11.20.26, AMNH 608795–797 (3); Waghar (Wagr, Wogr), AMNH 608801–802 (2), BMNH 1905.11.27.168–169 (2).

Eritrea.—near Massawa, BMNH 1952.25.19; Rairo, Habab, BMNH 69.10.16.85 (type of *blanfordi.*).

Sudan.—Erba Mountains, BMNH 97.10.15.3; Erkowit, BMNH 1915.12.24.719–720 (2), 1916.9.20.671, 1919.12.17.700–703 (3), SGM 686, 2034, 2773, 3286; Port Sudan, BMNH 1965.M.13774; Sinkat, BMNH 1919.12.17.683–699 (17).

Egypt.—Wadi Aideib, Gebel Elba, UMMZ 224089–091 (3); Wadi Akwamtra, Gebel Elba, UMMZ 224092; Wadi Kansisrob, Gebel Elba, UMMZ 224088.

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NEW SPECIES OF FOSSIL VAMPIRE BATS (MAMMALIA: CHIROPTERA: DESMODONTIDAE) FROM FLORIDA AND VENEZUELA

Gary S. Morgan, Omar J. Linares, and Clayton E. Ray

Abstract.—A new species of vampire bat is described from a partial skull and several postcranial elements from the early Pleistocene of Florida. Similar in size to the living *Desmodus rotundus,* it is considerably smaller than the only previously recognized species of North American fossil vampire, *D. stocki.* Characters that distinguish the new species include the large mastoid process, narrow occiput, reduced ventral flexion and posterior inflation of the braincase, and posteriorly directed foramen magnum. It occurs in fossil deposits ranging in age from approximately 1.8 to 1.0 million years (early to middle Irvingtonian), and is more than one million years older than any previously known vampire bat.

A second new species of giant vampire bat is described from two partial skeletons recovered from surficial deposits of uncertain Late Quaternary age in Cueva del Guácharo, Monagas, Venezuela. This new species is larger than any other described vampire and differs as well in its relatively slender and delicate skull, and mandible with straight ventral border and pockets behind incisors almost lacking. Skeletal fragments from caves in West Virginia and Yucatán represent vampires of similarly large size but undetermined affinities.

Fossil remains, undoubtedly in part at least of Recent age, of the common vampire, *Desmodus rotundus,* were recognized by Lund from caves near Lagoa Santa, Minas Gerais, Brazil, in the course of his explorations of 1835–1844 (Ray et al. 1988). Remains thought to be Recent in age have been assigned to *Desmodus rotundus* from three caves, and to *Diphylla ecaudata* from one cave, in Venezuela (Linares 1968, 1970). The new species described here is the first evidence of an extinct vampire in South America. Fossil vampires were first reported from North America in a footnote to a paper on a new species of Pleistocene terrestrial gastropod from a cinnabar mine near Terlingua, Texas (Cockerell 1930). This large extinct vampire bat was later described as *Desmodus stocki* (Jones, 1958) from deposits of late Pleistocene (Rancholabrean) age in San Josecito Cave, Nuevo Leon, northern Mexico. Gut (1959) described a second species, *D. magnus,* from the late Pleistocene Reddick 1 fauna, Marion County, Florida. Fossils of *Desmodus* from outside the Recent North American range of *D. rotundus* are known from late Pleistocene sites in northern Mexico, California, Arizona, New Mexico, Texas, Florida, West Virginia, and Cuba (Ray et al. 1988). Hutchison (1967) synonymized *D. magnus* with *D. stocki* on the basis of their similarity in size and other cranial features. Most recent workers have followed Hutchison in recognizing *D. stocki* as the only extinct late Pleistocene species in North America. Ray et al. (1988) mapped and briefly summarized all known fossil occurrences of vampire bats.

In Florida, *Desmodus stocki* has been recorded from four Rancholabrean vertebrate faunas (Ray et al. 1988). Most of these fossils were referred originally to *Desmodus magnus.* Over the past 20 years numerous early Pleistocene (Irvingtonian) vertebrate fossil sites have been discovered in peninsular Florida. Screenwashing for microvertebrates from these Irvingtonian localities has revealed the presence of a new species of *Desmodus* in three faunas: the early Irvingtonian Inglis 1A Local Fauna, Citrus County, and the middle Irvingtonian Haile 16A and Haile 21A local faunas, Alachua County. These fossils represent the oldest known vampire bats.

Meanwhile, in conjunction with field studies of bats and surveys of caves in Venezuela, Linares in 1965 recovered two geologically young fragmentary skeletons of a very large new species of vampire bat. Efforts by Linares and Ray to determine the affinities of this form led to comprehensive study of the fossil record of vampires and to comparison of the hard parts of the three living species. Our mutually overlapping and converging interests in fossil vampires have resulted in presentation of a synopsis of our findings (Ray et al. 1988) and in a more detailed review we have in progress. Delay in publication of that review has caused premature allusion in print to the new species from Florida and Venezuela. This, together with the intense current interest in vampires, has induced us to validate the names of the two new species without further delay.

The fossils utilized for this paper are deposited in the vertebrate paleontological collections of the Florida State Museum, University of Florida (UF) and the Florida Geological Survey (UF/FGS), also housed at the Florida State Museum; the Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution (USNM); Department of Vertebrate Paleontology, Los Angeles County Museum of Natural History (LACM); Sección de Paleobiología, Museo de Ciencias Naturales, Universidad Simón Bolivar, Caracas, Venezuela (MUSB). Recent comparative material is from the Division of Mammals, National Museum of Natural History, Smithsonian Institution (USNM), the Department of Mammalogy, American Museum of Natural History (AMNH), and the mammalogy collection of the Florida State Museum (UF). All measurements were taken with dial calipers and rounded to the nearest 0.1 mm. Descriptive morphological terms and cranial measurements follow DeBlase and Martin (1981).

Systematic Paleontology

Class Mammalia Linnaeus
Order Chiroptera Blumenbach
Family Desmodontidae Gill
Genus *Desmodus* Maximilian
Desmodus archaeodaptes, new species
Fig. 1

D. praecursor.—Ray et al., 1988:20 (nomen nudum).

Desmodus archaeodaptes.—Ray et al., 1988: 22 et sqq. (nomen nudum).

Holotype.—UF 94526, nearly complete braincase posterior to interorbital constriction, lacking only zygomatic arches, with associated left periotic. Collected by Lawrence H. Martin, Jr., in May 1983.

Type locality.—Haile 21A Local Fauna of early Pleistocene (middle Irvingtonian) age, located 4.6 km northeast of Newberry, Alachua County, Florida.

Referred material.—UF 94527, UF 94528, two proximal ends of left humeri from type locality; UF 40046, complete right humerus, from Inglis 1A Local Fauna of early Pleistocene (early Irvingtonian) age, located 3 km southwest of Inglis, Citrus County, Florida; UF 24206, distal end of left humerus and UF 40047, proximal end of left radius, from Haile 16A Local Fauna of early Pleistocene (middle Irvingtonian) age, located 5.8 km northeast of Newberry, Alachua County, Florida.

Etymology.—From the Greek *archaios,* ancient, old, and *daptes,* eater of blood by

Table 1.—Cranial and mandibular measurements of *Desmodus archaeodaptes, D. rotundus, D. stocki,* and *D. draculae.* Mean, standard deviation, observed range (in parentheses), and sample size are given for each measurement.

Species and locality	Total length of skull	Condylobasal length	Breadth of rostrum	Interorbital constriction	Zygomatic breadth
Desmodus archaeodaptes (UF 94526, holotype) Haile 21A Florida	—	—	—	5.8	12.4
Desmodus rotundus murinus Mexico	23.7 ± 0.44 (22.7–24.3) 30	21.2 ± 0.36 (20.5–21.8) 30	6.0 ± 0.21 (5.5–6.5) 30	5.5 ± 0.17 (5.1–5.8) 30	12.0 ± 0.29 (11.5–12.7) 30
Desmodus r. rotundus Chile and Paraguay	24.8 ± 0.53 24.1–25.5 10	22.3 ± 0.56 (21.5–23.3) 10	6.6 ± 0.28 (6.1–7.0) 10	5.7 ± 0.23 (5.4–6.0) 10	12.8 ± 0.28 (12.3–13.1) 10
Desmodus stocki San Josecito Cave Mexico	27.3 ± 0.52 (26.5–28.2) 6	24.5 ± 0.18 (24.1–24.7) 6	7.4 ± 0.16 (7.1–7.6) 6	6.1 ± 0.11 (5.9–6.2) 9	14.0 ± 0 (14.0) 2
Desmodus stocki Reddick Florida	—	—	—	6.1 ± 0.21 (5.8–6.3) 3	14.3 ± 0.20 (14.1–14.5) 2
Desmodus draculae (MUSB 152-85 PB, holotype; USNM 23568, paratype) Cueva del Guácharo, Venezuela	31.2, —	29.7, —	9.2, —	5.7, 6.7	—

sucking. The name refers to the fact that this is the oldest known species of vampire bat.

Diagnosis.—Differs from other known species of *Desmodus* in possessing broad plate-like mastoid process, narrower occiput, lateral connection of nuchal crest to paroccipital process; and from all except *D. draculae* in nearly vertical orientation of supraoccipital, lack of inflation and ventral flexion of posterior portion of braincase, and posteriorly oriented foramen magnum with rounded dorsal margin. *Desmodus archaeodaptes* differs from *D. rotundus* in presence of larger glenoid fossa, reduced postglenoid process, smaller occipital protuberance, and weakly inflated supraoccipital; from *D. stocki* in smaller size, longer and narrower braincase, weaker cranial crests, ventrally deflected paroccipital process, shallow basicranial pits separated by low indistinct ridge, and weakly inflated posteromedial process of basisphenoid; and from *D. draculae* in much smaller size.

Measurements.—See Tables 1 and 2.

Description and comparisons.—The braincase of the holotype of *Desmodus archaeodaptes* from Haile 21A is nearly complete posterior to the interorbital constriction. The zygomatic arches are missing except for the base of the right squamosal process. This skull is within the size range of Recent *D. rotundus* and is considerably smaller than that of *D. stocki* and *D. draculae* (see Table 1 and Fig. 1).

Desmodus archaeodaptes more closely resembles *D. rotundus* than *D. stocki* in certain cranial features: these include narrower more elongated braincase, reduced cranial crests, ventral deflection of the paroccipital

Table 1.—Continued.

Mastoid breadth	Breadth of braincase	Length of braincase	Height of braincase	Total length of mandible	Length of mandibular tooth row	Height of coronoid
12.4	12.3	17.2	12.0	—	—	—
12.5 ± 0.29 (12.0–13.1) 30	11.9 ± 0.24 (11.5–12.5) 30	16.9 ± 0.35 (16.4–17.9) 30	11.9 ± 0.39 (11.1–12.6) 30	15.3 ± 0.33 (14.5–16.0) 30	4.7 ± 0.14 (4.4–5.0) 30	6.1 ± 0.20 (5.6–6.5) 3
13.0 ± 0.22 (12.6–13.3) 10	12.6 ± 0.32 (12.1–13.0) 10	17.4 ± 0.33 (17.1–18.2) 10	12.3 ± 0.36 (11.9–12.6) 10	15.8 ± 0.40 (15.3–16.6) 10	4.8 ± 0.09 (4.7–4.9) 10	6.3 ± 0.26 (6.0–6.8) 10
14.1 ± 0.33 (13.5–14.5) 8	13.8 ± 0.20 (13.6–14.2) 11	19.2 ± 0.32 (18.7–19.7) 9	13.5 ± 0.17 (13.2–13.8) 10	—	—	—
14.4 ± 0.25 (14.1–14.7) 5	14.1 ± 0.22 (13.8–14.4) 4	19.6 ± 0.08 (19.5–19.7) 3	13.2 ± 0.19 (13.0–13.5) 4	17.4 ± 0.26 (17.0–17.6) 3	5.3 ± 0.10 (5.1–5.4) 16	6.7 ± 0.21 (6.2–6.9) 7
15.2, 15.5	14.8, 14.5	21.1, 22.4	14.8, 13.4	21.9, —	8.5, 8.3	9.4, —

process, weakly inflated posteromedial process of the basisphenoid, and shallow basicranial pits. There are also many characters that distinguish the skulls of *D. archaeodaptes* and *D. rotundus.* The occipital protuberance only slightly overhangs the occipital condyles in *D. archaeodaptes,* whereas in *D. rotundus* the braincase is expanded posteriorly and flexed ventrally so that the occipital protuberance occupies a more posteroventral position. The occipital protuberance is also larger in the living species and has a prominent posteriorly projecting process. In lateral view, the supraoccipital of *D. archaeodaptes* is nearly vertical, but in *D. rotundus,* because of inflation and ventral flexion of the braincase, it is tilted posteriorly. In the essentially unmodified braincase of *D. archaeodaptes* the foramen magnum faces posteriorly, whereas in *D. rotundus* it is oriented ventrally. The supraoccipital in *D. archaeodaptes* is essentially flat, but in *D. rotundus* the region along the midline between the foramen magnum and the occipital protuberance is noticeably inflated. The occiput of *D. archaeodaptes* is narrower and higher than in the Recent species. The occipital protuberance is more dorsad, and the nuchal crests (forming the lateral borders of the occiput) make a more acute angle in *D. archaeodaptes* than in *D. rotundus* because they connect laterally to the paroccipital processes rather than to the mastoid processes. Laterally, the nuchal crest turns abruptly ventrad in *D. archaeodaptes* and becomes confluent with the lateral edge of the paroccipital process; a weak secondary crest branches from the lateral edge of the nuchal crest and connects with the mastoid process. In *D. rotundus* the mastoidal connection is emphasized and the paroccipital connection is lost.

The braincase of *Desmodus stocki* is larger overall and relatively shorter, broader, and more globose than that of *D. archaeodaptes* and *D. rotundus,* but is intermediate between these smaller species in certain oth-

Table 2.—Measurements of the humerus of Recent and fossil *Desmodus.* Mean, standard deviation, observed range (in parentheses), and sample size are given for all measurements, except those taken from Hutchison (1967).

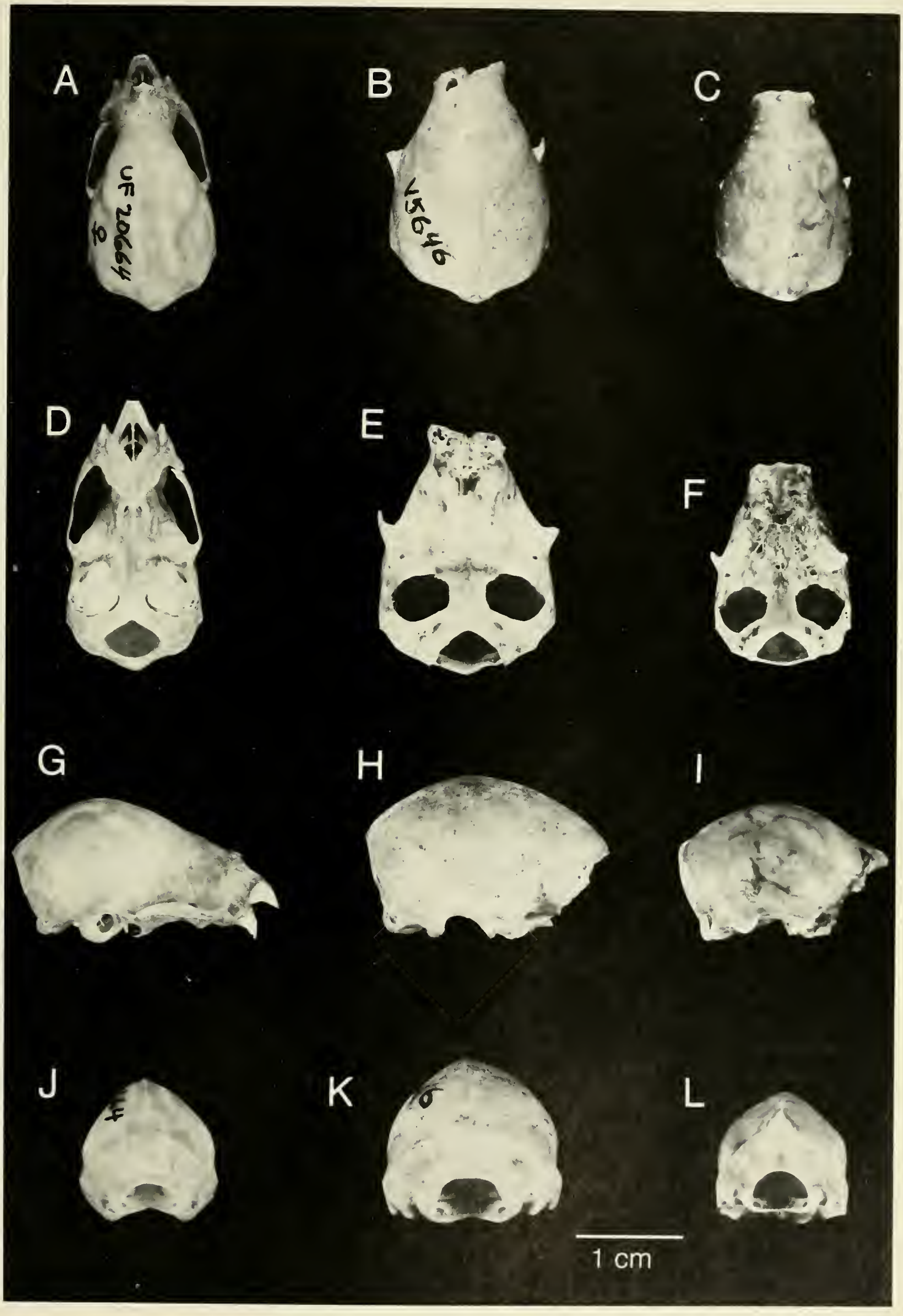
Species and locality	Total length	Proximal width	Distal width	Medial width of shaft
Desmodus archaeodaptes				
(UF 40046) Inglis 1A Florida	39.7	5.7	6.2	2.2
(UF 24206) Haile 16A Florida	—	—	5.9	—
(UF 94527) Haile 21A Florida	—	5.2	—	2.1
Desmodus rotundus	37.0 ± 2.33 (32.4–42.4) 19	4.9 ± 0.28 (4.4–5.6) 19	5.4 ± 0.30 (4.8–5.9) 19	2.1 ± 0.18 (1.7–2.4) 15
Desmodus stocki				
San Josecito Cave Mexico (from Hutchison, 1967)	43.6 (39.3–47.5) 42	6.3 (5.8–6.8) 47	6.8 (6.4–7.3) 52	2.5 (2.0–2.9) 56
Reddick Florida	41.8 ± 1.34 (39.4–44.3) 15	6.3 ± 0.16 (6.0–6.7) 38	6.8 ± 0.18 (6.4–7.2) 42	2.6 ± 0.11 (2.2–2.7) 42
Desmodus draculae (MUSB 152-85 PB, holotype) Cueva del Guácharo Venezuela	51.0 1	—	8.5 1	3.3 1

er characters. The posterior portion of the braincase of *D. stocki* is more inflated and the occipital protuberance and foramen magnum are located in a more ventral position than in *D. archaeodaptes.* Compared with *D. rotundus,* however, the braincase of *D. stocki* is not expanded as far posteriorly, nor does it attain the same degree of ventral flexion. The dorsal margin of the foramen magnum is rounded in *D. archaeodaptes* in contrast to its hexagonal shape in *D. stocki.* The cranium of *D. stocki* resembles that of the living species in the more ventral position of its occipital protuberance and the lateral connection of the nuchal crest to the mastoid process; these features give the occiput the appearance of being broader, but shallower, dorsoventrally than in *D. archaeodaptes.*

The articular surface of the glenoid fossa is relatively large in *Desmodus archaeodaptes* and *D. stocki,* and the postglenoid process is short and blunt. *Desmodus rotundus* has a smaller glenoid fossa and the postglenoid process is more elongated and triangular in shape. The smaller postglenoid

⟶

Fig. 1. Skulls of vampire bats in dorsal (A–C), ventral (D–F), right lateral (G–I), and posterior (J–L) aspect. A, D, G, J, *Desmodus rotundus,* UF 20664, Recent, Paraguay; B, E, H, K, *Desmodus stocki,* UF/FGS 5646, Rancholabrean, Reddick 1, Florida; C, F, I, L, *Desmodus archaeodaptes,* UF 94526 (holotype), Irvingtonian, Haile 21A, Florida. Scale is one cm.


A
B
C
UF 20664 ♀
V5646
D
E
F
G
H
I
J
K
L
1 cm

process of *D. archaeodaptes* and *D. stocki,* coupled with the larger articulating surface for the mandible, suggests that these extinct species may have had somewhat greater freedom of movement of the lower jaw than *D. rotundus.* The posteromedial process of the basisphenoid is weakly developed in the two smaller vampires, but is strongly inflated in *D. stocki.* The basicranial pits located anterior and medial to the tympanic cavity are barely noticeable depressions in *D. archaeodaptes,* but are larger, deeper, and extend farther posteriorly in *D. stocki.* In the larger species these pits are separated by a thin, knife-like ridge of bone that extends posteriorly to a point about halfway between the anterior and posterior edges of the tympanic cavity. This ridge is low and indistinct in *D. archaeodaptes* and disappears at the anterior edge of the tympanic cavity leaving the basioccipital almost perfectly flat. The basicranial pits and ridge are intermediate in their development in *D. rotundus.* The paroccipital process is ventrally deflected in *D. archaeodaptes* and *D. rotundus,* but oriented posteriorly in *D. stocki.* The broad ventrally rounded mastoid process of *D. archaeodaptes* is larger than that of *D. stocki* or *D. rotundus.*

The total length of the complete humerus from Inglis 1A referred to *Desmodus archaeodaptes* is within the observed range of humeri of Recent *D. rotundus,* although it is longer than any humerus measured of Middle American specimens referred to *D. rotundus murinus* (Table 2). The proximal and distal widths of this specimen slightly exceed those measurements in the same sample of *D. rotundus.* The length of the Inglis humerus barely overlaps the lower end of the range of variation of *D. stocki* humeri from Reddick 1C, while the proximal and distal widths are less than those for any humerus of *D. stocki* measured (Table 2). Two proximal ends of humeri from Haile 21A and a single distal end from Haile 16A are slightly smaller than the humerus from Inglis 1A, but are well within the observed range of measurements for Recent *D. rotundus.* There are no apparent characters, other than size, that differentiate the humeri of *D. rotundus, D. archaeodaptes,* and *D. stocki.*

Geologic age and localities.—Desmodus archaeodaptes is described on the basis of six specimens from three localities in northern peninsular Florida, all of which are early Pleistocene (Irvingtonian) in age. Biostratigraphic correlations with the North American Land Mammal biochronology establish Inglis 1A as very early Irvingtonian in age (between about 1.8 and 1.5 Ma), while Haile 16A and Haile 21A are middle Irvingtonian (between about 1.5 and 1.0 Ma). The oldest previously recorded vampire bats were samples of *D. stocki* from the late Pleistocene (early or middle Rancholabrean) Arredondo 2A and Reddick 1A, 1B, and 1C faunas, also from northern Florida. With the exception of the probably Recent remains from San Miguel Island, all fossils of *D. stocki* from the western United States and northern Mexico are latest Pleistocene (late Rancholabrean) in age (Kurten & Anderson 1980, Ray et al. 1988), a time interval during which *Desmodus* appears to have been absent from Florida (Morgan 1985).

Fossil sites representing former caves, fissures, and sinkholes are common in the karst terrain of northern peninsular Florida. Most of these sites are clastic infillings deposited in solution features developed in the soft marine limestones of the upper Eocene Ocala Group. These fossiliferous terrestrial sediments are most often exposed by commercial limestone mining. Many Florida State Museum vertebrate fossil sites are identified by numbers and letters following the general locality name (e.g., Haile 21A). The name (e.g., Haile) refers to the geographic location of the site, the number identifies the particular limestone quarry or specific area in which the site is (or was) located, and the letter refers to individual fossil deposits within one quarry or specific area. Even though two or more fossil sites may be found in the same limestone quarry, it cannot be assumed without strong evidence that they are necessarily close in age or formed through similar depositional processes.

The Inglis 1A Local Fauna was collected from the north bank of the now-defunct Cross Florida Barge Canal in Citrus County, Florida, 3 km SW of Inglis (29°01'N, 82°42'W), SE ¼, SE ¼, Sec. 9, T17S, R16E, Yankeetown 7.5 minute quadrangle, U.S. Geological Survey (1955). The fossiliferous sediments, now completely excavated, consisted of alternating layers of sand and clay filling a large solution cavity in the Eocene Inglis Formation. The geology and stratigraphy of Inglis 1A were discussed by Klein (1971). A diverse chiropteran fauna occurs at Inglis 1A supporting geological evidence that this deposit represents a former cave. Comprehensive studies have been conducted on the birds (Carr 1980) and snakes and lizards (Meylan 1982) of this fauna, and a list of the mammals was given by Webb & Wilkins (1984). Inglis 1A contains mammals found in both late Blancan and early Irvingtonian faunas in Florida, including *Glyptotherium* cf. *G. arizonae* (Gillette & Ray 1981), *Megalonyx leptostomus* (McDonald 1977), *Trigonictis* cf. *T. macrodon* (Ray et al. 1981), *Chasmaporthetes ossifragus* (Berta 1981), and *Capromeryx arizonensis* (Klein 1971), but lacks forms restricted to the Blancan, including *Borophagus, Nannippus phlegon,* and *Equus* (*Dolichohippus*). An early Irvingtonian age for this fauna is further indicated by the presence of *Geomys propinetis* (Wilkins, 1984) and *Sigmodon curtisi* (Martin 1979).

The Haile 16A Local Fauna was discovered in a limestone quarry 5.8 km NE of Newberry, Alachua County, Florida (29°41'N, 82°34'W), NE ¼, NE ¼, Sec. 25, T9S, R17E, Newberry 7.5 minute quadrangle, U.S. Geological Survey (1968). The fossil vertebrates at this site occurred in a large fissure with massive dark silty clays. The depth, areal extent, and stratigraphy of this deposit could not be determined accurately as it was destroyed by limestone quarrying operations before it could be excavated. Although all fossils from Haile 16A were obtained by screenwashing spoil piles, there is no evidence that the fauna is mixed. No list of the mammalian fauna from Haile 16A has been published; however, a few of the taxa have been studied, including *Trigonictis* (Ray et al. 1981), *Geomys* (Wilkins 1984), *Erethizon* (Frazier 1981), and *Sigmodon* (Martin 1979). According to Martin, *Sigmodon libitinus,* a species known only from Haile 16A, is intermediate between *S. curtisi* from the early Irvingtonian Inglis 1A fauna and *S. bakeri* from the late Irvingtonian Coleman 2A fauna. A middle Irvingtonian age for Haile 16A is also indicated by the presence of *Megalonyx wheatleyi* (McDonald 1977), *Tapirus haysii,* and an early species of *Pitymys,* and by the stage of evolution of *Holmesina.*

The Haile 21A Local Fauna is located 4.6 km northeast of Newberry, Alachua County, Florida (29°41'N, 82°33'W), SE ¼, NE ¼, Sec. 26, T9S, R17E, Newberry 7.5 minute quadrangle, U.S. Geological Survey (1968). This site was discovered in 1983 by Eric Kendrew and was worked by the Florida State Museum between October 1983 and March 1984. Fossils were initially recovered from Haile 21A after the land surface had been graded with heavy equipment in preparation for mining. The fossiliferous sediments consist of clays, sands, and limestone breccias filling a former cave or sinkhole roughly circular in outline, some 10 m in diameter and 5 to 7 m in depth. There are no previous published references to the Haile 21A vertebrate fauna. The fauna is overwhelmingly dominated by a large species of *Platygonus,* similar to samples of *Platygonus* from other Irvingtonian sites in Florida. The occurrence of *Smilodon gracilis* suggests a pre-late Irvingtonian age for Haile 21A (Berta 1987), and the presence of *Tapirus haysii* and the association of *Canis edwardii* and *C. armbrusteri* are in-

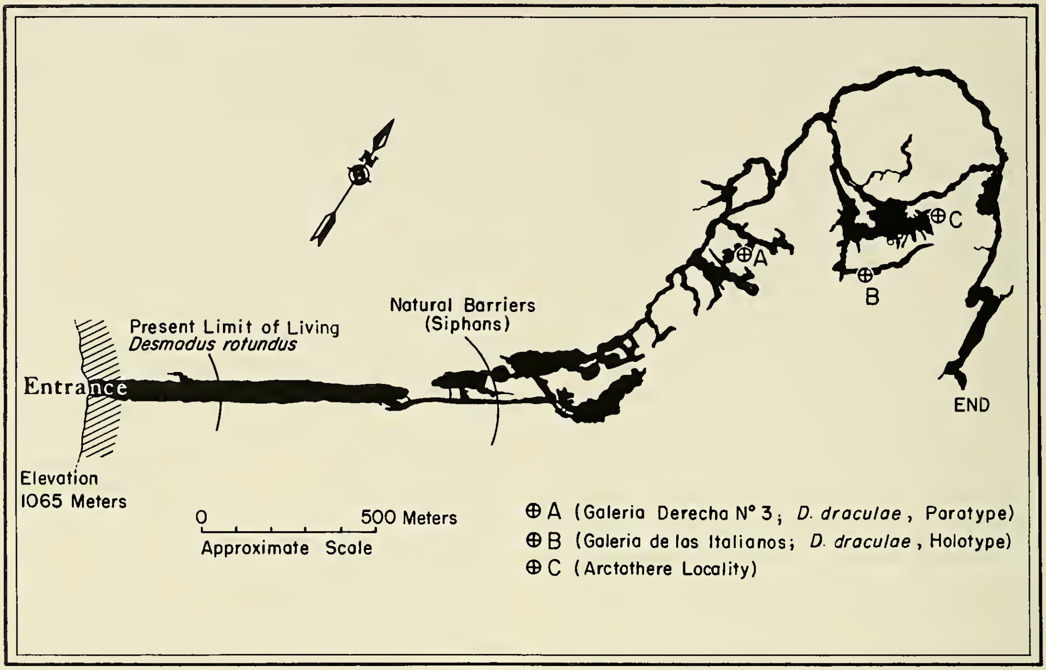


Fig. 2. Sketch map of Cueva del Guácharo, Monagas, Venezuela, the type locality of *Desmodus draculae*. In part after Anonymous, 1968, with modifications and additions by Linares.

dicative of Florida middle Irvingtonian faunas.

Desmodus draculae, new species
Fig. 2–8

"Una forma de *Desmodus* posiblemente del Pleistoceno . . . mayor que todas las conocidas . . . una nueva especie."—Linares 1968:138–139.

"A new species of *Desmodus* from Venezuela."—Martin 1972:326.

"A new species of fossil vampire bat from Venezuela."—Wołoszyn & Mayo 1974: 260.

Desmodus sp.—Smith, 1976:66.

"Fossil *Desmodus* larger than all previously known forms."—Greenhall et al. 1983:1.

Desmodus draculae.—Linares, 1987:11 (figured on p. 10).—Ray et al., 1988:20 et sqq., figs. 2–5 (nomen nudum).

Holotype.—MUSB 152-85 PB, skull, mandible, skeletal parts. Skull lacks zygomatic arches and all teeth save incisors; mandible essentially complete, retains right canine and all postcanine teeth and left P_4; skeletal parts include left humerus, distal two-thirds (with ulnar sesamoid in place) and head of right humerus, distal half or more of left and right radii, with vestiges of coossified ulnae, and three vertebrae. All elements white in color, thoroughly leached and chalky in texture though retaining sharp surface detail, except for the radii, which are in part deeply pitted. Collected by Omar J. Linares, 10–18 Apr 1965.

Type locality.—Cueva del Guácharo, District of Caripe, State of Monagas, Venezuela (Fig. 2), 10°10′27″N, 62°33′07″W. This cave has been described, illustrated, and mapped by the Sociedad Venezolana de Espeleología in its Boletín (Anonymous 1968, 1971). The cave is at least 9425 meters long, of which the first 1041 meters (known as the Tourist Zone) is the more readily accessible, and is terminated by nat-

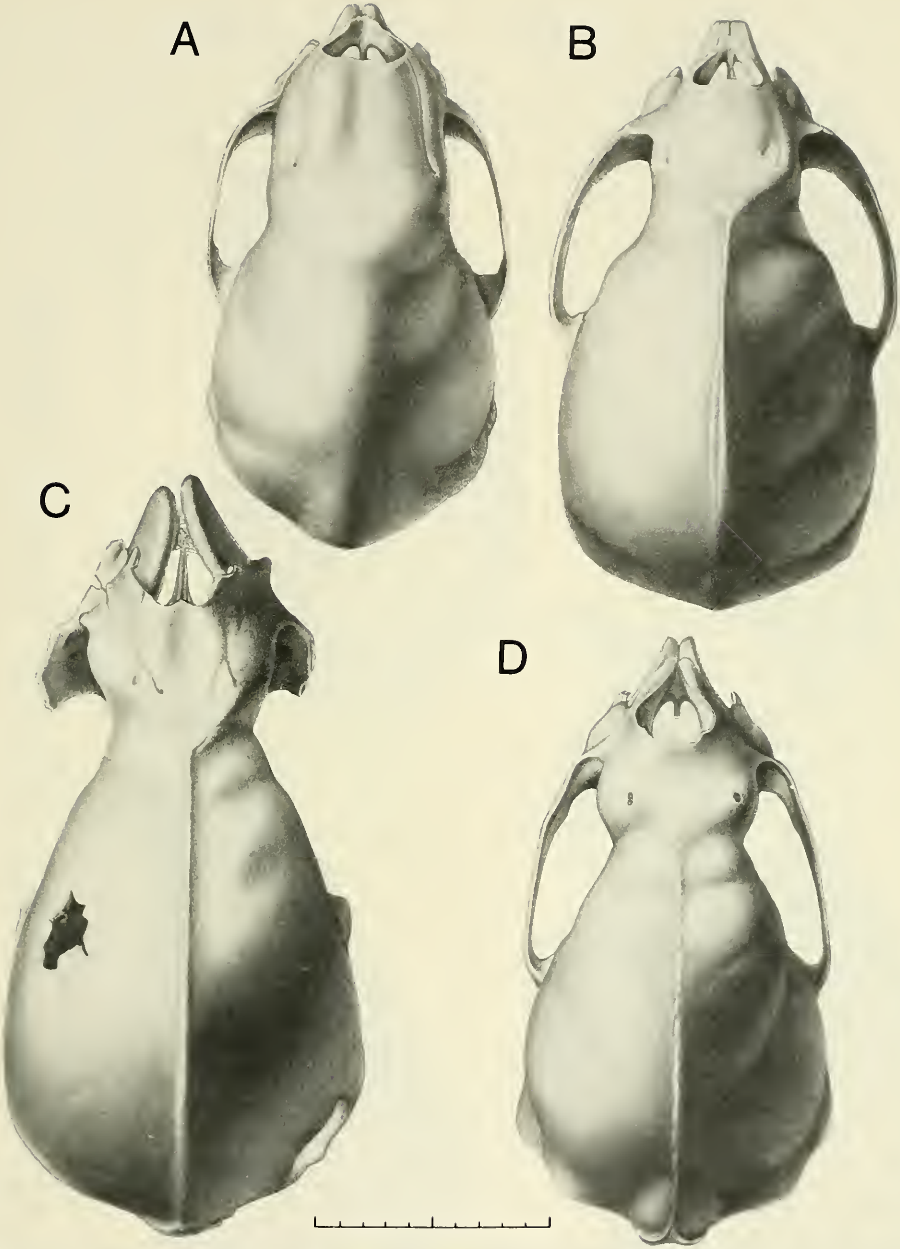


Fig. 3. Skulls of vampire bats in dorsal aspect: A, *Diphylla ecaudata,* USNM 269507: B, *Diaemus youngi,* AMNH 175654; C, *Desmodus draculae,* holotype, MUSB 152-85; D, *Desmodus rotundus,* USNM 114977. Scale is one cm.

ural barriers in the form of siphons. The type specimen of *D. draculae* was collected at the surface on the floor of the Galería de los Italianos, locality B on our sketch map (Fig. 2), at least 1973 meters from the present entrance of the cave, and some 1400 meters beyond the limit of living *D. rotundus.*

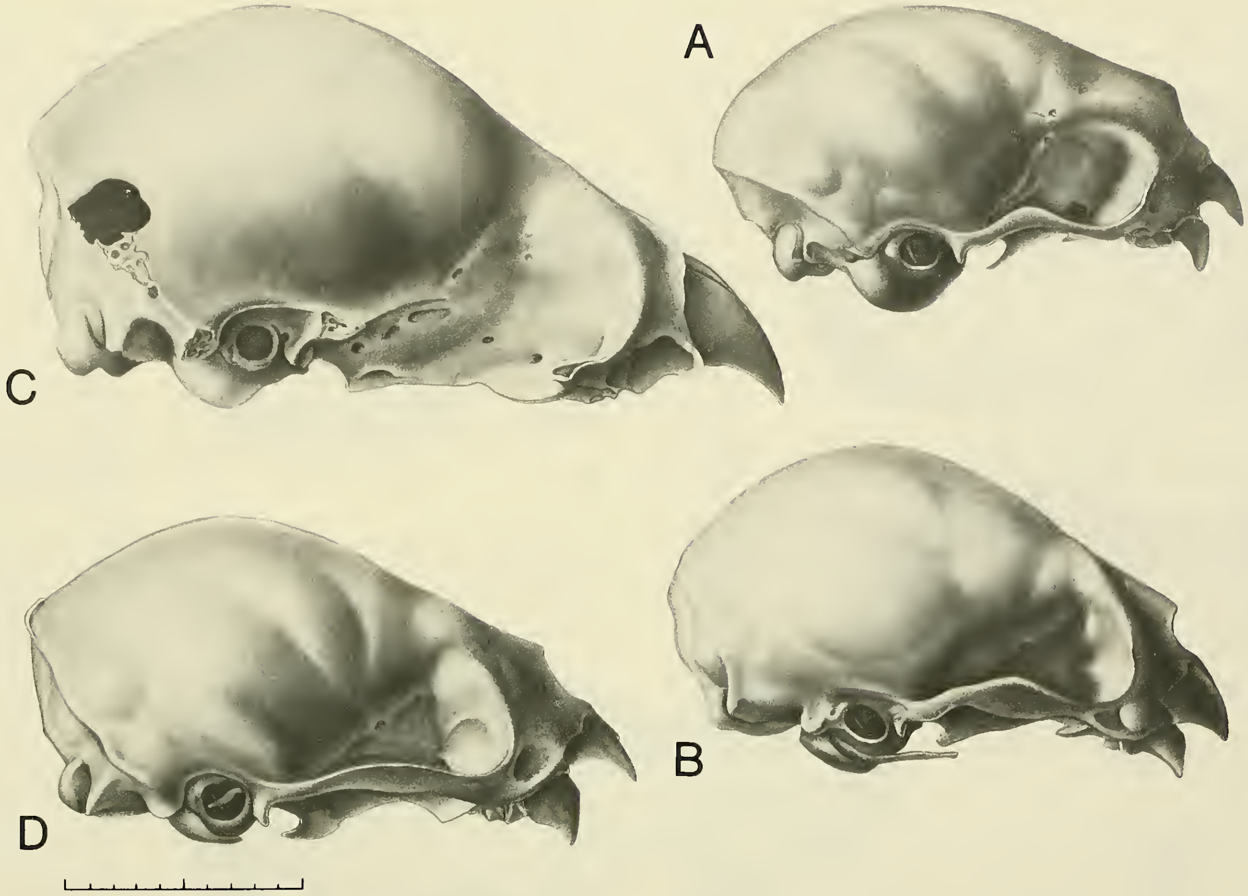


Fig. 4. Skulls of vampire bats in lateral aspect: A, *Diphylla ecaudata,* USNM 269507; B, *Diaemus youngi,* AMNH 175654; C, *Desmodus draculae,* holotype, MUSB 152-85 PB; D, *Desmodus rotundus,* USNM 114977. Scale is one cm.

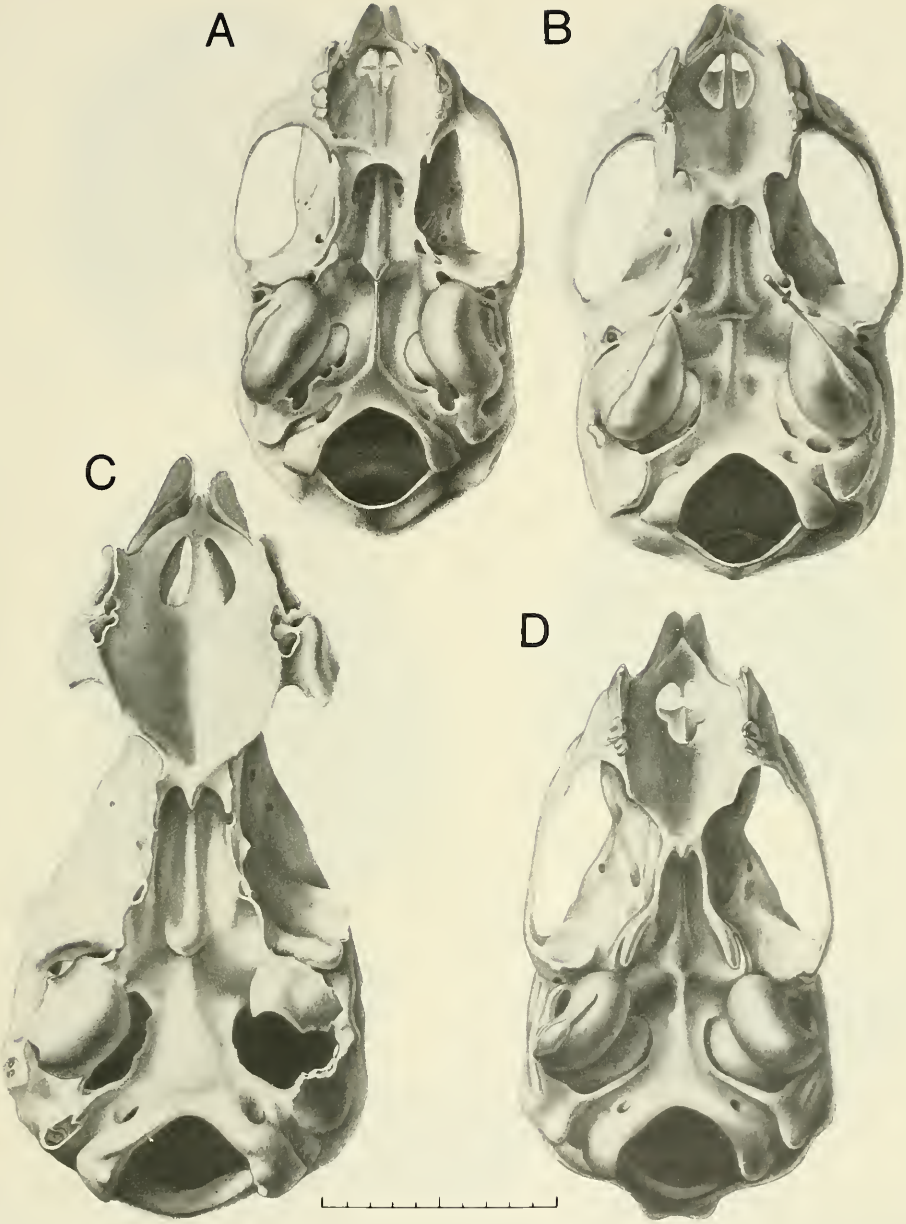


Fig. 5. Skulls of vampire bats in ventral aspect: A, *Diphylla ecaudata,* USNM 269507; B, *Diaemus youngi,* AMNH 175654. C, *Desmodus draculae,* holotype, MUSB 152-85 PB; D, *Desmodus rotundus,* USNM 114977. Scale is one cm.

Paratype.—USNM 23568, incomplete skull, lacking most of facial region and all teeth; incomplete mandible lacking posterior ends of rami and all teeth except base of right canine; postcranial fragments, including fragment of right scapula, and fragments of left and right humeri, radii (with coossified portions of ulnae), and femora.

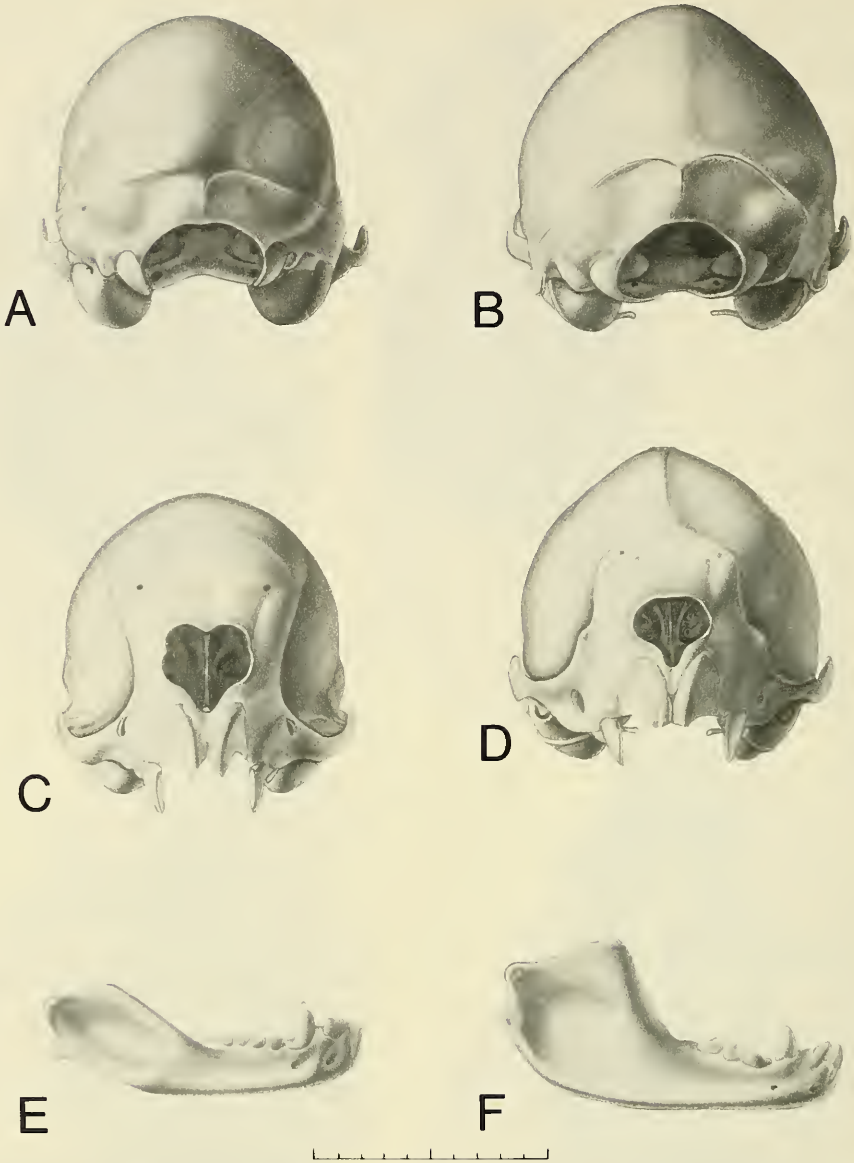


Fig. 6. Skulls and jaws of vampire bats. Skulls in posterior aspect: A, *Diphylla ecaudata,* USNM 269507; B, *Diaemus youngi,* AMNH 175654. Skulls in anterior aspect: C, *Diphylla ecaudata,* USNM 269507; D, *Diaemus youngi,* AMNH 175654. Right mandibular rami in labial aspect; E, *Diphylla ecaudata,* USNM 269507; F, *Diaemus youngi,* AMNH 175654. Scale is one cm.

Preservation similar to that of holotype, but not as good. Two proximal ends of right radii indicate still another individual. Collected by Omar J. Linares, 10–18 Apr 1965, at locality A, Cueva del Guácharo (Fig. 2).

Etymology.—The specific epithet of this largest known chiropteran vampire commemorates Count Dracula, the greatest human vampire of folklore (Wolf 1975).

Diagnosis.—A *Desmodus* larger than any other known form (greatest length of skull more than 31 mm vs. 27.4 maximum for *D. stocki,* length of humerus 51 mm vs. 47.5 maximum for *D. stocki*), but skull more

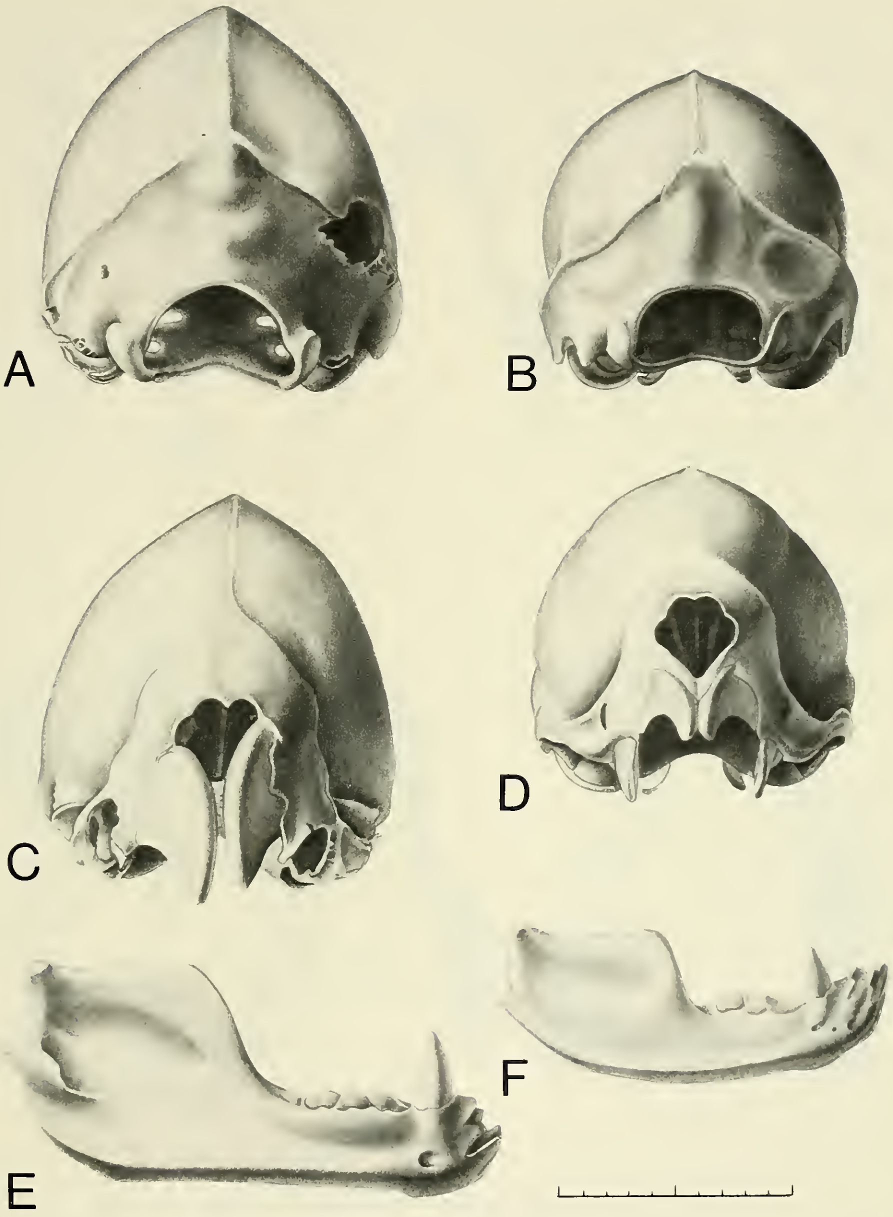


Fig. 7. Skulls and jaws of vampire bats. Skulls in posterior aspect: A, *Desmodus draculae,* holotype, MUSB 152-85 PB; B, *Desmodus rotundus,* USNM 114977. Skulls in anterior aspect: C, *Desmodus draculae,* holotype, MUSB 152-85 PB; D, *Desmodus rotundus,* USNM 114977. Right mandibular rami in labial aspect: E, *Desmodus draculae,* holotype, MUSB 152-85 PB; F, *Desmodus rotundus,* USNM 114977. Scale is one cm.

slender and delicate. Mandible with ventral border straight in lateral aspect and with pockets behind incisors virtually nonexistent.

Measurements.—See Tables 1 and 2.

Description and comparisons.—Except as otherwise indicated here, characters of skull of *Desmodus draculae* essentially as in *D. rotundus.* Skull long and narrow; facial region even more reduced; interorbital con-

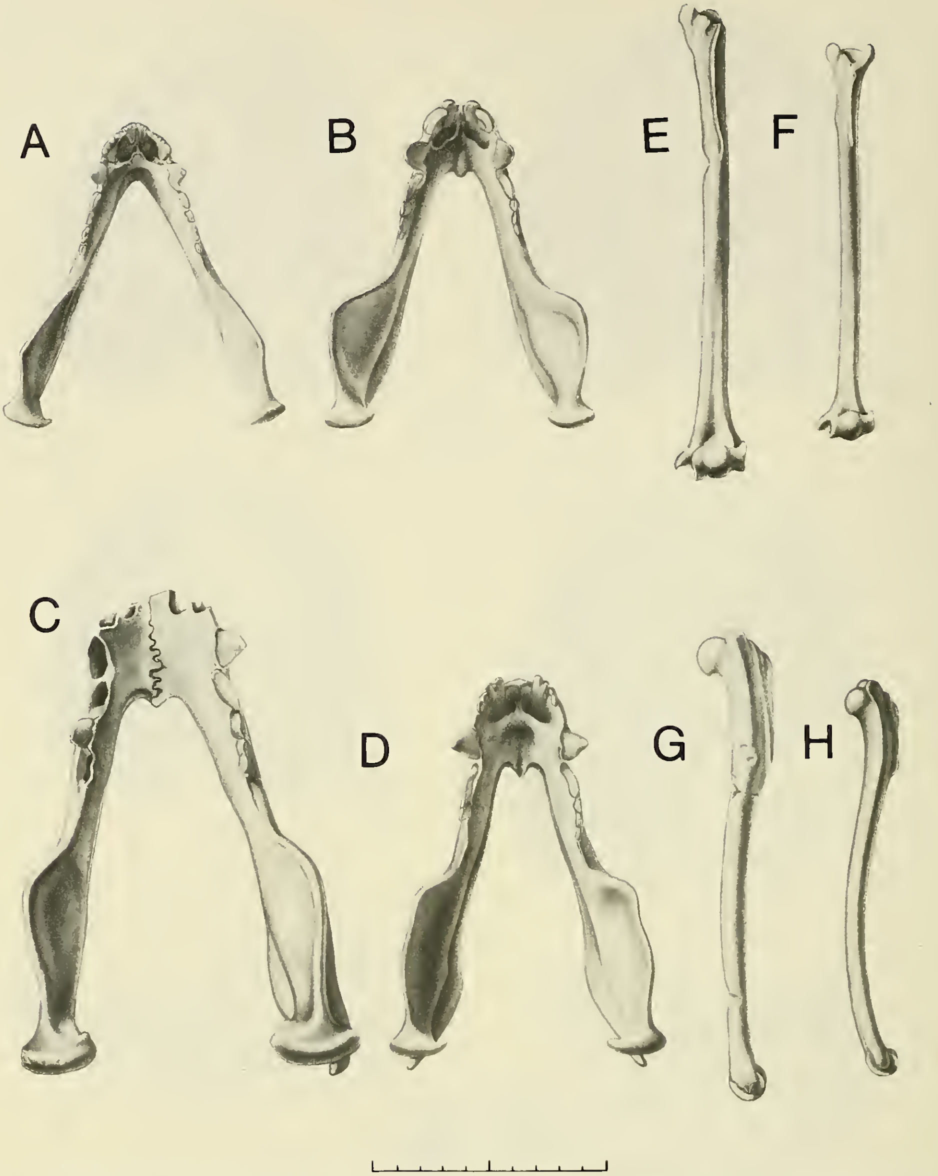


Fig. 8. Jaws and humeri of vampire bats. Mandibles in dorsal aspect: A, *Diphylla ecaudata,* USNM 269507; B, *Diaemus youngi,* AMNH 175654; C, *Desmodus draculae,* holotype, MUSB 152-85 PB; D, *Desmodus rotundus,* USNM 114977. Left humeri in cranial aspect: E, *Desmodus draculae,* holotype, MUSB 152-85 PB; F, *Desmodus rotundus,* USNM 114977. Left humeri in medial aspect; G, *Desmodus draculae,* holotype, MUSB 152-85 PB; H, *Desmodus rotundus,* USNM 114977. Scale is one cm, pertaining to A–D. Length of E and G is 51 mm, and F and H, 42.1 mm.

striction even farther forward and relatively greater; zygomatic ramus of maxilla directed more posteriad; occipital margin less clearly lyriform, with only suggestion of median lambdoidal extension; nasals even more reduced and depressed; maxillae scarcely expanded lateral to nasals. In lateral aspect, rostrum even more upturned and nares even more dorsally directed than in *D. rotundus*; dorsal profile of skull slopes forward from high braincase on a smooth line, uninterrupted by the slight nasal projection seen in *D. rotundus*. In ventral aspect, bullae are seen to be still more reduced than in *D. rotundus*, and are firmly coossified with skull anteriorly and posteriorly (as seen posteriorly in *Diphylla ecaudata*); palate longer and narrower, incisive foramina smaller than in *D. rotundus*.

Mandible also as in *D. rotundus* except as indicated here. Pockets behind incisors for reception of tips of upper incisors hardly discernible. Tips of upper incisors apparently would have rested medial to inner lower incisors, not in part behind them. In lateral aspect, ventral border of mandible quite straight, not curved as in *D. rotundus*; posteriorly it curves abruptly dorsad toward angular process. Posterior part of mandible overall resembles that of *Diaemus youngi* rather than *Desmodus rotundus*.

The postcranial parts preserved exhibit few distinctions from *Desmodus rotundus* and *D. stocki* other than larger size and concomitant robustness. The entepicondylar process of the humerus is more slender in proximodistal expansion than is that of *D. rotundus* and *D. stocki*. Although all specimens of the radius and ulna are incomplete, deeply pitted, and poorly preserved, it does appear that the shaft of the ulna distal to its coossification with the radius is more reduced than in *D. rotundus* and *D. stocki*. In none of the specimens can the ulnar shaft be traced with certainty far beyond the point of fusion; additional, better-preserved specimens will be needed to resolve the point.

A few fragments each from cave deposits in Yucatán and West Virginia represent large vampires of uncertain affinities, but possibly related to *D. draculae* (Ray et al. 1988).

Geologic age.—Quaternary. Unfortunately there is little basis on which to suggest an age for this material. The remoteness of the site within the cave, the occurrence of an arctothere in the same sector (Fig. 2, locality C), and the presumed extinct status of the species, all suggest an early, possibly late Pleistocene, age. The rotten condition of the bones and occurrence at the surface in a wet, active cave, in the same sector with similarly preserved remains of *Desmodus rotundus* and *Diphylla ecaudata*, are more consistent with a late, possibly Recent age. Only additional discoveries of fossils in a more revealing geologic context, or of living *D. draculae*, will resolve the problem.

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STUDIES IN THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE) IV. THE NEW GENUS, *LESSINGIANTHUS*

Harold Robinson

Abstract.—The genus *Lessingianthus* is described as new for a series of 101 neotropical species typified by *Vernonia buddleiifolia.* The typical subgenus is characterized by pollen with type B areolation and has a few species with type D pollen. A second subgenus, *Oligocephalus,* is established for three species having type C pollen areolation. The genus contains some of the species previously placed in the *Vernonia* series Buddleiifoliae, Brevifoliae, Macrolepidae, Remotiflorae, and Flexuosae. The members of the new genus have consistently lophate pollen, as do members of the related genus *Lepidaploa,* but the new genus lacks the rhizomatous condition of the pollen crests, lacks the basal node of the style, lacks glands on the achenes, and often has pedunculate heads. *Lessingianthus myrsinites,* is described as new, using an apparently unpublished species name of Ekman.

The present paper is the fourth in a series of seven devoted to the study of the neotropical *Lepidaploa* complex (Robinson 1987a, b, c, 1988). The element from the broad concept of *Vernonia* treated herein is the largest in the series other than *Lepidaploa* itself. My interest in the group first developed during a study of style bases in the Vernonieae, which demonstrated that the members of the present group lacked a node. Interest was increased by the realization that many species lacking nodes were of a group referred to in prior treatments of *Vernonia* as the section Lepidaploae Macrocephalae (Baker 1873). The fact that most species of the group have distinctive, large, lophate pollen (Jones 1979b), and the recent discovery of non-rhizomatous crests on the pollen grains has led to the conclusion that the group should be recognized as a new genus, herein named *Lessingianthus.*

Prior taxonomic treatments of *Vernonia* sensu lato have provided very imperfect approximations of the group treated here as *Lessingianthus.* Furthermore, the species were always included within the also imperfectly defined *Lepidaploa* subgroup of *Vernonia.* Both the sections Lepidaploae Macrocephalae of Baker (1873) and the series *Buddleiifoliae* of Jones (1982) were recognized on the basis of the relatively large size of the heads in many of the species of the group. Although large heads remained a prime distinction of the group for Jones (1982), the 22 species included in his comparatively refined treatment did not all have large heads. Subsequently, relationships have been traced to species included by Jones in his series Brevifoliae, Macrolepidae, Remotiflorae, and Flexuosae. In most of these taxonomic series, the members of *Lessingianthus* were intermixed with species placed in this series of studies in the related genus *Lepidaploa.* It is the accurate delimitation of *Lessingianthus* from *Lepidaploa* that is the primary aim of the following discussion. Four characters are most instructive in this: the presence or absence of a basal stylar node, the pollen structure, the form of the inflorescence, and the form of the involucre. Each of these will be discussed separately.

Basal Stylar Node

The presence of basal stylar nodes has been noted in various Asteraceae since at least the work of Cassini (1818), and they have been found taxonomically useful in some groups such as the Eupatorieae (Robinson & King 1977, King & Robinson 1987). Nodes seem to have a function in species of the tribe Heliantheae where they expand belatedly and tear the corolla base loose from the achene. In other tribes such as the Eupatorieae and Vernonieae, however, there is no function sufficiently important to prevent variability within the groups.

In the Vernonieae, the stylar node appears basic for the tribe, but seems to differ in commonness in the Eastern and Western Hemispheres. A highly developed node, such as that in the African-Indian Ocean genus *Distephanus* (Robinson & Kahn 1986), is otherwise found in comparatively few members of the tribe in the Eastern Hemisphere, where most Vernonieae lack nodes. In the Western Hemisphere, however, a stylar node is much more widely distributed and its absences appear to be more significant. The distribution of the character has been surveyed and has yielded some interesting results.

In the Western Hemisphere, the stylar node is lacking or poorly differentiated in a few small groups such as *Lepidonia* and *Stramentopappus* (Robinson & Funk 1987) in the *Leiboldia* group, and in *Stenocephalum* and *Chrysolaena* in the *Lepidaploa* group (Robinson 1987a, 1988), but it is well-developed in the genus *Lepidaploa* itself. The node is present in most other elements of *Vernonia* s.l., but is again lacking in a series of species traditionally placed in the genera *Eremanthus* and *Lychnophora* of the Lychnophorinae. In the latter group, the lack of a basal node correlates with the rather unique variation from the common cymose maturation pattern of the heads (Robinson 1980a). All these groups give the impression of many separate losses of a basal stylar node. Each loss seems correlated with other characters that favor recognition of the groups at generic or higher levels.

The essential lack of a basal stylar node in *Lessingianthus* contrasts strongly with the rather marked structure seen in almost all members of the related *Lepidaploa.* In the species of *Lessingianthus,* there is no enlargement whatsoever, and there may or may not be a sclerified ring. The sclerified ring may appear enlarged when the softer upper tissue has collapsed. Some species included here, such as *Vernonia regis* and *V. brevifolia,* seem to have a slight but distinct enlargement at the base of the style, but fully soaked material of styles shows the lower shaft equals the sclerified ring in width. The ring differs from that of *Lepidaploa* by its slight angle and the wide area of attachment that remains inside the ring. In *Lepidaploa* the sclerified surface cuts under the base of the style and leaves a very narrow area of attachment.

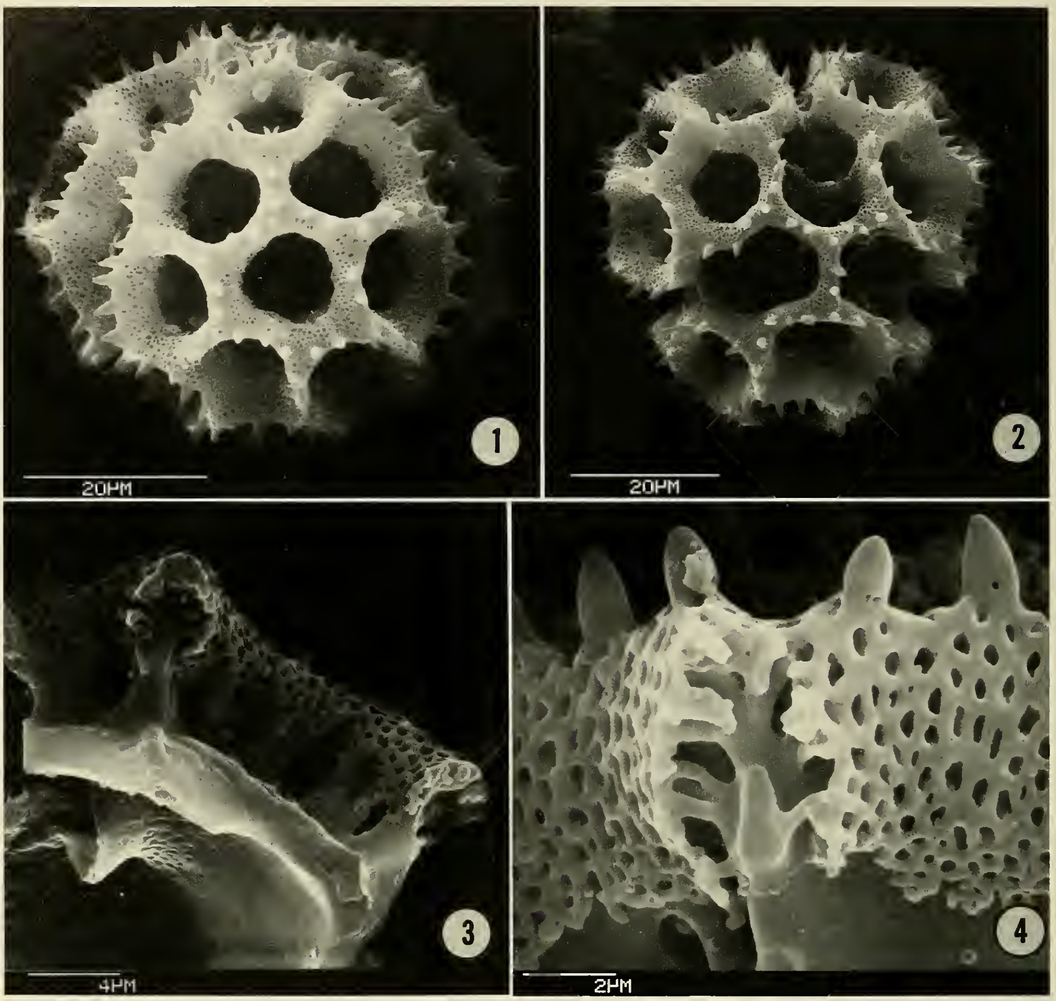
Immaturity of style bases may lead to misinterpretation, but mistakes in observation are usually caused by failure to extract the complete style. The typical *Lessingianthus* style base closely resembles a broken *Lepidaploa* style base. It should be noted that *Lessingianthus* style bases may be distinguishable even from broken bases of *Lepidaploa* because they are often larger.

Pollen

Two aspects of the pollen of *Lessingianthus* are significant for taxonomic discrimination. The pollen in both *Lessingianthus* and *Lepidaploa* is lophate with crests forming regular patterns. Regular patterns occur widely in both Eastern and Western Hemisphere Vernonieae, and they are regarded here as primitive in the tribe. The non-lophate types are regarded as reversions. The lophate types in both hemispheres show the perforated tectum restricted to the crests (Figs. 1–16) or completely lacking. The crests of the pollen of Eastern Hemisphere species and of genera such as *Stokesia, Mattfeldanthus,* and *Lessingianthus* from the Western Hemisphere have stout, high baculae separate from the point of attachment on the footlayer to the point above where they join the ridge of the crest (Figs. 3, 7, 9, 10, 15). This condition appears ancestral. The crests in the related *Lepidaploa* show a condition previously described as "rhizomatous" (Robinson 1987a, b, c), where the baculae under the crests are joined into a transverse basal rhizome and where the attachment of the rhizome to the footlayer is comparatively weak. The drawing by Stix (1960) of her general *Vernonia* type pollen seems to show this rhizomatous structure. If so, her inclusion of the *Vernonia argyrophylla* type pollen under this category was an error. The "rhizomatous" type of crest has a tendency to peel away from the pollen grain rather easily, a trait that can best be seen under SEM but which can also be seen under the light microscope. The *Lepidaploa*-type rhizomatous crest is reviewed more fully in the treatment of *Lepidaploa.* Only a few Brasilian species in *Lepidaploa,* mostly those having type D pollen, have an intermediate development of the rhizomatous character. Pollen with rhizomatous crests must be regarded as a restricted type within the tribe, which probably evolved only once. The precise form is known only in the Neotropical members of the tribe. There is reason to believe that all other genera characterized by such pollen, e.g., *Stenocephalum* (Robinson 1987a), and *Echinocoryne* (Robinson 1987b), are related directly to *Lepidaploa,* and one other occurrence of such pollen in *Eirmocephala* may be derived from an intergeneric hybridization involving *Lepidaploa* (Robinson 1987c). Because of the close relationship among the groups with such pollen, it is possible to conclude that the rather closely related *Lessingianthus* departs phyletically from a point slightly below the origin of the "rhizomatous" apomorphy. The pollen of *Lessingianthus* could be seen as being of a more ancestral type at the same time the style base is of a more derived type. It is possible that the crest structure has undergone reversals in the evolution of the group, but everything observed could be explained without such reversals.

The precise form of the lophate pattern of the pollen also distinguishes almost all species of *Lessingianthus* from any *Lepidaploa.* The *Vernonia argyrophylla*-type pollen described by Stix (1960), also called type B pollen by Jones (1979b), in its typical form appears to be restricted to *Lessingianthus* and is completely absent from *Lepidaploa.* Such pollen has colpar areolae extending the whole length of the grain and meeting at the poles at the same time that the intercolpi have three areolae across at the equator (Figs. 1, 2, 5, 6, 8). The three areolae across the intercolpar equator may be part of a 1:2:3:2:1 pattern (Fig. 1) or a 1:2:1:2:1 pattern (Fig. 6). The type B grains tend to have diameters greater than the other lophate types in the *Lepidaploa* relationship. They are mostly 50–80 μm in diameter in fluid. Most *Lepidaploa* have pollen grains 40–55 μm in diameter, rarely to 60 μm. The larger grains of *Lessingianthus* tend to occur in the species with the most robust flowers and heads. All neotropical species seen with *Vernonia argyrophylla* or type B grains are recognized here as members of *Lessingianthus.* A number of the species of *Lessingianthus* were included by Jones (1979b) under series Macrolepidae Benth. & Hook. with the pollen type listed as A, but the latter seems to have been a misprint.

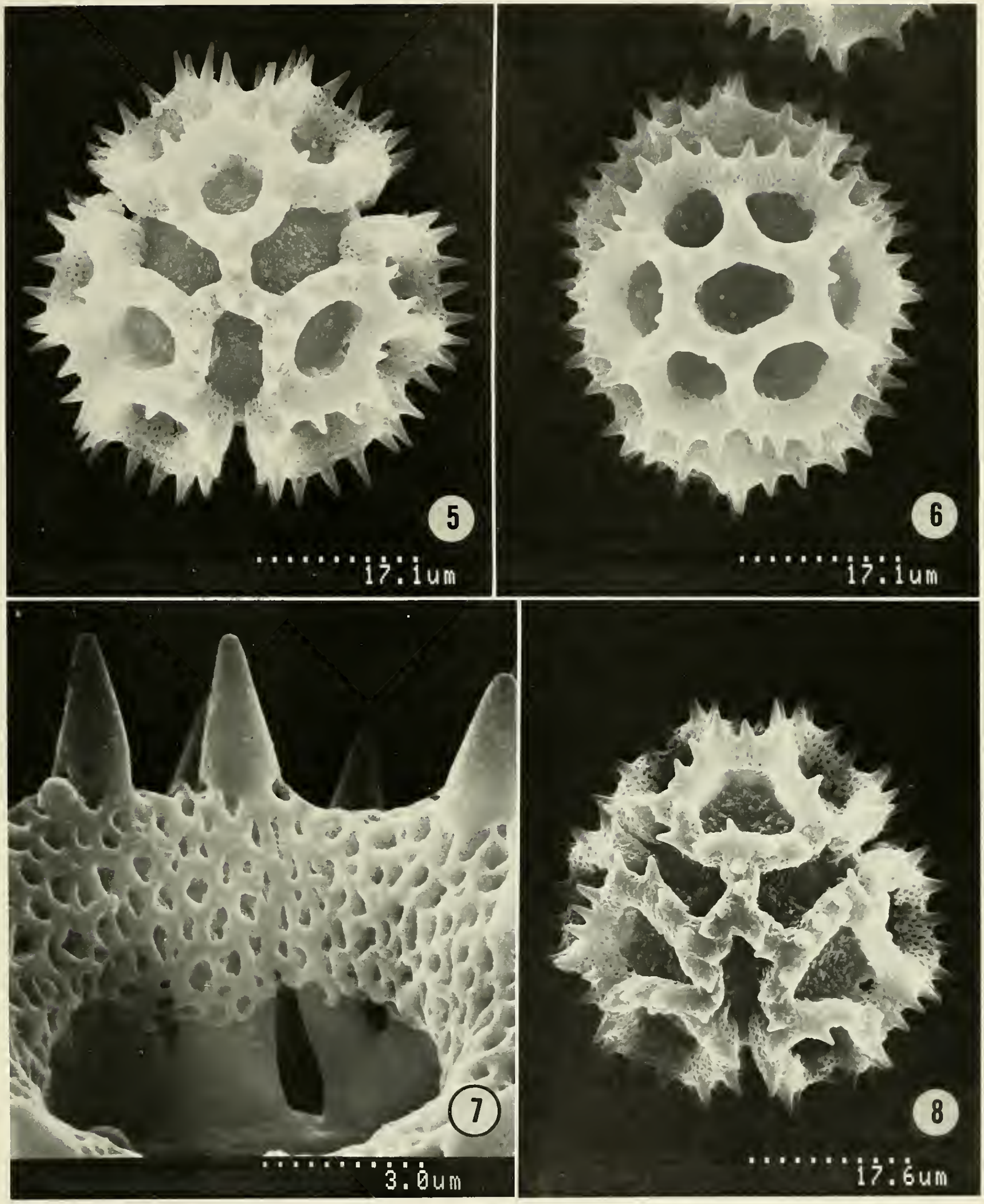
The *Vernonia argyrophylla* or type B pollen has been adequately distinguished by both Stix (1960) and Jones (1979b) from other types of lophate grains found in *Vernonia* that have separate areolae at the pollen poles or that have cross-walls across the colpar area above and below the pore. However, distinction has not been ordinarily made between the larger type B pollen with three areolae across the intercolpar region and the generally smaller forms with only



Figs. 1–4. Pollen of *Lessingianthus argyrophyllus* (Less.) H. Robins. 1. Intercolpar view showing 1:2:3:2:1 pattern. 2. Polar view showing the three colpi meeting at the pole. 3. Broken grain showing baculae. 4. Broken grain showing detail under perforated tectum.

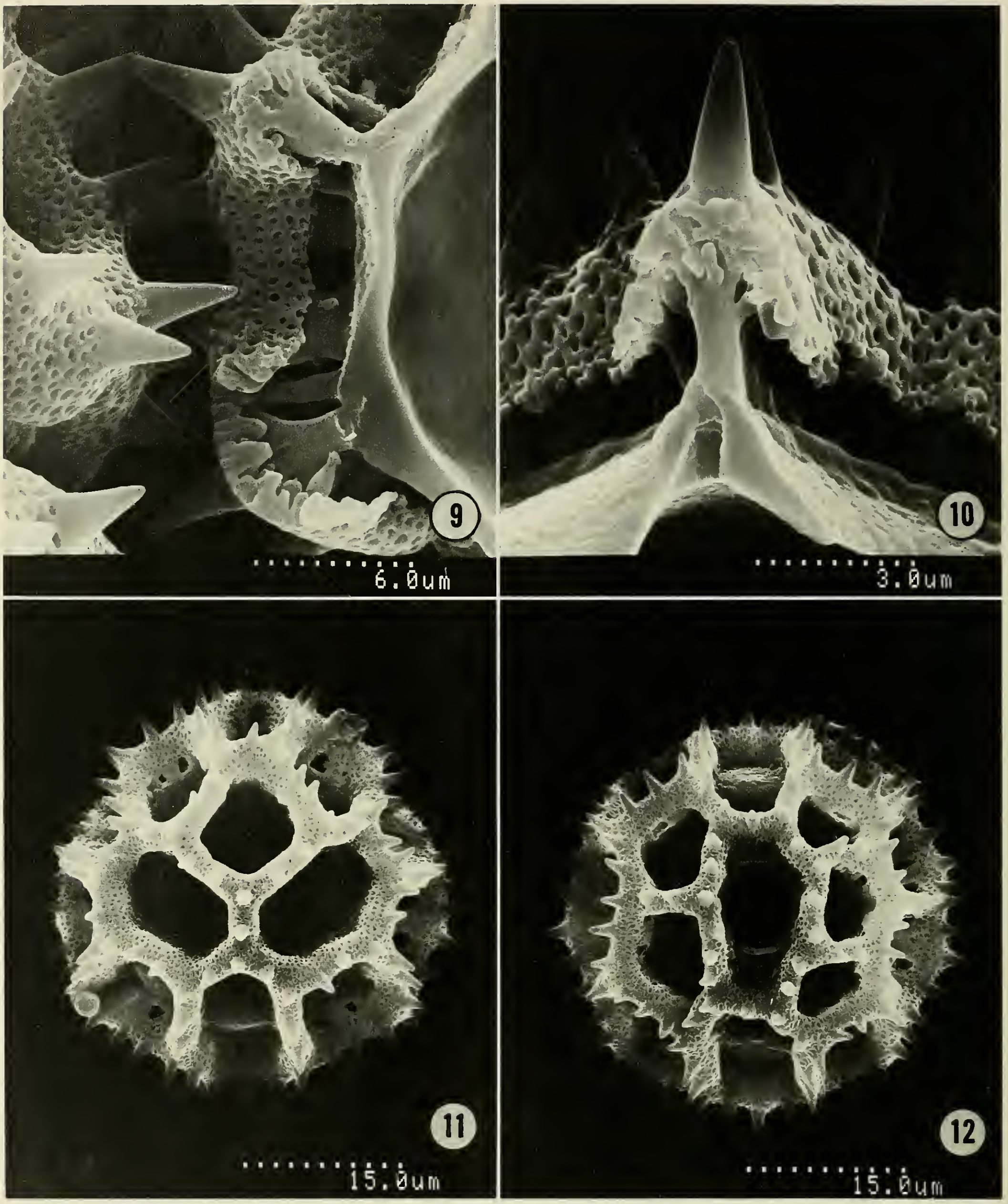
two areolae across the intercolpar region. The latter type has been recognized as the *V. geminata*-type by Robinson (1980b). Present observations show that the distinction is more than technical. All species with *V. geminata*-type pollen prove to be members of the genus *Lepidaploa* or *Echinocoryne.* They are more closely related to species with type C and D pollens than to the *Lessingianthus* species with regular type B pollen. The *V. geminata* type grains all have rhizomatous crests, which the typical type B grains do not have. Pollen with three areolae across in many of its intercolpar regions has been seen in *Lepidaploa* in *V. violiceps* H. Robins. from Ecuador and in a specimen of an unnamed *Vernonia* received from Badillo in Venezuela, and in some intercolpar regions of such species as *V. herbacea,* but the pollen involved is not true type B. The grains have rhizomatous crests and polar areolae that clearly indicate the identity of the species as *Lepidaploa* or *Chrysolaena.*

The only pollen in a *Lepidaploa* that might qualify as a true type B is in *V. psilostachya*

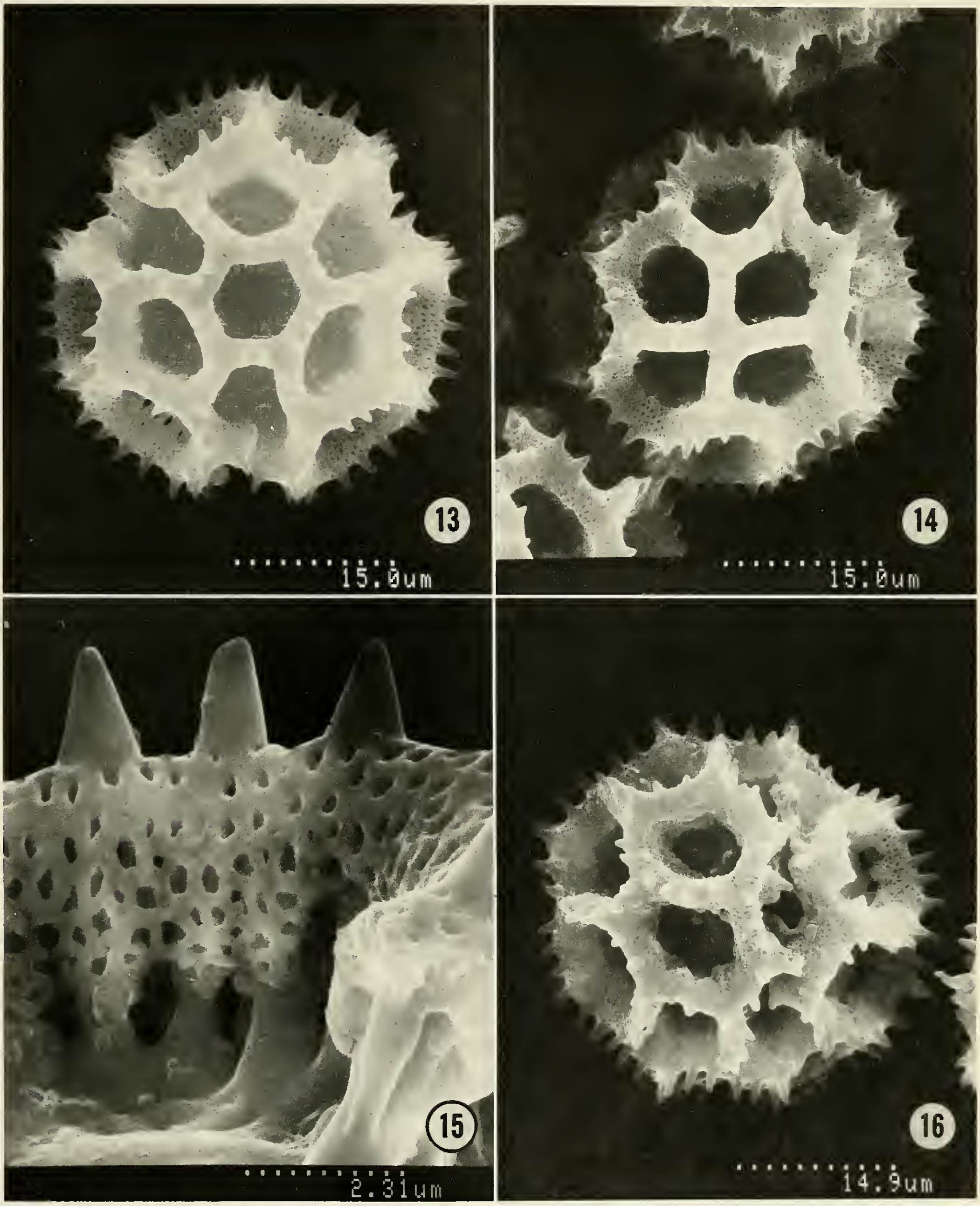


Figs. 5–8. Pollen of *Lessingianthus*. 5–7. *L. tomentellus* (Mart. ex DC.) H. Robins. 5. Polar view showing three colpi meeting at pole. 6. Intercolpar view showing 1:2:1:2:1 pattern. 7. Detail of pollen crest showing baculae. 8. *L. cephalotes* (DC.) H. Robins., polar view showing three colpi meeting at pole.

DC. The latter has colpi reaching the poles and a variable number of 2 or 3 areolae across the intercolpus in 1 or 2 tiers. Careful examination shows that very few of the grains actually match true type B in all the intercolpi simultaneously. The habit of the plants is small compared to any *Lessingianthus*, and the involucre is a *Lepidaploa*



Figs. 9–12. Pollen of *Lessingianthus.* 9. *L. laurifolius* (DC.) H. Robins., broken grain showing baculae. 10. *L. niederleinii* (Hieron.) H. Robins., broken grain showing baculae. 11, 12. *L. brevifolius* (Less.) H. Robins. 11. View with pole below middle showing three areolae above pores meeting at pole. 12. Colpar view showing crosswalls above and below pore.



Figs. 13–16. Pollen of *Lessingianthus.* 13–15. *L. simplex* (Less.) H. Robins. 13. Polar view showing polar areola. 14. Intercolpar view showing 1:2:2:1 pattern. 15. Detail of pollen crest showing baculae. 16. *L. virgulata* (Mart. ex DC.) H. Robins., near-colpar view showing truncate areolate poles and 1:2:2:1 intercolpar pattern.

type. The approximation of the pollen to type B might incline one to place the species in *Lessingianthus,* but SEM study shows a clearly rhizomatous structure under the crests.

There is one area of overlap in pollen areolation type. *Vernonia simplex* (Figs. 13–15) and *V. virgulata* (Fig. 16) have a type C lophate pattern with polar areolae. The intercolpar region usually is only two areolae wide in a 1:2:2:1 pattern (Figs. 14, 16). In the pattern of the areolae the pollen of these species is like the pollen that occurs in such species as *V.* (*Chrysolaena*) *flexuosa.* The pollen in *V. simplex* and *V. virgulata* differs from that of *Lepidaploa* and is like that of *Lessingianthus* in that the baculae attach directly to the foot-layer without a "rhizome." Previous treatments have associated these *Lessingianthus* species with two specialized groups now placed in *Chrysolaena* (Robinson 1988) and *Echinocoryne* (Robinson 1987b). *Vernonia simplex* was included by Jones (1981) in his series *Flexuosae* in his refined concept of the group. In this latter case, the pubescence of the plants and the lophate pattern of the pollen seemed to re-enforce the relationship between species in the series. However, the pollen distinction seems to correlate rather well with the presence of pedunculate heads in the group. The series *Flexuosae,* in spite of initial appearances, actually consists of two totally separate elements, one in *Lessingianthus* and the other, *Chrysolaena,* having rhizomatous crests on the pollen and glanduliferous anther appendages. The latter group is closer to *Lepidaploa.* Although its pollen has not been examined with the SEM, *V. desertorum,* which Jones (1981) also placed in series *Flexuosae* apparently is a *Lessingianthus.* Light microscope observations of the crests indicate that they are not rhizomatous. The three pedunculate species with type C pollen, including the two from the series *Flexuosae,* have grains of ca. 50 μm diameter, in the size range common to both *Lessingianthus* and *Lepidaploa.* *Vernonia virgulata* was placed by Jones (1979b) in his series *Subulatae,* which otherwise proves to belong to the genus *Echinocoryne.* The Jones (1979b) citation of type B pollen from *V. virgulata* seemed to correlate with the type cited for the remainder of the series, but none of grains involved were actually type B. As stated above, the pollen of *V. virgulata* is closest to type C; and as indicated by Robinson (1987b), the species of *Echinocoryne* have pollen of the *V. geminata* type with only two rows of intercolpar areoles and no polar areolae.

Two additional pollen variations occur in *Lessingianthus.* The pollen of *V. brevifolia* (Figs. 11, 12) and *V. dura* have crests of exine aross the colpi above and below the pores. Such crosswalls were characteristic of the *Vernonia arenaria*-type of Stix (1960) and the type D of Jones (1979b). The *V. brevifolia* and *V. dura* pollen differs from type D and resembles other *Lessingianthus* pollen in the presence of non-rhizomatous crests with high baculae and by the presence of three areolae equatorially across the intercolpus. It should be recognized that these type D grains differ from the type B only in the presence of the crosswalls above and below the pores, and the genetic difference may not be very great.

Although *V. cephalotes* normally shows type B pollen (Fig. 8), some specimens have grains with an irregular surface pattern best classified as type A. Type A pollen has been considered a reversion type in the tribe because of the wider distribution of lophate types, but *V. cephalotes* is the only specific example of such a reversion thus far known in the Western Hemisphere. The grains measure ca. 45 μm in fluid, larger than the common type A. The irregular pattern of colpi and spines suggests the influence of irregular meiosis. Another species in which only large type A pollen has been seen, *V. glazioviana* is included here in the belief it represents a similar reversion from a type A pollen.

The size of pollen in Asteraceae often correlates with chromosome number, but the larger size of pollen in many species of *Lessingianthus* is not particularly correlated with known polyploidy, except to the extent that the $\bar{X} = 17$ basic to Neotropical Vernonieae is a polyploidy. Jones (1979a) provided counts for four members of the genus. Two of the species, *V. bardanioides,* and *V. glabrata* include higher polyploids having N = 34, but each also has lower counts of N = 17. A similar mixture of lower counts and higher polyploidy is also seen in at least one member of *Chrysolaena* (as *V. cognata* in Jones 1979a).

Inflorescence Form

The general *Lepidaploa* and *Lessingianthus* group is notable for a type of inflorescence that can best be termed seriate-cymose. *Lepidaploa* itself exemplifies the structure where each head is technically terminal with a lateral branch from immediately below the head bearing the rest of the series. The result looks like a series of lateral sessile heads except for the usual slight deflection at each head. This form is seen in every species presently recognized as a true *Lepidaploa,* and it seems to derive from ancestors more like the Brasilian *Vernonia diffusa* Less. that have less regular cymes and are outside of the *Lepidaploa* complex. Such ancestral stocks seem to have produced some other strongly seriate-cymose forms like those of the neotropical *Cyrtocymura* and *Eirmocephala* (Robinson 1987c) and the Colombian *Dipterocypsela* Blake. The latter are considered to be basically outside the *Lepidaploa* complex. All of the other marked examples of such cymes except *V. peculiaris* Verdcourt of Africa seem to be in *Lepidaploa* or its close relatives. These include *Mattfeldanthus* Robins. & King of Brasil that has lophate pollen. The cymes have been retained with smaller, less distinct heads in *Stenocephalum* (Robinson 1987a). In the closely related *Echinocephalum* the inflorescence is drastically altered by the presence of peduncles, sometimes very long peduncles, under the heads. The latter condition seems derived within the complex.

Lessingianthus has many species that show the same seriate-cymose condition noted for *Lepidaploa,* but includes variations of this form that differ from anything in the latter genus. One variation is the development of pedunculate heads. This character occurs in members of the genus, such as *V. psilophylla* and *V. secunda* that have a closer relationship to species with sessile heads than to each other. Many of the species such as *V. sellowii, V. carvalhoi, V. santosii,* and *V. scaposa* have scapose inflorescences from abbreviated vegetative plants, but the species do not form a related group within the genus. The pedunculate and scapose characters represent general trends in *Lessingianthus* that are lacking in *Lepidaploa.* The species group with type C pollen, which has been misplaced in the series *Subulatae* and *Flexuosae,* is characterized by pedunculate heads. *Vernonia virgulata* is not distinguishable from *Echinocoryne* on the basis of that character, but differs in other features including its pollen. In both the pedunculate heads and the non-rhizomatous crests of the pollen, the latter species along with *V. simplex* and *V. desertorum* fall easily within *Lessingianthus.*

One other modification in a few species of *Lessingianthus* was discussed by Robinson (1980c) in connection with the description of *V. eitenii.* Although the small group of species involved has inflorescences closely resembling the seriate-cymes of their relatives, the sequence of maturation of the heads is reversed, so that the uppermost head matures first and the progress is downward. This sequence indicates that developmentally the inflorescence has converted to a cyme with the lower heads truly lateral. It is another variation that does not occur in *Lepidaploa.*

The species with seriate cymes in *Lessingianthus* and *Lepidaploa* are often distinguishable by an additional feature. In those species having distinct foliose bracts in the cymes, the bracts in *Lessingianthus* never seem to have the abrupt reduction in size from leaves to bracts that is seen at the base of the cyme in many species of *Lepidaploa.*

Involucral Bracts

Lessingianthus is essentially the same as *Lepidaploa* in the ratio of involucral bracts to flowers in the head. The bracts are usually twice to three times as many as the flowers. *Lessingianthus* never has excessive numbers of involucral bracts, as is seen in *Echinocoryne.* In other aspects of the involucre, however, there are characters that help to distinguish the two genera. One of these is the degree of differentiation between the outer and inner bracts.

In *Lessingianthus* and *Lepidaploa,* the involucral bracts are graduated with the inner bracts progressively larger and longer than the outer ones. The bracts in *Lessingianthus* show only the differences to be expected in such graduated structures. In those where the bracts are narrow and pointed, as in *V. bardanioides,* or those where they are short, as is *V. buddleiifolia* and *V. argyrophylla,* the slender or obtuse tips occur throughout the involucre. In *Lepidaploa* the outer bracts are often very different in shape from the inner ones. The innermost bracts may often be rather abruptly wider and the outermost bracts are often very aristate and spreading. Such differences are not found in all *Lepidaploa,* but they are found in almost no species of *Lessingianthus.* The condition is approached in *Vernonia glabrata* and *V. neiderleinii* which are otherwise like *Lessingianthus* in their rather large habit. A number of species of *Lessingianthus,* such as *V. arachniolepis* and *V. pseudosquarrosa,* have outer bracts with spreading, rather foliose tips, a feature not noted in *Lepidaploa.*

The tips of the involucral bracts in *Lessingianthus* are often very short in an almost reptilian scale pattern. Such a pattern is characteristic of the typical element of the genus characterized by larger heads, but it also occurs in some smaller-headed species such as *V. psilophylla.* The narrowly pointed bracts of *V. bardanioides, V. eitenii, V. irwinii,* and their relatives taper evenly to the tips and have a distinct longitudinal median costa externally of a type not seen in *Lepidaploa.* They do not have the apical mucros or aristae seen in many *Lepidaploa* species. The latter short apical mucros occur in *Lessingianthus* in only a few species such as *V. elegans.*

The involucral bracts of most species of *Lessingianthus* are imbricate in many series, but some species such as *V. carvalhoi* and *V. brevifolia* have involucres that appear less imbricate because of the narrower bracts. The most significant examples of reduced involucres in *Lessingianthus* are in the three species, *V. virgulata, V. simplex,* and *V. desertorum* that have been noted above as having type C pollen. These species are treated below as part of a distinct subgenus within *Lessingianthus.*

A number of other characters show variations of interest in *Lessingianthus* although they are not as useful for delimiting the genus. In many species of *Lessingianthus* the tendency for pedunculate heads seems correlated to some extent with the occurrence of distinct petioles. Nevertheless, shortly petiolate and sessile leaves occur in both genera. The corolla lobes of *Lessingianthus* show a broad fusion and enlargement of the vascular strands at the tip, a feature that seems rather characteristic of most of the *Lepidaploa* complex. The vascular strands of the corolla lobes of most other American Vernonieae are only narrowly fused or separated at the tips. The inner pappus in both genera is unfailingly capillary, but in *Lessingianthus* the bristles are comparatively short in a number of species such as *V. eitenii* and *V. bardanioides.* The pappus in these species is shorter in relation to the involucre and corolla, and the corolla throat is mostly exposed. Short pappus bristles of this type do not occur in *Lepidaploa.* The achenes in the genus are normally densely setuliferous, but a few species such as *V. pseudopiptocarpha* and *V. ixiamensis* have glabrous achenes, whereas *V. glabrata, V. saltensis,* and *V. westermanii* have achenes with few setulae. The density of setulae on the achenes of most species allows little space for glands, and unlike many *Lepidaploa* species, no glands have been seen in the genus. A few species such as *V. ammophila* and *V. pycnostachya* have resin cells on the surface of the achene as single cells or small groups of two or three cells. The raphides in the achene wall are usually elongate, but are quadrate in some species such as *V. regis, V. pseudopiptocarpha,* and *V. ammophila.*

In one species of *Lessingianthus, V. santosii* Robinson (1980b), the flowers in the heads have been noted as opening in two sets, the outer rows first and then the inner disk flowers later as a separate group. The initial phase offers the superficial appearance of a head with ray flowers. The full distribution of the character is not known, but it has been seen again in the comparatively unrelated Vernonian genus *Centratherum,* where the two stages occur on separate days. The character is most obvious in the field, and studies in Brazil might show how common the character is in *Lessingianthus.* The character would obviously not be found in Vernonieae with smaller, fewer-flowered heads such as *Stenocephalum.*

The two generic concepts *Lessingianthus* and *Lepidaploa* represent two elements with basically differing aspects and different geography. The most obvious reason for recognizing two genera is the form of the inflorescence, which in *Lessingianthus* frequently has pedicellate heads and in *Lepidaploa* has all heads essentially sessile in the seriate cymes. It is the form of the pollen that seems to correlate best phyletically with the two groups, the one with many pedunculate heads and mostly undifferentiated involucres, and the second with exclusively sessile heads and mostly differentiated involucres. The generic distinction is therefore placed here technically at the point of the difference between non-rhizomatous pollen crests with large discrete baculae versus the mostly rhizomatous pollen. Every species of *Lessingianthus* can be assigned either by its pedunculate heads or by its type B or D pollen having no polar areolae in conjunction with 1:2:3:2:1 or 1:2:1:2:1 intercolpar patterns. This distinction creates problems in only a few species. One species falling into *Lessingianthus* on the basis of non-rhizomatous type D pollen having a 1:2:1:2:1 intercolpar pattern seems uncomfortable in the genus on the basis of habit. *Vernonia regis* is most unusual in the genus by the rather prominent ring at the base of the style. Collapse of the softer shaft leaves a more marked enlargement than in any other *Lessingianthus.* Nevertheless, the structure is not truly broader than the shaft and it does not show the narrow attachment commonly seen in *Lepidaploa.* The species is further distinctive in its crowded narrow heads with distinct herbaceous outer bracts. *Vernonia regis* does not look like a *Lepidaploa* but rather like a *Stenocephalum.* The differences from *Stenocephalum* are discussed by Robinson (1987a). This particular species may reflect some area of evolutionary complexity such as hybridization not yet resolved, but for the present the Type D non-rhizomatous pollen character is applied rigorously to include it within *Lessingianthus.*

In the present view, *Lessingianthus* may be circumscribed too broadly in some cases, but the genus is not too narrowly delimited.

The new genus is named in honor of Carl F. Lessing 1809–1862 who was the author of many of the species of the genus.

Lessingianthus, gen. nov.

Plantae herbaceae perennes plerumque erectae ad 1.5–2.0 m altae in caulibus foliis pedunculis et bracteis involucri variabiliter pubescentes. Folia alterna breviter petiolata vel sessilia. Inflorescentiae simplices vel cymosae saepe scorpioideo-cymosae vel seriate subcapitulate proliferatae vel rare stricte cymosae, pedunculis nullis vel variabiliter elongatis. Capitula late plerumque campanulata; bracteae involucri 2–3-plo plus quam flores in capitulo subimbricatae plerumque multiseriatae plerumque late oblongae et obtusae interdum lineari-lanceolatae raro leniter imbricatae. Flores in capitulo 15–50; corollae plerumque lavandulae saepe in tubis et faucibus glabris in lobis distaliter plerumque minute glanduliferae vel setuliferae apice in nervis conjunctae et incrassatae; appendices antherarum non glanduliferae; basi stylorum non noduliferi raro distincte annuliferi. Achaenia prismatica plerumque 5-costata plerumque dense sericeo-setulifera non glandulifera raro cellulis resiniferis sparse obtecta; carpopodia cylindrica vel obturaculiformia et turbinata, cellulis plerumque oblongis in parietibus striate porulosis; setae pappi interiores capillares longitudinaliter ad corollas subaequales vel multo breviores, seriebus exterioribus longe squamiformibus. Grana pollinis (45–)50–75(–80) μm in diametro lophata in cristis non rhizomata, colpis ad polos attingentibus, areolaris intercolpis aequatorialiter triplicibus (typus B), raro grana ad polos areolata et in areolaris intercolpis aequatorialiter duplicibus (typus C).

Type.—*Vernonia argyrophylla* Less. The genus is geographically mostly concentrated in Brasil with a comparatively few species occurring westward in Argentina, Paraguay, and Bolivia. The genus has two representatives in Peru, only one, *L. rubricaulis,* as far north as Colombia, and only *L. morilloi* in southern Venezuela.

The following 101 species are recognized in the genus.

Lessingianthus adenophyllus
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia adenophylla Mart. ex DC., Prodr. 5:17. 1836. Brasil (Paraná).

Lessingianthus ammophilus (Gardn.)
H. Robinson, comb. nov.

Vernonia ammophila Gardn., Lond. J. Bot. 5:227. 1846. *Cacalia ammophila* (Gardn.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Goiás, Minas Gerais).

Lessingianthus arachniolepis
(Ekman & Dusen) H. Robinson,
comb. nov.

Vernonia arachniolepis Ekman & Dusen in Malme, Kungl. Svenska Vetenskacademiens Handlingar 12(2):17. 1933. Brasil (Paraná, Rio Grande do Sul).

Lessingianthus argenteus (Less.)
H. Robinson, comb. nov.

Vernonia argentea Less., Linnaea 6:672. 1831. *Cacalia argentea* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Paraná, São Paulo).

Lessingianthus argyrophyllus (Less.)
H. Robinson, comb. nov. (Figs. 1–4)

Vernonia argyrophylla Less., Linnaea 6:627. 1831. *Cacalia argyrophylla* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus asteriflorus
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia asteriflora Mart. ex DC., Prodr. 5:29. 1836. *Cacalia asteriflora* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Vernonia kuntzei* Hieron., Engl. Bot. Jahrb. 22:678. 1897. *Vernonia kuntzei* (Hieron.) Kuntze, Rev. Gen. Pl. 3:138. 1898. Bolivia, Brasil (Paraná, São Paulo, Santa Catarina).

Lessingianthus bardanioides (Less.)
H. Robinson, comb. nov.

Vernonia bardanioides Less., Linnaea 6:669. 1831. *Vernonia reticulata* Gardn., Lond. J. Bot. 5:226. 1846. *Vernonia lappoides* Baker in Mart., Fl. Bras. 6(2):35. 1873. *Vernonia cirsiiflora* Mart. ex Baker in Mart., Fl. Bras. 6(2):36. 1873, nomen nudum *Cacalia bardanioides* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Cacalia lap-*

poides (Baker) Kuntze, Rev. Gen. Pl. 2: 970. 1891. Brasil (Bahia, D.F., Goiás, Mato Grosso do Sul, Minas Gerais, São Paulo).

Lessingianthus bishopii (H. Robinson) H. Robinson, comb. nov.

Vernonia bishopii H. Robinson, Phytologia 49:261. 1981. *Vernonia flavescens* Glaz., Bull. Soc. Bot. France Mém. 3, 56:369. 1909, nomen nudum, non *V. flavescens* Less. *Vernonia goiasensis* S. B. Jones, Brittonia 34:107. 1982, nomen nudum Brasil (Goiás, Mato Grosso do Sul).

Lessingianthus brevifolius (Less.) H. Robinson, comb. nov. (Figs. 11, 12)

Vernonia brevifolia Less., Linnaea 4:285. 1829; 6:659. 1831. *Vernonia ericaefolia* Hook. & Arnott, Comp. Bot. Mag. 1:236. 1835. *Cacalia brevifolia* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Vernonia linosyrifolia* Chod., Bull. Herb. Boiss., ser. 2, 2:300. 1902. Argentina, Brasil (Paraná, Rio Grande do Sul, São Paulo, Santa Catarina), Paraguay.

Lessingianthus brevipetiolatus (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia brevipetiolata Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):85. 1873. *Cacalia brevipetiolata* (Sch. Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Minas Gerais).

Lessingianthus buddleiifolius (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia buddleiifolia Mart. ex DC., Prodr. 5:45. 1836, as "*Buddleiaefolia.*" *Vernonia squamosa* Gardner, Lond. J. Bot. 6: 419. 1847. *Cacalia buddleiaefolia* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus bupleurifolius (DC.) H. Robinson, comb. nov.

Vernonia laevigata var. *bupleurifolia* DC., Prodr. 5:56. 1836. *Vernonia pupleurifolia* (DC.) Sch.Bip. ex Malme, Arkiv. Bot. 24A(8):13. 1932. Brasil (Goiás, Mato Grosso).

Near *L. obtusatus,* see Malme (1932).

Lessingianthus caiapoensis (H. Robinson) H. Robinson, comb. nov.

Vernonia caiapoensis H. Robinson, Phytologia 45:171. 1980. Brasil (Goiás).

Lessingianthus carduoides (Baker) H. Robinson, comb. nov.

Vernonia carduoides Baker in Mart., Fl. Bras. 6(2):34. 1873. *Cacalia carduoides* (Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Minas Gerais).

Lessingianthus carvalhoi (H. Robinson) H. Robinson, comb. nov.

Vernonia carvalhoi H. Robinson, Phytologia 53:394. 1983. Brasil (Bahia).

Lessingianthus cataractarum (Hieron.) H. Robinson, comb. nov.

Vernonia cataractarum Hieron., Bot. Jahrb. Syst. 22:681. 1897. Brasil (Santa Catarina).

Lessingianthus cephalotes (DC.) H. Robinson, comb. nov. (Fig. 8)

Vernonia cephalotes DC., Prodr. 5:57. 1836. Brasil (Goiás, Minas Gerais, Sào Paulo).

DeCandolle (1836) in his original description cited *Chrysocoma oligophylla* Vell. as a questionable synonym. Kuntze (1891) synonymized the two. The Vellozo description and plate (1825, 1835) indicate a pilose plant with much more pointed, graduated involucral bracts. The Vellozo species is evidently not *L. cephalotes* but the habitally very similar *V. hypochlora* Malme, which is a *Chrysolaena.*

Lessingianthus chamaepeuces (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia chamaepeuces Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):31. 1873. *Cacalia chamaepeuces* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Goiás, Mato Grosso).

Lessingianthus compactiflorus (Mart. ex Baker) H. Robinson, comb. nov.

Vernonia compactiflora Mart. ex Baker in Mart., Fl Bras. 6(2):44. 1873. *Cacalia compactiflora* (Mart. ex Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus cordiger (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia cordigera Mart. ex DC., Prodr. 5: 58. 1836. *Cacalia cordigera* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Minas Gerais).

Lessingianthus coriaceus (Less.) H. Robinson, comb. nov.

Vernonia coriacea Less., Linnaea 6:661. 1831. *Vernonia hecatantha* DC., Prodr. 5:53. 1836 (as *hexacantha,* corr. 5:696. 1836). *Cacalia coriacea* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Bolivia, Brasil (Bahia, D.F., Goiás, Maranhão, Mato Grosso, Minas Gerais, São Paulo). Peru.

Lessingianthus cristalinae (H. Robinson) H. Robinson, comb. nov.

Vernonia cristalinae H. Robinson, Phytologia 45: 172. 1980. Brasil (Goiás).

Lessingianthus dorsiventralis (Chodat) H. Robinson, comb. nov.

Vernonia dorsiventralis Chodat, Bull. Herb. Boiss. ser. 2, 1:410. 1901. Paraguay.

Lessingianthus durus (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia dura Mart. ex DC., Prodr. 5:59. 1836. *Cacalia dura* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:970.1891. *Vernonia macedoi* Barroso, Arq. Jard. Bot. Rio de Janeiro 13:9. 1954. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais).

Lessingianthus eitenii (H. Robinson) H. Robinson, comb. nov.

Vernonia eitenii H. Robinson, Phytologia 46:109. 1980. *Vernonia wasshausenii* S. B. Jones, Brittonia 34:110. 1982. Brasil (D.F., Goiás).

The species concept includes one paratype of *L. cristalinae* (Irwin et al. 32817). Specimens with only a few apical heads can be distinguished from *L. cristalinae* most easily by the less appressed and more yellowish pubescence of the stems.

Lessingianthus elegans (Gardn.) H. Robinson, comb. nov.

Vernonia elegans Gardn., Lond. J. Bot. 6: 421. 1847. *Cacalia elegans* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus erythrophilus (DC.) H. Robinson, comb. nov.

Vernonia erythrophila DC., Prodr. 5:56. 1836. *Cacalia erythrophila* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Minas Gerais).

Lessingianthus exiguus (Cabrera) H. Robinson, comb. nov.

Vernonia exigua Cabrera, Sellowia 13:166. 1961. Brasil (Paraná, Santa Catarina, São Paulo).

Lessingianthus farinosus (Baker)
H. Robinson, comb. nov.

Vernonia farinosa Baker. in Mart., Fl. Bras. 6(2):84. 1873. *Cacalia farinosa* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia).

Lessingianthus floccosus (Gardn.)
H. Robinson, comb. nov.

Vernonia floccosa Gardn., Lond. J. Bot. 5: 225. 1846. *Cacalia floccosa* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia robusta* Glaz., Bull. Soc. Bot. France Mém. 3, 56:369. 1909, nomen nudum. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus fonsecae (H. Robinson)
H. Robinson, comb. nov.

Vernonia fonsecae H. Robinson, Phytologia 45:174. 1980. Brasil (Goiás).

Lessingianthus glabratus (Less.)
H. Robinson, comb. nov.

Vernonia glabrata Less., Linnaea 4:294. 1829; 6:661. 1831. *Vernonia radula* Mart. ex DC., Prodr. 5:52. 1836. *Cacalia glabrata* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Cacalia radula* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. *Vernonia oxydonta* Malme, Ark. Bot. 24A(6): 19. 1932. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, Paraná, Rio Grande do Sul).

Lessingianthus glaziovianus (Baker)
H. Robinson, comb. nov.

Vernonia glazioviana Baker in Mart., Fl. Bras. 6(2):41. 1873. *Cacalia glaziouana* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Rio de Janeiro).

Lessingianthus glomeratus
(Baker ex Warming)
H. Robinson, comb. nov.

Vernonia glomerata Baker ex Warming, Vidensk. Medd. Forh. Kjöb. 1890:185. 1890. Brasil (D.F., Minas Gerais).

Lessingianthus grandiflorus (Less.)
H. Robinson, comb. nov.

Vernonia grandiflora Less., Linnaea 6:660. 1831. Brasil (Minas Gerais, Paraná, São Paulo), Paraguay.

Kuntze (1891) equated this species with *Chrysocoma pumilla* of Vellozo (1825), but the plate of the latter (1835) is interpreted here as representing the species commonly known as *Vernonia sessilifolia* Less.

Lessingianthus grearii (H. Robinson)
H. Robinson, comb. nov.

Vernonia grearii H. Robinson, Phytologia 45:175. 1980. Brasil (Goiás).

Lessingianthus heringeri (H. Robinson)
H. Robinson, comb. nov.

Vernonia heringeri H. Robinson, Phytologia 53:395. 1983. Brasil (D.F., Goiás).

Lessingianthus hoveaefolius (Gardn.)
H. Robinson, comb. nov.

Vernonia hoveaefolia Gardn., Lond. J. Bot. 6:423. 1847. Cacalia hoveaefolia (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Near *L. obtusatus.* Brasil (Goiás, Minas Gerais).

Lessingianthus hypochaeris (DC.)
H. Robinson, comb. nov.

Vernonia hypochaeris DC., Prodr. 5:45. 1836. *Cacalia hypochaeris* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Paraná).

Lessingianthus irwinii (Barroso)
H. Robinson, comb. nov.

Vernonia irwinii Barroso, Loefgrenia 36:2. 1969. Brasil (D.F.).

Lessingianthus ixiamensis (Rusby) H. Robinson, comb. nov.

Vernonia ixiamensis Rusby, Bull. New York Bot. Gard. 8:125. 1912. Bolivia.

Lessingianthus lacunosus (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia lacunosa Mart. ex DC., Prodr. 5: 56. 1836. *Cacalia lacunosa* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus laevigatus (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia laevigata Mart. ex DC., Prodr. 5: 56. 1836. Near *L. obtusata*; see Malme (1932). Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, Paraná).

Lessingianthus laurifolius (DC.) H. Robinson, comb. nov. (Fig. 9)

Vernonia laurifolia DC., Prodr. 5:30. 1836. *Cacalia laurifolia* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Bolivia, Brasil, Peru.

Lessingianthus ligulifolius (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia ligulifolia Mart. ex DC., Prodr. 46. 1836. as "*ligulaefolia*." *Cacalia ligulifolia* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia cotaniensis* Hieron., Bot. Jahrb, Syst. 40:352. 1908. Brasil (D.F., Goiás, São Paulo).

The species is close to *L. coriaceus.*

Lessingianthus linearifolius (Less.) H. Robinson, comb. nov.

Vernonia linearifolia Less., Linnaea 4:287. 1829. *Cacalia linearifolia* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Minas Gerais).

Lessingianthus linearis (Spreng.) H. Robinson, comb. nov.

Vernonia linearis Spreng., Syst. Veg., ed. 16, 3:437. 1826. *Cacalia linearis* (Spreng.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia, D.F., Goiás, Minas Gerais).

Lessingianthus lorentzii (Hieron.) H. Robinson, comb. nov.

Vernonia lorentzii Hieron., Engl. Bot. Jahrb. 22:674. 1898. Argentina, Paraguay.

Lessingianthus macrocephalus (Less.) H. Robinson, comb. nov.

Vernonia macrocephala Less., Linnaea 4: 298. 1829. *Cacalia macrocephala* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Rio Grande do Sul, São Paulo), Uruguay.

Lessingianthus macrophyllus (Less.) H. Robinson, comb. nov.

Vernonia macrophylla Less., Linnaea 6:668. 1831. *Cacalia macrophylla* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia, Espirito Santo, Minas Gerais, Rio de Janeiro).

Lessingianthus mansoanus (Baker) H. Robinson, comb. nov.

Vernonia mansoana Baker in Mart., Fl. Bras. 6(2):84. 1873. *Cacalia mansoana* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Goiás, Mato Grosso).

Lessingianthus mollissimus (D. Don ex Hook. & Arn.) H. Robinson, comb. nov.

Vernonia mollissima D. Don ex Hook. & Arn., Comp. Bot. Mag. 1:237. 1835. *Cacalia mollissima* (D. Don ex Hook. & Arn.) Kuntze, Rev. Gen. Pl. 2:970. 1891.

Argentina, Brasil (Mato Grosso, Paraná, Rio Grande do Sul), Paraguay.

Lessingianthus monocephalus (Gardn.) H. Robinson, comb. nov.

Vernonia monocephala Gardn., Lond. J. Bot. 6:418. 1847. *Cacalia monocephala* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia, D.F., Goiás).

Lessingianthus morii (H. Robinson) H. Robinson, comb. nov.

Vernonia morii H. Robinson, Phytologia 44: 290. 1979. Brasil (Bahia).

Lessingianthus morilloi (Badillo) H. Robinson, comb. nov.

Vernonia morilloi Badillo, Ernstia 1:2. 1981. Venezuela (Amazonas).

Lessingianthus myrsinites H. Robinson, sp. nov.

Vernonia myrsinites Ekman, in herb.

Plantae fruticosae ad 0.5–1.0 m altae superne ramosae dense foliosae. Caules superne lanosi base xylopodiales. Folia sessilia oblonga 2–7 cm longae et 1.0–3.5 cm latae base truncatae vel breviter cordatae margine integrae apice obtusae vel breviter acutae supra subglabrae et sublucidae subtus pilulosae et glandulo-punctatae utrinque in nervulis prominentes, nervis secundariis 3–8 erecto-patentibus. Inflorescentiae in ramis abrupte terminales fasciculatae plerumque ca. 3-capitatae; capitula late cylindrica ca. 12 mm longa et 5 mm lata; squamae involucri subimbricatae appressae 36–40 gradatim ca. 6-seriatae, bracteae exteriores late ovatae 2–3 mm longae apice glabrae breviter acutae et minute apiculatae extus plerumque dense pilosulae, bracteae interiores oblongae 4–7 mm longae apice roundatae vel saepe eroso-fimbriatae extus glabrae; corollae lavandulae vel purpureae ca. 11 mm longae plerumque glabrae, tubis ca. 5 mm longis, faucibus ca. 1 mm longis, lobis ca. 5 mm longis et 0.6 mm latis apice minute scabridulis extus superne pauce glanduliferis; thecae antherarum ca. 3 mm longae, appendices antherarum ca. 0.7 mm longae et base 2.3 mm latae. Achaenia ca. 3 mm longa sericeo-setulifera; setae pappi interiores ca. 30 ca. 7 mm longae apice leniter incrassatae, squamae exteriores lineares ca. 1.2 mm longae. Grana pollinis in diametro ca. 60 μm distincte lophata (typus B).

Type.—Brasil: Goiás: Chapada dos Veadeiros. 18–19 km N of Alto Paraiso. Wet campo at 4300 ft. elevation. Coarse suffrutescent herb to 1 m tall. Florets lavender. Local in sandy areas within rocky outcrops. Jan 24 1980. R. M. King and F. Almeda 8281 (Holotype UB; Isotype US).

Paratypes.—Brasil: Goiás: Chapada dos Veadeiros, 14°S, 47°W, ca. 15 km W of Veadeiros. Elev. 1000 m. Much-branched subshrub ca. 60 cm tall. Heads lavender-purple. Frequent. Campo. Feb 8 1966. H. S. Irwin, J. W. Grear, Jr., R. Souza, R. Reis dos Santos 12342 (US); ca. 20 km W of Veadeiros. Elev. 1000 m. Erect subshrub ca. 1 m tall. Heads magenta. Creek margin, among rocks. Feb 9 1966. Irwin et al. 12408 (US); herb ca. 1 m tall. Heads magenta. Frequent. Rocky slopes and wet campo. Feb 11 1966. Irwin et al. 12569 (US); ca. 15 km W of Veadeiros. Shrub to ca. 50 cm tall. Heads cream. Rocky slope and creek margin. Feb 14 1966. Irwin et al. 12839 (US); ca. 10 km S of Alto do Paraiso (formerly Veadeiros). Elev. 1000 m. Subshrub ca. 50 cm tall. Heads in fruit. Rocky slopes. Mar 23 1969. H. S. Irwin, R. Reis dos Santos, R. Souza, & S. F da Fonseca 24953 (US); ca. 19 km N of Alto do Paraiso, elev. ca. 1250 m. Subshrub ca. 1 m tall. Heads in fruit. Outcrops. Cerrado on steep rocky slopes, surrounded by campo. Mar 20 1971. H. S. Irwin, R. M. Harley, G. L. Smith 32812 (US); 18–19 km N of Alto Paraiso. Wet campo at 4300 ft. elev. Shrub 1 m tall. Pappus tawny at maturity. Jan 24 1980. R. M. King & F. Almeda 8282 (US); 20 and 30 km N of Alto Paraiso de Goiás, along road to Monte Alegre de Goiás. Elev. 4200 ft. Subshrub ¾ m tall, flowers lavender or purple. Feb 7 1981. R. M. King & L. E. Bishop 8810 and 8818A (US); West of road to Monte Alegre de Goiás, 12–20 km N of Alto Paraiso de Goiás. Elev. 4000–4400 ft. Shrubs ½–¾ m tall, flowers past anthesis and lavender. Feb 7 1981. King & Bishop 8827 and 8828 (US).

The species is in herbaria under the name *Vernonia myrsinites* Ekman, and a type photograph has been seen of a specimen that was once in the Berlin Herbarium annotated by Ekman in 1912. Unfortunately, no place of publication has been found, and the name does not appear in any of the indices. It is not among the Ekman names validated by Malme (1933). Part of the reason for the oversight is the restricted distribution of the species, with recollections occurring in quantity only comparatively recently. The species is therefore described here as new. Ekman is cited only in synonymy since he proposed the name in a different combination.

There is no evidence that the present species has been confused in the past with the vegetatively similar *Lessingianthus cordigera* of Minas Gerais. The latter has a more branching inflorescence with densely hairy tips on the inner involucral bracts as the most obvious differences.

Lessingianthus niederleinii (Hieron.)
H. Robinson, comb. nov. (Fig. 10)

Vernonia niederleinii Hieron., Bot. Jahrb. Syst. 22:681. 1897. *Vernonia valenzuelae* Chod., Bull. Herb. Boiss. ser. 2, 3:641. 1903. Argentina, Brasil (Paraná), Paraguay.

Lessingianthus obscurus (Less.)
H. Robinson, comb. nov.

Vernonia obscura Lessing, Linnaea 4:296. 1829; 6:663. 1831. *Vernonia davalliifolia* Gardn., Lond. J. Bot. 6:422. 1847, as "*davalliaefolia*". *Cacalia obscura* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Goiás, São Paulo).

Lessingianthus obtusatus (Less.)
H. Robinson, comb. nov.

Vernonia obtusata Lessing, Linnaea 6:662. 1831. *Cacalia obtusata* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia subacuminata* Hieron., Bot. Jahrb. Syst. 22: 691. 1897. Bolivia, Brasil (Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus octandrus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia octandra Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):87. 1873. *Cacalia octandra* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Goiás?).

Lessingianthus onoporoides (Baker)
H. Robinson, comb. nov.

Vernonia onoporoides Baker in Mart., Fl. Bras. 6(2):36. 1873. *Cacalia onoporoides* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus pentacontus (DC.)
H. Robinson, comb. nov.

Vernonia pentaconta DC., Prodr. 5:30. 1836, as *pentacantha,* corr. 5:696. 1836. *Cacalia pentacantha* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil?

Lessingianthus platyphyllus (Chod.)
H. Robinson, comb. nov.

Vernonia platyphylla Chod., Bull. Herb. Boiss., ser. 2, 2:299. 1902. Brasil (Mato Grosso), Paraguay.

Lessingianthus polyphyllus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia polyphylla Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):63. 1873. Brasil (Paraná), Paraguay.

Lessingianthus pseudopiptocarphus (H. Robinson) H. Robinson, comb. nov.

Vernonia pseudopiptocarpha H. Robinson, Phytologia 45:180. 1980. Brasil (Goiás, Mato Grosso).

Lessingianthus plantaginodes (Kuntze) H. Robinson, comb. nov.

Vernonia rubricaulis var. *squarrosa* Less., Linnaea 4:300. 1829. *Vernonia squarrosa* (Less.) Less., Linnaea 6:678. 1831, non *V. squarrosa* [Don] Less., Linnaea 6:627. 1831 which was given precedence by Kuntze (1891). *Cacalia plantaginodes* Kuntze, Rev. Gen. Pl. 2:969. 1891, non *V. plantaginoides* Hieron. *Vernonia pseudosquarrosa* Hieron., Bot. Jahrb. 22:685. 1897. *Vernonia sancti-pauli* Hieron., Bot. Jahrb. Syst. 22:687. 1897. *Vernonia squarrulosa* Mattfeld ex Malme, Ark. Bot. 24A(6):18. 1931. Argentina, Brasil (Paraná, Rio Grande do Sul, São Paulo), Uruguay.

Lessingianthus psilophyllus (DC.) H. Robinson, comb. nov.

Vernonia psilophylla DC., Prodr. 5:28. 1836. *Vernonia graminifolia* Gardn., Lond. J. Bot. 6:421. 1847. *Cacalia graminifolia* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Cacalia psilophylla* (DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás, Minas Gerais, Pará, Paraná).

Lessingianthus pulverulentus (Baker) H. Robinson, comb. nov.

Vernonia pulverulenta Baker in Mart., Fl. Bras. 6(2):42. 1873. *Cacalia pulverulenta* (Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus pumilla (Vell.) H. Robinson, comb. nov.

Chrysocoma pumilla Vell., Fl. Flum. 331. 1825; 8, pl. 32. 1835. *Vernonia sessilifolia* Less., Linnaea 6:659. 1831. *Cacalia pumila* (Vell.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Cacalia sessilifolia* (Less.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Paraná).

Lessingianthus pycnostachyus (DC.) H. Robinson, comb. nov.

Vernonia pycnostachya DC., Prodr. 5:58. 1836. *Cacalia pycnostachya* (DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus regis (H. Robinson) H. Robinson, comb. nov.

Vernonia regis H. Robinson, Phytologia 45: 181. 1980. Brasil (Bahia).

Lessingianthus reitzianus (Cabrera) H. Robinson, comb. nov.

Vernonia reitziana Cabrera, Sellowia 13: 160. 1961. Brasil (Paraná, Santa Catarina).

Lessingianthus robustus (Rusby) H. Robinson, comb. nov.

Vernonia robusta Rusby, Mem. Torrey Bot. Club 6:54. 1896, non *V. robusta* Glaz., nomen nudum. Bolivia.

Lessingianthus roseus (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia rosea Mart. ex DC., Prodr. 5:59. 1836. *Cacalia rosea* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus rosmarinifolius (Less.) H. Robinson, comb. nov.

Vernonia rosmarinifolia Less., Linnaea 4: 285. 1829. *Cacalia rosmarinifolia* (Less.)

Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Bahia, Minas Gerais).

Lessingianthus rubricaulis (Humb. & Bonpl.) H. Robinson, comb. nov.

Vernonia rubricaulis Humb. & Bonpl., Pl. Aequin. 2:66. tab. 99. 1809. *Vernonia intermedia* DC., Prodr. 5:27. 1836. *Cacalia intermedia* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Cacalia rubricaulis* (Humb. & Bonpl.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Argentina, Brasil (Mato Grosso, Minas Gerais, Paraná, Santa Catarina), Colombia, Paraguay, Peru.

Lessingianthus rugulosus (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia rugulosa Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):83. 1873. *Cacalia rugulosa* (Sch. Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus saltensis (Hieron.) H. Robinson, comb. nov.

Vernonia saltensis Hieron., Bot. Jahrb. Syst. 22:691. 1897. Argentina, Bolivia.

Lessingianthus santosii (H. Robinson) H. Robinson, comb. nov.

Vernonia santosii H. Robinson, Phytologia 45:182. 1980. Brasil (Bahia).

Lessingianthus scaposus (Barroso) H. Robinson, comb. nov.

Vernonia scaposa Barroso, Loefgrenia 36: 2. 1969. Brasil (Minas Gerais).

Lessingianthus secundus (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia secunda Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):93. 1973. *Cacalia secunda* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás).

Lessingianthus sellowii (Less.) H. Robinson, comb. nov.

Vernonia sellowii Lessing, Linnaea 4:301. 1829. *Cacalia sellowii* (Less.) Kuntze, Rev. Gen. Pl. 2:971. 1891. *Vernonia hassleriana* Chod., Bull. Herb. Boiss., ser. 2, 2:302. 1902. Argentina, Brasil (Paraná, Rio Grande do Sul, Santa Catarina), Uruguay.

Lessingianthus soderstroemii (H. Robinson) H. Robinson, comb. nov.

Vernonia soderstroemii H. Robinson, Phytologia 45:183. 1980. Brasil (D.F., Goiás).

Lessingianthus souzae (H. Robinson) H. Robinson, comb. nov.

Vernonia souzae H. Robinson, Phytologia 45:184. 1980. Brasil (Goiás).

Lessingianthus stoechas (Mart. ex Baker) H. Robinson, comb. nov.

Vernonia stoechas Mart. ex Baker in Mart., Fl. Bras. 6(2):49. 1873. *Cacalia stoechas* (Mart. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás, Minas Gerais).

Lessingianthus subcarduoides (H. Robinson) H. Robinson, comb. nov.

Vernonia subcarduoides H. Robinson, Phytologia 45:185. 1980. Brasil (Minas Gerais).

Lessingianthus subobtusus (Malme) H. Robinson, comb. nov.

Vernonia subobtusa Malme, Ark. Bot. 24A(8):13. 1932. Brasil (Mato Grosso).

Lessingianthus syncephalus (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia syncephala Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):64. 1873. *Cacalia syncephala* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás?).

Lessingianthus tomentellus (Mart. ex DC.) H. Robinson, comb. nov. (Figs. 5–7)

Vernonia tomentella Mart. ex DC., Prodr. 5:59. 1836. *Cacalia tomentella* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais, São Paulo).

Lessingianthus ulei (Hieron.) H. Robinson, comb. nov.

Vernonia ulei Hieron., Bot. Jahrb. 22:686. 1897. Brasil (Minas Gerais).

Lessingianthus varroniifolius (DC.) H. Robinson, comb. nov.

Vernonia varroniifolia DC., Prodr. 5:56. 1836. *Cacalia varroniifolia* (DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Bolivia, Brasil.

Lessingianthus venosissimus (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia venosissima Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):30. 1873. *Cacalia venosissima* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. *Vernonia urbaniana* Glaz., Bull. Soc. Bot. France Mém. 3, 57:369. 1909., nomen nudum. Brasil (D.F., Goiás, Mato Grosso).

Lessingianthus vepretorum (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia vepretorum Mart. ex DC., Prodr. 5:59. 1836. *Cacalia vepretorum* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus vestitus (Baker) H. Robinson, comb. nov.

Vernonia vestita Baker in Mart., Fl. Bras. 6(2):83. 1873. *Cacalia vestita* (Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus warmingianus (Baker) H. Robinson, comb. nov.

Vernonia warmingiana Baker in Mart., Fl. Bras. 6(2):68. 1873. *Cacalia warmingiana* (Baker) Kuntze, Rev. Gen. Pl. 2: 971. 1891. Brasil (Goiás, Minas Gerais).

Lessingianthus westermanii (Ekman & Dusen) H. Robinson, comb. nov.

Vernonia westermanii Ekman & Dusen ex Malme, Kungl. Svenska Vetenskapsakad. Handl. 12(2):10. 1933. Brasil (Paraná).

Lessingianthus xanthophyllus (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia xanthophylla Mart. ex DC., Prodr. 5:58. 1836. *Cacalia xanthophylla* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Bahia).

Lessingianthus zuccarianus (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia zuccariana Mart. ex DC., Prodr. 5:55. 1836. *Cacalia zuccariana* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais).

Lessingianthus subg. **Oligocephalus** H. Robinson, subg. nov.

Vernonia sect. *Lepidaploa* subsect. *Oligocephalae* Baker in Mart., Fl. Bras. 6(2): 46. 1873, pro parte.

Lessingianthis subg. Lessingianthis typicis similis sed squamae involucri subaequales et granae pollines polariter areolatae et intercolpe aequatorialiter biareolatae; a

Lepidaplois in capitulis pedunculatis et in cristis pollinis non rhizomatibus differt.

Type.—Vernonia simplex Less. (=*Lessingianthus simplex* (Less.) H. Robinson.

Lessingianthus desertorum
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia desertorum Mart. ex DC., Prodr. 5:43. 1836. *Vernonia campestris* DC., Prodr. 5:43. 1836. *Vernonia desertorum* var. *campestris* (DC.) Baker in Mart., Fl. Bras. 6(2):48. 1873. *Vernonia desertorum* var. *longipes* Baker in Mart., Fl. Bras. 6(2): 48. 1873. *Cacalia desertorum* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:290. 1981. *Vernonia desertorum* var. *macrocephala* Chod., Bull. Herb. Boissier, ser. 2, 2:300. 1902. Brasil (Bahia, D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo), Paraguay.

Lessingianthus simplex (Lessing)
H. Robinson, comb. nov. (Figs. 13–15)

Vernonia simplex Lessing, Linnaea 4:280. 1829. *Vernonia simplex* var. *angustifolia* Less., Linnaea 4:280. 1829. *Vernonia simplex* var. *latifolia* Less., Linnaea 4:280. 1829. *Vernonia simplex* var. *regnellii* Baker in Mart., Fl. Bras. 6(2):53. 1873. *Vernonia erigerontis* Mart. ex DC., Prod. 5:43. 1836, nomen nudum. Bolivia, Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, Santa Catarina, São Paulo).

Lessingianthus virgulatus
(Mart. ex DC.)
H. Robinson, comb. nov. (Fig. 16)

Vernonia virgulata Mart. ex DC., Prodr. 5: 42. 1836. *Cacalia virgulata* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás, Minas Gerais).

The species is placed in the subgenus because of the polar areolae, but it is probably not closely related to the other two species.

Acknowledgments

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STUDIES IN THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE) V. THE NEW GENUS *CHRYSOLAENA*

Harold Robinson

Abstract.—The genus *Chrysolaena* is described for seven neotropical species, most of which were previously placed in *Vernonia* series *Flexuosae.* The genus has the lophate and rhizomatous exine structure of *Lepidaploa,* but these xylopodial herbs differ in being mostly unbranched below the inflorescence, in having glanduliferous anther appendages, and in lacking basal nodes on the styles.

The present paper is the fifth in a series of seven devoted to the study of the neotropical *Lepidaploa* complex (Robinson 1987a, b, c) The group treated in the present study includes some well-known species of central and southern Brazil and adjacent Argentina and Bolivia. General similarity of habit and pubescence has resulted in some accurate grouping of the species in previous studies. Jones (1981) made the observation that all the species associated with the group had his type C pollen. The discovery of additional anther appendage and style base characters for the group during the present study has resulted in the recognition of the new genus *Chrysolaena.*

Previous treatments of species of *Chrysolaena* have recognized some of the relationships, but these treatments have always shown some omissions and have usually included some species that are not *Chrysolaena.* Both Baker (1873) and Cabrera (1944) placed the species that they recognized within the overall *Vernonia* Sect. *Lepidaploa.* Jones (1981) placed the group under sect. *Vernonia,* of which he made sect. *Lepidaploa* a synonym. In more detail, Baker (1873) placed the then known species now placed in *Chrysolaena* among others in his subsects. *Macrocephalae* and *Scorpioideae.* Two other species later considered to be related by Jones (1981), *V. simplex* and *V. desertorum,* were placed by Baker among other species in his subsect. *Oligocephalae.* Cabrera (1944) established subsect. *Flexuosae* for four species of Argentina, which all proved to be *Chrysolaena*; but like Baker, he kept *V. verbascifolia* separated in subsect. *Macrocephalae.* The recent study by Jones (1981) reduced the rank of the *Flexuosae* to a series. Jones included all the presently recognized members of *Chrysolaena* in his series, except the species commonly known as *V. hypochlora* (syn. *Chysocoma oligophylla*). He also included the two species of somewhat similar habit from Baker's (1873) subsect. *Oligocephalae.* Jones' (1981) description of series *Flexuosae* emphasized the xylopodial habit, the usual lack of branching below the inflorescence, the yellowish to brownish trichomes, the few to numerous sessile heads, the lanceolate acuminate to aristate involucral bracts, the strigose to pilose achenes, and the type C lophate pollen. Only the two oligocephalous species violated the cited characters by having pedunculate heads.

The circumscription of the *Flexuosae* of Jones (1981) was believed to be totally accurate by the present author at the time the present series of studies began because of the basic similarities of habit and pollen type. The concept did not come into question until the pollen of the *Lepidaploa* complex was subjected to detailed SEM study. The recognition of two groups based on pollen differences was followed by the discovery of style base and glandular trichome characters that are of generic importance. The present redisposition of the series *Flexuosae* of Jones is based on the characteristics discussed below under the headings pollen, inflorescences, involucres, nonglandular trichomes, style bases, and glands. The latter refer particularly to the glands of the anther appendage. The generic distinctions emphasized are those from the two larger members of the complex, *Lepidaploa* and *Lessingianthus*.

Pollen

As in all members of the *Lepidaploa* complex, the pollen of *Chrysolaena* has the exine organized into a lophate pattern. The actual pattern is one referred to by Stix (1960) in her major study of Asteraceous pollen as the *Vernonia cognata*-Type. The same type has more recently been designated by Jones (1979a) as type C. The type is distinguished by having a single areolae at each pole, no cross-walls in the colpus immediately above or below the pores, and usually two areolae equatorially across the intercolpar region. There are sometimes three areolae in one or two of the intercolpar regions of a grain (Fig. 1). The type C pattern is found in all the species that have been placed in the series *Flexuosae,* and all those recognized here as *Chrysolaena.*

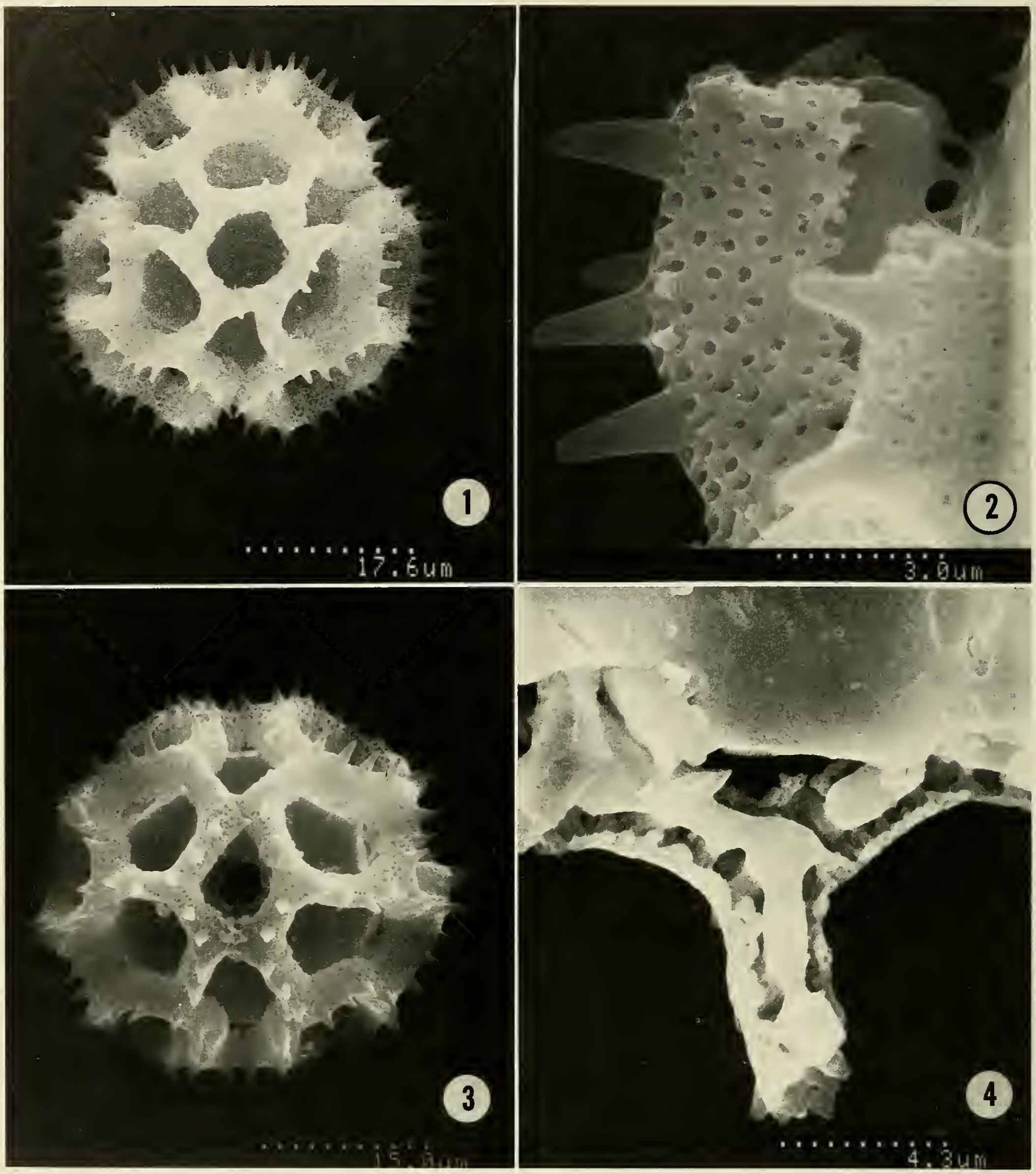
Under detailed SEM examination, the pollen of series *Flexuosae* of Jones (1981) shows two types. The majority of the species shows the "rhizomatous" structure of the exine crests (Figs. 1–4) that is characteristic of the genus *Lepidaploa* and its close relatives *Stenocephalum* and *Echinocoryne* (Robinson 1987a, b). The remaining two species, examined by SEM and light microscopy, *V. simplex* and *V. desertorum,* show no such rhizomatous structure. The latter species are the same ones that Baker (1873) placed in his subsect. *Oligocephalae,* separate from his placement of those now included in *Chrysolaena.* These two species have pedunculate heads, which distinguishes them from others included in the *Flexuosae* by Jones. The characters by which the latter two species resemble *Chrysolaena* can be considered comparatively superficial. The non-rhizomatous pollen crests, the pedunculate condition of the heads, and the lack of glands on the achenes and anther appendages are all characters that distinguish the species from *Chrysolaena* and indicate their proper placement in *Lessingianthus* (Robinson 1988).

Inflorescences

The sessile condition of the heads in all the members of *Chrysolaena* that were recognized by Jones in his series *Flexuosae* correlate with the rhizomatous pollen crests in indicating a close relationship to the genus *Lepidaploa.* As in the latter genus, the inflorescences of *Chrysolaena* characteristically show a seriate-cymose condition where every head has a terminal position and the continuation of the apparent primary branch is through a lateral branch. Each head except the terminal one appears sessile as a result of the lateral branch being immediately below the head. The only member of *Chrysolaena* in which the character seems to fail is the species added to the group in this treatment, *Chrysocoma oligophylla.* Even in this species, displacement of the lateral branches from immediately below the heads seems rare. The pedunculate appearance seems to be mostly derived from the presence of many branches that usually have only one head. No other character indicates that the species should be excluded from the genus.

Involucres

The involucres of *Chrysolaena* have bracts of graduated lengths, but they show none of



Figs. 1–4. *Chrysolaena herbacea* (Vell.) H. Robinson, pollen. 1. Polar view showing polar areola and variation between two and three intercolpar areolae at periphery. 2. Lateral view of crest showing weak basal attachment of rhizome. 3. Colpar view with colpus partially collapsed and appearing interrupted. 4. Crest stripped from surface showing underside with rhizome.

the additional differentiation in shape and texture seen in many species of *Lepidaploa.* The lack of differentiation is reminiscent of *Lessingianthus,* and it may be a retained primitive condition, rather than a reduction.

The ratio of involucral bracts to flowers in the heads of *Chrysolaena* is 1:1–2:1. The comparative number of bracts is generally less than in either *Lepidaploa* or *Lessingianthus,* both of which tend to have 2:1–3:1 ratios. The shift in basic ratio is in the opposite direction from that seen in two other genera of the complex, *Stenocephalum* and *Echinocoryne,* where the involucral bracts occur in comparatively higher numbers.

Nonglandular Trichomes

The stems, leaves, and involucral bracts of *Chrysolaena* bear long sericeous or lanate hairs that contribute to the similarity in appearance of the plants. The hairs are yellowish to brownish and vary from straight to slightly flexuous. The hairs on the leaves vary from very dense in *V. herbacea* to sparse in *V. platensis.* Pubescence density in the inflorescence on the branches and involucral bracts is comparatively uniform in all the species. The hairs as seen in the species *V. herbacea* are the basis of the generic name *Chrysolaena.*

Style Bases

The presence or absence of nodular style bases is discussed in greater detail in treatments of the genera *Lessingianthus* (Robinson 1988) and *Lepidaploa* (Robinson in prep). The presence of a node seems basic to many neotropical members of the tribe Vernonieae and is regarded as basic to the *Lepidaploa* complex. However, three different genera of the complex appear to have lost the node. There is little or no node in *Stenocephalum* (Robinson 1987a), and *Lessingianthus* has essentially no node in its more than ninety species (Robinson 1988). *Chrysolaena* also lacks a distinct node. The only enlargements seen are the result of the basal row of sclerified cells holding their shape while the softer tissue above contracts. This condition contrasts strongly with the usually large and sometimes ornamented basal disk seen in *Lepidaploa.* Apparently, the three genera lacking basal stylar nodes have separately lost this structure. No function is presently known for the structure in the tribe, and therefore no functional shift is known that could explain the three separate losses. The essential coincidence of the character with generic concepts is convenient for the taxonomist, but it does raise unresolved questions about the precise nature of the phyletic gaps between the genera.

Glands

Structures sometimes referred to as short-stalked capitate glands are a type of a biseriate hair characteristic of the Asteraceae. They are notable in the family for the sesquiterpene lactones that they produce. They can be found on stems, leaves, involucres, corollas, anthers, style branches and achenes, but their appearance on vegetative parts, involucres, or corollas does not necessarily correlate with occurrence on anthers or achenes. In fact, only the tribes Heliantheae and Vernonieae commonly have glands on the anther appendages. *Chrysolaena* is one genus of the Vernonieae that seems to characteristically have glands on the anther appendages, but it is the only such genus in the *Lepidaploa* complex. In *Chrysolaena* the glands occur over most of the length of the appendage. They have been seen in all specimens of all but one species. The anther appendages of *V. herbacea* usually lack glands, although a few have been seen in some specimens.

The achenes of *Chrysolaena* also usually have glands among the setulae, at least near the base. Such glands do not occur in *Lessingianthus,* but they are found in various species of *Lepidaploa.* Glandular achenes and rhizomatous pollen crests both indicate a closer relationship of *Chrysolaena* to *Lepidaploa* than to *Lessingianthus.*

The various characters cited for *Chrysolaena* in some cases correlate with *Lepidaploa* and in others with *Lessingianthus.* The rhizomatous pollen crests are considered evidence that the relationship is closer to *Lepidaploa.* The latter view is strengthened by the basically sessile condition of the heads and by the common occurrence of glands on the achene. The lack of a basal stylar node and the habital resemblance to *Lessingianthus* subg. *Oligocephalus* seems to be the only basis for relating *Chrysolaena* to *Lessingianthus,* but these resemblances seem to be the result of independent reductions. *Chrysolaena* violates the generic limits of the two larger genera in a number of minor characters, such as the involucre/flower ratio and the pedunculate heads found rarely in one species. Still, one character, the glands on the anther appendages, is a unique departure from all other members of the *Lepidaploa* complex. Even though the glands are usually missing in one of the species, their presence is too consistent in the genus as a whole to be ignored. The combination of the glanduliferous appendages and the other discrepancies from *Lepidaploa* and *Lessingianthus* lead to the present recognition of *Chrysolaena* as a distinct genus.

The generic name is derived from the words *Chryso-* meaning golden and *laena* meaning cloak.

Chrysolaena H. Robinson, gen. nov.

Vernonia subsect. *Flexuosae* Cabrera, Darwiniana 6:329. 1944. Type: *Vernonia flexuosa* Sims.

Vernonia series *Flexuosae* (Cabrera) Jones, Rhodora 81:442. 1979. Type: *Vernonia flexuosa* Sims.

Vernonia series *Verbascifoliae* Jones, Rhodora 81:438. 1979 as to type but not as to intent. Type: *Vernonia verbascifolia* Less.

Plantae herbaceae perennes ad 2.5–15.0 dm altae xylopodiales, caules folia et bracteae involucri flave vel fulve sericeae vel lanatae. Caules erecti interdum abbreviati sub inflorescentia non ramosi. Folia alterna vel basilares saepe superne descrescentia sessilia ovata vel linearia vel obovata supra et subtus parce vel dense sericeae vel lanatae, nervis secondariis ascendentiter pinnatis vel sublongitudinalibus. Inflorescentiae interdum scaposae distincte cymosae saepe seriate cymosae, ramis dense sericeis; capitula sessilia raro breviter pedunculata. Involucra leniter subimbricata subgraduata 1–2-plo quam floribus 3–5-seriata, bracteis lanceolatis acutis. Flores 10–65; corollae purpureae, lobis plerumque glanduliferis caetera glabris in nervis apice conjunctis et leniter incrassatis; appendices antherarum plerumque glanduliferae; basi stylorum non noduliferi. Achaenia dense setulifera et plerumque glandulifera plerumque 5-costata; carpopodia turbinata, cellulis oblongis in parietibus lateralibus porulosis; setae pappi interiores capillares elongatae apice non lateriores, squamae exteriores breviores. Grana pollinis in diametro 40–50 μm lophata ad polos uni-areolata intercolpe dupliciter areolata (typus C), cristis rhizomataceis.

Type.—*Vernonia flexuosa* Sims.

Chromosome numbers of N = 17 and N = 34 have been reported in members of *Chrysolaena* (Jones 1979b).

The genus is concentrated geographically in central and southern Brazil and northern Argentina, and extends westward into Bolivia with one occurrence in Peru. The genus contains the following seven species of which six have been recently treated by Jones (1981) as members of the *Vernonia* series *Flexuosae.*

Chrysolaena flexuosa (Sims)
H. Robinson, comb. nov.

Vernonia flexuosa Sims, Bot. Mag. 51, pl. 2477. 1824. *Vernonia montevidensis* Nees ex Otto & Dietr., Allg. Gartenzeitung 1: 229. 1833. *Cacalia flexuosa* (Sims) Kuntze, Rev. Gen. Pl. 2:970. 1891. Argentina, Brazil (Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay, Uruguay.

Chrysolaena herbacea (Vell.)
H. Robinson, comb. nov.

Chrysocoma herbacea Vell., Fl. Flum. 330. 1825. *Vernonia obovta* Less., Linnaea 4:

279. 1829. *Vernonia densevillosa* Mart. ex DC., Prodr. 5:43. 1836. *Vernonia chrysophylla* Gardn., Lond. J. Bot. 6:417. 1847. *Cacalia obovata* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia paucifolia* Rusby, Mem. Torrey Bot. Club 3: 50. 1893. *Vernonia herbacea* (Vell.) Rusby, Mem. Torrey Bot. Club 4:209. 1895. Bolivia, Brazil (Amazonas, D.F., Goiás, Mato Grosso, Minas Gerais, Paraná, Rio de Janeiro, São Paulo), Peru (Junin).

Chrysolaena lithospermifolia (Hieron.) H. Robinson, comb. nov.

Vernonia lithospermifolia Hieron., Bot. Jahrb. Syst. 22:694. 1897. Brazil (Mato Grosso, Minas Gerais, Paraná, Santa Catarina, São Paulo), Paraguay.

Chrysolaena oligophylla (Vell.) H. Robinson, comb. nov.

Chrysocoma oligophylla Vell., Fl. Flum. 324. 1825, Atlas 8: pl. 2. 1835. *Cacalia oligophylla* (Vell.) Kuntze, Rev. Gen. Pl. 2: 968. 1891. *Vernonia hypochlora* Malme, Kungl. Svensk Vetenskapsakad. Handl. 12(2):12. 1933. Brazil (Paraná, Santa Catarina, São Paulo). The identity of the Vellozo species is briefly discussed in the treatment of *Lessingianthus* (Robinson 1988). The species name has been incorrectly associated with the habitally very similar *V. cephalotes* DC.

Chrysolaena platensis (Spreng.) H. Robinson, comb. nov.

Conyza platensis Spreng., Syst. Veg. 3:509. 1826. *Vernonia platensis* (Spreng.) Less., Linnaea 4:312. 1829. *Vernonia cognata* Less., Linnaea 6:670. 1831. *Vernonia senecionea* Mart. ex DC., Prodr. 5:54. 1836. *Cacalia cognata* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Cacalia platensis* (Spreng.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia sceptrum* Chod., Bull. Herb. Boissier, ser. 2, 2:303. 1902. Argentina, Brazil (Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay, Uruguay.

Chrysolaena propinqua (Hieron.) H. Robinson, comb. nov.

Vernonia propinqua Hieron., Bot. Jahrb. Syst. 22:695. 1897. *Vernonia lepidifera* Chod., Bull. Herb. Boissier, ser. 2, 2:304. 1902. Argentina (Misiones), Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay.

Chrysolaena verbascifolia (Less.) H. Robinson, comb. nov.

Vernonia verbascifolia Less., Linnaea 4: 310. 1829. Argentina (Corrientes, Misiones), Brazil (Paraná), Paraguay.

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STUDIES IN THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE) VI. A NEW GENUS, *AYNIA*

Harold Robinson

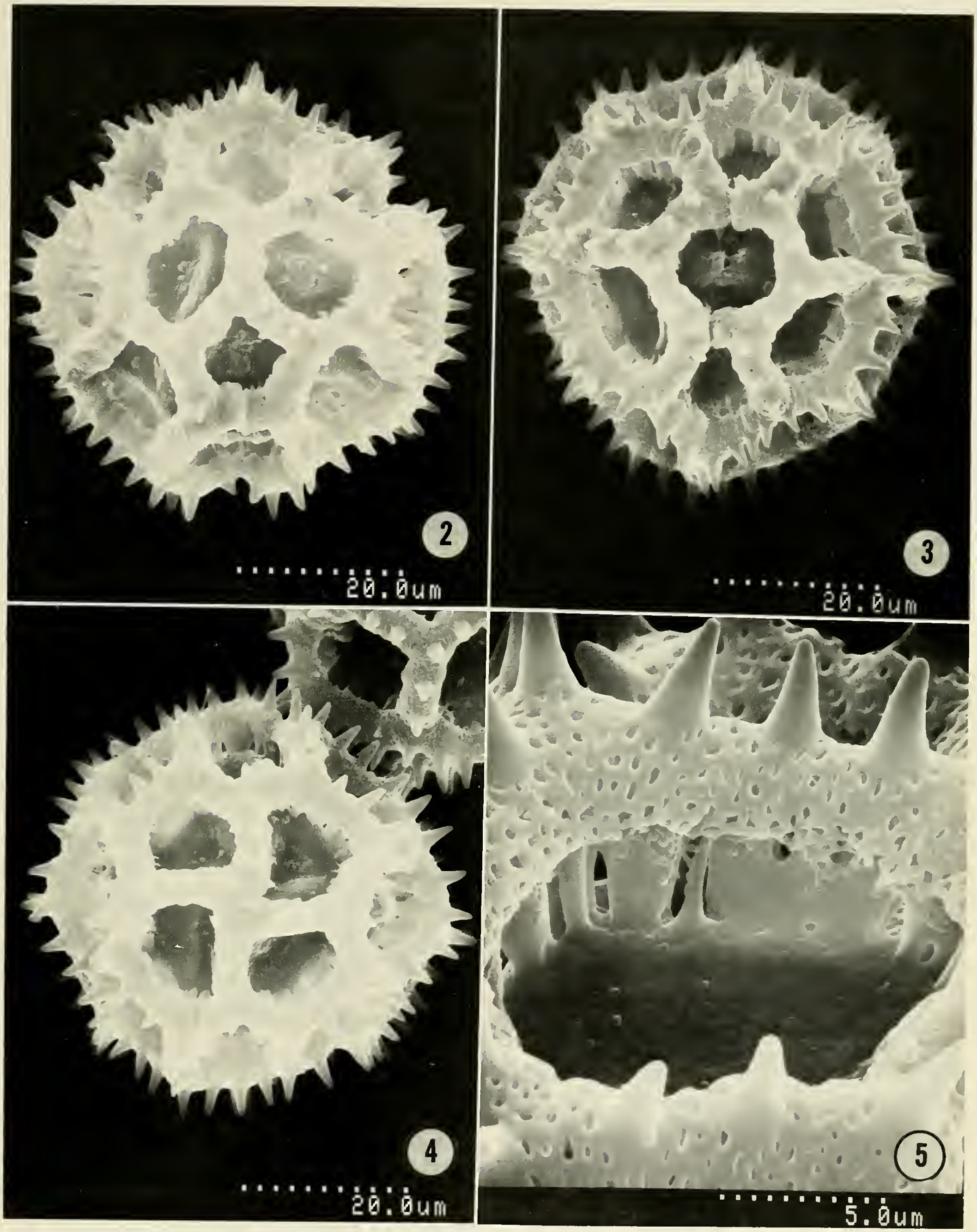
Abstract.—*Aynia pseudascaricida* is described as a new genus and species on the basis of collections from Ayacucho, Peru. The plants superficially resemble *Baccharoides* of India and Africa, but belong to the Neotropical *Lepidaploa* complex. Numerous leaf-like basal involucral bracts distinguish the genus from others of the complex. The non-rhizomatous lophate pollen is unique among the Vernonieae in having three intercolpar areolae at the poles.

Efforts to resolve the neotropical *Lepidaploa* complex of the tribe Vernonieae (Robinson 1987a, b, c) have resulted in the discovery of a totally undescribed member of the complex from southern Peru. For nearly sixty years since the collection by Killip and Smith the specimens have remained undetermined. The species has a superficial resemblance to *Baccharoides anthelmintica* of India that is sometimes cultivated as a medicinal plant, but the new genus is most easily distinguished from *Baccharoides* and from various potentially related neotropical genera by its more robust habit with larger heads (Fig. 1). The pollen is also unique in its details (Figs. 2–5). The non-type A pollen and the *Lepidaploa*-like ratio of involucral bracts clearly distinguish the genus from typical *Vernonia,* where it would be placed under older, artificial systems of classification of the tribe. The genus and species are as follows.

Aynia pseudascaricida H. Robinson, gen. et sp. nov.
(Figs. 1–5)

Plantae alte herbaceae vel suffrutescentes erectae ad 2.5 m altae laxae ramosae. Caules pallides teretes striati puberuli evanescentes, internodis ad 8 cm longis. Folia alterna, petiolis 1–2 cm longis anguste alatis; laminae late ellipticae ad 12–15 cm longae et 4–8 cm latae base breviter acuminatae margine remote mucronato-denticulatae apice supra viridis erecte puberulae parce immerse glandulo-punctatae subtus cinereo-tomentosae obscure glandulo-punctatae, nervis secundariis patentiter pinnatis utrinque 12–15. Inflorescentiae cymosae laxe lateraliter ramosae; ramis pilosulis; capitula plerumque pedunculata raro sessilia, pedunculis plerumque 3–13 cm longis. Involucrum hemisphaericum; bracteae involucri basilares foliiformes patentes elliptico-lanceolatae 2–7 cm longae et 0.5–2.0 cm latae base anguste cuneatae margine apice supra et subtus ut in foliis; bracteae ceterum fulvae rubro-tinctae appressae chartaceae subimbricatae ca. 100 in seriebus 4–5 lineari-lanceolatae 10–25 mm longae et base 2–3 mm latae apice peranguste acutae extus appresse puberulae et leniter pallide tomentellae ad medio distincte longitudinaliter unicostatae. Flores ca. 50 in capitulo; corollae puniceae vel lavandulae plerumque glabrae, tubis cylindricis ca. 8 mm longis, faucibus leniter infundibularibus 3–4 mm longis, lobis angustis ca. 10 mm longis et 0.8 mm latis apice dense spiculiferis in nervis incrassatis sensim sclerificatis; filamenta angusta carnosa in partibus superioribus ca. 0.65 mm longa, cellulis oblongis vel laxe oblongis vix noduliferis vel incrassatis; the-

Fig. 1. *Aynia pseudascaricida* H. Robinson, Holotype, United States National Herbarium, Washington, D.C.



Figs. 2–5. Pollen of *Aynia pseudascaricida.* 2. Polar view showing three intercolpar polar areolae. 3. Colpar view showing incomplete muri above and below pore. 4. Intercolpar view showing two tiers of two areolae. 5. Detail of pollen crest showing underlying large baculae attached to footlayer.

cae antherarum ca. 5.5 mm longae, cellulis endothecialibus suboblongis leniter asymmetrice lineate ornatis; appendices antherarum lanceolatae ca. 1.8 mm longae ad medio costatae margine leniter reflexae apice pungentes; basi stylorum distincte noduliferi; rami stylorum ca. 5.5 mm longi et abaxialiter dense hirsuti non glanduliferi. Achaenia ca. 4.5 mm longa et 1.5 mm lata superne in zonis 1 mm longis laeva et sclerificata inferne sensim 10-nervata a videtur glabra base et apice parce et minute glandulifera raro superne minute setulifera, raphidis plerumque quadratis; carpopodia ca. 0.5 mm alta et 1 mm lata ad foraminem valde incurvata, cellulis oblongis in parietibus incrassatis lateraliter porosis; setae pappi flavidae capillares rigidae ca. 75 in seriebus 2–3 longiores plerumque 13–17 mm longae apice sensim angustiores pungentes extus convexae extus et margine scabridae; setae exteriores breves paucae indistinctae ca. 0.5 mm longae squamiformes vel subulatae et base alatae. Grana pollinis in diametro ca. 60 μm lophata, cristis non rhizomataceis, areolis intercolpi aequatoriale in seriebus duplicibus binis, areolis intercolpi unicis superioribus et inferioribus ad polem attingentibus (*Aynia*-type, Figs. 2–5).

Type.—Peru: Ayacucho: Aina (Ayna), between Huanta and Rio Apurimac; alt. 750–1000 meters; open woods. Herb to 6 ft; stem simple; corolla tubes deep pink; styles white to pink; stamens deep pink. May 7, 17 1929. E. P. Killip & A. C. Smith 22514 (Holotype US). Paratype: Peru; Ayacucho: Aina, between Huanta and Río Apurimac; alt. 750–1000 meters. Thickets. Shrub 5–8 ft, with elongate branches; florets deep pink. May 7, 17 1929. E. P. Killip & A. C. Smith 23101 (US).

The generic name derives from the collection locality in northern Ayacucho in Peru. The species name derives from the resemblance to the well known *Baccharoides anthelmintica* (L.) Moench of India that is sometimes introduced into the Neotropical Region.

The ease of distinction of *Aynia* as a genus leaves the question of its closest relationship unresolved. There is no problem once certain assumptions are made. Some of the most important information that would determine the placement of the new genus in the paleotropical or neotropical members of the tribe is lacking in the present material. At present there is no information on the chemistry and chromosome number, characteristics that were found to differ in the new and old world groups (Jones 1977). Nevertheless, *Aynia* is presumed to be native to the area where it was collected, and in the absence of any characters specifically relating the genus to paleotropical genera such as *Baccharoides,* it is supposed that relationship is to the neotropical members of the *Lepidaploa* complex. Examination of details shows ample differences in *Baccharoides* such as the form of the inflorescence, the presence of appendages on the involucral bracts, the long, narrow, basal tube of the corolla rather abruptly expanding into a cylindrical throat, the lack of thickened veins and the presence of glands rather than numerous spicules at the tips of the corolla lobes, the smaller cells of the anther collar, the lack of broad appendages in the bases of the anther thecae, the transversely oblong and closely vertically striated endothecial cells, the smaller and blunter anther appendages, the lack of a node at the base of the style, and the more elongate achenes densely covered with setulae and glands. For this reason the new genus is seen as unrelated to *Baccharoides* and is regarded as a member of the Neotropical element of the tribe. The chromosome number is expected to be based on $\bar{x} = 17$ when it is determined, rather than $\bar{x} = 9$ or 10 as in paleotropical members of the tribe.

The relationship of *Aynia* within the Neotropical Vernonieae can be understood best by a review of various individual features in detail as follows under the headings, pollen, inflorescence, corolla lobes, anther, style base, pappus, and geography.

Pollen

The pollen of *Aynia* is lophate with non-rhizomatous crests attached to the footlayer by large baculae (Fig. 5). The general form occurs widely in the Vernonieae in both paleotropical genera such as *Baccharoides* and American genera such as *Stokesia, Mattfeldanthus* and *Lessingianthus.* Typical *Baccharoides* differs by having more than one row of smaller baculae under the crests, but other species of that genus have a single row of larger baculae as in the American genera. Relationship to the paleotropical and American groups cannot be determined on the basis of the pollen alone.

The pollen grains of *Aynia* are distinct from all the genera mentioned, both paleo- and neo-tropical, in the detail of the areolation. The unique form can be viewed as having intercolpar groups of six areolae (1:2:2:1) that are unique in reaching the poles of the grain (Figs. 2–4). In other pollen types with similar intercolpar groupings, the groupings are always separated from each other at the poles by colpi or extra areolae. In all other lophate grains in the Vernonieae with three areolae grouped at the poles, the areolae involved are aligned with the pores. The phyletic value of a distinct pollen form must be judged by the ease with which it can be derived from other types in related genera. In this case, the pollen is not duplicated in any other member of the Vernonieae. This is in spite of the fact that a 1:2:2:1 intercolpar pattern which does not reach the poles is one of the most common patterns in the tribe, and it is even seen in a crude form in most type A grains.

Inflorescence

The two specimens seen show an inflorescence with heads in one cymose series (Fig. 1). Most of the heads are terminal, with the remainder of the inflorescence arising laterally from the axil of a leaf-like bract. In only one of the heads is the lateral branch from immediately below the head with the head appearing sessile. In two of the seven heads observed, the head rather than the branch is axillary, and it is less mature than the head to which it is lateral. The inflorescence structure is simpler than any in *Baccharoides,* where the branch origins often lack bracts. In the regularly bracteate condition, *Aynia* is more like the Neotropical *Lepidaploa* complex. Within the latter complex, the inflorescence superficially most resembles *Lessingianthus* by its usually long-pedunculate heads.

The large, foliose, basal bracts of the head, by which *Aynia* superficially resembles typical *Baccharoides,* are obviously not evidence of close relationship to the latter genus. Still, the bracts readily distinguish *Aynia* from all members of the *Lepidaploa* complex to which *Aynia* is apparently related. The other members of the complex with foliose outer bracts have a gradual transition, and their foliose bract tips are never very large. The bracts in *Aynia* are totally leaf-like and show almost no intergradation.

The inner involucre of *Aynia* has bracts of a totally different texture from the basal series. The ratio of the inner bracts to the flowers is 2:1, a ratio characteristic of *Lepidaploa* and *Lessingianthus.* Such a ratio is widely distributed in the Neotropical Vernonieae, but it is not found in typical *Vernonia* from eastern North America.

Corolla Lobes

On the basis of an incomplete survey, the veins in the corolla lobes of the *Lepidaploa* complex seem distinct among the Vernonieae by the extent to which they fuse broadly and form an enlargement at the apex. The least amounts of fusion seen in the complex in the genus *Chrysolaena* are as strongly fused as those of any other genus examined in the tribe. In this respect *Aynia* is most clearly a member of the *Lepidaploa* complex. The veins at the tips of the corolla lobes expand into a large shield that is equalled in the complex only in the genus

Mattfeldanthus. The tracheids and fibers form a mass that makes the tip of the lobe very stiff in both *Aynia* and *Mattfeldanthus.* The type species of the latter genus, *M. mutisioides* H. Robins. & R. M. King, further resembles *Aynia* by the densely spiculiferous outer surface of the lobe-tip. *Mattfeldanthus nobilis* (H. Robins.) H. Robins. differs in having numerous small glands rather than spicules on the outer surface. The lobe character, more than any other, specifies the relationship of *Aynia* to the *Lepidaploa* complex.

Anther

The anther thecae of *Aynia* are like those of *Mattfeldanthus* and unlike those of *Baccharoides* in both basal appendages and endothecial cells. The two Neotropical genera both have broadly truncate differentiated bases on the thecae. The marginal cells are obviously specialized and form slight lobes. *Baccharoides,* in contrast, has shortly pointed anther bases with almost no differentiated marginal cells. The endothecial cells of the Neotropical genera are also alike in their curved, thickened bands that usually leave the median surfaces of the cells unthickened. In *Baccharoides* the cells are shorter and have vertical bands usually rather evenly spaced and straight across the surface.

The apical anther appendage of *Aynia* is distinct from those of all the other genera discussed by the lanceolate shape and the median costa. The appendage differs from *Baccharoides* additionally by the somewhat recurved margins and the laxer cells. The appendages of *Baccharoides* are much shorter, blunter, denser and flatter. The anther collars of *Baccharoides* are like the apical appendages in having smaller cells than in *Aynia* and *Mattfeldanthus.*

Style Base

The presence of a node at the base of the style is of some use in determining relationships in the Vernonieae. *Aynia* has a distinct node and in that way differs from the majority of paleotropical Vernonieae including *Baccharoides.* Those paleotropical Vernonieae having a stylar node such as *Distephanus* (Robinson & Kahn 1986) also tend to differ by having a much larger node. Nodes of the type seen in *Aynia* are most common in the neotropical Vernonieae and exactly the same form can be found in *Mattfeldanthus.* It is notable that distinct nodes are lacking in the other genus of the *Lepidaploa* complex having non-rhizomatous pollen, *Lessingianthus.* Thus, the stylar node, like the corolla lobes, places *Aynia* closer to *Mattfeldanthus,* which differs in inflorescence form and corolla symmetry; and it tends to separate *Aynia* from *Lessingianthus,* which it resembles more in the latter two characters.

Pappus

The pappus of *Aynia* looks different from that of related genera in color and persistence, but the actual character differences are more subtle. The comparative persistence seems related to the presence of more rows of bristles. The color difference is, at least partly, due to the thicker bristles. The bristles are convex and scabrid on the outer surface. In contrast, the bristles of *Mattfeldanthus* are flattened and smooth on the outer surface, and the bristles of *Baccharoides* are flattened and scabrid. A well-marked outer pappus series is not so obvious in *Aynia* as in most Vernonieae including *Mattfeldanthus*; however, some shorter outer papper segments are present. They are of various lengths and a few have broadened alariform bases with shortly awned tips. The form of the pappus is not unique within the Vernonieae, but it seems unique within the *Lepidaploa* complex.

Geography

The occurrence of *Aynia* in the Andes is a prime reason for relating the genus to other neotropical Vernonieae rather than to paleotropical genera such as *Baccharoides* which has superficially similar basal involucral bracts. All details of structure appear to reenforce the geographical evidence, and there is no reason to doubt that *Aynia* is related to the neotropical Vernonieae with which it occurs. Nevertheless, the geography does not correlate perfectly with the genera to which the new genus is evidently most closely related. *Lepidaploa,* which is common in the Andes, belongs to a more specialized element of the *Lepidaploa* complex that has rhizomatous crests on the pollen. The two other genera of the complex that have non-rhizomatous pollen are concentrated in Brazil. Both species of *Mattfeldanthus* are presently known only from Bahia in Brazil. *Lessingianthus,* which occurs in Peru, is represented there only by species extending their ranges from farther east. The geography seems to reenforce the distinct nature of *Aynia* in the *Lepidaploa* complex, with the new genus being the only element with non-rhizomatous pollen crests that is not centered in Brazil.

Acknowledgments

The pollen specimens were prepared by Barbara Eastwood using facilities of the Botany Department Palynological Laboratory. The photographs were prepared by Brian Kahn of the Smithsonian Museum of Natural History SEM Laboratory using a Hitachi 570 scanning electron microscope. The photograph of the holotype was made by Victor E. Krantz, Staff Photographer, Museum of Natural History.

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Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

BIOLOGICAL SOCIETY OF WASHINGTON

115th Annual Meeting, 18 April 1988

The meeting was called to order by Austin Williams at 1:00 p.m. in the Waldo Schmitt Room, National Museum of Natural History.

Austin announced the election results. The new elected officers are listed on the inside front cover of this issue.

Don Wilson, Treasurer, reported that income from dues, subscriptions, page-charges, and sale of past issues of the Proceedings in 1987 was lower than for 1986. Total income for 1987 was $88,476.70. The estimated income for 1988 is $75,800.00, and the estimated expenditures are $68,550.00—leaving $7,250.00 available to subsidize page charges. Austin noted that the report had been approved by the Council.

Austin announced a change in the editorial staff of the Proceedings. Brian Kensley, Editor for the past seven years (Volume 94–100), understandably, had retired. He received our many thanks and a standing ovation from the members present. Kensley still served as editor for Bulletin No. 8 (Results of recent research on Aldabra Atol, Indian Ocean), which was published in 1988. The new editor, C. Brian Robbins, was introduced. Also, Stephen D. Cairns agreed to serve as an additional associate editor for Invertebrate Zoology papers.

Brian Robbins, Editor, then reported on Volume 100 of the Proceedings. One hundred papers totaling 1050 pages, were published in 1987. It was noted that papers submitted by individuals unable to pay full page-charges were currently subject to a publications delay of one year. Unpaid papers now account for about 60 pages per issue. Don Wilson indicated that funds were available to increase this to 80 pages per issue; this will be implemented for Volume 101 (1988). Brian reported that a motion to limit the number of subsidized pages per author(s) per year to 12 printed pages (approximately 27 manuscript pages, including figures and tables), was approved by the Council. Also, Brian announced that our manuscript review policy, including suggestions and guidelines for reviewers and associate editor forms, was being revised and will affect all future manuscripts.

The 100 Year Index is currently being prepared by Phyllis Spangler. A format has been agreed to by the editorial staff. Copy will be ready for comments, revisions, etc. by Fall of 1988.

A motion was made and seconded that the meeting be adjourned; Kristian Fauchald, the new President, adjourned the meeting at 1:45 p.m.

Respectfully submitted,
C. Brian Robbins
Editor

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 a summary in an alternate language when appropriate.

Submission of manuscripts.—Submit manuscripts to the Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed in order of receipt by a board of Associate Editors and appropriate referees.

Proofs.—First proofs are submitted to authors for correction and approval. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, changes at proof stages, and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

Presentation.—Manuscripts should be typed **double-spaced throughout** (including tables, legends, and footnotes) on one side of 8½ × 11 inch sheets, with at least one inch of margin all around. Submit two facsimiles (including illustrations) with the original, and retain an author's copy. Pages must be numbered consecutively. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s') Address(es), Appendix, Figure Legends, Figures (each numbered and identified), Tables (**double-spaced throughout,** each table numbered with an Arabic numeral and with heading provided).

Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is required for descriptions and diagnoses. Literature citations in the text should be in abbreviated style (author, date, page), except in botanical synonymies, with unabbreviated citations of journals and books in the Literature Cited sections. Direct quotations in the text must be accompanied by author, date, **and pagination.** The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate figure and table placement in pencil in the margin of the manuscript. Plan illustrations in proportions that will efficiently use space on the type bed of the Proceedings. **Original illustrations should not exceed 15 × 24 inches.** Figures requiring solid black backgrounds should be indicated as such when the manuscript is submitted, but should not be masked.

CONTENTS