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## VOLUME 99

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

# PROCEEDINGS
# OF THE
# BIOLOGICAL SOCIETY
# OF
# WASHINGTON

THIS ISSUE IS DEDICATED TO
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ON THE OCCASION OF HIS 80TH BIRTHDAY,
AND IN RECOGNITION OF HIS LONG SERVICE
TO THE SOCIETY

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## PROCEEDINGS

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# *NEPHTYS CRYPTOMMA,* NEW SPECIES (POLYCHAETA: NEPHTYIDAE) FROM THE NORTHERN GULF OF MEXICO

Donald E. Harper, Jr.

*Abstract.*—A new species of polychaetous annelid, *Nephtys cryptomma,* is described from the northern Gulf of Mexico. The species is most abundant on sandy bottoms and appears to reproduce during the spring.

The species described herein as *Nephtys cryptomma* was first collected in 1978 during a benthic study conducted off Freeport, Texas. Specimens were subsequently collected off Louisiana in 1978–79 during the Central Gulf Platform Study (CGPS) conducted for the Bureau of Land Management, and off Cameron in 1983. The specimens were initially identified as *Nephtys magellanica* Augener (1912:208), based on the description by Hartman (1968:587), especially because of obvious eyespots visible in young specimens. However, more detailed examination of the specimens and comparison with the redescription of the syntypes of *N. magellanica* from the Straits of Magellan by Perkins (1980:34) revealed several differences. The specimens were thus designated *Nephtys* "subdermal eyes" while the description was in progress.

The type and additional specimens of *Nephtys cryptomma* have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Other specimens were deposited in the Texas A&M University, Department of Oceanography reference collection, College Station (TAMU), and the Texas A&M Marine Laboratory reference collection, Galveston (AMML).

### *Nephtys cryptomma,* new species
Figs. 1–4

*Material examined.*—TEXAS, Freeport, 19 km offshore, 28°44′N, 95°15′W, sandy to muddy sand bottoms, 21-m depth, 3 Apr 1980, Holotype (USNM 67778): 4 paratypes (USNM 67779), 2 paratypes (AMML PLY-24); 24 Feb 1978, 1 adult (USNM 67780); 16 Dec 1979, 1 adult (TAMU 1-2289); 13 Feb 1980, 1 young (USNM 67781), 1 young (TAMU 1-2290); 10 Mar 1980, 7 young (AMML PLY-25); 30 Jun 1980, 1 young (USNM 67782); 24 Jul 1980, 3 young (AMML PLY-28); 25 Aug 1980, 3 young (USNM 67783); 17 Apr 1981, 1 adult (AMML PLY-27); Freeport, 9 km offshore, 28°41′N, 95°17′W, muddy bottom, 16-m depth, 28 Jan 1980, 1 young (USNM 67784).

LOUISIANA, Grand Isle, 27 km offshore, 29°02′N, 90°09′W, muddy sand bottom, 13-m depth; 27 May 1978, 1 young (AMML PLY-29); Grand Isle, 54 km SSW offshore, 28°39′N, 90°14′W, sandy to silty sand bottom, 36-m depth; 26 Aug 1978, 4 young (USNM 69962), 1 adult (TAMU 1-2291), 1 young (AMML PLY-26).

VIRGINIA, York River, 3 to 10-m depth, Jan–Mar 1961, 4 adults (USNM 33327); Nov 1960, 1 adult (USNM 33326), 3–6 m; Mar 1961, 1 adult, 6 young (USNM 33328).

FLORIDA, Seahorse Key, 6 Feb 1960, 3 adults (USNM 33330).

*Diagnosis.*—Prostomium squarish anteriorly, tapering posteriorly, with paired anterolateral and ventrolateral antennae; middorsal pigment spot. First or tentacular segment extended lateral to prostomium with weakly developed setigerous parapodia bearing small dorsal tentacular cirri and

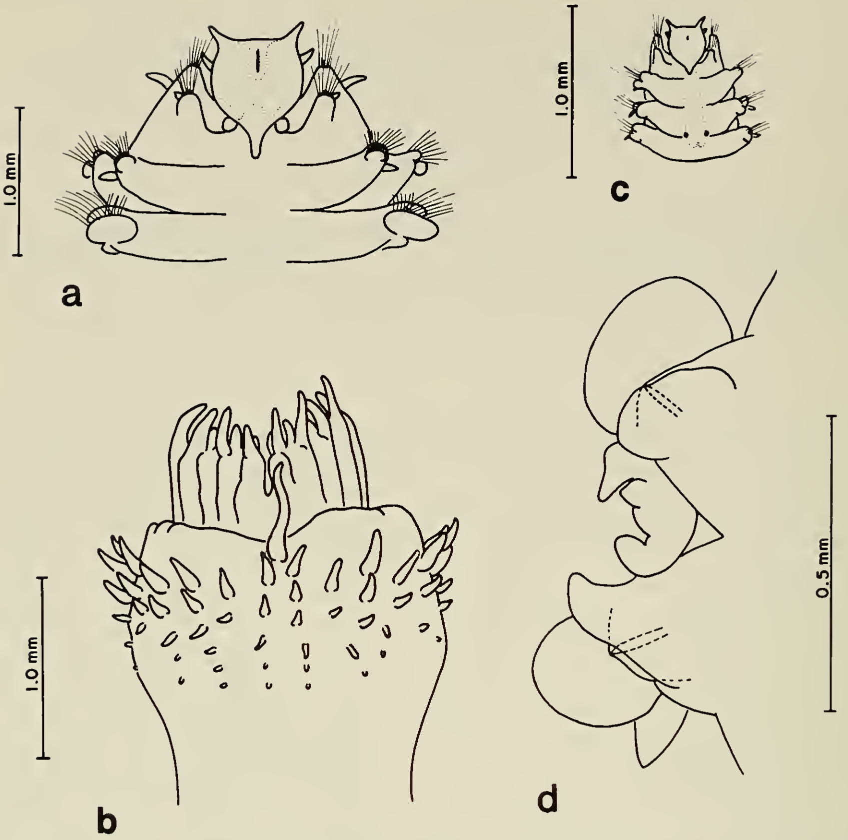

Fig. 1. *Nephtys cryptomma* (holotype): a, Anterior end, dorsal view; b, Distal end of everted proboscis, dorsal view; c, Anterior end of juvenile showing location of eyespots and brain (dotted); d, right parapodium 3, anterior view (setae not shown).

larger ventral tentacular cirri. Proboscis barrel-shaped, with 22 subterminal longitudinal rows of papillae in addition to long tapering middorsal and shorter midventral papillae. Parapodia biramous, with acicular lobes conical; notopodial presetal lamellae shorter than acicular lobes, with shallow excavations; postsetal lamellae broadly oval, longer than acicular lobes. Branchiae sickle-shaped, beginning on setiger 3, terminating about 3 segments from pygidium. Dorsal cirri begin on setiger 2, small in anterior segments, becoming elongate, thin, strap-like, almost as long as branchiae by midbody, continuing to posterior end. Preacicular setae barred capillaries, postacicular setae longer flowing capillaries with mostly fine teeth. Pygidium with dorsal anus and single anal cirrus.

*Description.*—Prostomium squarish anteriorly, tapering posteriorly, with pair of antennae at anterior corners, pair of ventrolateral antennae just anterior to neuropodia of peristomium, pair of nuchal organs at posterolateral angles, and medial spot or streak of reddish-brown pigment (Fig. 1a). Peristomial or tentacular segment with biramous parapodia directed anteriorly; notopodia with presetal lamellae smaller than acicular lobes, postsetal lamellae slightly larger, dorsal tentacular cirri small, notosetae directed anterodorsally; neuropodia with weakly developed lamellae and larger tentacular cirri, neurosetae directed ante-

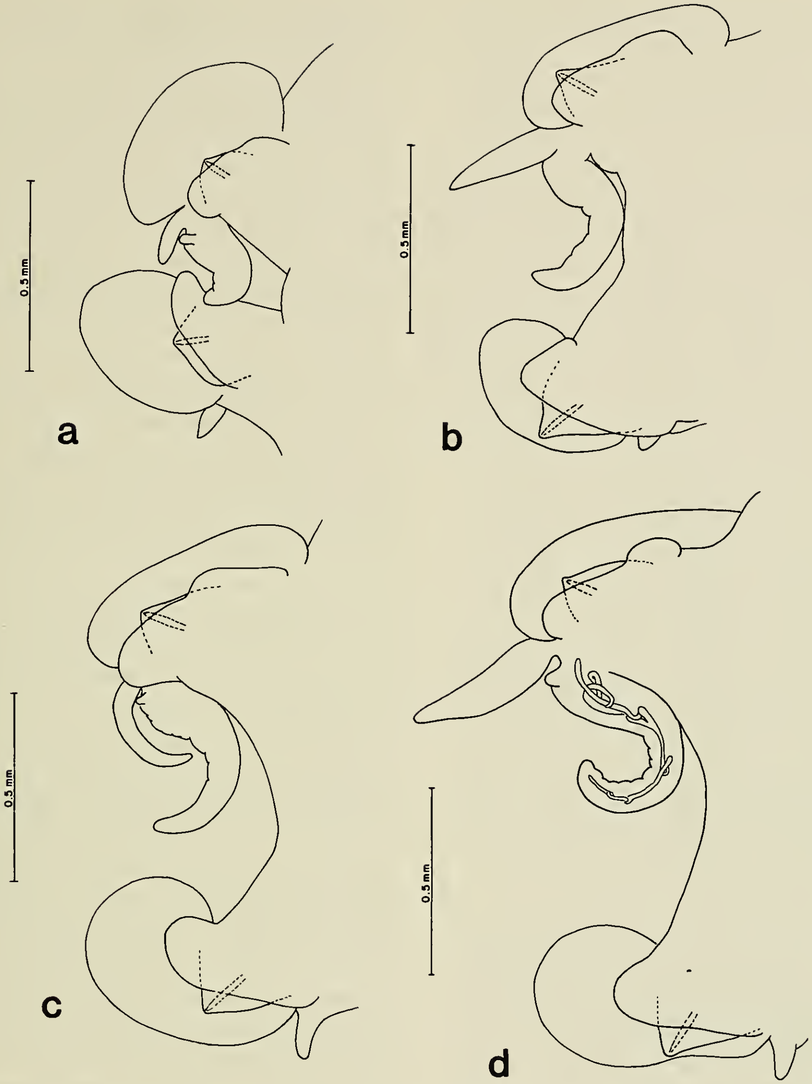

Fig. 2. *Nephtys cryptomma*: a, Right parapodium 10, anterior view; b, Right parapodium 38, anterior view; c, Right parapodium 50, anterior view; d, Right parapodium 70, anterior view.

riorly (Fig. 1a). Mouth flanked by lateral lobes. Subterminal part of everted proboscis with long, tapering, middorsal papilla, shorter midventral median papilla and 22 longitudinal rows of conical papillae, usually 4–6 per row, decreasing in size proximally; on both dorsal and ventral surfaces, second row of papillae on either side of midline with only 2 (sometimes 1) papillae; occasionally some ventral rows merge in V-shape; terminal part of proboscis with 11 pairs of bifid papillae (Fig. 1b). Internal deep lateral grooves begin at proximal end and terminate about one-quarter of length before distal end; single brown tooth in terminus of each groove. Pair of black eyespots on posterolateral surface of brain, visible through integument of juvenile and young specimens (Fig. 1c), but obscured by more opaque integument in adults. Notopodia of setiger 2 with small pre- and postsetal lamellae and small dorsal cirri. Parapodia fully developed from setiger 3 (Fig. 1d), reaching maximum size about setiger 10 (Fig. 2a). Acicular lobes conical or, on few anterior segments, slightly bilobed. Notopodial presetal lamellae shorter than acicular lobes, with shallow excavations in anterior segments, becoming more pronounced toward mid-body; postsetal lamellae longer than acicular lobes, broadly oval, without excavations (Figs. 2a–d). Neuropodial presetal lamellae shorter than acicular lobes, oval; postsetal lamellae much larger than acicular lobes, oval. From mid-body posteriorly, lamellae gradually reduced in size, and quite small in far posterior segments. Interramal branchiae present from setiger 3 (Fig. 1d), well-developed in mature specimens, large, recurved on all segments, with small conical projections just below insertion of dorsal cirri (Figs. 1d, 2a–d). Dorsal cirri attached to dorsal part of notopodia, small anteriorly, attaining maximum size in anterior third of body and continuing posteriorly; when fully developed in mid-body and posterior segments, thin, lanceolate (Figs. 2a–d). Ventral cirri present from peristomial segment. Setae all capillaries of 2 basic types forming 2 fan-shaped rows in both rami. Preacicular setae shorter, straighter, appearing cross-barred internally (Fig. 3a). Postacicular setae longer, flowing, spinous; most neurosetae finely spinous along entire blade, but 2 to 3 in middle of row with few large basal teeth in addition to fine spines (Fig. 3b); some upper neurosetae appearing smooth (Fig. 3c). Notosetae directed dorsolaterally, neurosetae directed ventrolaterally. Pygidium rounded, enclosed in posterior small segments, with dorsal anus and single terminal anal cirrus (Fig. 3d).

*Etymology.*—The specific epithet is from the Greek "kryptos" (hidden) and "omma" (eye) referring to the deep-set eyespots which are evident in juveniles, but hidden beneath integument in adults.

*Size range.*—The holotype is a complete ovigerous female, 43 mm long, 3 mm wide (including parapodia), having 82 fully formed segments, followed by 3 incomplete ones, the last represented by setae only. The largest specimen, complete but broken, is 65 mm long, 4 mm wide, with 98 segments, including 2 incomplete ones (USNM 67780).

*Color.*—Living worms are cream-colored, except for the nearly transparent posterior few segments and anal cirrus, reddish-brown prostomial spot and black eyes. Setae and tips of acicula dark golden. Blood red. Gut visible as dark area from about setiger 16 to end of body. Preserved worms are uniformly opaque white to pale yellow, except for the prostomial spot.

*Distribution.*—The species is presently known from the northern and eastern Gulf of Mexico (Florida, Louisiana, and Texas) and Virginia.

*Remarks.*—The dark prostomial spot could cause *N. cryptomma* to be mistaken for other species. *Nephtys simoni* Perkins (1980:37) has the spot and eyespots, but the paratypes (USNM 55684) have slightly bilobed acicular lobes rather than conical lobes, rounded notopodial presetal lamellae with the lamellae smaller than in *N. cryptomma,* and slightly bilobed postsetal lobes. *Nephtys parva* Clark and Jones (1955:143) has the pigment spot and eyes, and entire acicular lobes, but has reduced pre- and postsetal lamellae and branchiae beginning on setiger 4. *Nephtys magellanica,* the species with which *Nephtys cryptomma* was originally confused, lacks the prostomial pigment spot, has bilobed acicular lobes, shorter presetal lobes, and only 20 rows of papillae on the proboscis.

Several lots of specimens collected from the Chesapeake Bay area by Wass (1965:16; USNM 33326–28, 38738) and Seahorse Key, Florida, by Taylor (1971:103–104; USNM 33330) were examined. These specimens, originally identified as *N. magellanica* were re-examined by Perkins (1980), determined to be similar to *N. hombergii* Savigny (1818:314) and labelled *N.* cf. *hombergi.* Perkins (1980:41–42) stated that these specimens differed from *N. simoni* in lacking dorsal cirri on segment 1, yet they all bear small papilla-like dorsal cirri on the tentacular segment, arising from the lateral surface of the parapodia. In some cases the cirri are very small and inconspicuous, causing the parapodium to appear bilobed. Furthermore, the dorsal presetal lamellae have shallow excavations as in *N. cryptomma* rather than the deeply cleft lamellae as in *N. hombergii* (Fauvel 1923:367–368, fig. 143c, d; Fauchald 1963:12, fig. 3E). These specimens have therefore been referred to *N. cryptomma.*

*Nephtys cryptomma* is probably more abundant in the eastern Gulf of Mexico than the single record indicates. Re-examination of the specimens identified as *N. simoni* collected during the MAFLA study for the Bureau of Land Management (Taylor 1984:9) may show that some of the individuals are actually *N. cryptomma.*

Ecological notes.—*Nephtys cryptomma* has been collected most frequently on sandy and muddy sand bottoms. Depths ranged from 16 m off the Texas coast to 36 m off Louisiana. The species was never a numerically dominant member of its assemblage. During a 6-year (1978–1983) benthic study off Freeport, Texas, in which 15 stations were sampled at each of two sites, the maximum monthly abundance was 12 individuals at the deeper sandy bottom site. Data from both the Freeport and CGPS studies indicate that *N. cryptomma* is a spring breeder. The few ovigerous females obtained were collected in the spring. Off Freeport, only a few specimens were collected in 1978 and 1982. In 1979–1981, maximum abundances occurred in early spring, followed by decreases through summer, while in 1983 the largest numbers were col-

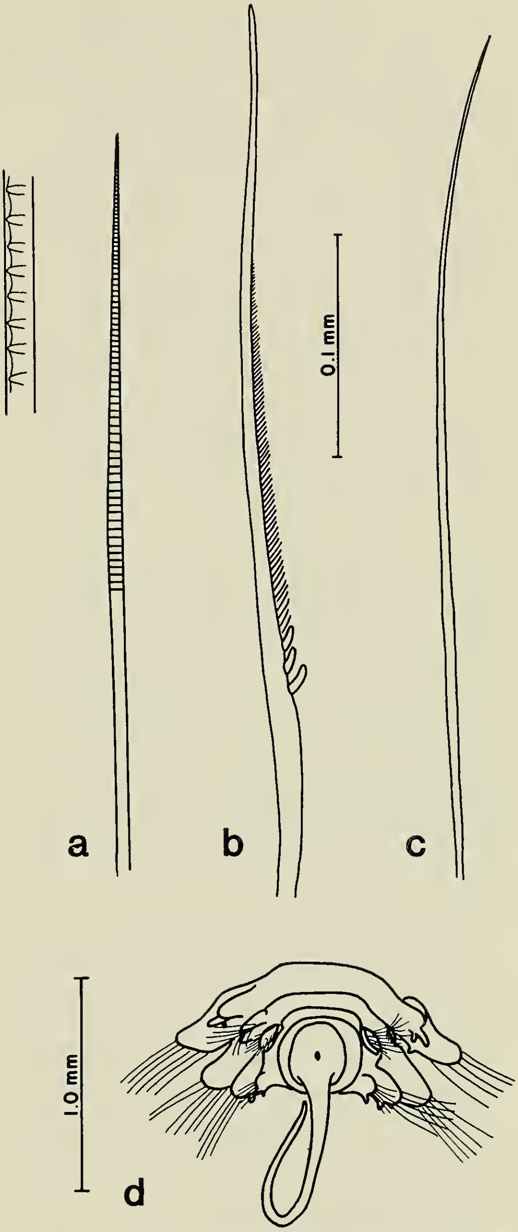

Fig. 3. *Nephtys cryptomma*: a, Barred preacicular capillary seta: inset showing details of cross-barring, highly magnified; b, Spinous postacicular neuroseta from middle of row; c, Smooth postacicular neuroseta from lower part of row; d, Posterior end and pygidium.

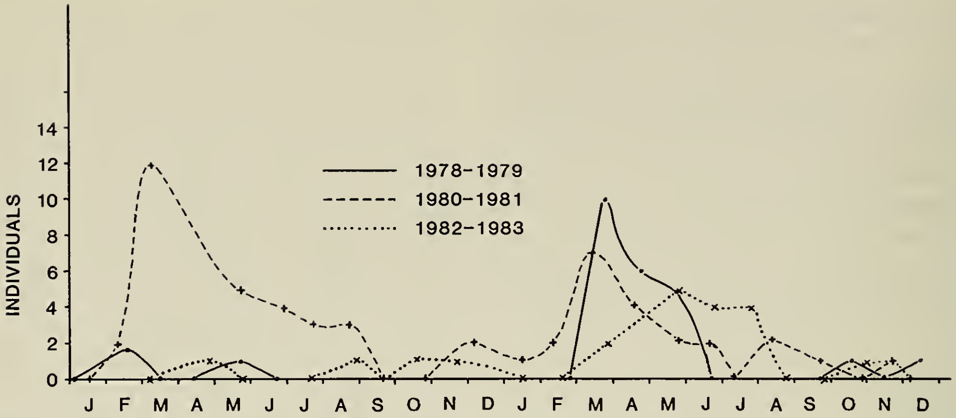

Fig. 4. Seasonal distribution of *Nephtys cryptomma* off Freeport, Texas, 1978–1983 on sandy bottom study area in 21-m depth.

lected in late spring (Fig. 4). The rapid decline in June 1979 coincided with the occurrence of hypoxic, hydrogen sulfide-laden water (Harper et al. 1981) and was probably not indicative of the usual seasonal trend. During the 3-season, 36-station CGPS study off Louisiana in 1978–79, *N. cryptomma* abundances were: May–June—84; August–September—9; January—8, which agrees with the seasonal data collected off Freeport.

*Notes on living worms.*—Living worms were collected on 3 April 1980 from the type-locality off Freeport, Texas, and observed in the laboratory in a finger bowl. The worms were generally passive, lying on their backs. When prodded they swam vigorously by undulating the posterior three-quarters of the body. The proboscis was never everted unless the worm was immersed in 70% ethanol.

Cilia on the branchiae and interramal body walls created water currents that flowed posteriorly in the interramal channel. The branchiae were kept away from the body wall in this current, and were frequently snapped backward, either singly or in unison, which dislodged small adhering particles.

The mid-dorsal longitudinal blood vessel was mostly obscured by musculature. It emerged from the musculature in the vicinity of setiger 25, and disappeared again at the base of the prostomium. Between setiger 25 and 15 the vessel was large, contractile and fixed in position. From setiger 15 to 9 the position of the vessel was not fixed, and it moved from side to side as the worm flexed. From setiger 9 to the base of the prostomium the vessel was fixed in the dorsal midline. Paired contractile longitudinal ventral vessels, lying alongside the ventral nerve cord, were visible from about setiger 4 to the pygidium; they were largest anteriorly. Blood flowed posteriorly in the right vessel and anteriorly in the left. Lateral vessels were small, forming networks of vessels in the body wall posterior to the parapodia, and in the branchiae (Fig. 2d). The gut was visible as a dark line from about setiger 16 to the posterior end of the body.

## Acknowledgments

I thank the numerous graduate and undergraduate students who participated in the cruises off Freeport and sorted the samples, and particularly my associates Larry McKinney and Robert Salzer, who analyzed most of the benthic samples. This research was sponsored by the Department of Energy Contract No. DE-FC96-79P010114 administered by the Texas A&M Research Foundation, directed by Roy W. Hann, Jr., and Robert E. Randall, both of the Environmental Engineering Division, Civil Engineering Department, Texas A&M University. The Central Gulf Platform Study was supported by Bureau of Land Management Contract AA551CT817 to Southwest Research Institute, Houston, Texas, managed by C. A. Bedinger, Jr.

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Texas A&M Marine Laboratory, Bldg. 311, Ft. Crockett, Galveston, Texas 77550.

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# NEW SOUTH AMERICAN GASTROPODS IN THE GENERA *CONUS* (CONIDAE) AND *LATIRUS* (FASCIOLARIIDAE)

Edward J. Petuch

*Abstract.*—Additions to the marine gastropod fauna of South America, including six new species of *Conus* (Conidae) and a new *Latirus* (Fasciolariidae), are described. Two of the new cones, *Conus carioca* n. sp. and *C. riosi* n. sp., range along the northern and eastern coasts of Brazil, while two others, *C. tostesi* n. sp. and *C. xanthocinctus* n. sp., are restricted to the Patagonian region of southern Brazil and Uruguay. Two northern South American cones are also described: *C. gibsonsmithorum* n. sp. from the Paraguaná Peninsula, Venezuela, and *C. penchaszadehi* n. sp. from the Goajira Peninsula of Colombia. The new fasciolariid, *Latirus vermeiji* n. sp., is endemic to Fernando de Noronha Island off northern Brazil.

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The northern and eastern coasts of South America, in particular Venezuela, Colombia, and Brazil, have recently been shown to harbor atypical Caribbean molluscan faunas with archaic appearances (Vermeij 1978:231–235; Petuch 1981). Through the works of Venezuelan authors, such as Gibson-Smith, Penchaszadeh, Princz, and Flores, the gastropod fauna of that coastline is now becoming better known. The Brazilian coast, on the other hand, is still poorly known, with the compendium of Rios (1975) being the only comprehensive faunal guide to that area.

Through the kindness of several South American malacologists, including Sr. Luiz Roberto Tostes, Rio de Janeiro, and Prof. E. C. Rios, Rio Grande do Sul, Brazil, and Dr. Pablo Penchaszadeh, Universidad Simon Bolivar, and Dr. and Mrs Gibson-Smith, Caracas, Venezuela, I was given study material of interesting new species from their respective countries. These unusual new gastropods include, amongst others, six new species of *Conus*. Dr. Geerat Vermeij, University of Maryland, has also kindly donated a number of specimens of a new *Latirus* from Fernando de Noronha Island off the northern Brazilian coast. These were collected during a research trip to the island in 1968. These important new additions to the fauna of South America are described here.

Gastropoda
Neogastropoda
Fasciolariidae
*Latirus* Montfort, 1810

### *Latirus vermeiji*, new species

Figs. 3, 4

*Material examined.*—Holotype: Length 25 mm, width 13 mm, on rocks at low tide line, south coast of Fernando de Noronha Island, Brazil, 1968, number 14243, type collection of the Museu Oceanográfico Centro de Ciencias do Mar, Fundação Universidade do Rio Grande, Brazil; Paratypes: length 27 mm, same locality and date as holotype, collection of the Division of Mollusks, National Museum of Natural History, Smithsonian Institution, USNM 784685; three specimens, lengths 15–26 mm, collection of Geerat J. Vermeij, Department of Zoology, University of Maryland.

*Description.*—Shell fusiform in outline, spire protracted; siphonal canal short for genus; adults with 8 whorls; sculpture consisting of 8–10 large spiral cords with finer threads in between; whorls with 8–9 prominent axial ribs; shoulder sharply angled, producing faint knob at posterior end of each rib; columella with 3 large plications; outer lip with numerous lirae; lirae extending into aperture; siphon slightly umbilicate; shell uniformly deep orange colored; interior of aperture white; periostracum and operculum dark brown.

*Etymology.*—Named for Dr. Geerat J. Vermeij, of the University of Maryland, who collected the type material on Fernando de Noronha.

*Distribution.*—Endemic to the island of Fernando de Noronha off northern Brazil.

*Discussion.*—This new species somewhat resembles a stumpier version of the Abrolhos Islands endemic, *Latirus ogum* Petuch, 1979, but differs in having a much shorter siphonal canal and more angled shoulder. In these last two characters, *L. vermeiji* resembles a small *Leucozonia* species. The new species is a true *Latirus,* however, in that it lacks the tooth on the outer lip and the color banding of that fasciolariid genus. Interestingly enough, *Latirus vermeiji* is morphologically closer to the Panamic *L. socorroensis* Hertlein and Strong, 1951, which is also endemic to offshore island groups.

### Conacea
### Conidae
### *Conus* Linnaeus, 1758
### *Conus carioca,* new species
Figs. 1, 2

*Material examined.*—Holotype: Length 52 mm, width 24 mm, trawled by commercial fishermen from 100 m depth off Cabo Frio, Rio de Janeiro State, Brazil, 1975, collection of the Museu Oceanográfico de Fundação Universidade de Rio Grande do Sul #20-915; Paratypes: length 45 mm, same locality and depth as holotype, Museu Oceanográfico #20-915; 2 specimens, lengths 53 mm and 53 mm, trawled by Brazilian fisheries research vessel, from 150 m depth off Recife, Pernambuco, Brazil, 1968, Museu Oceanográfico #14-242; length 57 mm, same depth and locality as holotype, collection of the Division of Mollusks, National Museum of Natural History, Smithsonian Institution USNM 784686.

*Description.*—Shell elongate, straight-sided, smooth and shiny, shoulder sharp-edged, carinated; spire flattened but slightly protracted in early whorls; color white with revolving bands of bright orange and orange-pink; orange bands overlaid with rows of pale brown dots and dashes; mid-body with white band; central white band bordered on both sides by bands of dark brown flammules; spire pale orange with crescent-shaped brown flammules; interior of aperture pale salmon; periostracum thin, smooth, translucent brown; operculum small, oval in shape.

*Etymology.*—Named for the "cariocas," the inhabitants of Rio de Janeiro.

*Discussion.*—*Conus carioca* most closely resembles the deep water, slope species *C. villepini* Fischer and Bernardi, 1857. The new continental shelf species differs from its slope-inhabiting relative in being more elongate, in having a much flatter spire, and in being a much more colorful shell, with bands of bright orange and salmon-pink.

### *Conus gibsonsmithorum,* new species
Figs. 5, 6

*Material examined.*—Holotype: Length 20 mm, width 18 mm, trawled by commercial shrimp boats from 35 m depth off north coast of the Paraguaná Peninsula, Falcón State, Venezuela, 1978, Museu Oceanográfico #14244; Paratype: length 18 mm, same depth and locality as holotype, USNM 784687.

*Description.*—Shell turnip-shaped, obese, thick and heavy; anterior one-third of shell greatly constricted; body whorl smooth and shiny, with anterior one-third having heavy grooving and thick spiral cords; aperture very narrow; spire elevated on early whorls, becoming planar on later whorls; shoulder sharp-edged, carinated; slight constriction just below shoulder carina; shell pale cream-yellow colored with pale tan band around middle; spire pale yellow, becoming tan on early whorls; periostracum thin, smooth, translucent yellow.

*Etymology.*—Named for Dr. and Mrs. Jack Gibson-Smith (Jack and Winifred) of Caracas, Venezuela, in recognition of their contributions to Venezuelan malacology.

*Discussion.*—This small new species is the only South American cone shell to have a squat, turnip-shaped body form. In this respect, *C. gibsonsmithorum* most closely resembles *C. sennottorum* Rehder and Abbott, 1951, from the Gulf of Mexico. The new Venezuelan species differs from its northern relative by lacking any spottings or color patterns, by having a more sharply carinated shoulder with sub-shoulder constriction, and by being a smaller, stockier species.

At present, *C. gibsonsmithorum* is known only from the Gulf of Venezuela region, to which it is most probably endemic.

### *Conus penchaszadehi,* new species
Figs. 13, 14

*Material examined.*—Holotype: Length 18 mm, width 9 mm, trawled by commercial shrimpers from 35 m depth off Cabo La Vela, Goajira Peninsula, Colombia, 1974, Museu Oceanográfico #14245.

*Description.*—Shell elongate, thin, fragile; spire elevated; body whorl shiny, totally covered with numerous fine spiral threads; spiral threads becoming coarser at anterior end; shell pinkish-white with scattered orange flammules on body whorl; solid, dark orange band around anterior one-third of body whorl; anterior tip bright pinkish-orange; spire white with crescent-shaped orange flammules; interior of aperture pale salmon-pink; protoconch and early whorls bright orange; periostracum thick, brown, with rows of fine tufts.

*Etymology.*—Named for Dr. Pablo Penchaszadeh, Department of Biology, Simon Bolivar University, Caracas, Venezuela.

*Discussion.*—This distinctive little shell is unlike any other northern South American cone. *Conus penchaszadehi* may be related to *C. atractus* Tomlin, 1937, but differs from that species by having the bright orange color band and flammules and by having finer spiral sculpture. The new Venezuelan species, however, closely resembles pale color forms of the Panamic *C. orion* Broderip, 1833, and may be the Caribbean cognate species.

*Conus penchaszadehi* is only known from off the Goajira Peninsula of Colombia, but it most probably ranges all along the Colombian coast and into the Gulf of Venezuela.

### *Conus riosi,* new species
Fig. 7, 8

*Material examined.*—Holotype: Length 54 mm, width 32 mm, trawled from 50 m depth off Salvador, Bahia State, Brazil, by Brazilian fisheries research vessel R/V RIOBALDO, 1975, Museu Oceanográfico #18757; Paratypes: length 37 mm, same locality and depth as holotype, Museu Oceanográfico #14242.

*Description.*—Shell thick, heavy, wide-shouldered, tapering toward anterior end; spire completely flattened with only first few whorls being protracted; body whorl and spire shiny with waxy feel; shoulder sharp-edged with prominent carina; shells varying in color from yellow to orange with numerous crowded vertical flammules of dark brown or reddish-brown; mid-body with clear white band; white band bordered by, or sometimes covered by, band of dark brown checkers; second band of dark flammules around anterior end; anterior tip bright apricot-orange; spire orange with numerous crescent-shaped dark brown flammules; interior of aperture pale orange; periostracum thin, translucent yellow-brown, with scattered tufts of large hairs.

*Etymology.*—Named for Prof. E. C. Rios, of the Fundação Universidade do Rio Grande, in recognition of his invaluable works on the Brazilian molluscan fauna.

*Discussion.*—This new species is closely related to, and is often confused with, the common, widespread *Conus daucus* Hwass, 1792. The new Brazilian species differs from its Caribbean relative by being a larger, heavier shell, by having a different color pattern with a prominent white or brown central band, and by having an undulating suture on the spire whorls. *Conus riosi* also prefers deeper waters along the southern coast of Brazil, while *C. daucus* generally prefers shallow water reef areas around the Caribbean region. Of the specimens of *C. riosi* examined, none had the deep red-orange color or the rows of tiny spots seen on *C. daucus.*

*Conus daucus* may range only into northern Brazil, since many of the records of that species from further south have turned out to be *C. riosi.* The "*C. daucus*" illustrated by Van Mol, Tursch, and Kempf (1967: plate 7, fig. 2) and that of Rios (1975: Fig. 542) both appear to be referable to the new species.

## The Patagonian *Conus* Species

The last two new cones described here belong to a distinctive and close-knit species group that is restricted to the cold water Patagonian region, from Santa Catarina, Brazil, to south of Mar del Plata, Argentina. Included in this group are *Conus clenchi* Martins, 1943, *C. tostesi* n. sp., and *C. xanthocinctus* n. sp., from southernmost Brazil, and *C. carcellesi* Martins, 1945, *C. iheringi* Frenguelli, 1946, and *C. platensis* Frenguelli, 1946 from Uruguay and Argentina. All species in this group have highly polished shells with rounded shoulders, relatively high to protracted spires, and large, mamillate protoconchs. Because of its sharp-angled shoulder and small protoconch, *C. clerii* Reeve, 1844, which is sympatric with *C. clenchi, C. tostesi,* and *C. xanthocinctus* along the southern Brazilian coast, does not appear to belong to this group. Instead, *C. clerii* appears to be related to southern Caribbean species such as *C. undatus* Kiener, 1848, *C. cingulatus* Lamarck, 1810, and *C. centurio* Born, 1780.

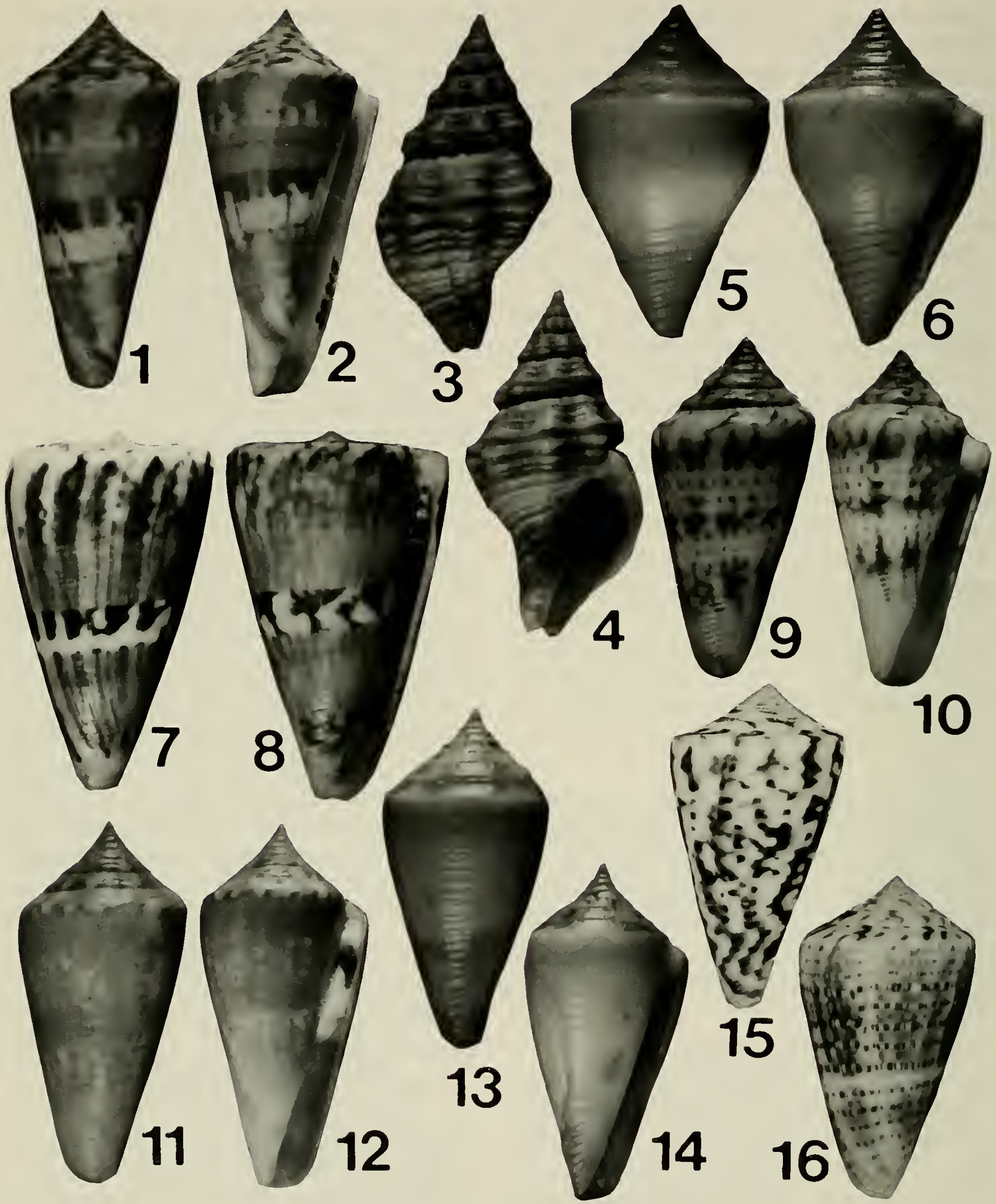
The six Patagonian cones represent remnants of a large cold water molluscan fauna that extended down a large part of the coast of Argentina during the Late Pliocene (Frenguelli 1932). This fauna was typified by conid species such as *C. patagonicus* Frenguelli, 1932, and a large number of interesting volutacean genera that includes *Minicymbiola, Odontocymbiola, Zidona, Adelomelon, Pachycymbiola, Weaveria, Orbignytesta, Olivancillaria,* and *Olivina,* and a remarkable trophonine (Muricidae) fauna. Descendants of these distinctive species radiations are still extant along the Patagonian coast, with the greatest number of species being found from southernmost Brazil to, and into, the Mar del Plata. In the Recent, the descendant Patagonian cones represent the southernmost limit of the family in the Americas.

### *Conus tostesi,* new species

Figs. 9, 10

*Material examined.*—Holotype: Length 35 mm, width 18 mm, trawled by commercial fishermen from 100 m depth off Cabo Frio, Rio de Janeiro State, Brazil, 1977, Museu Oceanográfico #14246; Paratypes: length 29 mm, same locality and depth as holotype, Museu Oceanográfico #14247; length 27 mm, USNM 784688.

*Description.*—Shell elongate, thin fragile;



Figs. 1–16. Species of *Latirus* and *Conus* from South America. 1, 2, *Conus carioca,* dorsal and ventral aspects of holotype; 3, 4, *Latirus vermeiji,* dorsal and ventral aspects of holotype; 5, 6, *Conus gibsonsmithorum,* dorsal and ventral aspects of holotype; 7, 8, *Conus riosi,* dorsal and ventral aspects of holotype; 9, 10, *Conus tostesi,* dorsal and ventral aspects of holotype; 11, 12, *Conus xanthocinctus,* dorsal and ventral aspects of holotype; 13, 14, *Conus penchaszadehi,* dorsal and ventral aspects of holotype; 15, *Conus clerii* Reeve, 1844, specimen from 100 m off Cabo Frio, Rio de Janeiro State, Brazil; 16, *Conus clenchi* Martins, 1943, specimen from 100 m off Cabo Frio, Rio de Janeiro State, Brazil.

spire protracted, slightly scalariform; body whorl shiny, with anterior one-third covered with numerous fine spiral threads; shoulder produced but slightly rounded; color pale violet to darker violet with three wide bands of reddish-brown, one just below shoulder, one around mid-body, and one around anterior end; banded color pattern overlaid by 10–14 rows of brown dots; anterior tip darker violet on some specimens; spire white with numerous crescent-shaped flammules; protoconch large, mamillate; periostracum thin, smooth translucent yellow.

*Etymology.*—The new taxon honors Sr. Luiz Roberto Tostes of Rio de Janeiro, Brazil, who kindly donated large amounts of material for study.

*Discussion.*—*Conus tostesi* is closest to the sympatric *C. clerii* Reeve, 1844, but differs in being a much smaller, more elongate shell, by having a higher, scalariform spire, by being of a violet color instead of white, and by having a much larger, mamillate protoconch. A typical specimen of *C. clerii,* from the type locality of *C. tostesi,* is illustrated here for comparison (Fig. 15).

This new Brazilian species actually shows a closer affinity to some of the rare Paolinian-Submagellanic species such as *C. carcellesi* Martins, 1945 and *C. platensis* Frenguelli, 1946 from the Mar del Plata (Frenguelli 1946). *Conus tostesi* differs from both of these species, however, by having a three-banded color pattern, finer body sculpture, and by lacking spiral grooves on the spire.

### *Conus xanthocinctus,* new species
Figs. 11, 12

*Material examined.*—Holotype: Length 47 mm, width 22 mm, trawled by commercial fishermen from 100 m depth off Cabo Frio, Rio de Janeiro State, Brazil, Museu Oceanográfico #14248; Paratype: Length 45 mm, same locality and depth as holotype, Museu Oceanográfico #14249.

*Description.*—Shell elongate, slender, thin and fragile; spire protracted, stepped; body whorl and spire smooth, shiny; shoulder only slightly produced, rounded, anterior end of shell with few weak spiral striae; aperture narrow; shell color bright golden-yellow with three darker, orange-yellow bands, one just below shoulder, one around mid-body, and one around anterior end; mid-body band darkest, deep orange colored; bands overlaid with 12–14 spiral rows of brown dashes and scattered white flammules; spire golden-yellow with numerous crescent-shaped tan flammules; shoulder and suture of spire whorls ornamented with bands of alternating dark tan and white flammules; interior of aperture pale golden colored; periostracum thin, smooth, translucent yellow; operculum small, oval.

*Etymology.*—"Yellow-belted," in reference to the characteristic and distinctive bright orange-yellow band around the mid-body.

*Discussion.*—This distinctive new species could only be confused with the sympatric *C. clenchi* Martins, 1943, and then only in general shell shape. The bright golden color bands and characteristic shoulder coloration readily separates *C. xanthocinctus* from *C. clenchi.* A typical specimen of *C. clenchi,* from the type locality of *C. xanthocinctus,* is illustrated here for comparison (Fig. 16).

## Acknowledgments

I thank Dr. M. G. Harasewych, Division of Mollusks, Smithsonian Institution, for taking the excellent photographs used in this paper.

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# THE AUSTRAL-AFRICAN CONID SUBGENUS *FLORACONUS* IREDALE, 1930, TAKEN OFF BERMUDA (GASTROPODA: CONIDAE)

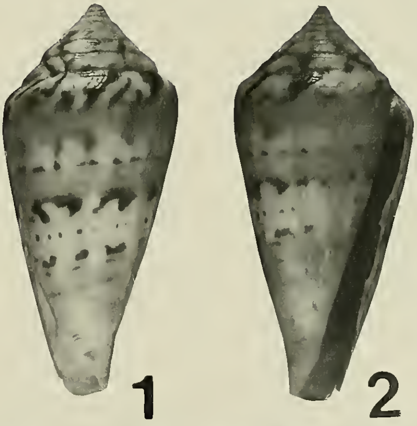
Edward J. Petuch

*Abstract.*—Baited lobster traps have recently been used to sample the deep water molluscan fauna of the slope of Bermuda. Among the many unusual gastropods collected was the first known northern Atlantic member of the Austral-African conid subgenus *Floraconus* Iredale, 1930. The discovery of this species, which is geographically widely separated from related forms and is here named *Conus* (*Floraconus*) *lightbourni* new species, points to the relict nature of the subgenus.

Mollusks from the deep waters around Bermuda have recently been taken by a novel new collecting technique. This method, undertaken by the well known Bermudan malacologists Messrs. John R. H. Lightbourn and Arthur T. Guest, involves dropping baited lobster traps into deep water and leaving them there for a number of days. At the end of that time, the traps are retrieved and the hermit crab-occupied shells are collected. Since dredging on the steep slope of the Bermuda seamount is difficult, this simple method is proving itself to be the best way to explore the unknown slope fauna.

To date, a large number of interesting new gastropod shells, all occupied by hermit crabs, have been collected from the lobster pots. These include unusual species such as the newly described *Pterynotus lightbourni* Harasewych and Jensen, a number of *Pleurotomaria* (*Perotrochus*) species, the "Hawaiian endemic" *Gyrineum loisae* Lewis, the eastern and southern Atlantic *Gyrineum olearium* Linnaeus (Jensen, pers. comm.), and the first known northern Atlantic species of the Austral-African conid subgenus *Floraconus* Iredale, 1930. All of these elements give the Bermudan slope fauna a distinctly Indo-Pacific and Japonic appearance.

The subgenus *Floraconus* was previously thought to be restricted to the southern and eastern shores of Australia and to the Cape Province region of South Africa. Because of this distributional pattern, this conid subgenus may represent a Paleogene relict group, much like the sympatric Austral-African relict volutid genus *Athleta* (Petuch 1981:1127). The presence of *Floraconus* in the northern Atlantic indicates that the group was once very widespread but has survived into the Recent in only three widely separated areas.



Figs. 1, 2. Dorsal and ventral aspects of the holotype of *Conus* (*Floraconus*) *lightbourni*, from 497 m off Bermuda.

The new *Floraconus* is the only known truly endemic Bermudan cone shell. A large, common, shallow water species, named *Conus bermudensis* by Clench in 1942, was originally thought to be endemic to the island but has now been found to be conspecific with the widespread western Atlantic *C. mindanus* Hwass, 1792 (Walls 1979:726–730). Along with *C. mus* Hwass, 1792, *C. mindanus,* and *C. villepinii* Fischer and Bernardi, 1857, the new *Floraconus* brings the total number of known Bermudan cone species to four. This unexpected mid-Atlantic member of an Austral-African group is described here.

Gastropoda
Neogastropoda
Conacea
Conidae
*Conus* Linnaeus, 1758
*Floraconus* Iredale, 1930
*Conus* (*Floraconus*) *lightbourni,*
new species Figs. 1, 2

*Material examined.*—Holotype: Length 35 mm, width 16 mm, occupied by hermit crab, taken in lobster pot from 180 fathoms (approx. 497 m), 1½ miles (2.5 km) due south of Castle Island, Bermuda, July 1973, by J. R. H. Lightbourn; collection of the Department of Malacology, Delaware Museum of Natural History, DMNH 134938; Paratypes: 3 specimens, lengths 26.0 mm–47.7 mm, same depth and locality as holotype, DMNH 134939; 5 specimens, lengths 22.4 mm–44 mm, collection of Mr. J. R. H. Lightbourn, Bermuda.

*Description.*—Shell elongate, slender, obconical, thin, lightweight; spire elevated; shoulder and spire whorls rounded; body whorl and spire shiny, polished; anterior end of body whorl with numerous faint, raised spiral threads; aperture narrow, straight; base shell color bright orange, overlaid with two wide bands of deep salmon-pink, one at mid-body, one between mid-body and shoulder; some specimens with third salmon band around anterior end; salmon-pink bands ornamented with rows of large brown spots; spots often coalesce into large brown flammules, usually on either side of central band; some specimens with rows of small brown dots on orange bands; spire salmon-pink with large crescent-shaped brown flammules; protoconch mamillate; interior of aperture pale violet-purple; operculum and periostracum unknown.

*Etymology.*—Named for Mr. John R. H. Lightbourn of Bermuda, in recognition of his many important discoveries of new deep water Bermudan mollusks.

*Remarks.*—The narrow, highly polished body and rounded shoulder of *C. lightbourni* readily separates the new species from any other known western Atlantic cone shell. The new species is closest to the South African *C.* (*Floraconus*) *pictus* Reeve, 1843, in color pattern, but is more like the eastern Australian *C.* (*Floraconus*) *wallangra* (Garrard, 1961) or *C.* (*Floraconus*) *angasi* Tryon, 1883, in shape.

## Acknowledgments

I thank Dr. M. G. Harasewych, of the Smithsonian Institution, Washington, D.C., for the excellent photographs.

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# THE STATUS OF *PSEUDORHABDOSYNOCHUS* YAMAGUTI, 1958, AND *CYCLOPLECTANUM* OLIVER, 1968 (MONOGENEA: DIPLECTANIDAE)

Delane C. Kritsky and Mary Beverley-Burton

*Abstract.*—*Cycloplectanum* Oliver, 1968, is considered a junior subjective synonym of *Pseudorhabdosynochus* Yamaguti, 1958. *Diplectanum epinepheli* Yamaguti, 1938, *P. epinepheli* Yamaguti, 1958, and *C. hongkongensis* Beverley-Burton and Suriano, 1981, are synonyms, resulting in the valid name of the species being *P. epinepheli* (Yamaguti, 1938) new combination.

During our independent investigations on diplectanids from fishes in the Neotropics (DCK) and in the Pacific and Caribbean (MB-B), it became apparent that a problem exists concerning the status of the genera *Pseudorhabdosynochus* Yamaguti, 1958, and *Cycloplectanum* Oliver, 1968. In this paper, we present a historical review of these taxa and offer a solution to the systematic problem.

Yamaguti (1958) established *Pseudorhabdosynochus* for *P. epinepheli* Yamaguti, 1958, from the gills of *Epinephelus akaara* (Temm. and Schleg.) collected from the Inland Sea of Japan. The genus was characterized, in part, by the presence of squamodiscs reduced to membranous plaques with several curved, transverse ridges. Oliver (1968) proposed *Cycloplectanum* for diplectanids in which the two interior rows of rods on the squamodiscs formed closed circles. He designated *Diplectanum americanum* Price, 1937, as the type-species, of which *D. epinepheli* Yamaguti, 1938, *D. serrani* Yamaguti, 1953, *D. amplidiscatum* Bravo-Hollis, 1954, *D. latesi* Tripathi, 1957, *D. melanesiensis* Laird, 1958, and *Pseudorhabdosynochus epinepheli* Yamaguti, 1958, were considered junior synonyms. Beverley-Burton and Suriano (1981) emended *Cycloplectanum* on the basis of morphologic characteristics of the terminal genitalia (i.e., copulatory complex and vagina). These authors did not accept Oliver's (1968) synonymies of species, but considered all six taxa listed to be distinct. Recognizing that their arrangement would result in homonymy between the then congeneric *epinepheli* (Yamaguti, 1938) and *epinepheli* (Yamaguti, 1958), Beverley-Burton and Suriano (1981) proposed *C. yamagutii* to replace the latter.

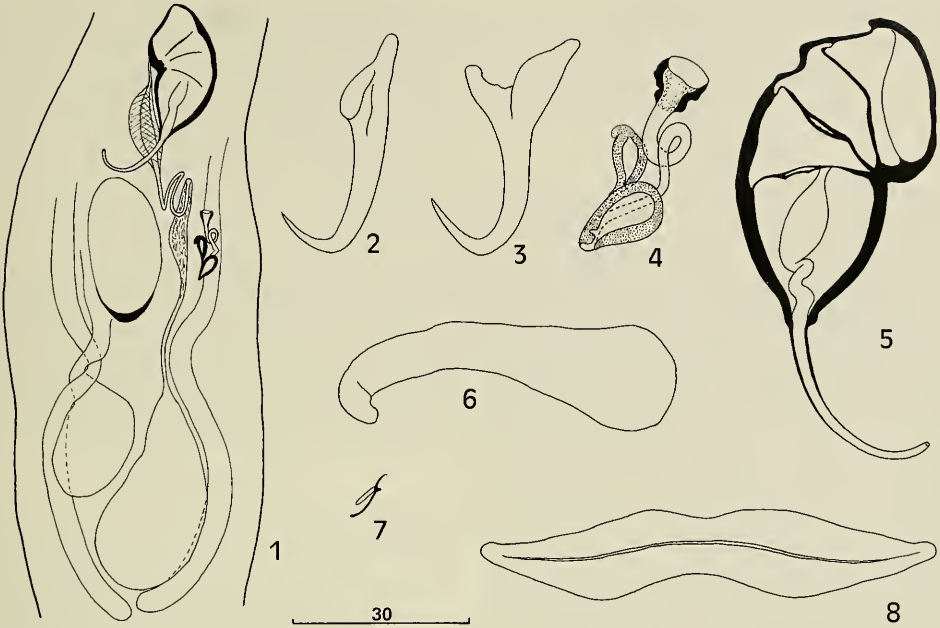
It is evident that the proposals of Oliver (1968) concerning *Pseudorhabdosynochus epinepheli* and the establishment of *Cycloplectanum* are based on incorrect interpretations of the International Code of Zoological Nomenclature (ICZN). His determination that *P. epinepheli* was a junior synonym of *Diplectanum americanum* does not invalidate the status of the former as the name-bearing type of *Pseudorhabdosynochus* (Art. 61, ICZN). Thus, *Cycloplectanum* is a subjective junior synonym of *Pseudorhabdosynochus* since the taxon contains two type-species (*P. epinepheli* and *D. americanum*) with *Pseudorhabdosynochus* having priority. As long as *D. americanum* and *P. epinepheli* are congeneric, *Cycloplectanum* must be suppressed (Art. 23, ICZN).

Based on the most recent revision of *Cycloplectanum* by Beverley-Burton and Suriano (1981), *Pseudorhabdosynochus* (= *Cycloplectanum*) currently contains the species listed in Table 1. From Yamaguti's (1958)

Table 1.—Pseudorhabdosynochus species and their synonyms.

| Species | Synonyms |
|---|---|
| *Pseudorhabdosynochus epinepheli* (Yamaguti, 1938) (senior subjective synonym of the type species, *P. epinepheli* Yamaguti, 1958) | *Diplectanum epinepheli* Yamaguti, 1938<br>*Pseudorhabosynochus epinepheli* Yamaguti, 1958 (type species)<br>*Cycloplectanum hongkongensis* Beverley-Burton and Suriano, 1981<br>*C. americanum* (Price, 1937) Oliver, 1968 (partim)<br>*C. yamagutii* Beverley-Burton and Suriano, 1981 |
| *P. americanum* (Price, 1937) | *D. americanum* Price, 1937<br>*C. americanum* (Price, 1937) Oliver, 1968 (partim) |
| *P. amplidiscatum* (Bravo-Hollis, 1954) | *D. amplidiscatum* Bravo-Hollis, 1954<br>*C. amplidiscatum* (Bravo-Hollis, 1954) Beverley-Burton and Suriano, 1981<br>*C. americanum* (Price, 1937) Oliver, 1968 (partim) |
| *P. beverleyburtonae* (Oliver, 1984) | *C. beverleyburtonae* Oliver, 1984<br>*C. americanum* (Price, 1937) Oliver, 1968 (misidentification)<br>*D. americanum* Price, 1937 of Euzet and Oliver (1965) (misidentification) |
| *P. bocquetae* (Oliver and Paperna, 1984) | *C. boquetae* Oliver and Paperna, 1984 |
| *P. caballeroi* (Oliver, 1984) | *C. caballeroi* Oliver, 1984<br>*C. americanum* (Price, 1937) Oliver, 1968 (partim)<br>*D. americanum* Price, 1937 of Caballero and Bravo-Hollis (1961) (misidentification) |
| *P. cupatum* (Young, 1969) | *D. cupatum* Young, 1969<br>*C. cupatum* (Young, 1969) Beverley-Burton and Suriano, 1981 |
| *P. lantauensis* (Beverley-Burton and Suriano, 1981) | *C. lantauensis* Beverley-Burton and Suriano, 1981 |
| *P. latesi* (Tripathi, 1955) | *D. latesi* Tripathi, 1955<br>*C. latesi* (Tripathi, 1955) Beverley-Burton and Suriano, 1981<br>*C. americanum* (Price, 1937) Oliver, 1968 (partim) |
| *P. melanesiensis* (Laird, 1958) | *D. melanesiensis* Laird, 1958<br>*C. melanesiensis* (Laird, 1958) Beverley-Burton and Suriano, 1981<br>*C. americanum* (Price, 1937) Oliver, 1968 (partim) |
| *P. querni* (Yamaguti, 1968) | *D. querni* Yamaguti, 1968<br>*C. querni* (Yamaguti, 1968) Beverley-Burton and Suriano, 1981 |
| *P. serrani* (Yamaguti, 1953) | *D. serrani* Yamaguti, 1953<br>*C. serrani* (Yamaguti, 1953) Beverley-Burton and Suriano, 1981 |
| *P. summanae* (Young, 1969) | *D. summanae* Young, 1969<br>*C. summanae* (Young, 1969) Beverley-Burton and Suriano, 1981 |
| *P. vagampullum* (Young, 1969) | *D. vagampullum* Young, 1969<br>*C. vagampullum* (Young, 1969) Beverley-Burton and Suriano, 1981 |

description of the internal anatomy and structure of the squamodisc of *P. epinepheli*, it might be argued that this species is not congeneric with others included in the table. Relevant to this is that Yamaguti (1958) indicated an intercecal ovary which does not loop the right intestinal crus. *Pseudorhabdosynochus epinepheli* was also considered to have unarmed squamodiscs which distinguished it, at that time, from other known species of Diplectanidae. However, our study of the holotype and paratype of *P. epinepheli* Yamaguti, 1958 (Meguro Parasitological Museum No. 22375) under No-



Figs. 1–8. *Pseudorhabdosynochus epinepheli* (Yamaguti, 1938). 1, Diagram of median region of body (ventral); 2, Ventral anchor; 3, Dorsal anchor; 4, Vagina (ventral); 5, Cirrus; 6, Dorsal bar; 7, Hook; 8, Ventral bar. All figures are drawn to the same scale (30 micrometers) except Figure 1.

marksi (direct interference contrast) illumination confirmed that the ovary does loop the right intestinal crus as it does in all other species of the complex (Fig. 1). While both the holotype and paratype lack scaled squamodiscs, this feature also is not sufficient to exclude *P. epinepheli* from the complex since squamodisc scales are easily lost if fixation does not occur immediately after death of the diplectanid.

Confusion concerning the valid name of the type-species of *Pseudorhabdosynochus* also exists. Originally indicated by monotypy, the species, *P. epinepheli* Yamaguti, 1958, has undergone name changes (to *C. americanum* by Oliver, 1968, and to *C. yamagutii* by Beverley-Burton and Suriano, 1981) as a result of the proposal and subsequent revision of *Cycloplectanum.* Now, our examination of holotypes and paratypes of *Diplectanum epinepheli* Yamaguti, 1938 (Meguro Parasitological Museum No. 22259), *P. epinepheli* Yamaguti, 1958 (Meguro Parasitological Museum No. 22375) and *C. hongkongensis* Beverley-Burton and Suriano, 1981 (USNM Helm. Coll. Nos. 76720, 76726, 76727) has revealed that all of these forms are conspecific. The type-series of *Diplectanum epinepheli* includes specimens which have squamodiscs partially or completely lacking scales, and sclerites of the haptor and terminal genitalia are indistinguishable from those of *P. epinepheli.* Thus, since the three species listed above are herein considered conspecific, the senior available name (i.e., valid name, Art. 23a, ICZN) for this taxon is *P. epinepheli* (Yamaguti, 1938).

In his descriptions of *D. epinepheli* and *P. epinepheli,* Yamaguti (1938, 1958) did not provide detailed drawings of the sclerites of the haptor and genitalia. Those presented herein (Figs. 2–8) are based on the holotype and paratype of *P. epinepheli* Yamaguti, 1958, the specimens on which *Pseudorhabdosynochus* was originally proposed.

## Discussion

Blackwelder (1967:503–505) has shown that the 1961 ICZN was not clear regarding the definition of what the type of a genus is, i.e., a species (a taxon) or a species name, although the preface (page v) to this edition of the Code clearly indicates the former. However, the Glossary of the 1985 edition of the ICZN expresses that a type-species is a nominal species, a nomenclatural concept having no defined taxonomic boundaries. Although many authors (taxonomists) have apparently believed that the type of a genus is a species rather than a species name, the definitions provided by the 1985 Code clearly indicate that the type of a generic taxon is a name. Thus, the type, designated by monotypy, of *Pseudorhabdosynochus* remains *P. epinepheli* Yamaguti, 1958, which is a junior subjective synonym of *P. epinepheli* (Yamaguti, 1938) n. comb.

The nominal genus, *Cycloplectanum* Oliver, 1968, while a junior subjective synonym of *Pseudorhabdosynochus,* satisfies all criteria of the Code (Arts. 10–20) and is therefore an available name. If at some later revision of the species group, *americanum* and *epinepheli* are determined not to be congeneric, *Cycloplectanum* is available for the group containing *americanum.*

## Acknowledgments

We wish to thank Dr. S. Kamegai, Director of the Meguro Parasitological Museum, Tokyo, Japan, for the loan of type-specimens of *Pseudorhabdosynochus epinepheli* Yamaguti, 1958, and *Diplectanum epinepheli* Yamaguti, 1938; Dr. J. R. Lichtenfels, Animal Parasitology Institute, Beltsville, Maryland, for loan of the type-specimens of *Cycloplectanum hongkongensis* Beverley-Burton and Suriano, 1981; and Drs. R. C. Anderson, Idaho State University, Pocatello, and R. L. Rausch, University of Washington, Seattle, for critical and useful comments concerning our analysis. Financial support was provided by the National Sciences and Engineering Research Council of Canada (Grant No. 801-81).

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# A NEW RECORD OF *PARACOROPHIUM HARTMANNORUM* ANDRES, 1975, FROM THE CHILEAN COAST, WITH A DESCRIPTION OF THE ADULT (AMPHIPODA: COROPHIIDAE)

Exequiel González

*Abstract.*—The adult male and female of *Paracorophium hartmannorum* Andres, 1975, are described, and *P. chilensis* Varela, 1983, is placed in synonymy. The main differences between adults and juveniles are longer dactyl teeth on the palm of the second gnathopod and the toothed posterior margin of the bases of pereopods 6 and 7 in the adults. The present material extends the geographical range of the species north of Valparaiso.

*Paracorophium hartmannorum* was described by Andres (1975) from a juvenile male 2.8 mm in length collected by G. Hartmann-Schröder from Estero Lenga (36°46′S, 73°10′W) near Concepción, Chile. Andres recorded his new species from four localities between Constitución and Valdivia, in southern Chile. Collections made in 1976 from the mouth of Rio La Ligua (32°25′S, 71°26′W), north of Valparaiso (Fig. 1), extend the known range to the north, and enable me to describe the adults. The latter have been compared with Varela's description and figures of *P. chilensis,* from Valdivia, which is considered a synonym of *P. hartmannorum.*

### *Paracorophium hartmannorum* Andres
Figs. 2–4

*Paracorophium hartmannorum.*—Andres, 1975:127–130, figs. I–V.
*Paracorophium chilensis.*—Varela, 1983: 32–36, figs. 5–6.

*Description of male.*—Length 3.8–4.4 mm. Head with lateral lobes produced. Antennae 1 and 2 as described by Andres (1975); segments 2 and 3 of antenna 2 almost 3 times as wide as segment 4. Lower lip, mandible, maxilla 2, and maxilliped similar to Andres' description. First maxilla, outer plate wide, distal margin with 8 to 9 bifid spines, second segment of palp with 5 simple apical spines. Second maxilla like that of *Paracorophium excavatum* Hurley, inner plate slightly shorter, inner margin fringed with long fine setae along about ⅔ of its length, setae also on distal margin; outer plate with setae only on distal margin. First gnathopod: coxal plate large, slightly constricted proximally, with 2 strong spines on posterior margin, 15 setae on ventral margin; basis proximally constricted, group of 3 long simple setae and 4th more distal seta on posterior margin, inner surface with 2 simple setae on middle region, distal end with 5 long simple setae on medial surface; ischium with same proportions as in *P. excavatum*; merus with same proportions as ischium, 3 short plumose setae on posterior margin, inner surface of distal end toward posterior with 3 or 4 short plumose setae; carpus, anterior margin with 4 or 5 long simple setae in middle to distal region, anteriodistal angle with 3 long plumose setae, posterior margin with 16 long slender plumose setae on outer surface and 10 long slender plumose setae on border, inner surface with oblique row of long and fine plumose setae from posteroproximal to ⅔ anterodistal end of segment; propod, anterior margin with 2 long simple setae on middle region, anterodistal angle with 5 long simple setae, first shortest, inner surface with 2 or 3 setae, palm with 8 short spines on outer surface, and 5 or 6 on inner surface, margin of palm and distal part of posterior margin of propod with several fine teeth giving appearance of little brush; dactyl slightly longer than palm, with long spine on proximal anterior margin, posterior margin with inconspicuous tooth at proximal end and strong spine about ⅓ from distal end, margin finely serrate proximal to spine. Second gnathopod, coxal plate subrectangular with 7 or 8 short spines on ventral margin, 1 or 2 strong spines on posterior margin; basis constricted proximally, posteriorly convex as Hurley (1954) described for *P. excavatum,* 2 or 3 long setae on posterior margin, 1 or 2 little spines on distal end of anterior margin, proximal end ½ width of distal end; ischium ⅓ basis length with 2 spines on distal posterior margin; merus with distal end free, anterior margin divided, forming inner and outer borders, latter forms with posterior margin almost rectangle, merus length 3 times its width, distal end with 9 long strong plumose setae, most of them reaching distal end of propod, inner border of anterior margin and posterior margin forming lanceolate structure with 18 long plumose setae on inner border, posterior margin with 3 or 4 simple setae on distal third; carpus, posterior end articulating with anterior margin of merus, posterior margin of carpus with 13 or 14 long plumose setae, anterodistal angle with 4 or 5 long simple setae, inner surface with oblique row of long plumose setae directed from anterodistal to posteroproximal; propod quadrate, anterior margin with 6 or 7 plumose setae forming 2 or 3 groups, anterodistal angle with 3 or 4 simple setae, posterior margin produced distally into strong, narrow defining tooth, palm with strong median tooth ½ as long as defining tooth, deep excavation between teeth with 3 plumose setae, median tooth with 3 or 4 plumose setae on its base, defining tooth with 2 or 3 plumose setae on its tooth base, inner surface of palm with 2 or 3 short plumose setae on tooth base and 2 on deep excavation between teeth; dactyl strong, curved, reaching by half its length beyond defining tooth, anterior margin with simple spine near proximal end, posterior margin with 2 or 3 short simple spines on distal ⅓ and 3 or 4 on proximal end. Pereopods: Third, Fourth and Fifth without differences from Andres' (1975) description. Basis of Pereopod 5 with proximal posterior lobe. Basis of Pereopod 6 with proximal posterior lobe, distal lobe less evident but with conspicuous toothed margin, short plumose spines on margins of both lobes. Pereopod 7, basis with strongly toothed posterodistal lobe, short plumose spines on margin. Uropods: First similar to Andres' description, peduncle produced into ventral process beneath rami as in *P. excavatum* and *P. lucasi* (Thompson), 4 spines on peduncle outer dorsal margin and 2 on inner dorsal margin; outer ramus with 2 lateral spines at about midlength and 3 or 4 dorsal spines at apex; inner ramus with one spine on lateral margin and 3 or 4 at apex. Second with single dorsal spine on peduncle distolateral corner, outer ramus shorter than inner with single spine at midlength of lateral margin and 4 at apex; inner ramus with 2 spines near midlength on dorsal surface and 4 at apex. Third as in Andres' description, with a few more apical setae than shown by Varela (1983). Telson similar to Andres' description, with slightly different setation as shown in Figure 4. Epimera: First with 3 or 4 plumose setae (Varela, 1983, shows 2 setae); second, with long plumose setae on ventral margin and distal part of posterior margin which is slightly toothed; third wide, without setae.

*Description of female.*—Length 2.5–4.8 mm. Antenna 2 with second and third pe-

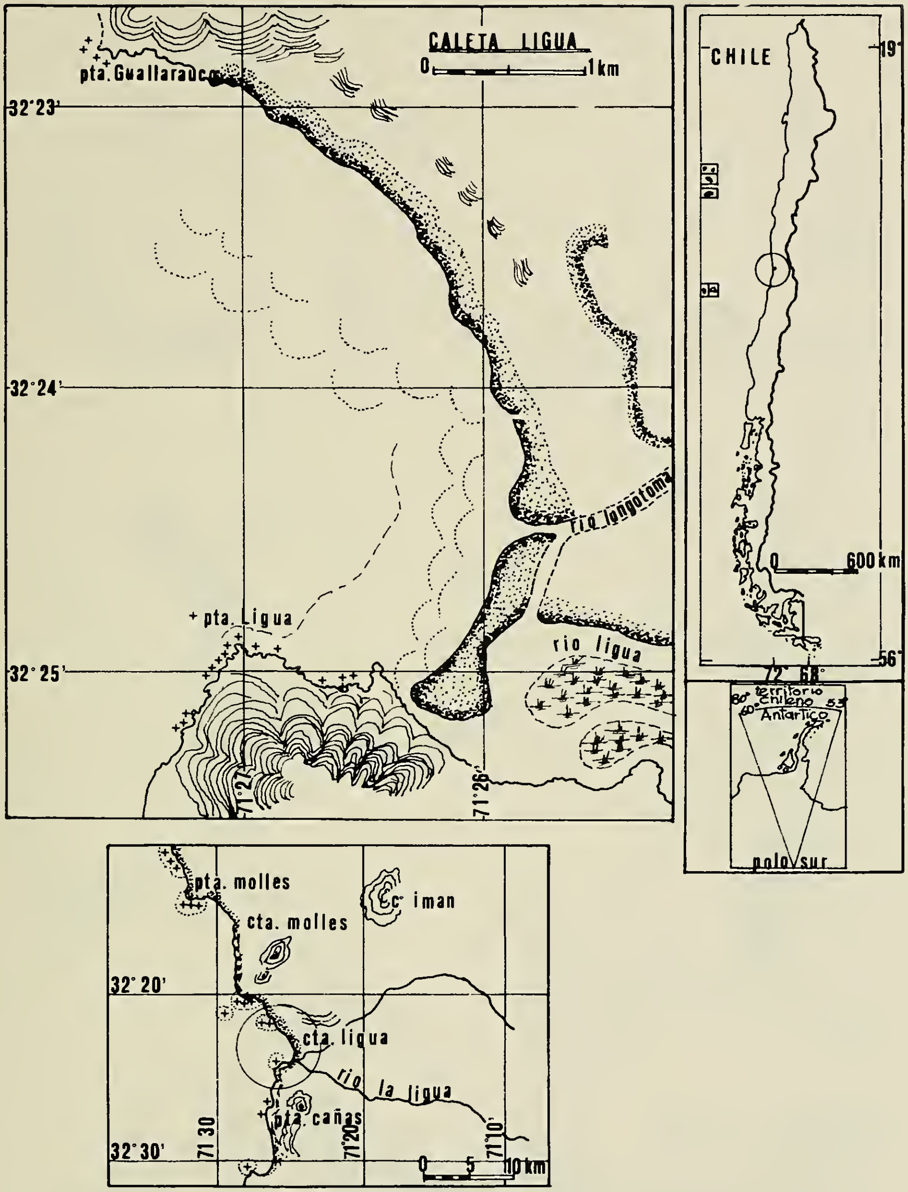

Fig. 1. Map of Central Chile showing the collection site.

duncle segments not wide, just twice length of fourth segment. Gnathopods: First much as in male. Second with propod and carpus slender, palm shorter than in male, without teeth, armed only with long plumose setae, defining tooth inconspicuous. Pereopods: Sixth with basis without teeth on posterior margin, posterior lobes not evident. Seventh with basis without teeth on posterior margin or if present, teeth very weak; lobes not evident, general appearance as in Figure Vc of Andres (1975).

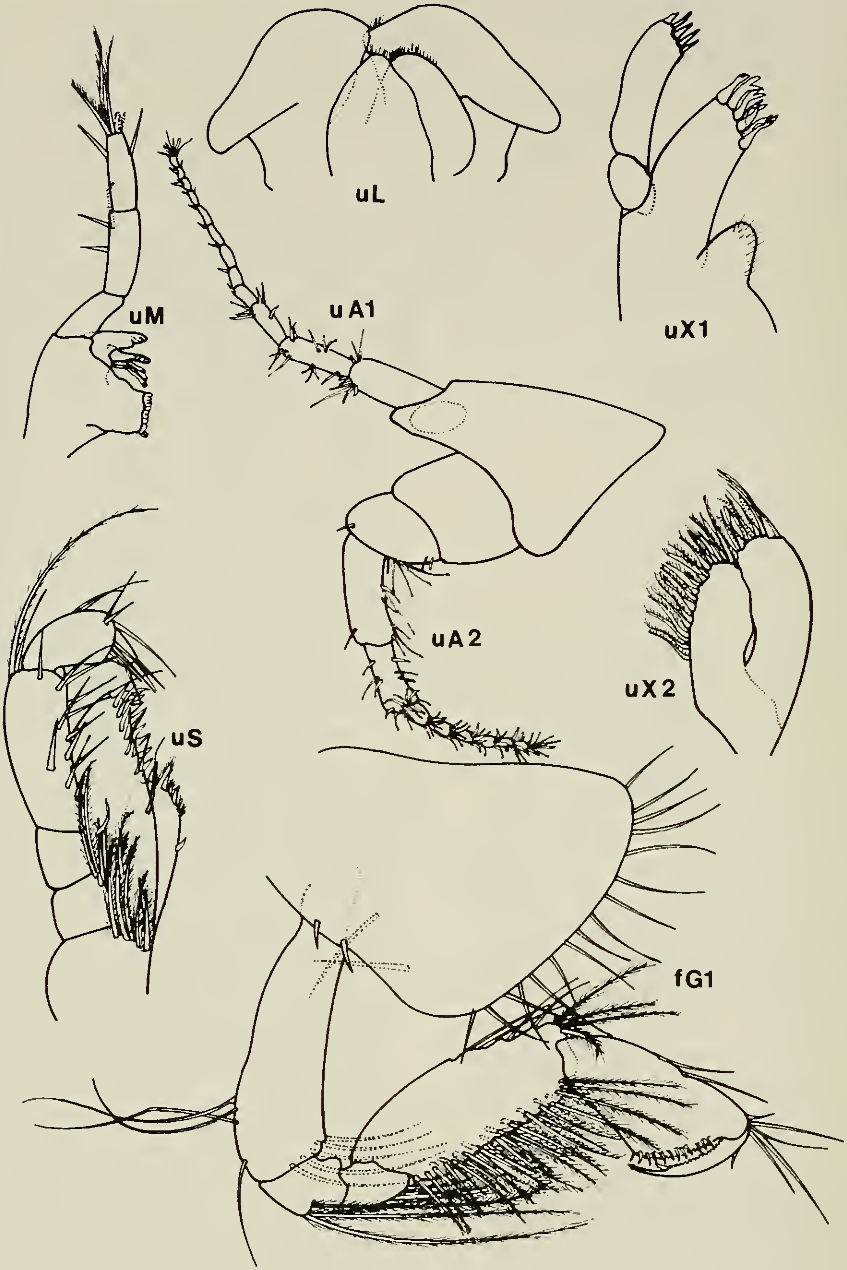

Fig. 2. *Paracorophium hartmannorum,* male "u" modified from Andres (1975); Male "f," length 3.8 mm. A, Antenna; C, Head; G, Gnathopod; I, Inner plate or ramus; L, Lower lip; M, Mandible; P, Pereopod; R, Uropod; S, Maxilliped; T, Telson; W, Pleon; X, Maxilla. Lower case letters to left of capital letters refer to specimens cited in captions; lower case letters to the right are as follows: d, dorsal; r, right; l, left.

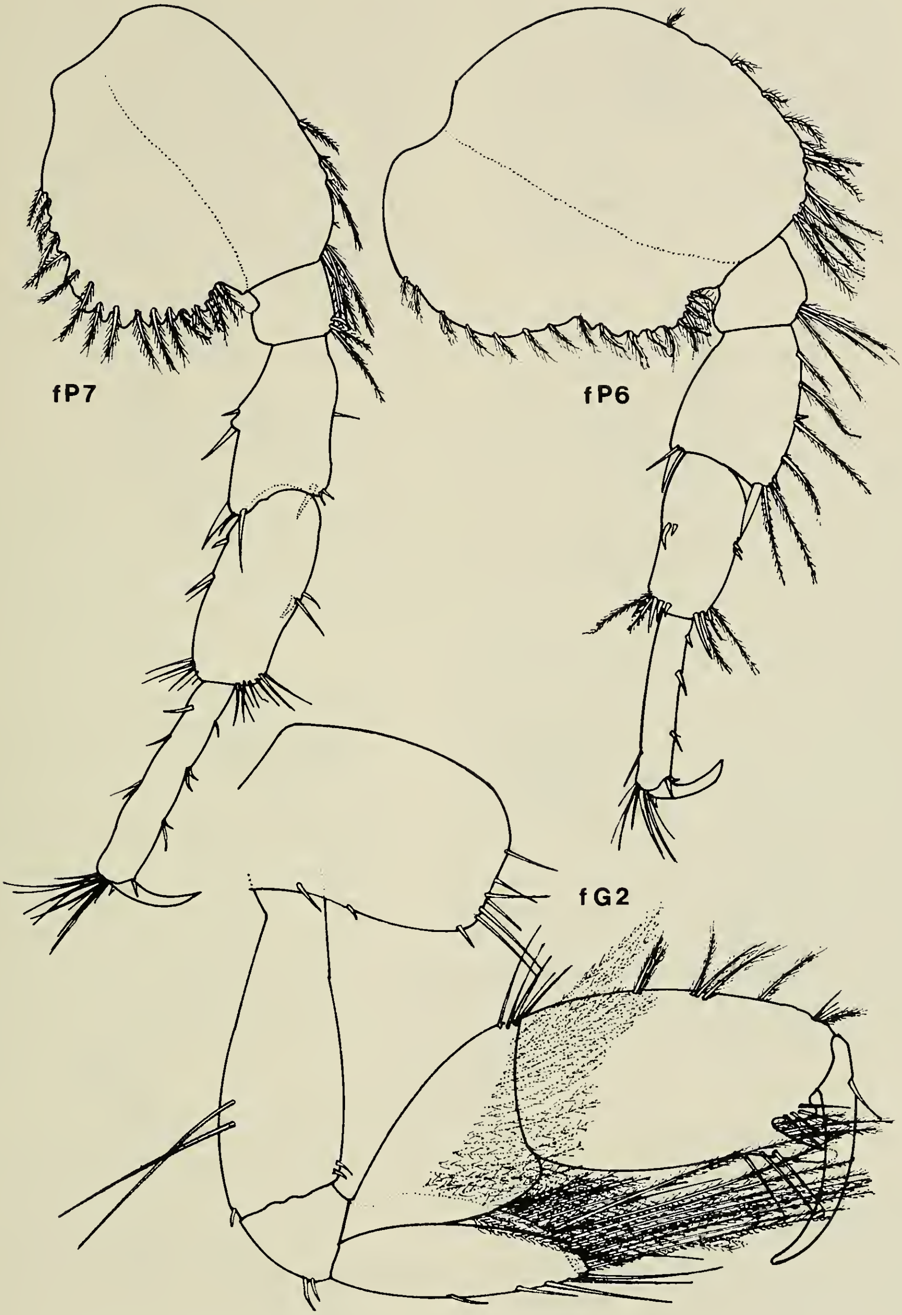

Fig. 3. *Paracorophium hartmannorum,* male "f," length 3.8 mm. Symbols as in Fig. 2.

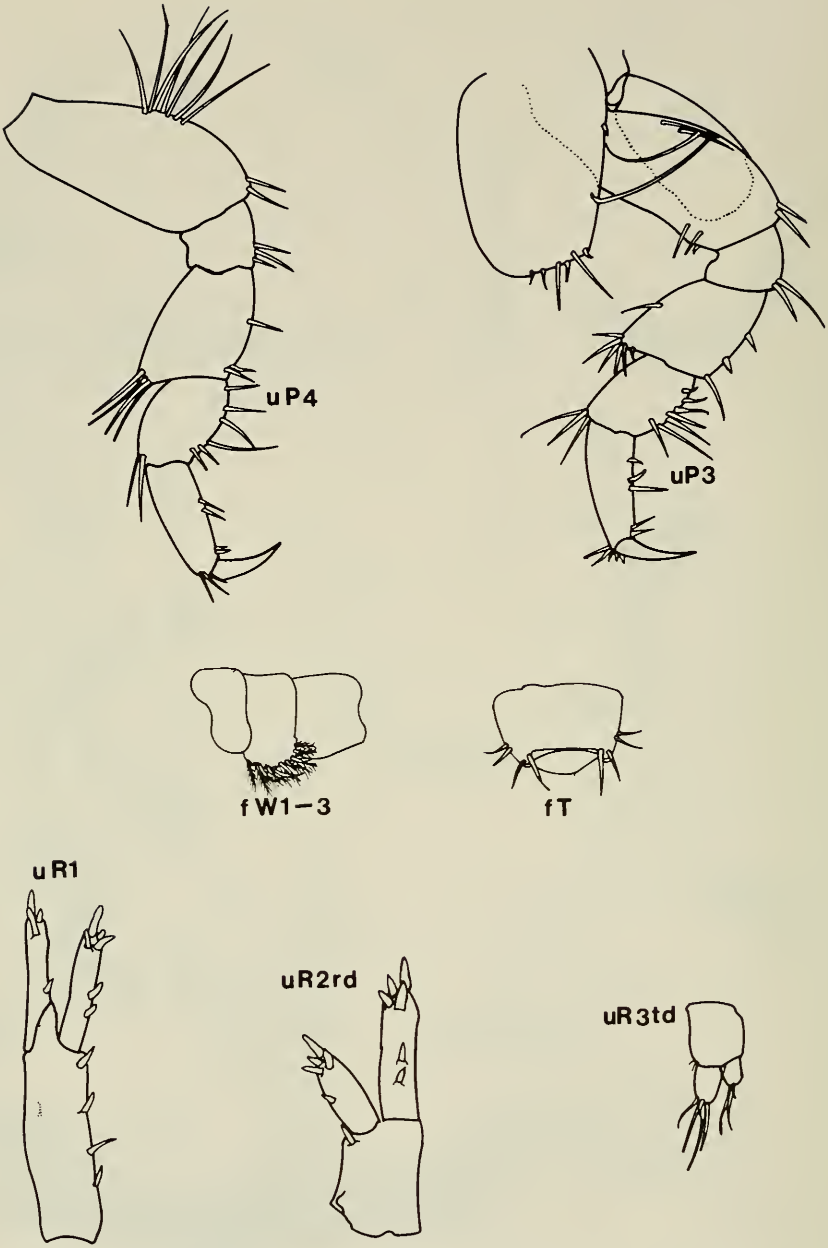

Fig. 4. *Paracorophium hartmannorum,* male "u" modified from Andres (1975); Male "f," length 3.8 mm. Symbols as in Fig. 2.

## General Remarks

*Paracorophium hartmannorum* closely resembles *P. excavatum,* but setation and proportional lengths of articles of the appendages are different as stated by Andres (1975). The most conspicuous characteristics in the adult form are greater dactyl length and presence of teeth on palm of second gnathopod, and toothed posterior margins of basis in fourth and fifth pereopods. The geographical distributions given by Andres (1975) is from Constitución (35°20'S, 72°25'W) to Valdivia (Niebla, Río Valdivia, 39°51'S, 73°24'W); there were two intermediate localities, Río Andalien (36°44'S, 73°01'W) in Concepción Bay and Estero Lenga (36°46'S, 73°01'W) in San Vicente Bay. Varela's specimens of *P. chilensis* were from Playa Caleta, Mehuín (39°26'S, 73°13'W). The present material extends the northern geographical range to La Ligua (32°25'S, 71°26'W). All these localities have similar environmental characteristics, especially fluctuating salinity, from 0.67‰ to 38.2‰ (Andres 1975). In the mouth of Río La Ligua the salinity varied from 8‰ to 22‰ depending on the effects of tides. The species is found mainly in fine sand (0.15–0.20 mm in diameter).

### Key to the Species of *Paracorophium* (modified and expanded from Hurley (1954) and Andres (1975)

1. Outer plate of maxilliped with fringe of many fine setae along inner margin; first, second and third epimera all with marginal fringes of long slender setae; pereopods 5–7 with long fine setae marginally on most segments; antenna 2 of male with 4th peduncle segment not produced forward markedly as lobe .................... *P. lucasi* Hurley
– Outer plate of maxilliped with 8 or 9 slender spines along inner margin; third epimeral plate lacking marginal fringe of setae; pereopods 5–7 with only a few marginal setae ......... 2
2. Antenna 2 in male, 4th peduncle segment produced distoventrally into distinct lobe; median tooth on palm of gnathopod 2 almost as long as defining tooth; dactyl not reaching beyond defining tooth; posterior margin of basis of pereopods 6–7 entire ..... *P. excavatum* (Thompson)
– Antenna 2 in male 4th peduncle segment not produced distoventrally into lobe; median tooth on palm of gnathopod 2 half as long as defining tooth; dactyl overreaching defining tooth by about half its length; posterior margin of basis of pereopods 6–7 toothed .......... *Paracorophium hartmannorum* Andres

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# DESCRIPTION OF A PAEDOPHAGOUS DEEP-WATER CICHLID (TELEOSTEI: CICHLIDAE) FROM LAKE MALAWI, AFRICA

Jay R. Stauffer, Jr. and Kenneth R. McKaye

*Abstract.*—A deep-water paedophagous cichlid of the genus *Diplotaxodon* is described from Lake Malawi, Africa. Similarity of jaw morphology between this species and shallow-water paedophages which obtain eggs and larvae by ramming brooding females, suggest that this deep-water cichlid obtains food in the same manner.

The exploitation of fish eggs, embryos, and larvae (i.e., paedophagy) was first reported for haplochromine fishes by Greenwood (1959, 1967, 1974). Recent studies of the shallow water fauna of Lake Malawi led to the discovery of a group of three fish species which specialized in ramming females to take young from their mouths (McKaye and Kocher 1983). This ramming mode of feeding was suggested, contrary to hypotheses from earlier studies (Greenwood 1959, Fryer and Iles 1972, Wilhelm 1980), to be one of the general methods by which paedophagous cichlids gathered their prey in the lakes of Africa. The other method is to steal eggs after they are laid, but before the female can gather them into her mouth, as done by *Cyrtocara ovatus, Cyrtocara insignis,* and *Cyrtocara labifer* (McKaye 1984).

Deep water trawls in Lake Malawi produced four specimens of an undescribed species of *Diplotaxodon,* one of which had cichlid eggs in its stomach. The purpose of this paper is to describe this deep-water paedophage. External counts and measurements follow Barel et al. (1977).

## *Diplotaxodon greenwoodi,* new species
Fig. 1

*Holotype.*—National Museum of Natural History (USNM) 270847, adult female (ripe) (Fig. 1), 198.7 mm standard length (SL), 8 km south of Mumbo Island, 34°45′E, 14°04′S, Cape Maclear, Lake Malawi, at 86 m. Collected by KRM and JRS, Field Collection Number JRS-84-29, 17 Apr 1984.

*Paratypes.*—USNM 270848 (3 specimens, females, 167.2 (ripe) 111.9 (immature), 140.3 (immature) mm SL), same data as holotype.

*Description.*—This description is based upon the holotype and 3 paratypes. Principal morphometric ratios and meristics are presented in Table 1.

*Body form.*—The body is moderately compressed. Body depth ranges between 342–365 thousandths of standard length. Distances between snout and dorsal fin origin and snout and pelvic fin origin range between 382–404 and 452–472 thousandths of standard length, respectively. The holotype had 16 abdominal vertebrae and 18 caudal vertebrae. The three paratypes had 16 + 17, 15 + 17, and 15 + 18 abdominal and caudal vertebrae (counts from radiographs).

*Head.*—Head length ranges between 374–381 thousandths of SL. The eye is large (horizontal eye diameter, 275–354 thousandths of HL). There are either two or three scale rows on the cheek. The jaw is prognathus and the gape inclination ranges between 57–66 degrees. The mean length of the lower jaw is 487 thousandths of HL.

Table 1.—Principal morphometric and meristic characteristics of *Diplotaxodon greenwoodi* (n = 4 and includes holotype).

| | Holotype | Mean | Range | SD |
|---|---|---|---|---|
| Standard length, mm | 198.7 | 154.5 | 111.9–198.7 | 37.1 |
| Head length, mm | 75.1 | 58.3 | 42.1–75.1 | 14.2 |
| Thousandths of HL | | | | |
| Horizontal eye diameter | 275 | 309 | 276–354 | 34 |
| Vertical eye diameter | 278 | 310 | 278–352 | 33 |
| Snout length | 317 | 299 | 242–342 | 43 |
| Postorbital head length | 406 | 389 | 380–406 | 12 |
| Premaxillary pedicel | 173 | 191 | 173–200 | 13 |
| Lower jaw length | 519 | 487 | 460–519 | 25 |
| Interorbital width | 189 | 176 | 166–193 | 18 |
| Cheek depth | 217 | 185 | 159–201 | 28 |
| Head depth | 870 | 850 | 824–870 | 21 |
| Thousandths of SL | | | | |
| Head length | 378 | 377 | 374–381 | 3 |
| Snout to dorsal | 383 | 396 | 383–404 | 10 |
| Snout to pelvic | 453 | 459 | 453–472 | 9 |
| Body depth | 355 | 354 | 342–365 | 9 |
| Least caudal peduncle length | 196 | 185 | 168-196 | 14 |
| Least caudal peduncle depth | 113 | 112 | 109–115 | 3 |
| Pectoral fin length | 329 | 320 | 306–332 | 13 |
| Pelvic fin length | 199 | 198 | 180–210 | 13 |
| Dorsal fin base length | 459 | 447 | 426–459 | 15 |
| Gape inclination (degrees) | 63 | 62.3 | 57–66 | 3.8 |
| Lateral line scales | 34 | 34 | 34 | — |
| Scale rows on cheek | 2 | 2.5 | 2–3 | 0.58 |
| Pectoral fin rays | 13 | 12.5 | 12–13 | 0.58 |
| Pelvic fin rays | 5 | 5 | 5 | — |
| Anal fin spines | 3 | 3 | 3 | — |
| Anal fin rays | 10 | 10.3 | 10–11 | 0.5 |
| Gill rakers on ceratobranchial | 20 | 19.3 | 19–20 | 0.5 |
| Gill rakers on epibranchial | 6 | 5.3 | 5–6 | 0.5 |

There is a small ventral protrusion present at the symphysis of the dentaries.

Teeth on the lower jaw of the holotype are in three rows, while those on the upper jaw are in four rows. Teeth in fourth row do not extend as far posteriorly as the others. All teeth are unicuspid. Those on the lower jaw are embedded in the soft tissue of the jaws.

Gill rakers are single filaments and on the ceratobranchial range in number between 19–20. There are 6 on the epibranchial, with one in the angle between the ceratobranchial and epibranchial bones.

*Fins.*—Mean dorsal fin base length is 447 (426–459) thousandths of standard length. Pectoral fins are comprised of 12–13 segmented rays. Anal fins have three spines and 10–11 segmented rays.

*Lower pharyngeal bone.*—The lower pharyngeal bone was dissected from the holotype. It is triangular in outline with two tooth forms (Fig. 1). Both tooth forms are conical, with those on the posterior part of the bone straight, while those laterally are slightly recurved.

*Squamation.*—Scales are ctenoid, with 34 pored lateral line scales. Scales uniformly

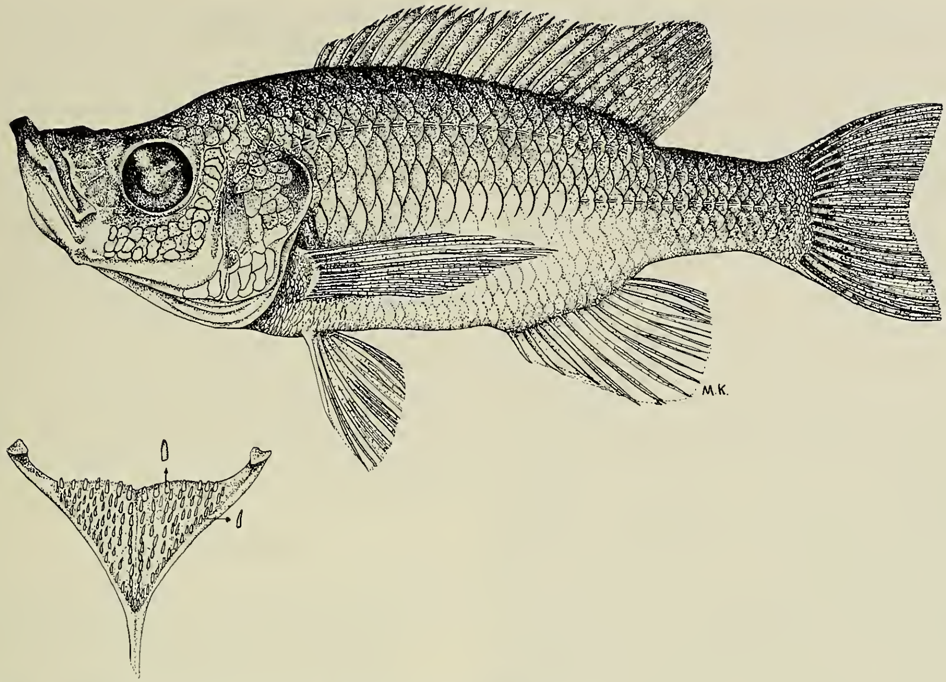

Fig. 1. Holotype (USNM 270847) of *Diplotaxodon greenwoodi.*

cover the anterior third of the caudal fin, partially cover the middle third, and are essentially absent from the posterior third.

*Coloration.*—Freshly collected specimens are dark dorsally, with a purple sheen. The lateral surfaces are silver, but fade to white ventrally.

*Diagnosis.*—Trewavas (1935:68) distinguished the genus *Diplotaxodon* as follows: "third, or third and fourth vertebrae with inferior apophyses which are short, and do not approach each other below dorsal aorta; vertebra 16 + 18; teeth conical, in two series; premaxillaries not beak-like." *Diplotaxodon greenwoodi* differs from the other two described species in the genus, *D. argenteus* and *D. eccelsi,* by the increase in gape inclination, and vertebral number. There is also a fourth row of teeth on the upper jaw. An analysis of the phylogenetic relationships of *D. greenwoodi* must await revision of the genus, which probably contains some 20 undescribed species (Iles, pers. comm.).

*Discussion.*—Most specimens trawled from below 70 meters had completely everted guts when they reached the surface. However, the gut of the holotype contained eggs, which were identical in shape and size with those contained in the ovaries of *Lethrinops gossei* which were collected simultaneously. It is conceivable that the eggs in the stomach of *D. greenwoodi* were a result of "trawl snatching." However, the presence of numerous ripe male and female *L. gossei* in the trawl sample indicates that the trawl was made over an *L. gossei* breeding arena where the presence of a paedophage would be expected. That the paedophage was relatively rare (< 0.1% of cichlids caught in trawl) is consistent with data collected on shallow-water paedophages (Fryer and Iles 1972, McKaye and Kocher 1983).

The feeding behavior of *D. greenwoodi*

has not yet been observed because it occurs at depths below our present diving capabilities. Nevertheless we hypothesize that *D. greenwoodi* is a paedophage which obtains eggs and larvae by ramming brooding females, in a manner convergent with that in *Cyrtocara orthognathus* and *Cyrtocara liemi* (McKaye and Kocher 1983). This behavioral hypothesis is inferred from the morphology of *D. greenwoodi.* The head shape, particularly gape inclination (ranging between 57–66 degrees), closely resembles that of *C. orthognathus* and *C. liemi,* which are known ramming paedophages (McKaye and Kocher 1983). Examination of the gape inclination of the holotype (USNM 227497), and two paratypes (USNM 227501; 227503) of *C. liemi* showed that the gape inclination ranged between 41–45 degrees. Gape inclination of three specimens of *C. orthognathus* (British Museum Natural History [BMNH] 1973.3.26:88; 1956.6.4:4; 1969.3.11:17) ranged between 67–74 degrees. Both *C. liemi* and *C. orthognathus* obtain eggs and larvae by stalking brooding females in the water column, and approaching these females from underneath and behind before ramming them.

Convergence in form among paedophages is further supported by *D. greenwoodi* dentition. Teeth are restricted to the anterolateral parts of the upper and lower jaw bones and are buried in a thickened oral mucosa. A similar condition exists in both Lake Victoria haplochromine lineages of paedophagous fishes which are now placed in the genus *Lipochromis* and given subgeneric rank of *Lipochromis* and *Cleptochromis* (Greenwood 1979).

*Etymology.*—Named after P. H. Greenwood in recognition of his renowned studies of cichlid fishes, and for being the first to discover this unique feeding specialization in cichlids.

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# *AEGLA SPECTABILIS,* A NEW SPECIES OF FRESHWATER CRAB FROM THE EASTERN SLOPE OF THE NAHUELBUTA COASTAL CORDILLERA, CHILE

Carlos G. Jara

*Abstract.*—A new species, *Aegla spectabilis* (Crustacea: Anomura: Aeglidae), is described from the Nahuelbuta region in central southern Chile. Morphologically it is related to *A. rostrata* and *A. denticulata,* both from Chile. Its most prominent feature is the robust spinulation on the margins of the carapace and dorsum of legs. It can be distinguished from all other species of *Aegla* by its spiniform palmar crest and the strong spine on the dorsum of carpus of the chelipeds.

The Chilean aeglid fauna is currently represented by 12 species of *Aegla* Leach (1821) (see Retamal 1981 and Jara 1982). Among them, three, namely *A. denticulata* Nicolet (1849), *A. rostrata* Jara (1977), and *A. bahamondei* Jara (1982) stand out from the remaining Chilean species mostly because of the prominent spinulation on the margins of the carapace (Jara 1982). All three occur in the region between Concepción (36°50′S) and Valdivia (39°30′S) (see Jara 1977, 1980, 1982), but *A. denticulata* ranges farther to the south (Bahamonde and López 1963). The Nahuelbuta Coastal Range, in which the type-locality of *A. bahamondei* is located (Jara 1982), extends into this part of the country. The same author mentions that specimens of *Aegla,* referable with doubt to *A. bahamondei,* were collected at a locality situated to the southeast of the Nahuelbuta Range. However, no previous record of *Aegla* from the eastern slope of Nahuelbuta proper exists.

In this paper, a fourth strongly ornamented form of *Aegla,* found in a river system that drains part of the eastern slope of Nahuelbuta, is described as a new species.

## *Aegla spectabilis,* new species
Fig. 1

*Holotype.*—Instituto de Zoología, Universidad Austral de Chile, IZUA C-637, adult female, Chol Chol River under bridge on outskirts of Chol Chol, 29 km northwest of Temuco (38°36′S, 72°51′W) by road, Chile, 21 Dec 1982, coll. C. G. Jara.

*Paratype.*—IZUA C-633, young female, Perquenco River at Galvarino town, 27 km north of Chol Chol (38°25′S, 72°47′W) by road, Chile, 22 Dec 1982, coll. C. G. Jara.

*Diagnosis.*—Rostrum long, styliform, acute; orbital spine well developed; first hepatic lobe spiniform; anterior and posterior branchial margins strongly denticulate; anterolateral angle of second abdominal epimeron upturned, spiniform; fourth thoracic sternum with median spiniform tubercle; palmar crest as single acute projecting spine; dorsum of carpus of chelae with long acute spine; dorsal margin of carpus of ambulatory legs denticulate; merus of ambulatory legs with distodorsal and distoventral ends spiniform.

*Description of holotype.*—Carapace ovoid, dorsoventrally depressed and laterally expanded in branchial regions. Middorsal line elevated but not forming longitudinal carina; dorsum of carapace more ridge-roofed than convex, bearing sparse long fine setae arising in groups from small pits; setae denser, shorter, and stiffer on both sides of middorsal line of abdominal terga. Precervical region of carapace much narrower than postcervical.

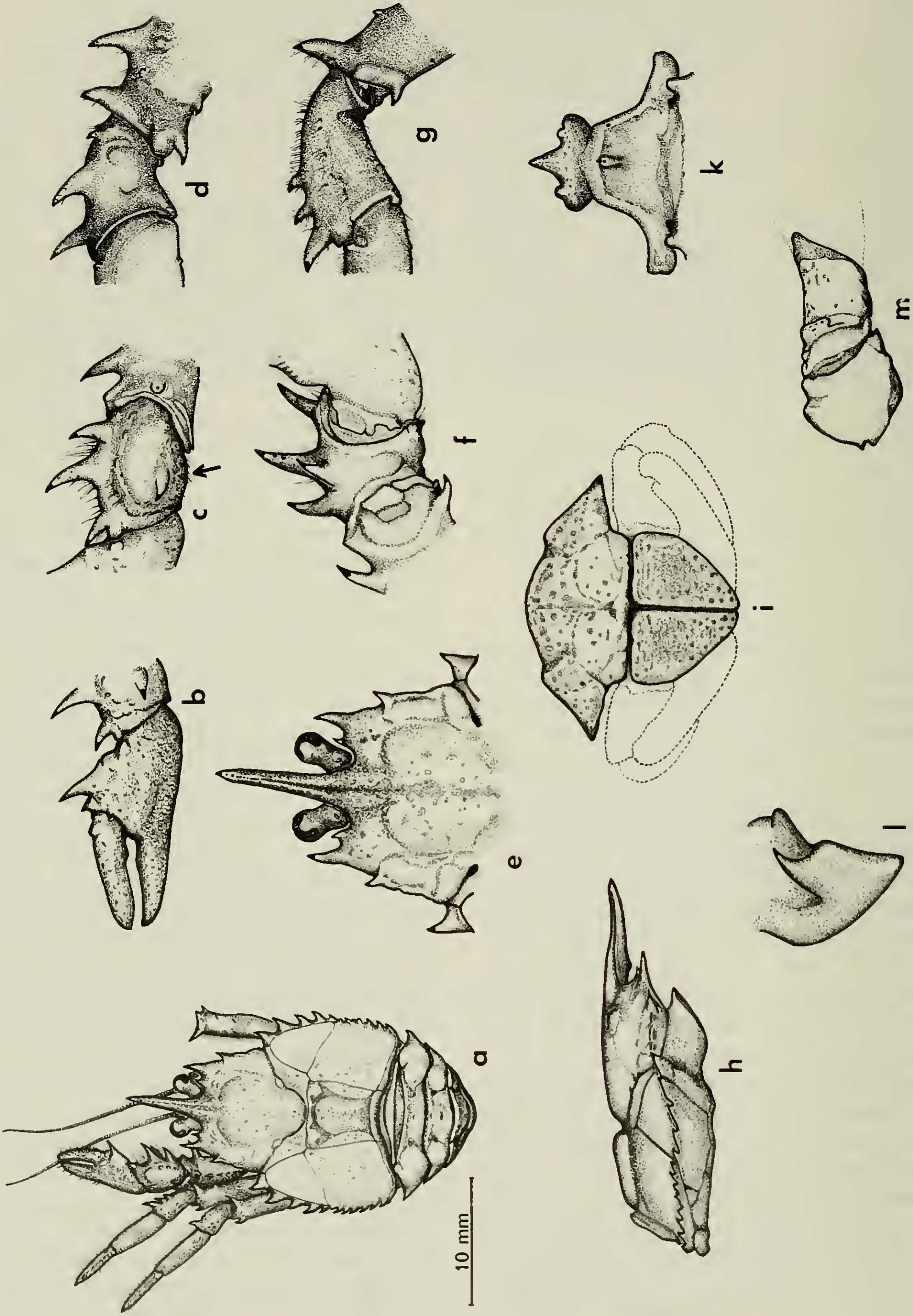
Rostrum long, slender, tipped with acute conical scale; distal third slightly upturned and dorsally flattened. Rostral carina narrow but well marked along proximal half of rostrum, bearing irregular row of small scales intermingled with setae; shallow grooves on both sides fading out beyond midlength of rostrum; height of rostral carina at level of corneae less than depth of ventral keel. Rostral tip surpassing eyestalks by 2.5 length of cornea. Rostral and orbital margins without scales.

Orbits U-shaped, wide, moderately deep; orbital spine large, conical, acute, inclined toward anterolateral angle of carapace; extraorbital sinus wide, deep, subrectangular, its maximum aperture little less than half maximum orbital aperture. Anterolateral lobe of carapace not particularly flattened and produced as large conical spine reaching midlength of cornea; main part of spine directed laterally while acuminate tip inclined toward midline. External margin of anterolateral lobe little scabrous but not scaly.

Hepatic area expanded laterally, somewhat flattened dorsally and limited inwardly by shallow groove separated from more elevated gastric area; first hepatic lobe separated from anterolateral lobe by wide subcrescentic moderately deep notch, its free angle produced as strong, laterally divergent, acute spine. Second and third hepatic lobes relatively well defined and limited by small blunt-angled notches; dorsum of third moderately inflated. Epigastric eminences consisting of slender, arcuate, little protuberant nodulose ridge behind which semicircular finely punctate depression extending to base of protogastric eminences. Latter moderately prominent, forming small blunt conical protuberance tipped with small lenticular scale separated from base of rostral carina by shallow concavity. Gastric area protuberant, its uppermost zone flat. Branchial areas expanded laterally, their free margins denticulate. Anterior branchial margin with 5 broad based, conical, somewhat dorsally depressed denticles, their frontally recurved tips with acute scale, decreasing in size posteriorly and separated by wide semicircular indentations. Posterior branchial margin with 6 (right) and 8 (left) small but clear cut, acute, conical denticles almost uniform in size, incurved frontally, and markedly upturned, especially the last. Dorsal surface of anterior branchial area slightly concave; posterior branchial area convex toward midline but concave behind free margin. Cardiac area subrectangular, slightly wider at frontal than at rear end. Areola limited laterally by subparallel grooves, subrectangular, about 1.5 times longer than broad, markedly protuberant, and regularly convex from side to side.

Abdominal terga deeply sculptured, with narrow, shallow groove devoid of setae along midline. Anterolateral angle of second abdominal epimeron noticeably upturned and produced as broad based, triangular, laterally compressed, sharp spine; tip rising above dorsal surface of epimeron reaching laterally to level of tips of posterior branchial denticles; anteroventral margin of epimeron below anterolateral angle almost straight, ending in blunt ventral angle. Lateral surface of epimeron between anterolateral and ventral angle quite concave. Angles of third and fourth epimera also sharply acute. Telson plate dimerous, subpentagonal. Fourth thoracic sternum with projecting, subconical, slightly compressed, corneous tipped, but almost blunt, ventromedial tubercle.

Cheliped (only left one present) slender. Chela subrectangular in dorsal view, dor-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soventrally depressed, its dorsal surface with short stiff setae and tiny scales. Fingers slightly curved; when closed leaving wide open gap between finely crenulate inner margins. Movable finger with small acute tubercle on its dorsal edge close to propodus. Anteromesial lobe of palm small, spiniform, separated from palmar crest by narrow deep notch. Palmar crest consisting of single, long, conical, sharply acuminate spine; its proximal base bearing 2 very small swellings tipped with setae. Carpal lobe produced in slender, acute spine. Carpal crest forming 2 long, sharp, slightly recurved, and widely separated spines; proximal spine about two-thirds as long as distal one; row of 4 small blunt tubercles tipped with setae present above carpal crest and behind carpal lobe; another dorsal crest situated external to and clearly separated from former consisting of long sharp acuminate curved spine, as long as the second in inner crest, followed by blunt tubercle. Ventral face of carpus armed with long acute spine about size of second spine of inner carpal crest. Space between ventral spine and inner crest with several long thin setae. Merus with dorsal row of 4 spiniform tubercles, distalmost longest and second shortest; distodorsal vertex also spiniform; inner ventral margin smooth with single distal long curved spine; outer ventral margin with 3 spines of which proximalmost longest and second shortest. Ventromedial margin of ischium smooth, with only broad blunt tubercle proximally. Distodorsal and distal ventrolateral angles of merus of pereiopods projected in strong conical acute spine; merus of second left pereiopod also with minute acute tubercle on distal fifth of dorsal margin; distodorsal angle of carpus of pereiopods strongly spiniform, preceded by 1 to 3 smaller but also strong spines in row decreasing in size proximally.

Table 1.—Somatometry of *A. spectabilis*, new species, type series. All measurements in mm. CL, carapace length, distance between rostral apex and posterior margin of cephalothorax; RL, rostral length, distance between rostral tip and midpoint of transverse line tangent to deepest points of orbital margins; PCL, precervical length, distance between rostral tip and midpoint of cervical groove; FW, frontal width, distance between tips of anterolateral angles of carapace; PCW, maximum precervical width, distance across third hepatic lobes; CW, maximum carapace width; LCL, left cheliped length; RCL, right cheliped length; L2PL, length of second left pereiopod; L2DL, dactylar length of second left pereiopod; L4DL, dactylar length of fourth left pereiopod; TL, telson length. F: female.

| Collection | | IZUA-C 637 | IZUA-C 633 |
|---|---|---|---|
| Specimen | : | Holotype | Paratype |
| Sex | : | F | F |
| CL | : | 19.5 | 15.0 |
| RL | : | 6.1 | 4.1 |
| PCL | : | 13.9 | 10.6 |
| FW | : | 6.1 | 4.9 |
| PCW | : | 9.9 | 8.3 |
| CW | : | 15.5 | 13.0 |
| LCL | : | 20.7 | 16.1 |
| RCL | : | – | 15.4 |
| L2PL | : | 23.5 | 17.9 |
| L2DL | : | 5.7 | 4.1 |
| L4DL | : | 5.9 | 4.3 |
| TL | : | 3.2 | 2.9 |

*Color* (alcohol fixed specimens).—Dorsum of carapace vinaceous (Ruber 3) as background color but with several changes of intensity in different regions. Margins of rostrum, orbits, and crest of rostral carina dark blood red (Ruber 8). Epigastric areas between proto and epigastric eminences

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Fig. 1. *Aegla spectabilis* (all illustrations from holotype): a, Dorsal view; b, Left chela (dorsal); c, Carpus of left cheliped (dorsal), arrow points to large middorsal spine; d, Carpus of left cheliped showing large middorsal spine in profile; e, Dorsal view of rostral area; f, Carpus of left cheliped (ventral); g, Carpus of second left pereiopod; h, Lateral view of cephalothorax; i, Telson plate; k, Third and fourth thoracic sterna; l, Lateral view of second abdominal epimeron; m, Ventral view of ischium of left cheliped.

purplish black (Purpureus 9). Midline behind epigastric eminences and dorsum of posterior branchial areas sepia (Aurantiacus 9). Distal half of marginal spines of branchial areas apricot (Aurantiacus 2) while corneous apex of all spines translucent saffron yellow (Aurantiacus 3). Dorsum of pereiopods orange (Aurantiacus 4) or honey yellow (Flavus 5). Ventral surface of body and appendages marmoreous white or slightly yellowish with some iridescences. (Color standards according to Paclt 1958).

*Variation and measurements.*—The single female paratype differs from the holotype in the following respects: rostrum shorter, surpassing eyestalks by 1.5 times length of corneae; dorsum of carapace more regularly convex; front comparatively narrower; branchial margins less upturned and expanded laterally but clearly denticulate; in dorsal view, anterior margin of anterolateral angle of second abdominal epimeron closer to posterolateral angle of carapace; dorsal spiniform process of movable finger very small, lacking apical scale; ventromedial tubercle on fourth thoracic sternum blunt, without apical scale.

Measurements of the holotype and paratype specimens are presented in Table 1. Measurements were made with calipers to the nearest 0.1 mm; the morphometric characters here considered are those defined by Jara and López (1981).

*Distribution.*—Known only from the type-locality and from Galvarino, 27 km north of the type-locality, in the Perquenco River which is a tributary of the Chol Chol River.

*Natural history.*—The river section where the holotype of *A. spectabilis* was collected corresponds to an epipotamal facies; there the current velocity reached about 0.8 m $sec^{-1}$. The greenish turbid water flowed over a sand and gravel bottom limited on the sides by steep banks covered by bushes and bamboo-like vegetation. The water temperature on 21 December 1982 was 20°C, pH 7.9, and conductivity 53 uS $cm^{-1}$; dissolved oxygen reached 13.3 mg $l^{-1}$. The paratype was collected in a river section of hyporithral characteristics where current velocity reached an average of 0.6 m $sec^{-1}$ flowing over boulders and stones without gravel or sand. Water was transparent, its temperature on 22 December 1982 was 17.5°C, ph 7.0, conductivity 95 uS $cm^{-1}$, and dissolved oxygen 13.6 mg $l^{-1}$. At both localities *A. spectabilis* was collected together with a second, largely more abundant, species of *Aegla* not yet identified but very similar to *A. rostrata* Jara. As samplings were done tracking counter-current for long stretches of the bottom with a sack-like kick net, the microhabitat conditions preferred by *A. spectabilis* are not known.

*Etymology.*—From *spectabilis* (Latin), amazing. The specific name refers to the surprisingly heavy ornamentation of this species of *Aegla.*

*Comparison.*—*Aegla spectabilis* resembles *A. denticulata* Nicolet, 1849, and *A. rostrata* Jara, 1977, both from Chile. With them it shares a rather short ovoid carapace greatly expanded at the branchial level, a long, tapered, acute rostrum, robust acute spines on the anterolateral angles of the carapace, well developed orbital spines, an acute and somewhat exserted first hepatic angle, conspicuously denticulate branchial margins, and strongly armed chelipeds; moreover, the dorsodistal angle of the carpus and merus of the ambulatory legs are acute or spiniform and the anterolateral angle of the second abdominal epimeron is spiniform and buttressed behind by a ridge which arises from the tergum. In *A. spectabilis,* however, the dorsum of the carapace appears to be more depressed, the denticles on the branchial are better defined and more prominent, and the chelae are less massive than in the other two species. The areola of *A. spectabilis* is more protuberant than that of *A. rostrata* but less than that of *A. denticulata* though in *A. spectabilis* the areola has a faint keel along its midline. The anterolateral angle of the second abdominal epimeron of *A. spectabilis* is more upturned than it is in *A. rostrata* and *A. denticulata.* With *A. denticulata* it shares the prominent conical tubercle on the fourth thoracic sternum and the scarcely defined proto- and epigastric prominences, but *A. spectabilis* lacks the pronounced carina along the dorsum of the carapace which distinguishes *A. denticulata.* On the other hand, *A. spectabilis* resembles *A. rostrata* in possessing a long, narrow rostrum and wide U-shaped extraorbital sinuses but differs from it in several other respects, mainly in the form and size of the chelae and the distinctness of the branchial denticles.

Neither *A. denticulata* nor *A. rostrata* has a row of spines along the dorsal margin of the carpus of the ambulatory legs as *A. spectabilis* has. Two spines on the distodorsal vertex of the carpus of the ambulatory legs are mentioned for *A. lenitica* Buckup and Rossi, 1977, from Brazil, and a row of spiniform scabrosities along the carpal margin are drawn but not mentioned in the description of *A. parana* Schmitt, 1942, also from Brazil. However, in no other species of *Aegla* are these spines as well developed as in *A. spectabilis.*

A single-spined carpal crest of the chelipeds, such as that found in *A. spectabilis,* is approached only by that drawn and described by Schmitt (1942) for the holotype of *A. sanlorenzo* Schmitt, 1942, from Argentina; however, the character was absent in the specimens of *A. sanlorenzo* examined by Ringuelet (1949a). Finally, the long slender spine on the external half of the dorsum of the chelipedal carpus in *A. spectabilis* is a unique feature, not shared with any other aeglid. Whereas in *A. parana* Schmitt, 1942, a middorsal row of spiniform tubercles is located in a position similar to that occupied by the spine in *A. spectabilis,* no tubercle is markedly larger than the others.

*Remarks.*—*Aegla spectabilis* is the most profusely ornamented form of *Aegla* yet described. Because of the shape of its rostrum, it could be included in the Pacific rostrum type group of *Aegla* proposed by Schmitt (1942). However, because of its two most distinctive characters, namely the spiniform carpal crest and the spine on the dorsum of the chelipedal carpus, it clearly departs from the remaining species of *Aegla.* Due to these particular attributes it perhaps deserves to be allocated to a separate subgeneric or generic taxon but such a decision seems premature in view of the need for a revision of all the species assigned to the unique genus *Aegla.* The current diagnosis of the genus *Aegla* (see Leach 1821, Nicolet 1849, Girard 1855, Hobbs, Hobbs et al., 1977) seems too broad, not adequately assessing the morphological variation displayed by aeglids. At least several subgeneric categories should be recognized in order to arrange the species according to their presumed phylogenetical relationships which, up to now, have been partially scrutinized only by Ringuelet (1949b).

The degree of spinulation varies greatly among aeglids and some ideas about their possible phylogeny have been advanced regarding tendencies of morphological transformation among the species. Schmitt (1942: 442) supposed that "the least differentiated, least spiny or ornamented species stands nearest the ancestral *Aegla.*" If Schmitt's opinion is correct then the spinulation of *A. spectabilis* would be apomorphic. At variance with Schmitt's opinion, Ringuelet (1949a, b) stated that a common trend among several Argentinian species is toward reduction of orbital spines and extraorbital sinuses. According to him (1949), the species of *Aegla* "nearest the ancestor" are those which possess wide concave extraorbital sinuses, large orbital spines, a wide front, long anterolateral spines, a prominent rostrum with a sharp carina not throughed on both sides, and a spiniform second abdominal epimeron. If Ringuelet's opinion is correct then *A. spectabilis* morphology would be plesiomorphic in several respects.

The tendencies of character transformation observed among Chilean aeglids seem to indicate that an extreme reduction of ornamentation as well as an extreme development of spinulation may be considered as apomorphic conditions. In fact, the greatest reduction of spines is shown by *A. alacalufi* Jara and López, 1981, and, to a lesser degree, by *A. papudo* Schmitt, 1942. Both species share an undivided telson plate while the remaining aeglids have dimerous ones (Jara and López 1981). The monomerous telson plate is undoubtedly apomorphic. Other Chilean aeglids which show reduced spinulation are: *A. maulensis* Bahamonde and López, 1963, *A. manni* Jara, 1980, and *A. concepcionensis* Schmitt, 1940. With the exception of *A. maulensis,* all of these species live in small brooks and streams associated with the Chilean western continental slope, and possibly, they are phylogenetically related.

On the other hand, the trend toward profuse spinulation seems to be correlated with living in lentic environments. Thus, *A. rostrata,* from Lake Riñihue, most likely represents a lacustrine lineage derived from less spiny riverine forms (see Jara 1977, 1982). The same trend is demonstrated by *A. denticulata* which is widespread in small, moderately fast running streams in the provinces of Valdivia, Osorno, and Llanquihue. Recently, a large population of this species was found in the sub-littoral of Lake Rupanco (Osorno); those specimens show a remarkably more prominent and profuse spinulation than those collected from streams. Since Lake Rupanco, like Lake Riñihue, is a young lake (in geological time), it is unlikely that its population of *A. denticulata* is the stem population of the less spiny riverine form. Considered from this point of view, an exceedingly prominent spinulation would be apomorphic. It is then possible that the spinulation of *A. spectabilis* was developed in a lentic environment. Such a possibility is strongly supported by the fact that during the Pliocene the region of Angol, about 70 km to the north of the type-locality of *A. spectabilis,* was occupied by lakes formed by accumulation of glacial waters along the eastern slope of the Nahuelbuta Coastal Range (Börgel 1983). If this is so, the low population density of *A. spectabilis* in the Chol Chol river basin may be indicative of its relictual condition. Nahuelbuta has been advocated as a refugial area for the preglacial Tertiary freshwater fauna of central southern Chile (Arenas 1976). Jara (1982) hypothesized that *A. bahamondei,* from the western slope of Nahuelbbuta, might represent the ancestral stock from which the lacustrine *A. rostrata* might have evolved. The finding of *A. spectabilis* on the eastern slope of Nahuelbuta reinforces the notion that this area harbours peculiar faunistic elements which render it important from a zoogeographical point of view.

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# NOMENCLATURAL NOTES ON THE ANURA (AMPHIBIA)

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*Abstract.* —The status and availability of the family-group names Hylodidae, Allophrynidae, and Pelodryadidae and the generic name *Crepidus* are reviewed and clarified.

Through the kindness of several colleagues, a number of nomenclatural problems or inconsistencies with the International Code of Zoological Nomenclature (reference to pertinent articles of the Code are indicated as Art. in the rest of this paper) that have appeared or been perpetuated by my published works, have been recently called to my attention. Three of these relate to the use of family-group names in the classification proposed for my biogeographical analysis of frog distribution (1973), the other to the correct name of an endemic Central American bufonid.

In the original manuscript (completed in 1971) of my 1973 paper, documentation for several novel features of classification was provided but later removed in the editing process. This circumstance makes ambiguous certain family-group names used in that report and adopted by several subsequent authors. The first of these is the name Hylodinae for a subfamily of the Leptodactylidae. The family-group name Hylodidae was originally proposed by Günther (1859) for the genera *Crossodactylus, Phyllobates, Hylodes,* and *Platymantis.* The type-genus is *Hylodes* Fitzinger, 1826 (monotype: *Hyla ranoides* Spix, 1824, a synonym of *Hyla nasus* Lichtenstein, 1823). Several authors including Myers (1962) and Lynch (1971) argue that Fitzinger proposed exactly the same generic name again in 1843 for a second genus of frogs. It is clear from the 1843 work that this is not the case as the name is listed as *Hylodes* (Fitz.), which in this paper represents a genus previously named. As pointed out by Fitzinger (footnote p. 15), the parentheses around the author's name indicate that the scientific name was proposed by that person, but is not used by Fitzinger strictly in its original sense (i.e., to have the same composition). Thus *Leptodactylus* (Fitz.), *Rana* (Linné), and *Hyla* (Laurent) as well as others are so listed. Names newly proposed in the paper lack an indication of Fitzinger's name, as for example *Limnodynastes* and *Lithodytes.* Fitzinger (1843) designated *Hylodes martinicensis* Tschudi, 1838, as the type of the subgenus *Hylodes,* but because this form was not included in the original description of the genus-group name, it cannot be considered the type-species (Art. 67g). In addition, the type-species of *Hylodes* was established in 1826 as *Hyla ranoides* Spix (by monotypy) since the only other species included by Fitzinger in the genus was *Hylodes gravenhorstii* Fitzinger, a nomen nudum. Obviously, Fitzinger had no way to know that things would work out this way since there were no commonly accepted rules relating to nomenclature in his day. Consequently, contrary to the argument of Lynch (1971), the type of the family-group name Hylodidae (and Hylodinae) is *Hylodes* Fitzinger, 1826. This name has priority over Elosiinae Miranda-Ribeiro (1926) under Art. 23 and the latter has no claim for exemption, under Art. 40b, as having won general acceptance prior to 1961.

The second problem relates to my use of

the family-group name Allophrynidae (monotypic for the genus *Allophryne* Gaige, 1926). Mention of the family name by me did not constitute an appropriate proposal of a new name under Art. 13 of the Code and the name was not made available by my action. To remedy the situation, I herewith reintroduce the name Allophrynidae for the single genus and species *Allophryne ruthveni* Gaige, 1926. This family is characterized by the features presented by Lynch and Freeman (1966), who give a description and definition of *Allophryne* which separates it from all currently recognized families of frogs. I have elsewhere (Savage 1973) suggested that the family is a derivative of a leptodactylid ancestor and cannot be placed in the Hylidae as proposed by Lynch and Freeman (1966) and Dowling and Duellman (1978).

A third matter involves the use of the name Pelodryadidae Günther, 1859, for the Australopapuan tree-frogs allied to the genus *Litoria* and often placed in the family Hylidae. When I (1973) proposed that the Pelodryadidae be recognized, it was on the basis of the throat muscle characteristic used by Tyler (1971) to separate the Australopapuan forms from the New World hylids. Since that time, although few have recognized the pelodryadids as a separate family, the family-group name Pelodryadinae has been used as a subfamilial appellation (Dowling and Duellman 1978; Tyler 1979). Unfortunately, the generic type of this taxon, *Pelodryas* Günther, 1859 (monotype: *Rana caerulea* White, 1790) is often regarded as a subjective, junior synonym of *Litoria* Tschudi, 1838 (monotype: *Litoria freycineti* Tschudi, 1838). Some will argue that the proper name for this family-group should have been proposed as "Litoriidae" from the oldest generic name. However, Pelodryadidae is the oldest available name for this taxon, since the family-group name Pelobii Fitzinger, 1843 (type–genus *Pelobius* Fitzinger, 1843, with *Litoria freycineti* as monotype) is preoccupied in Coleoptera by Pelobini Erichson, 1832 (generic type and senior homonym to Fitzinger's genus: *Pelobius* Erichson, 1832) and no one has ever proposed "Litoriidae" as a name. In addition, I was convined that the type-species, the well-known large, green tree-frog (*Pelodryas caeruleus*) was generically distinct from the type-species of *Litoria* (*L. freycineti*). Since that time a second species has been described (named *Litoria splendida* by Tyler, Davies, and Martin 1977) which is closely allied to *caeruleus* and should also be placed in *Pelodryas* according to the characteristics presented by Tyler and Davies (1978). The following features taken from the latter report diagnose the genus: large green frogs with broadly fringed and partially webbed fingers: cartilaginous intercalary elements in digits; hyoid plate with pedunculate alary processes; prominent parotoid or supracranial glands.

For these several reasons, the appropriate family-group name for Australopapuan tree-frogs is Pelodryadidae. If subsequent workers decide to replace *Pelodryas* in the synonymy of *Litoria,* Art. 40a provides that the family-group name will remain Pelodryadidae.

The final problem relates to the correct generic name for the lower Central American toad originally described by Cope (1875) as *Crepidius epioticus.* In 1966, I pointed out that the name *Crepidius* Cope is preoccupied by *Crepidius* Candeze, 1859, in Coleoptera and used the replacement name *Crepidophryne* Cope, 1889, for *epioticus,* the sole species placed in the genus. In doing so I overlooked the use by Brocchi (1882) of the name *Crepidus* for this taxon. Brocchi lists the name as *Crepidus* Cope and cites Cope's 1875 usage as *Crepidus* (sic), "Cope, *On the Batr. and Rept of Costa Rica* . . . ." The sole included species is also listed as *Crepidus epioticus.* Brocchi obviously had no intention of proposing a new name for Cope's genus so that *Crepidus* must be either a correction of the original spelling, an unjustified emendation of the spelling of *Cre-*

*pidius* or an incorrect subsequent spelling. Under Art. 33c misspellings have no independent status in nomenclature but a correction of an original spelling (Art. 32d) or even an unjustified emendation (Art. 33b) must be regarded as an available name. If *Crepidus* is recognized as a correction of an original spelling or as an unjustified emendation it becomes available and has priority over *Crepidophryne.*

In this case it is very difficult to determine which of the three possibilities apply. 1) Brocchi may have concluded that the correct classical spelling for *Crepidius* was *Crepidus* (a correction of an incorrect original spelling); his citation of Cope as the author of *Creidus* supports this view. 2) on the other hand, he may have misspelled Cope's genus as *Crepidus*; 3) or then again, he may have preferred *Crepidus* over *Crepidius,* as an alternate acceptable classically correct spelling, to produce an unjustified emendation of the former name.

It appears that alternate 1 is the most likely since Brocchi lists Cope as the author of *Crepidus.* There is no way to establish that alternate 2 is correct. Alternate 3 requires that Brocchi chose to modify Cope's spelling for some other reason than to correct the original spelling. However, Art. 33b requires that Brocchi use of *Crepidus* instead of *Crepidius* is demonstrably intentional. Since this cannot be done, *Crepidus* must stand as an incorrect subsequent spelling (Art. 33c) and has no standing. The name *Crepidophryne* Cope, 1889 (monotype: *Crepidius epioticus* Cope, 1875) stands as the correct name for the taxon involved and replaces the preoccupied name *Crepidius* Cope, 1875, with the same monotype.

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# *SEROLIS AGASSIZI,* NEW SPECIES, FROM THE DEEP SEA OFF CAPE FEAR, NORTH CAROLINA (CRUSTACEA: ISOPODA)

Robert Y. George

*Abstract.*—A new species of isopod *Serolis agassizi* is described. This blind deep-sea species was collected at 3840 meters over the continental rise off the coast of North Carolina. The abyssal species is the fourth member of the polytypic genus *Serolis* occurring north of the equator and its affinity with two shallow Northern Hemisphere species, *S. carinata* from the California coast, and *S. mgrayi* from the Georgia coast, is discussed. Its resemblance to the other abyssal blind species *S. vemae* is pointed out.

The isopod species belonging to the family Serolidae are morphologicaly distinctive due to their flattened body form. Out of the approximately 50 known species of the genus *Serolis,* only three have been found so far to occur north of the equator; all other species live in the Southern Hemisphere where they are particularly diverse and abundant in the cold waters of the Antarctic shelf and subantarctic islands (Nordenstam 1933; Sheppard 1933). Lockington (1877) discovered *Serolis carinata,* the first record of this genus in the Northern Hemisphere, in shallow waters off the coast of southern California. A second serolid species, *S. mgrayi,* was described by Menzies and Frankenberg (1966) from the continental shelf off Georgia. Hessler (1972) pointed out that these two shallow-water serolid species from the Northern Hemisphere, one from the Atlantic and the other from the Pacific coast, are closely related sibling species isolated geographically by the Central American land bridge. The speciation of these two species took place as a consequence of their geographic separation.

The third known Northern Hemisphere serolid species, *S. vemae,* was first reported from a depth of 5024 meters over the Argentine Rise southeast of Rio Grande in the South Atlantic Ocean (Menzies 1962). *Serolis vemae* was later captured in good numbers from a depth of 2862–4749 meters in the North Atlantic Ocean (Hessler 1967). The present paper describes the second abyssal species of *Serolis* from a depth of 3840 meters over the continental rise off North Carolina in the Northwest Atlantic Ocean. This new serolid species, *S. agassizi,* was collected during a cruise of R/V *Eastward* and is named in honor of Alexander Agassiz who made significant contributions to our understanding of the deep-sea fauna of the North Atlantic Ocean.

### *Serolis* Leach, 1818

*Diagnosis.*—Serolidae markedly flattened, not known to conglobate; coxal plates laterally expanded. Mandible with lacinia mobilis. Maxilliped with 3-articled palp. Pereopod 2 sexually dimorphic, in female ambulatory and in male subchelate. Pleopods 1–3 each with elongate peduncle and subelliptical rami. Uropoda biramous.

### *Serolis agassizi,* new species

Figs. 1, 2

*Diagnosis.*—*Serolis* with coxal plates visible dorsally in pereonal somites 2 to 4. Body configuration somewhat globular. Cephalon lacking eyes. Lateral margin of all pereonal

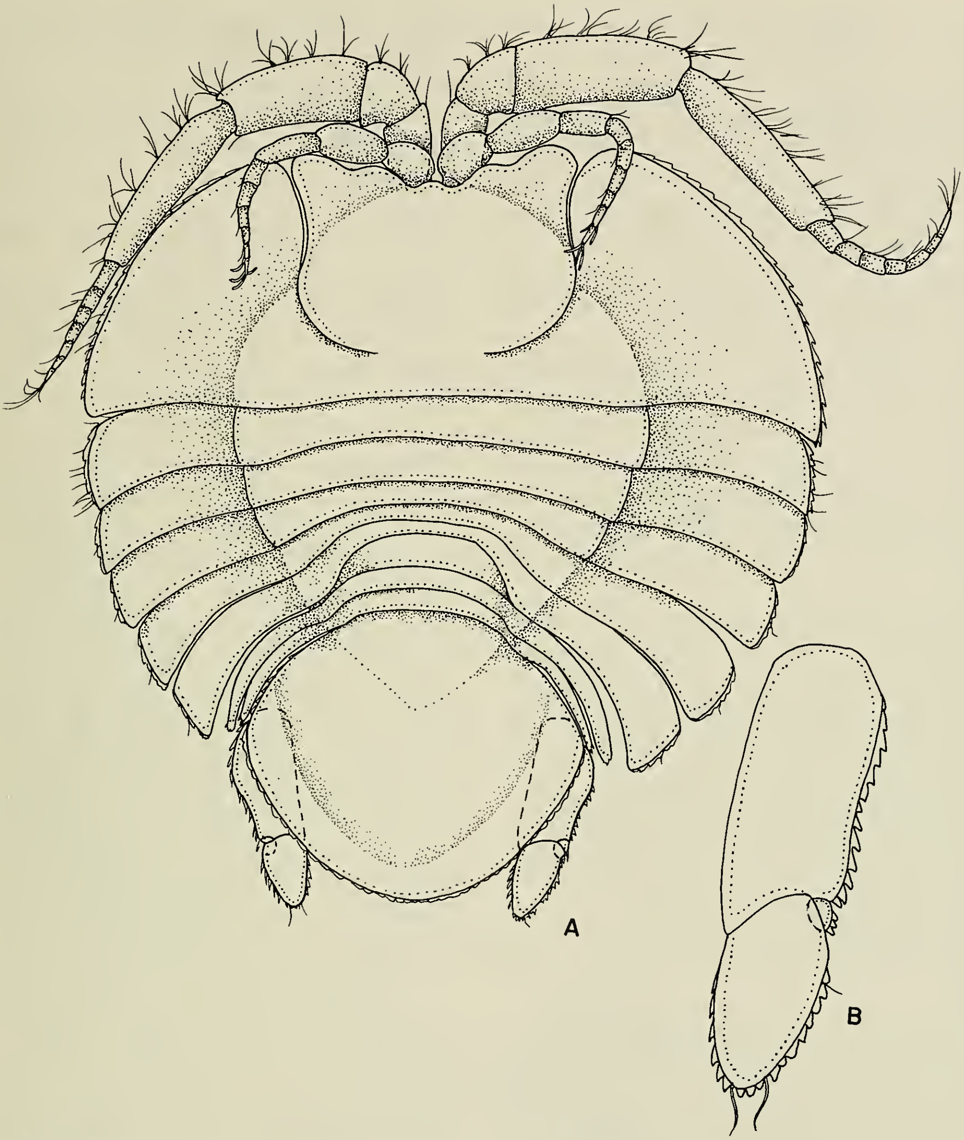

Fig. 1. *Serolis agassizi,* holotype female, length 3.0 mm: A, Dorsal view; B, Uropod.

somites denticulate. Pereonal somite 1 fused with cephalon. Pleotelson globular; posterior margin broadly rounded, denticulate. Lateral margin of uropod biramous; exopod minute; endopod enlarged, with lateral margin denticulate.

*Material examined.*—Holotype female, length 3 mm, width 2.5 mm (USNM 138717).

*Type-locality.*—Continental rise off North Carolina coast. R/V *Eastward* Sta 6214, 1 female, 3840–3975 m, 33°01.5′–33°03.0′N, 75°06.2′–75°6.5′W, 5 Nov 1966; collected with Small Biological Trawl.

*Description.*—Body shape globular with lateral margin denticulate and furnished with minute setae. Cephalon with large rostrum separated from lateral lobes by narrow furrow on either side of rostrum. Eyes entirely absent, ocular ridge lacking. Cephalon almost as long as pereonal somites 2–7 combined.

First pereonal somite with lateral margin denticulate. Pereonal somites 2–3 showing distinct coxal plates. Somites 1 and 2 subequal in length at midline; fourth somite less than one-half as long at middorsal region than at lateral region. Fifth and sixth somites similar in shape, lateral parts produced posteriorly to approximately half the length of pleotelson. Seventh pereonal somite uniformly narrow. Pleonite somewhat narrower than seventh pereonite. Pleotelson broadly rounded; posterior margin studded with minute tubercles similar to those on lateral margin of pereonal somites. Dorsal surface of pleotelson smooth, completely devoid of any ridges, tubercles or spines.

First antenna composed of 9 articles. Basal 4 articles constitute peduncle; first article bulbous; second article longest article of peduncle; third article longer and broader than fourth. Flagellum consisting of 5 articles, all bearing sensory setae. Second antenna with well developed peduncle composed of 4 articles. Basal 2 articles small, subequal; third and fourth articles elongate. Flagellum with 7 articles; total length of flagellum less than length of fourth peduncular article. Outer margin of second antenna furnished with setae.

Maxilliped with 3-jointed palp. Basal article of palp about as long as terminal article; second article twice as wide as terminal article. Endite furnished with 2 stout setae at distal end. Epipodite marked off from basopodite by distinct suture.

First pereopod with elongate basis longer than carpus, ischium and merus combined. Propodus enlarged, displaying row of spines along inner margin. Dactylus about as long as propodus; both combined into claw-like configuration. Seventh pereopod with subequal joints and reduced dactylus; merus bearing 3 leaf-like setae at outer distal edge.

Third pleopod with triangular basopodite; endopodite larger than exopodite. Exopodite with 3 distal plumose setae. Endopodite with long plumose setae along distal and outer margins.

Uropoda biramous, exopod extremely small; endopod large and denticulate along margins.

## Affinity with Other Three North Atlantic Species of *Serolis*

The new abyssal serolid species *S. agassizi* is markedly different from the two eye-bearing shallow water species, *S. mgrayi* from the Atlantic shelf (200–266 m) and *S. carinata* from the California coast (13–56 m) in the absence of eyes. As Hessler (1967) pointed out, these two shallow serolid species are quite similar in morphology but there are substantial differences to distinguish them as distinct species which may have a common origin in the Northern Hemisphere. However, *S. agassizi* is closely related to *S. vemae,* the other blind serolid species known from the abyssal depths (2862–5024 m) in the North and South Atlantic Ocean. Both species are small (less than 5 mm). The presence of a minute exopod of the uropod and a flagellum shorter than the last peduncular article of the second antenna are features shared by these two species. There are obviously well-defined morphological differences between these two deep sea North Atlantic serolid species. *Serolis agassizi* has rounded anterolateral angles of the cephalon but *S. vemae* has a cephalon with acute anterolateral angles. The coxal plate is marked off in pereonal somite 5 in *S. vemae* but not in this new species. *Serolis agassizi* has a smooth dorsal surface but denticulate lateral margin. *Serolis vemae* has a small tubercle on pereonal somites 5 and 6 and a smooth lateral margin. The pleotelson shape is very different between these two species, the apex broadly rounded in *S. agassizi* and somewhat tapering in *S. vemae.* The second article of the maxilliped palp is elongate and the terminal third article small in *S. vemae.* The second article of the maxilliped palp is

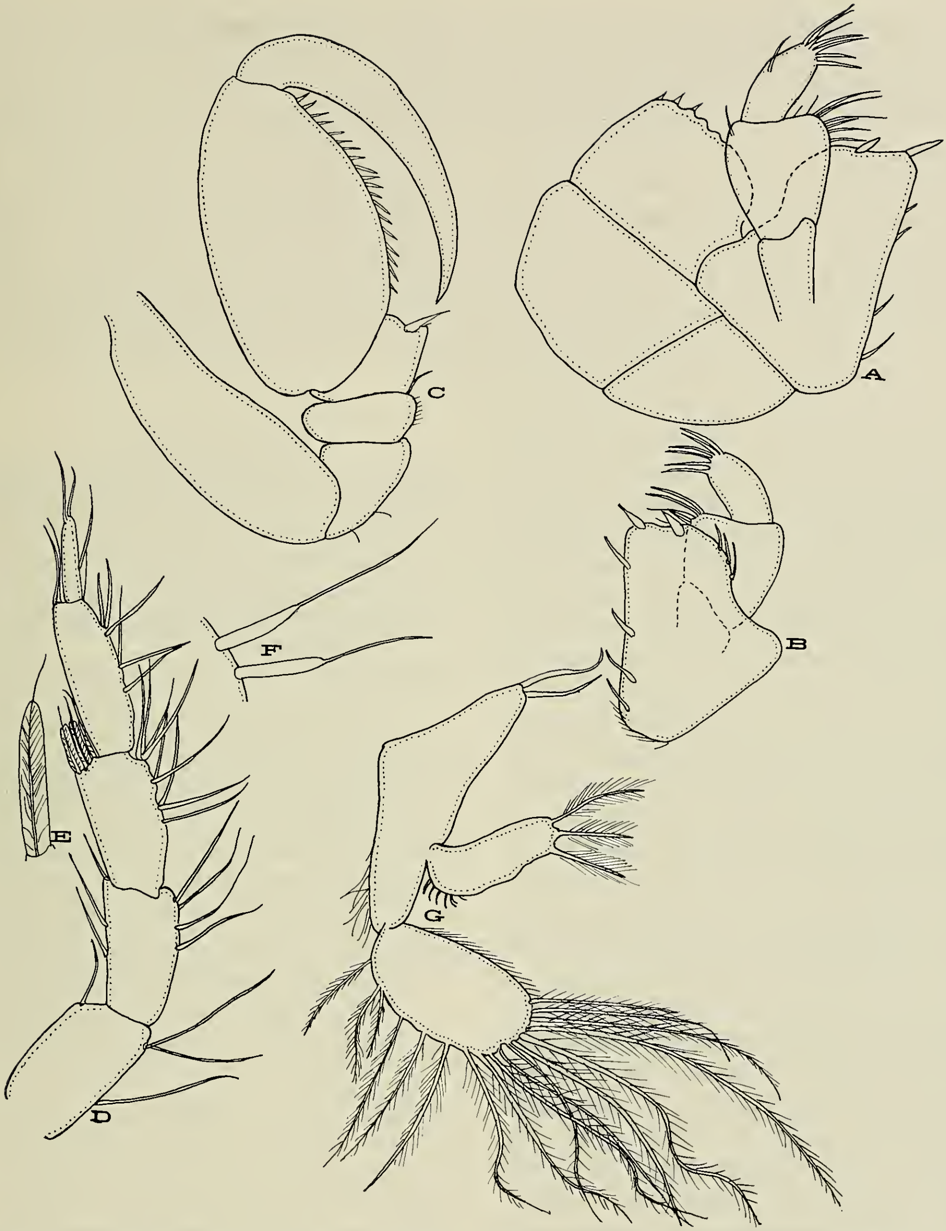

Fig. 2. *Serolis agassizi,* holotype female, length 3.0 mm: A, Maxilliped; B, Maxilliped, ventral view; C, first pereopod; D, Second pereopod; E–F, setae enlarged; G, Second pleopod.

only slightly longer than the terminal third article in *S. agassizi.* These points of difference clearly differentiate the two abyssal species of *Serolis* in the Northern Hemisphere.

## Affinity with Abyssal Species of *Serolis* from the South Atlantic Ocean

Besides these two species, there are only three other species of *Serolis* known to live exclusively at depths greater than 2500 meters. These three abyssal species are known from the subantarctic regions in the Scotia Sea. *Serolis maryannae* Menzies, from the continental rise, south of Staten Island (55°31.2'S, 64°07.5'W) at 3839 meters, is about four times larger than *S. agassizi.* This species also has reduced eyes, middorsal tubercles on the pereonal somites and elongate lateral margins of the posterior pereonal somites. *Serolis macdonellae* Menzies, from the lower slope depths in a region west of South Sandwich Island (56°43'S, 27°41'W) at 2741 meters, is strikingly different from *S. agassizi* in general body dimension, in possessing tubercles on the dorsal surface of the pereonal somites and in having a middorsal carinae on the pleon. The uropods do not extend beyond the posterior margin of pleotelson and the lateral margins of the last two pereonal somites are elongate in *S. macdonellae.* The third abyssal species from the Southern Hemisphere, *S. margaretae,* is known from the continental rise in the northwestern part of the Scotia Sea, south of Staten Island (55°42.9'S, 62°21.6'W) at 3813 meters. This species resembles *S. agassizi* in general body shape shape and also in having a similar pleonal configuration. However, there are obvious differences between these two species in the cephalon, which has a middorsal tubercle at the posterior end and conspicuous eyelobes in *S. margaretae.* The epimera of the sixth pereonal somite extend slightly beyond the apex of the telson and this feature evidently demarcates this species from *S. agassizi.* The closest known relative of *S. agassizi* is undoubtedly *S. vemae* which inhabits the abyssal depths of both northern and southern hemispheres in the Atlantic Ocean.

From a zoogeographic and evolutionary point of view, the distribution of the species of the genus *Serolis* is exceedingly interesting because of its dominant representation in the shelf-slope depths of the Antarctic and subantarctic zones. Their meager representation in the aybss (5 out of 50 known species) in depths greater than 2500 meters indicates that *Serolis* is generally a shelf-slope genus and speciation into the abyss probably took place after the Miocene glaciation when cooling of the deep sea came about.

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# A NEW SPECIES OF RED-EYED TREEFROG OF THE *HYLA URANOCHROA* GROUP (ANURA: HYLIDAE) FROM NORTHERN HONDURAS

James R. McCranie and Larry David Wilson

*Abstract.*—A new species of the *Hyla uranochroa* group is described from the Cordillera de Nombre de Dios, Departamento de Atlántida, Honduras. Relationships to other members of the group are discussed.

Until recently, the *Hyla uranochroa* group was considered to be confined to lower Central America (Duellman 1970). However, in 1982 and 1983 we discovered specimens representing a new species of this group from western Honduras which we subsequently described as *Hyla soralia* Wilson and McCranie, 1985. In August 1982 and 1984 we collected additional material representing another new species in this group from the Cordillera de Nombre de Dios in the Honduran department of Atlántida. The type-locality of this new species is alongside the Quebrada de Oro, a stream flowing out of the cordillera into the Río Viejo, in turn a tributary of the Río Cangrejal which flows into the Caribbean Sea at La Ceiba.

## *Hyla salvavida,* new species

Fig. 1

*Holotype.*—University of Kansas Museum of Natural History (KU) 200999, adult male, from Quebrada de Oro (15°38′N, 86°47′W), elevation 880 m, tributary of Río Viejo, south slope of Cerro Búfalo, Cordillera de Nombre de Dios, Departamento de Atlántida, Honduras, collected 16 Aug 1984 by James R. McCranie, Kenneth L. Williams, and Larry David Wilson. Original number LDW 6501.

*Paratopotypes.*—KU 201000-008, 201010-013, adult males, and KU 201009, adult female, 16 Aug 1982 and 16–18 Aug 1984, elevation and collectors as for holotype.

*Diagnosis.*—A member of the *Hyla uranochroa* group distinguished from the other members by the following combination of characters: dorsum uniform dark leaf green; venter pale yellow; pale lip stripe thin, diffuse, expanded below eye; lateral pale stripe poorly developed, consisting of broken series of flecks; snout–vent length (SVL) 25.2–27.5 mm in males, 34.3 in single female; tympanum diameter 38.7–43.8% of eye diameter in males; snout rounded in lateral profile; plantar surfaces of feet pigmented; anterior arm of squamosal extending one-third of distance to maxilla; quadratojugal present only as spur posteriorly.

*Description of holotype.*—Adult male with SVL of 26.2 mm; tibia length 14.2 mm; tibia length/SVL 0.542; hand length 7.6 mm; hand length/SVL 0.290; foot length 11.0 mm; foot length/SVL 0.420; head length 10.0 mm; head length/SVL 0.382; head width 9.7 mm; head width/SVL 0.370; diameter of eye 3.1 mm; diameter of tympanum 1.2 mm; tympanum/eye diameter 0.387. Snout in lateral profile rounded, in dorsal profile rounded; canthus rounded; loreal region slightly concave; lips moderately thick and unflared; nostrils protuberant; internarial distance 2.1 mm; internarial distance/head width 0.216; top of head flat; interorbital distance 3.9 mm; interorbital distance/head width 0.402; width of eyelid

Fig. 1. Female paratopotype (KU 201009) of *Hyla salvavida.*

2.2 mm; eyelid width/head width 0.227; snout length 2.7 mm; snout length/head length 0.270; snout length/eye diameter 0.871. Moderately heavy dermal fold extending from posterior corner of eye above tympanum to point above base of forearm, obscuring upper edge of tympanum; tympanum round, its diameter 1.25 times its distance from eye. Forearm moderately robust, having well-developed dermal fold on wrist; raised dermal fold along outer edge of forearm; pollex slightly enlarged with poorly cornified patch of nuptial excrescences; second finger noticeably shorter than first; subarticular tubercles round, those on third and fourth fingers bifid; discs on fingers moderate in size, that on third finger equal to diameter of tympanum; webbing vestigial between first and second fingers; webbing formula II 1½–3 III 2½–2 IV (sensu Myers and Duellman 1982); heels broadly overlapping when hindlimbs adpressed; tarsal fold moderately developed, extending length of tarsus; inner metatarsal tubercle ovoid, visible from above; subarticular tubercles rounded, conical; length of toes from shortest to longest 1-2-3-5-4; webbing formula I 2–2 II 1–2½ III 1½–3½ IV 2½–1 V; discs of toes distinctly smaller than those of fingers. Anal opening directed posteroventrally at upper level of thighs. Skin of dorsum smooth, that of throat and belly granular, that of ventral surfaces of thighs smooth. Tongue elongately ovoid, barely free behind; prevomerine teeth 4–5, situated on posteromedially-inclined ridges, narrowly separated and between moderately large ovoid choanae; vocal slits large, extending from posterolateral base of tongue to angle of jaws. Vocal sac single, median, and subgular.

In life, the color pattern was as follows: dorsum dark leaf-green; exposed surfaces of limbs same; upper jaw with a thin, diffuse lip stripe that is expanded below eye; outer edge of forearm with series of interrupted pale dashes from elbow to wrist; outer edge of tarsus with thin, diffuse pale stripe; pale anal stripe poorly developed; tubercles below anal opening tipped with white; venter pale yellow; iris blood red.

*Variation in the paratopotypes.* —The

pertinent data on thirteen males (range followed by mean in parentheses) and one female (separated from the former by a comma) are as follows (all measurements are in millimeters): SVL 25.2–27.5 (26.5), 34.3; tibia length 14.3–15.5 (14.8), 18.6; tibia length/SVL 0.532–0.587 (0.559), 0.542; foot length 10.2–11.5 (10.8), 13.8; foot length/SVL 0.385–0.437 (0.408), 0.402; hand length 6.9–8.0 (7.6), 10.0; hand length/SVL 0.256–0.317 (0.286), 0.292; head length 9.5–10.3 (9.9), 12.3; head length/SVL 0.359–0.398 (0.376), 0.359; head width 9.3–10.1 (9.8), 11.9; head width/SVL 0.358–0.388 (0.369), 0.347; diameter of eye 2.8–3.3 (3.1), 3.5; diameter of tympanum 1.2–1.4 (1.3), 1.3; tympanum/eye diameter 0.387–0.438 (0.409), 0.371; interorbital distance 3.6–4.1 (3.9), 4.7; interorbital distance/head width 0.367–0.418 (0.399), 0.395; width of eyelid 2.1–2.5 (2.3), 3.0; eyelid width/head width 0.208–0.258 (0.235), 0.252; internarial distance 2.0–2.3 (2.2), 2.9; internarial distance/head width 0.198–0.237 (0.224), 0.244; snout length 2.7–3.0 (2.8), 3.3; snout length/head length 0.262–0.303 (0.285), 0.268; snout length/eye diameter 0.871–1.00 (0.928), 0.943.

Variation in color and pattern of the paratopotypes is minimal, with the exceptions of KU 201008 in which the labial stripe is well-developed, complete, and confluent with the relatively well-developed lateral stripe and in the presence of a large cream-colored spot just above the groin in the single female (KU 201009).

*Metamorphosing froglets.*—On 16 August 1984 we collected two metamorphosing froglets (KU 201015-016) in stages 44 and 45 (Gosner 1960) respectively, at the type-locality. Mensural data on the specimens are as follows: SVL 15.2, 16.6; tail length 14.6, nub only in the latter; tibia length 7.8, 8.3; tibia length/SVL 0.513, 0.500; hand length 4.4, 4.6; hand length/SVL 0.289, 0.277; foot length 5.6, 6.0; foot length/SVL 0.368, 0.361.

Color notes on KU 201015 in life are as follows: dorsum metallic coppery green; lime green on upper eyelid; venter yellow; limbs yellow with greenish-brown patina; enamel yellow spots at elbow, knee, and heel; undersurfaces of feet orangish-red; tail gray stippled with white; pale lip stripe present; iris red.

*Tadpole.*—A single poorly-preserved tadpole presumed to be of this species (KU 201014) was collected at 1070 m in the Quebrada de Oro. Allocation must be considered tentative at best but the tadpole definitely is of the type found in members of the *Hyla uranochroa* group (Duellman 1970; Wilson and McCranie 1985). Many features are obscured due to the desiccated condition of the specimen but the following features are determinable: mouth ventral, large, and funnel-shaped without lateral folds in the oral disc; oral disc entirely bordered by a row of minute papillae; large conical papillae present within oral disc; beaks relatively small with long pointed serrations; denticle rows ⅔, second upper row narrowly interrupted medially, third lower row noticeably shorter than other rows.

*Osteology.*—The following descriptive notes are based on a cleared and stained adult male specimen (KU 201017) of *Hyla salvavida.* The features of the skull are in complete agreement with those used by Duellman (1970) in diagnosing the *uranochroa* group (including a large frontoparietal fontanelle possessed by these frogs, Duellman's 1970 illustration of the region as ossified in *H. uranochroa* notwithstanding). Furthermore, the skull of *H. salvavida* has the anterior arm of the squamosal extending about one-third of the distance to the maxilla and the quadratojugal reduced to a spur posteriorly as is the case in *rufioculis* but not *uranochroa* (skull features are unknown for *lythrodes* and *soralia*).

*Etymology.*—The name *salvavida* is derived from the Spanish, meaning "lifesaver," in appreciation of the "lifesaving qualities" of our Honduran field companion, *La Cerveza Salvavida.*

*Natural history notes.*—The vegetation at the type-locality may be characterized as of the Subtropical Wet Forest formation of Holdridge (1967) and is described in more detail by McCranie et al. (in prep.).

All the members of the hypodigm were collected at night on low vegetation one to two meters off the ground alongside a shallow, broad slow-moving small stream and associated pools at a point just before it flows into the Quebrada de Oro. Extensive searches elsewhere in the area over several days in two different years produced no other specimens.

All the males were collected while calling. The call is a cricket-like chirp repeated three or four times.

The single female collected on 16 August 1984 contains eggs about ready to be deposited. The same evening two metamorphosing froglets were found and a tadpole presumed to be of this species was collected on 4 June 1980. These data suggest an extended breeding season.

*Relationships.*—*Hyla salvavida* is a member of the *uranochroa* group as defined by Duellman (1970). He included two species, *rufioculis* and *uranochroa,* in the group. Myers and Duellman (1982) resurrected *Hyla lythrodes* from the synonymy of *H. rufioculis,* and Wilson and McCranie (1985) described a fourth species, *H. soralia,* from Honduras. *Hyla salvavida* agrees in all features of the *uranochroa* group as detailed by Duellman (1970), Duellman and Campbell (1982), and Wilson and McCranie (1985).

Within this group of five species, *Hyla salvavida* most closely resembles *H. rufioculis.* They share a pale labial stripe expanded below the eye, pigmented plantar surfaces of the feet, similar tympanum/eye ratio, and the same features of osteology and larval denticle morphology. They differ in dorsal color (leaf green in *salvavida,* dull brown to olive green in *rufioculis*), nature of the lateral stripe (broken in *salvavida,* well-developed and complete in *rufioculis*), character of the labial stripe (broken and suffused with green in *salvavida,* well-developed and complete in *rufioculis*), ventral color (pale yellow in *salvavida,* creamy white in *rufioculis*), and snout shape (rounded in lateral profile in *salvavida,* truncate in *rufioculis*).

Wilson and McCranie (1985) discussed the relationships and biogeography of the *uranochroa* group, postulating a dispersal northward of a lower Central American stock across the Nicaraguan depression during a pluvial period which gave rise to *Hyla soralia* in western Honduras and the *H. schmidtorum* group in southern México. *Hyla salvavida* appears to fit in this scenario as an early offshoot of the northward-dispersing stock that still shows major resemblances to the less-derived forms in lower Central America.

## Acknowledgments

Our thanks go to Kelly M. Hogan, Walter Holmes, and Kenneth L. Williams for their assistance in the field. Jay M. Savage and Brian I. Crother kindly loaned comparative material from the CRE collections housed at the University of Miami. Wilberto Aguilar N., director of the Departamento de Recursos Naturales Renovables, as always, was instrumental in providing collecting permits. Our long-time friend, Jorge Porras Zúniga, opened his home to us, obtained our rented field vehicle, and assisted in numerous other ways. To all we owe a debt of gratitude.

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# HAWAIIAN XANTHIDAE (DECAPODA: BRACHYURA) II. DESCRIPTION OF *GARTHIELLA,* NEW GENUS, WITH A REDESCRIPTION OF *G. ABERRANS* (RATHBUN, 1906)

Richard H. Titgen

*Abstract.*—The new genus *Garthiella* is erected to accommodate the xanthid species described as *Chlorodopsis aberrans* Rathbun, 1906. It is readily distinguished from the genus *Pilodius* (=*Chlorodopsis*) by the sharp fingers of the chelipeds, the shape of the first pleopod of the male, and the wide orbital hiatus.

Rathbun (1906) published the first comprehensive study of Hawaiian Crustacea Decapoda. Her report was based primarily on the collections made in 1902 by the U.S.F.C. Steamer *Albatross* from waters surrounding the Hawaiian Islands, but included additional Hawaiian material from the U.S. National Museum of Natural History, the Museum of Comparative Zoology, and the Philadelphia Academy of Natural Science. She also cited literature records of an additional 28 species. Her report remains the basis of decapod research in the Hawaiian Islands.

Of the 213 species and subspecies of Brachyura she reported, Rathbun (1906) placed 94 species in the family Xanthidae, 21 of which were described as new species. One new species, *Chlorodopsis aberrans,* was described and placed in the genus *Chlorodopsis* A. Milne Edwards, 1873, because it "has much in common with *C. woodmasoni* Alcock." However, as noted by its specific epithet, Rathbun recognized that it was not a typical *Pilodius* Dana, 1851 (=*Chlorodopsis*) by reason of pointed tips on the fingers of its chelipeds. All species of *Pilodius* are presently recognized as having chelipeds with the fingers hollowed at the tip.

While studying the xanthid crabs in the Bishop Museum, the author noted that this species did not fit into the accepted concept for the genus *Pilodius* because of its aberrant chelipeds, nor could it be assigned to any other described xanthid genus. Accordingly, the new genus *Garthiella* is here erected to accommodate *Chlorodopsis aberrans.*

## *Garthiella,* new genus

*Diagnosis.*—Carapace hexagonal to transversely subovate, about ⅗ as long as wide, flattish from side to side, slightly convex longitudinally, front turned down and convex. Regions more or less separated anteriorly, but vague posteriorly; surface variously sculptured with spines or tubercles. Front bilobed, approximately ⅓ carapace width; frontal-orbital border about ⅗ carapace width. Anterolateral border divided into 4 granulated lobes or teeth (excluding external orbital angle). Posterolateral border slightly longer than anterolateral. Basal antennal article rather broad, inner angle touching ventral prolongation of front; outer angle prolonged partway into wide orbital hiatus, not closing hiatus to antenna. Palatal ridges developed only posteriorly, not extending forward to anterior boundary of buccal cavern. Chelipeds equal or subequal in both sexes, covered by tubercles; fingers pointed. Ambulatory legs anteriorly spinose, with scattered hairs. Male abdomen with 7 segments, 3–5 fused; gonopod curved and tapered, with several long setae near tip and conical spines on distal half.

*Type-species.*—*Chlorodopsis aberrans* Rathbun, 1906.

*Etymology.*—This genus is named for a student of the Xanthidae, Dr. John S. Garth of the Allan Hancock Foundation, Los Angeles, California; the gender is feminine.

*Remarks.*—The new genus *Garthiella* is erected to accommodate the "aberrant" species *Chlorodopsis aberrans* Rathbun, 1906. *Garthiella* resembles *Pilodius* (=*Chlorodopsis*) in general appearance, but can be distinguished by the pointed fingers on the chelipeds and the tip of the first pleopod of the male. All species of *Pilodius* are presently recognized as having chelipeds with the fingers hollowed at the tip. The reduced beak at the tip of the gonopod of *Garthiella aberrans* is not like the larger, fuller beaks of species of *Pilodius.*

In species of *Pilodius* the orbital hiatus varies from being open to give the antennal flagellum access to the eye, to being closed. In general, though, the orbital hiatus is not wide, whereas, in *Garthiella aberrans* the orbital hiatus is quite wide.

### *Garthiella aberrans* (Rathbun, 1906), new combination
Figs. 1, 2

*Chlorodopsis aberrans* Rathbun, 1906:859, fig. 20.—Edmondson, 1925:43; 1946:295; 1962:274, fig. 20a.—Serène & Van Luom, 1958:90, 91; 1959:302, 328, text-figs. 2L, 5L, pl. 2 fig. D, pl. 3 fig. K.—Forest & Guinot, 1961:89.

*Material examined.*—3 males, 6 females, 2 juveniles, BPBM S1351, Johnston Island, coll. C. H. Edmondson, Jul 1923.

*Redescription.*—Carapace hexagonal to transversely subovate, flattish from side to side, slightly convex longitudinally, front turned down and convex; length about ⅗ width (Fig. 1a). Regions and subregions separated by wide smooth grooves lacking hair. Gastric and branchial regions defined and subdivided; 2M incompletely subdivided. Cardiac and intestinal regions blending into branchial region with no clear divisions. Anterior of carapace sculptured with sharp tubercles decreasing in size posteriorly to granules; scattered short hairs originating at many tubercles and granules.

Front bilobed and slightly greater than ⅓ carapace width. Frontal lobes rounded, granular, and slightly produced adjacent to U-shaped median sinus; small lateral frontal lobes separated by shallow emarginations. Orbital margins spinulose with 1 median dorsal and 1 ventrolateral notch; wide smooth groove just posterior to orbital margins continuous behind front. Frontal-orbital border about ⅗ carapace width.

Anterolateral border of carapace granular and divided into 4 lobes or teeth (excluding external orbital angle). First lobe granular and blunt, originating behind and below outer orbital angle; posterior 3 lobes granular and spinose. First 3 lobes obliquely directed anteriorly, increasing in size posteriorly; fourth lobe slightly smaller than third, more laterally directed. Posterolateral border slightly longer than anterolateral, and rather straight; posterior border slightly emarginate at midline.

Pterygostomial region similar to dorsum, granular to spiny (Fig. 1b). Third maxilliped densely bristled medially, with scattered hairs over exterior surface (Fig. 2a). Palatal ridges developed only posteriorly, not extending forward to anterior border of buccal cavern. Basal antennal article broad, inner angle touching ventral prolongation of front; outer angle prolonged partway into wide orbital hiatus, not closing hiatus to antenna (Fig. 1b).

Chelipeds slightly unequal, tubercular, with scattered short hairs. Tubercles on wrist and most of hand conical and sharp; lower surface of propodus with rounded tubercles. Two teeth on inner margin of carpus, indicated by slightly larger tubercles. Upper and lower borders of palm rounded; spinules on outer surface of palm tend to form lines, especially middle row. Fingers deeply grooved, acute (Fig. 2b); spinous tubercles

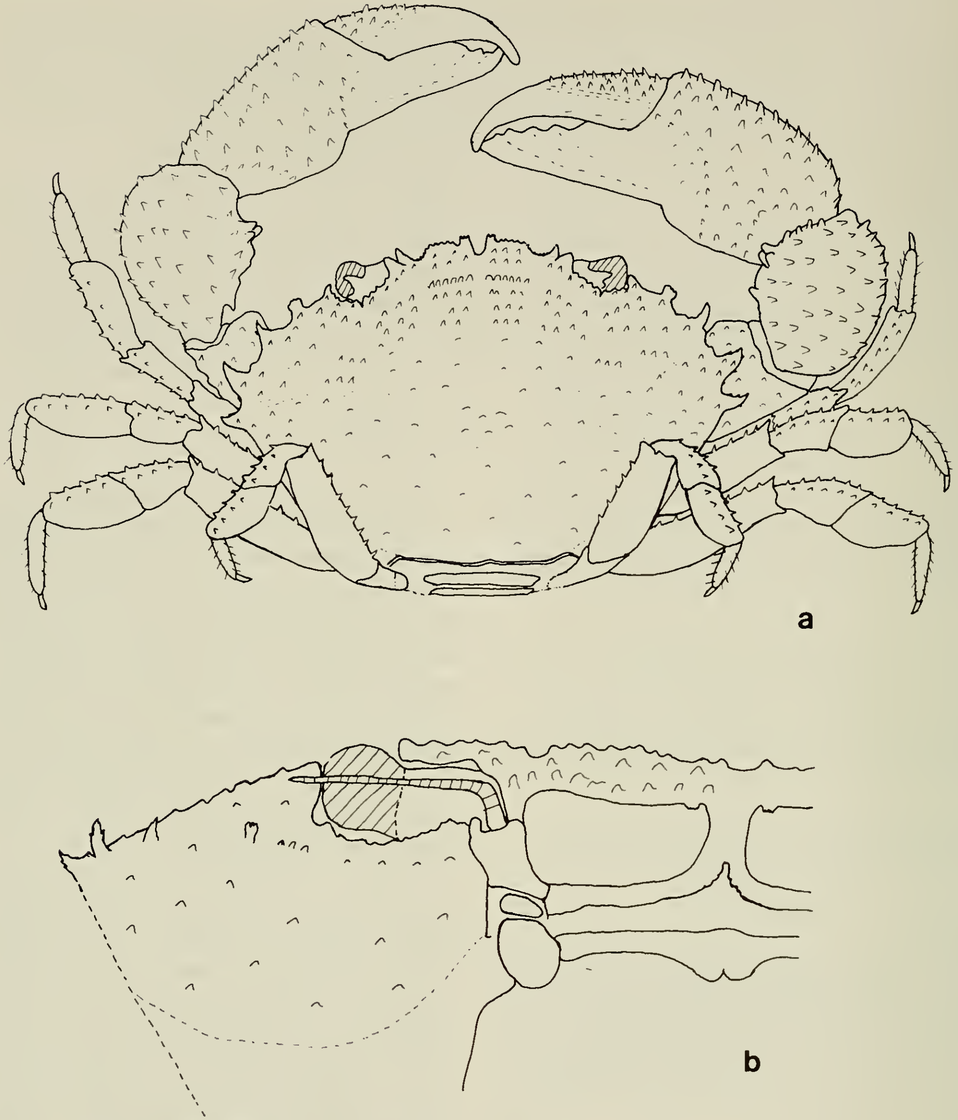

Fig. 1. *Garthiella aberrans*: a, Male, dorsal view; b, Front.

extending onto dorsal surface of dactylus about half its length, and onto outer face of pollex between grooves (more developed in females); teeth well developed; tip of dactylus curved, overlapping pollex internally when fingers closed, leaving no gap between teeth.

Ambulatory legs lightly granular, upper margins spinulate (Fig. 2c). Upper margin of propodus, and especially carpus, bicarinate. Legs with scattered long hairs, more dense on upper and lower margins.

Abdomen of male with 7 segments, third to fifth fused, suture lines not recognizable (Fig. 2d). Abdomen of female oval, with 2 longitudinal grooves joining at seventh segment (Fig. 2e); fringe of long hair around border, outer surface lightly covered by short hair.

First pleopod of male curved, with sev-

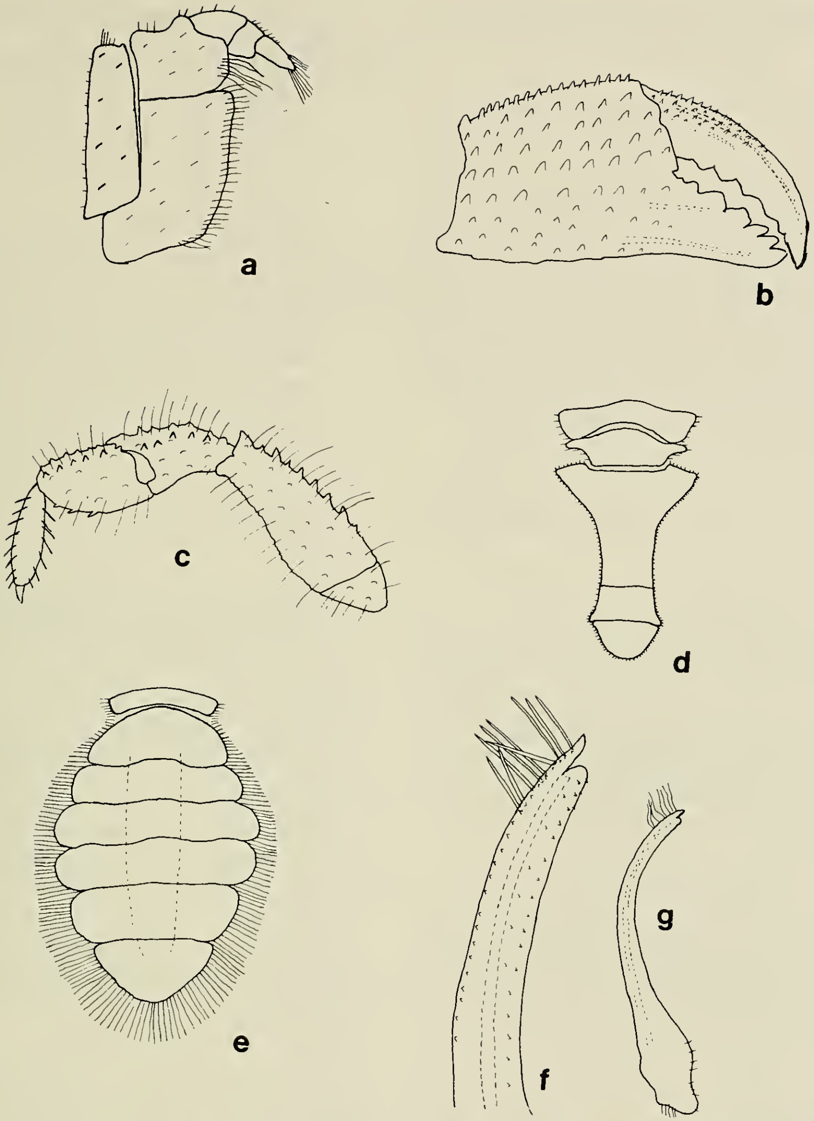

Fig. 2. *Garthiella aberrans*: a, Third maxilliped; b, Chela of male; c, Pereiopod; d, Abdomen of male; e, abdomen of female; f, g, First pleopod of male.

eral long setae near tip; conical spines on distal half; beak reduced (Fig. 2f, g).

*Remarks.*—*Garthiella aberrans* (Rathbun, 1906) was originally described from a single male specimen (USNM 29434). It was dredged in the vicinity of Nihoa Island (Modu [Moku] Manu or Bird Island) at U.S.F.C. Steamer *Albatross* Station D.4146, at a depth of 42–48 meters, on a bottom of coarse coral, sand, and forams. The only other reported specimens were collected at Johnston Island (Edmondson 1925). The Bishop Museum catalog states that 15 specimens were collected at Johnston Island, as reported by Edmondson (1925). However, Edmondson (1962) stated that there were

13 specimens in the Bishop Museum collections, of which only 11 can now be located.

Unlike the Nihoa specimen from deeper water (42–48 meters), Edmondson (1962) reported that the Johnston Island specimens were collected in shoal water. This information is not on the specimen label, in the Bishop Museum catalogue, or reported previously by Edmondson (1925). Because Edmondson collected the Johnston Island specimens, it must be presumed that these depth records are from memory or, less probably, from private field notes.

*Distribution.*—Near Nihoa Island, Northwestern Hawaiian Islands (Rathbun 1906); and Johnston Island (Edmondson 1925).

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I would like to thank Drs. C. C. Christensen, J. S. Garth, J. A. Titgen, and M. K. Wicksten for critically reading the manuscript and offering valuable comments. Dr. Garth was especially helpful by carefully examining some of the specimens.

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# GEOGRAPHIC VARIATION IN THE WHITE-MANTLED BARBET (*CAPITO HYPOLEUCUS*) OF COLOMBIA (AVES: CAPITONIDAE)

Gary R. Graves

*Abstract.*—*Capito hypoleucus,* a Colombian endemic currently considered monotypic, is divisible into three subspecies that differ in coloration. The nominate race is restricted to the foothills and lower slopes of the northern end of the central Andes from Valdivia, Antioquia, east to the eastern slope of the Serranía de San Lucas, Bolívar. Populations from the valley of the upper Río Porce (*C. h. carrikeri* n. subsp.) and the middle Magdalena Valley (*C. h. extinctus* n. subsp.) are described as new. Deforestation is responsible for the presumed extinction of *C. h. extinctus.*

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The White-mantled Barbet (*Capito hypoleucus*), a poorly-known Colombian endemic, is restricted to humid foothill forest (200–1500 m elevation) from the east bank of the lower Río Cauca, east around the northern end of the central Andes, and south to the middle Magdalena Valley (Hilty and Brown, in press). The species was known from fewer than a dozen specimens until Melbourne A. Carriker, Jr. and assistants (1947–1952) collected a series of 22 skins from four localities (Fig. 1) spanning the geographic range of the species. Examination of these specimens, now deposited in the National Museum of Natural History, Smithsonian Institution (USNM), indicates that *C. hypoleucus,* currently considered to be monotypic (Peters 1948), is divisible into three taxonomically distinct populations.

### *Capito hypoleucus hypoleucus* (Salvin)

*Capito hypoleucus* Salvin, 1897:xvi. Valdivia (3800 ft.), Antioquia, Colombia.

*Characters.*—The sides of the throat are lightly tinted with brown of the same color as that of the pectoral band. Dorsally, yellow pigment is restricted to the mantle. The flanks and belly are lightly washed with pale yellow.

*Distribution.*—Foothills and lower slopes at the northern end of the Central Andes from Valdivia, Antioquia, east to the east slope of the Serranía de San Lucas (Volador), Bolívar.

*Specimens examined.*—Antioquia: Puerto Valdivia (1 ♀, AMNH); Valdivia (3 ♂♂, 1 ♀, USNM); La Frijolera (1 ♂, AMNH).—Bolívar: Volador (2 ♂♂, 3 ♀♀, USNM).

*Remarks.*—The flanks of birds from Volador tend to be more intensely yellow than those of specimens from the west slopes of the Central Andes in Antioquia, but there appear to be no other significant plumage differences between the two populations. Specimens taken in the Valdivia region more than 40 years apart do not differ noticeably in plumage color. There is little difference in size among any of the populations examined.

Carriker and an assistant collected along the road above Puerto Valdivia from 19 May to 19 June 1948. The four USNM specimens (401684–687) were collected on 25 May, in "badly cut over" forest on steep slopes below the road (Carriker's field journal deposited in USNM). One male had enlarged testes.

Carriker collected at Volador from 5 May to 1 June 1947; the five *C. hypoleucus*

(USNM 392443–447) were taken on 19–31 May (♂, 23 May, testes enlarged).

### *Capito hypoleucus carrikeri*, new subspecies

*Holotype.*—USNM 425942, adult male from Botero, Antioquia, Colombia, elevation 3600 ft (1098 m). Collected 31 Aug 1950 by M. A. Carriker, Jr.; original number 18918.

*Characters.*—Yellow pigments in *carrikeri* are more extensive throughout the non-black portions of plumage than in *hypoleucus.* The yellow of the mantle extends up the nape to the rear of the crown, as opposed to being restricted to the mantle as in *hypoleucus.* Ventrally, the yellow of flanks, belly, and breast below the pectoral band is brighter and much more extensively distributed. The throat is white with a faint yellow tint, lacking the brown tint found in *hypoleucus.* The brown pectoral band is slightly lighter in shade than in *hypoleucus.*

*Measurements of holotype* (mm).—Wing chord, 88.2; tail, 57.7; exposed culmen, 24.2; width lower mandible, 13.7.

*Distribution.*—Known so far only from the type locality.

*Specimens examined.*—Antioquia: Botero (3 ♂♂, 6 ♀♀, USNM).

*Etymology.*—Named for Melbourne A. Carriker, Jr., who was responsible for collecting and preparing the type series.

*Remarks.*—This population is apparently restricted to the drainage of the northward flowing Río Porce, a tributary of the Río Nechí. Slopes above 1500 m elevation, deforestation, and semiarid habitat around the periphery of the valley form barriers to the east, west and south. Contact with *hypoleucus* may have occurred in the past at the foot of the steep valley formed by the Río Porce.

Carriker worked at Botero, a small village on the west bank of the Río Porce on the rail line to Medellín, from 17 August to 9 September 1950. Specimens of *C. hypoleucus* (USNM 425934–942) were collected on 30 August–8 September, from a "tall tree with small fruit" and "from large clumps of mistletoe in large tree," in the patchwork of forest and pasture on the west bank of the river. Three females and one male had enlarged gonads; a single bird of each sex was in an immature plumage, which lacks the brown pectoral band.

### *Capito hypoleucus extinctus*, new subspecies

*Holotype.*—USNM 436335, adult male from Hacienda Sofia, Río Samaná, Caldas, Colombia, elevation 3750 ft (1143 m). Collected 21 May 1951 by M. A. Carriker, Jr., original number 20235.

*Characters.*—Feather tips on the mantle and nape are white with a faint buffy tint, not strongly yellow as in *hypoleucus* (mantle) or *carrikeri* (mantle and nape). Yellow on the flanks and lower belly is much reduced. The pectoral band tends to be darker brown than in *hypoleucus* and much more so than in *carrikeri.* The throat is similar to *hypoleucus.*

*Measurements of holotype* (mm).—Wing chord, 89.0; tail, 58.0; exposed culmen, 23.5, width lower mandible, 14.0.

*Distribution.*—Foothills on both sides of the valley of the Río Magdalena in the vicinity of Honda.

*Specimens examined.*—Tolima: within 20 miles (west) of Honda (2 ♂♂, 1 ♀, AMNH).—Cundinamarca: Carmen de Yacopí (1 ♀, AMNH).—Caldas: Hacienda Sofia (2 ♂♂, 2 ♀♀, USNM).

*Etymology.*—Latin, *extinctus,* dead or destroyed, in reference to the probable extinction of this taxon through deforestation of the middle Magdalena Valley.

*Remarks.*—The series of specimens from the east bank of the Río Magdalena are inadequate to determine if populations east (Carmen de Yacopí) and west (Hacienda Sofia, west of Honda) of the Río Magdalena are subspecifically different.

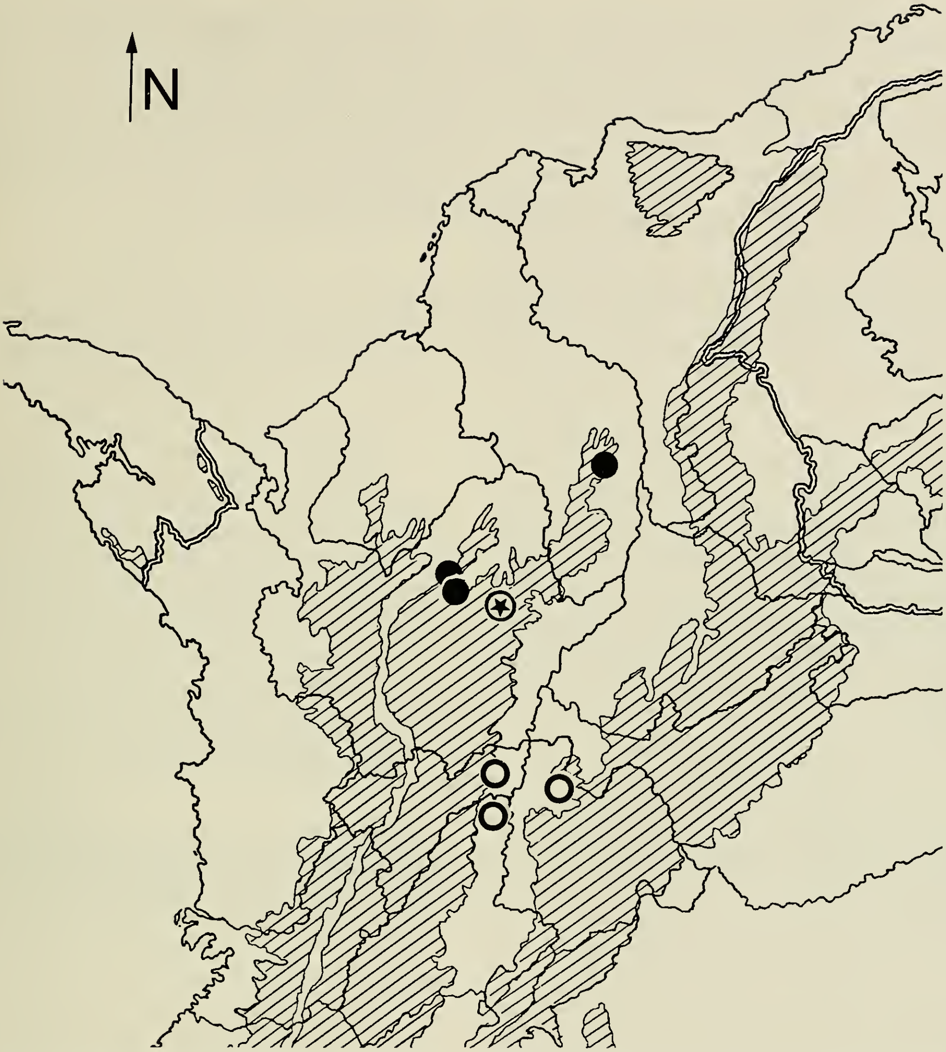

Fig. 1. Map showing the distribution of *Capito hypoleucus* in northwestern South America. Specimen localities are identified with symbols (filled circles = *C. h. hypoleucus*; starred circle = *C. h. carrikeri*; empty circles = *C. h. extinctus*). Fine lines indicate provincial boundaries; cross-hatched areas indicate elevations above 1000 m.

Carriker worked at Hacienda Sofia, along the road to Sonsón, from 10 May to 1 June 1951. Four specimens of *C. hypoleucus* (USNM 436334–337) were collected, two of which had enlarged gonads (♂, 31 May; ♀ 29 May). Carriker's only direct mention of *C. hypoleucus* from this locale was of an individual taken from a mixed-species flock.

## Discussion

The middle and lower Magdalena and Cauca valleys have been heavily deforested since the 19th century and perhaps as far back as Pre-Columbian times (see Chapman 1917, Hilty 1985). Hilty (1985) estimated that *Capito hypoleucus,* as well as a number of other species inhabiting humid forest on lower Andean slopes, have undergone a historic range loss of more than 50% due to habitat destruction. Before the era of habitat destruction by humans, populations of *C. hypoleucus* were probably in genetic contact, and geographic variation in plumage may have been more or less clinal in nature. The question of whether the recognized subspecies are arbitrary subdivisions of an unperceived cline or discrete populations, in all probability can no longer be answered. There are no data available on the present status or distribution of any of the historically known populations, but the fragmented state of the remaining lower montane humid forest suggests that any remaining populations are insular and genetically isolated. The complete deforestation of the floodplain and foothills of the middle Magdalena Valley during the past 30 years suggests that *C. h. extinctus* may already be extinct.

## Acknowledgments

I thank the curators of the National Museum of Natural History (USNM) and American Museum of Natural History (AMNH) for permission to examine specimens. William L. Brown, Steven L. Hilty, Storrs L. Olson, and J. V. Remsen, Jr. provided information and commented on the manuscript. Olson supplied the base map. This work was supported by a Smithsonian Postdoctoral Fellowship.

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# *LASIONECTES ENTRICHOMA,* NEW GENUS, NEW SPECIES, (CRUSTACEA: REMIPEDIA) FROM ANCHIALINE CAVES IN THE TURKS AND CAICOS, BRITISH WEST INDIES

Jill Yager and Frederick R. Schram

*Abstract.*—*Lasionectes entrichoma,* a new genus and species of remipede from the Turks and Caicos, British West Indies, is described. It possesses characters which warrant its placement into a new genus of the crustacean class Remipedia.

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In 1979, *Speleonectes lucayensis* Yager, the first species representing the new class of Crustacea, Remipedia, was collected from Lucayan Cavern, an anchialine cave on Grand Bahama Island in the northern Bahamas. Subsequent exploration of other caves in the West Indies has resulted in the discovery of the new genus and species of remipede described here, as well as several other new species of remipedes to be described later.

Although a separate country politically, the Turks and Caicos are geographically a southeast extension of the chain of islands making up the Bahamas. Their geologic makeup is also similar, in that the islands are the tops of exposed shallow water carbonate banks separated by deep water channels.

Old Blue Hill Cave, the type-locality for these new remipedes, is located on the island of Providenciales. The submerged cave system is developed in an inland ridge and has two entrances along the collapsed margin of a large sinkhole. The western opening is in a large, shallow, brackish pool which slopes abruptly down along the north margin of the sinkhole into the dark passages of the cave system. The pool is entirely open to sunlight, and is rich in organic material which has turned the water brown and reduced the level of visibility. The pool supports a rich biota of algae, the cyclopoid copepod *Apocyclops* (*Metacyclops*) *distans,* the amphipod *Spelaeonicippe provo* Stock and Vermeulen, and a very dense population of the caridean shrimp *Typhlatya garciai* Chace. The new remipede is found in the twilight zone which begins at about 5 m, and in the dark, deeper passages of the cave which have been explored to about 20 m. The eastern entrance into the cave system is at the bottom of a narrow, dimly illuminated fissure. In contrast to the western entrance, the water in this pool is very clear and the numbers of *Typhlatya* are greatly reduced from thousands of individuals to less than a hundred. The new remipede is relatively abundant, especially when compared to *Speleonectes lucayensis.* Hundreds of individuals have been seen while cave diving in both entrances of this cave system.

## *Lasionectes,* new genus

*Diagnosis.*—Second maxilla and maxilliped subchelate and distinctly more robust than first maxilla; terminal segments bearing trifid claw with comb-like row of spinules between large central spine and two flanking spines; both appendages with short setae along entire medial margin.

*Etymology.*—From the Greek *lasios* meaning hairy, and *nectes* meaning swimmer; a reference to the prevalence of fine

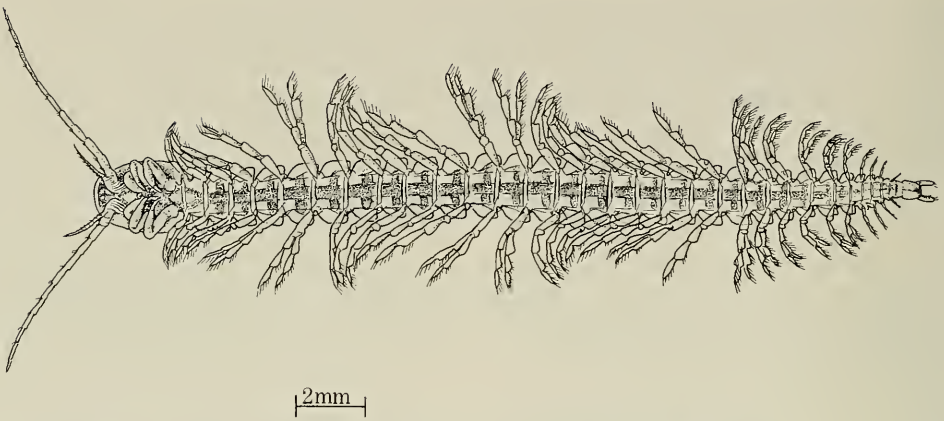

Fig. 1. *Lasionectes entrichoma*: Ventral view of animal showing swimming position.

hair-like setae on the second maxilla and maxilliped. Gender masculine.

*Type-species.*—(By monotypy) *Lasionectes entrichoma,* new species.

### *Lasionectes entrichoma,* new species
Figs. 1–3

*Type-material.*—Holotype. Adult, 31.5 mm, USNM 216978; in brackish water, Old Blue Hill Cave, Providenciales Island, Turks and Caicos, British West Indies, 6 Apr 1983.—Paratypes, 39 specimens, both juvenile and adult, from Old Blue Hill Cave and Airport Cave on Providenciales Island, and from Cottage Pond, Middle Caicos Island, Turks and Caicos, B.W.I., Coll. J. Yager and D. Williams. Retained for further studies in the collections of the San Diego Natural History Museum.

*Diagnosis.*—With characters of the genus.

*Description.*—Cephalon small, about 13% total body length (Fig. 1). Cephalic shield somewhat tapered anteriorly and folded over anterior margin of cephalon. Maximum of 32 postcephalic trunk segments; first trunk segment short, with greatly reduced pleura, partly covered by cephalic shield; pleura of trunk segments posterior to first well developed, projecting laterally, reduced in size anterior to anal segment. Trunk sternites with distinct transverse bars, not developed as plates; bar on segment 14 with large triangular process or flap on either end adjacent to limb base and covering genital pore; transverse bars posterior to segment 14 and continuing to about segment 24; thereafter developed as small triangular processes, becoming more prominent posteriorly in the series. Anal segment about as wide as long, anus terminal; caudal rami slightly less than length of anal segment, with 9 moderately long terminal setae and 2 distomedial setae (Fig. 2J).

Frontal filaments (Fig. 2A) small, rod-like, anteromedial to first antenna, with thumb-like process on posteromedial surface. Antenna 1 (Fig. 2B) large, well developed, biramous. Basal segment of peduncle enlarged, bearing 3–4 rows of densely packed, long, lash-like esthetascs draped posteriorly over antenna 2 toward labrum. Dorsal ramus long, with 12 segments; ventral ramus about one-half to two-thirds length of dorsal ramus, 8–9 segments; segments of both rami slender with fine hair-like setae along ventral margins and in tufts distoventrally; distal segment of both rami with 4–6 terminal setae.

Antenna 2 (Fig. 2C) biramous, well developed, moderate in size, not extending beyond cephalic shield. Two-segmented protopod, medial margins of which bearing short simple setae. Three-segmented endo-

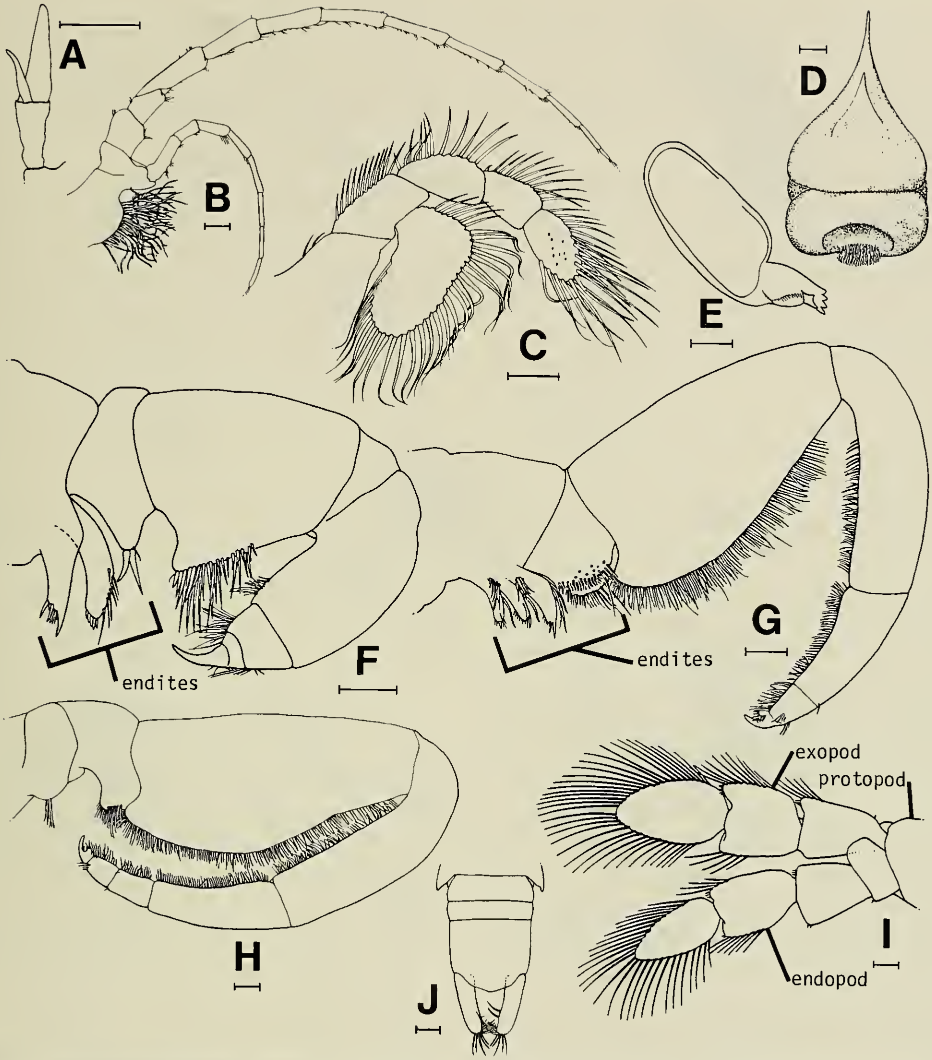

Fig. 2. Left appendages and related structures of *Lasionectes entrichoma*: A, Frontal filament; B, Antenna 1; C, Antenna 2; D, Labrum; E, Mandible; F, Maxilla 1; G, Maxilla 2; H, Maxilliped; I, Tenth trunk limb; J, Terminal part of body with caudal rami. Scales = 0.2 mm.

pod; first segment with about 13 plumose setae laterally, second segment with about 11 or 12, third segment with about 24 along entire margin and those most distal forming double row. Exopod a single, large, oval scale with about 35–40 long plumose setae along entire margin.

Labrum (Fig. 2D) a large fleshy lobe, narrow anteriorly, broad posterior section with transverse groove and fossa with densely packed short ribbon setae. Mandibles asymmetrical. Right mandible (Fig. 3B) with 3-cusped incisor process and 3-cusped lacinia mobilis. Left mandible (Figs. 2E, 3A) with 4-cusped incisor process and crescent-shaped lacinia mobilis. Molar processes densely spinose, semi-arcuate. Paragnaths round, flattened lobes, lateral and posterior to mouth, covered with fine ribbon setae.

First maxilla (Fig. 2F) 6-segmented, uni-

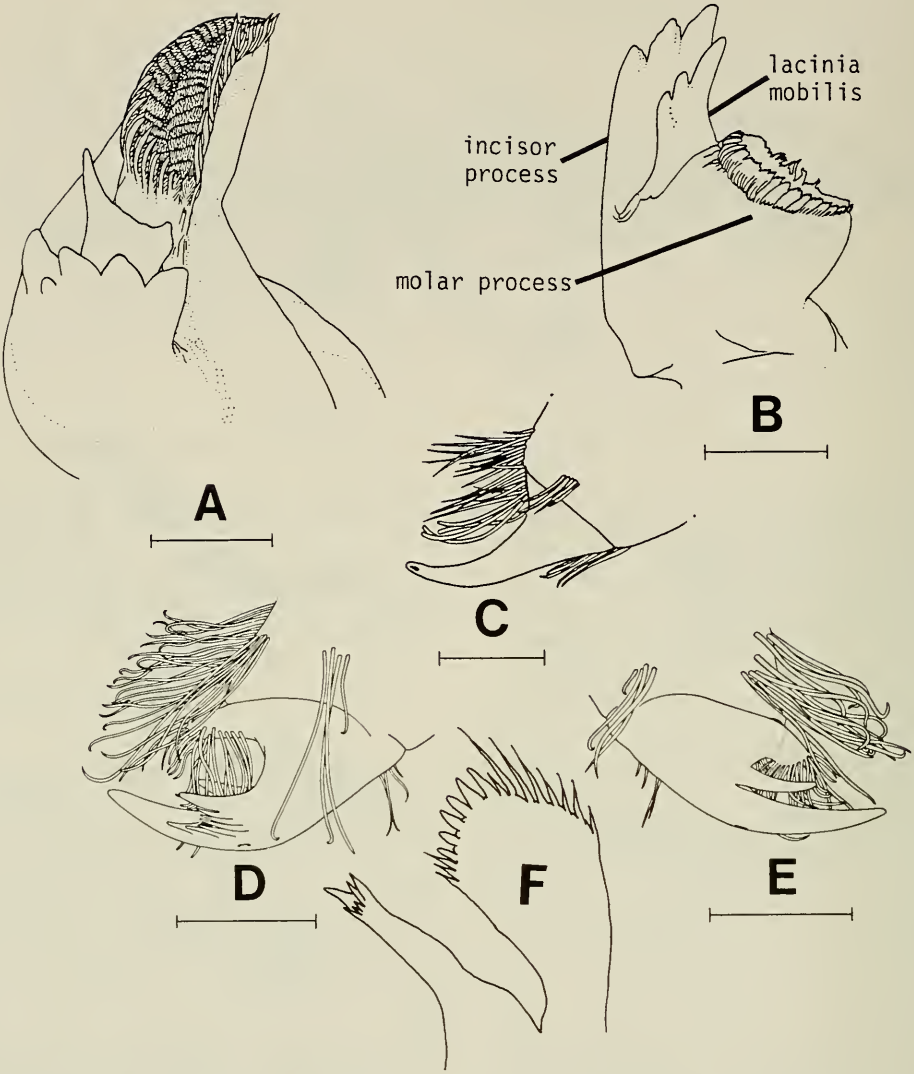

Fig. 3. Appendages of *Lasionectes entrichoma* in greater detail. A, left mandible; B, right mandible; C, Maxilla 1, tip; D, Maxilla 2 anterior view; E, Maxilla 2 posterior view; F, Maxilla 1 endites of first segment. Scales = 100 $\mu$m.

ramous, subchelate, robust. First or proximal segment with 2 well developed endites (Fig. 3F); proximal endite terminates ventro-posteriorly in long stout spine, with 4–6 stout spine-like setae dorsally; distal endite a broad, plate-like flap with 6 short, stout, spine-like setae along crest, flanked by many tiny setae, 8 short to long simple setae on anterodistal margin and 4 on posterodistal margin. Second segment with cone-like endite terminating in 2 robust spine-like sete and 1 or 2 small, simple setae. Third segment robust, with medial, subtriangular, double-crested endite bearing dense row of long, simple setae along each crest, and 1 short, stout terminal spine at apex of endite; anterior crest row with about 16 large setae, slightly longer than posterior row of about 24 short to moderate setae. Fourth segment long, robust, with about 8 simple setae on distomedial half of segment and 2 clusters of 8–10 simple setae on antero- and posterodistal margins. Fifth segment short, with 2 distal clusters of about 12 simple, moderately long setae on anterior and posterior medial margins and 2 distal clusters of about 6 on anterior and posterior lateral margin. Sixth segment (fig. 3C) very short, terminating in single, long, talon-like claw with large terminal pore; tuft of about 10 long, fine, simple setae at medial base of claw. Principle flexion point of appendage between segments 3 and 4, with segments 4–6 cradled in trough between double rows of setae on segment 3 when flexed. Secondary flexion occurring between segments 2 and 3, with 2 large setae of segment 2 held in opposition to apex of subtriangular endite of segment 3 during flexion.

Second maxilla (Fig. 2G) 7-segmented, long, about twice the length of first maxilla, uniramous, subchelate; first segment with 3 digitiform endites increasing in size distally, 2 small, subconical lobes posteriorly associated with second and third endites each bearing 3–5 short to moderate setae; first endite small, apex with 1 short, terminal spine and about 4–6 tiny hair-like setae, row of 4–6 small to moderate, simple setae on lateral margin; second endite with 1 moderately long terminal spine, about 6–8 small, simple, setae apically, a row of about 3 moderate, simple setae on lateral margin; third endite with 1 large spine terminal seta, 8–10 small, simple apical setae, a row of about 3–5 moderately long, simple, lateral setae. Segment 2 with large, medial, thumb-like lobe with clusters of moderate to long, simple setae in 2 rows, the anterior row of setae longer. Segment 3 long, wide, with subtriangular endite bearing 2 rows of dense, short, simple setae along entire medial margin of segment. Segments 4, 5, and 6 with dense rows of subequal setae along entire medial margin of segments; segment 5 with 1–2 simple setae on distolateral margin; segment 6 short, with 2 clusters of about 4 moderately long, simple setae on anterior and posterior distolateral margin and 2 clusters of about 8 long, fine setae on anterior and posterior distomedial margin. Segment 7 (Figs. 3D, 3E) very short, terminating in complex trifid claw with a central long spine and 2 shorter flanking spines, a comb-like row of several smaller spines between the central spine and posterior flanking spines. Thumb-like pad with fan-like setose margin opposed to claw.

Maxilliped (Fig. 2H) similar to second maxilla but markedly longer and more robust, with at least 8 segments. Segment 1 with several weakly developed median lobes, the most prominent of which with about 5 terminal, long, simple setae. Segment 2 with small, thumb-like lobe with two rows of clustered setae in V-shape, the anterior row with short to moderate simple setae, posterior with short, hair-like setae. Segment 3 long, wide, with subtriangular endite bearing 2 rows of setae along medial margin as in second maxilla. Segments 4, 5, 6 and 7 with dense rows of subequal setae as in second maxilla. Segment 6 with 1 short seta distolaterally. Segment 7 with several moderately long setae on anterior and posterior distolateral margin and 2 clusters of about 6 on anterior and posterior distomedial margin. Segment 8 with terminal trifid claw complex as in maxilla 2.

Trunk appendages (Fig. 2I) biramous, setose, laterally directed paddles. Protopod fleshy, exopod 3-segmented, endopod 4-segmented. Distal segments of both rami oval in shape.

*Etymology.*—From the Greek *entrichoma* meaning eyelash, a reference to the long lash-like setae on the base of the first antenna; used as a noun in apposition.

*Remarks.*—Additional specimens of *Lasionectes,* were collected from Airport Cave, another anchialine habitat on Providenciales. Associated fauna were a new family of caridean shrimp (C. W. Hart, Jr., pers.

comm.), a new genus of leptostracan, *Speonebalia cannoni* Bowman, Yager, and Iliffe, 1985, and the amphipod *Spelaeonicippe provo.* Cottage Pond on Middle Caicos Island was also found to be inhabited by *Lasionectes* and another as yet undescribed species of remipede. Although blind cave fish are known from many West Indian caves, they are noticeably absent in the abovementioned caves.

While *Lasionectes* bears some relationship to *Speleonectes lucayensis* Yager, 1981, the differences between the two taxa seem too great to maintain the two species within a single genus. The two species differ in the size ratio of the feeding appendages. The first maxilla of *Speleonectes* is the most robust when compared to the second maxilla and maxilliped. *Lasionectes* has a small first maxilla when compared to the second maxilla and the very robust maxilliped. With additional remipede material now available from other West Indian caves and also the Canary Islands, it will be possible to assess the relationships within the group in greater detail.

## Acknowledgments

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# A REDESCRIPTION OF *MICROCYCLOPS CEIBAENSIS* (MARSH, 1919) (COPEPODA: CYCLOPOIDA) FROM MARSH'S SPECIMENS IN THE NATIONAL MUSEUM OF NATURAL HISTORY

Janet W. Reid

*Abstract.*—The neotropical freshwater cyclopoid copepod species *Microcyclops ceibaensis* (Marsh, 1919) is redescribed from specimens from the type locality, deposited by Marsh in the National Museum of Natural History. *Microcyclops diversus* Kiefer, 1935, is a synonym. Locality records include Brazil, Costa Rica, Cuba, Haiti, Honduras, Uruguay, Venezuela, and possibly Mexico.

Species of the freshwater cyclopoid copepod genus *Microcyclops* may be distinguished by a complex of microcharacters. Because many characters now recognized to have taxonomic utility were not reported by earlier workers, and because some characters may be given different weight by contemporary investigators, assignment of specimens to particular species is still a tenuous business.

Marsh (1919) described *Cyclops ceibaënsis* from a collection made at La Ceiba, Honduras, by F. J. Dyer. This species is now assigned to the genus *Microcyclops* Kiefer, 1929a. Some confusion has resulted from inadequacies in Marsh's original description: Kiefer (1929b) tentatively synonymized *C. ceibaënsis* with *Microcyclops varicans* (O. Sars, 1863), an opinion shared by Gurney (1933). On the basis of broader experience with the range of variation within *M. varicans,* Kiefer later (1936) came to consider *M. ceibaensis* as a valid species and suggested that *M. diversus,* described by him from Uruguay (1935) might be a synonym of *ceibaensis.* Lindberg placed *M. ceibaensis* as "species incertae sedis" in his list of Cyclopoida from Central America and Mexico (1954b), though he later included it in a key to the genus (1957a). Smith and Fernando (1978) presented figures of a Cuban species which they attributed to *M. ceibaensis,* and commented that *M. diversus* is probably a synonym of the former species. On the other hand, Dussart (1984 and personal communication to the author) is of the opinion that *M. diversus* and *M. ceibaensis* are distinct species.

Marsh stated (1919) that the type specimen of *M. ceibaënsis* had been "catalogued under No. 57392 in the collection of the United States National Museum." This number is not traceable, and a careful search of the collections has failed to locate the type. However, several other specimens from the type locality, collected during the same period as the type, were found in the Marsh Collection of slides of Copepoda. The condition of the original slides permits a more extensive description than that furnished by Marsh. I here redescribe these specimens and compare them to closely related forms. Marsh (1919) designated no paratypic specimens. Since, however, his comments and unpublished notes make it clear that his observations of the specimens described in the present article were used in part for the original description, they may be considered to be paratypes.

## *Microcyclops ceibaensis* (Marsh, 1919)
Figs. 1–11

*Cyclops ceibaënsis* Marsh, 1919:546–547, figs. 1–5. (Honduras).

*Cyclops ceibaënsis.*—Kiefer, 1929a:36–37, 40; 1936:295–296.—Lindberg, 1954b: 486, 488.

*Cyclops varicans* (part).—Gurney, 1933:255.

*Cyclops* (*Microcyclops*) *varicans* (part).—Kiefer, 1929b:66; 1929a:36–37, 40.

*Microcyclops varicans* (part).—Comita, 1951:372.

*Microcyclops diversus* Kiefer, 1935:186–187, figs. 10–13. (Uruguay).—Brehm, 1935:298–299, 305. (Uruguay).—Collado et al., 1984:94–97, figs. 26–28. (Costa Rica).—Dussart, 1984:41, 43, 57, fig. 18. (Venezuela).—Herbst, 1959:70.—Lindberg, 1954a:214–216; 1954b:486–488; 1957a:168; 1957b:39.—Löffler, 1958:21; 1963:215; 1981:16.—Smith and Fernando, 1978:2020.

*Cyclops* (*Microcyclops*) cf. *diversus* und *ceibaënsis.*—Kiefer, 1936:265, 267, 295–296, figs. 68–70. (Haiti).

*Microcyclops ceibaensis.*—Lindberg, 1954b: 488; 1957a:168.—Osorio Tafall, 1941: 343. (Mexico).—Smith and Fernando, 1978:2020, figs. 30–32. (Cuba); 1980:11, 18, figs. 7G–7I. (Cuba).

*Cyclops* (*Microcyclops*) spec.—Herbst, 1959: 70–71, fig. 42. (Brazil).

non *Microcyclops diversus.*—Harding, 1955: 243, figs. 68–69. (Peru).

non *Cyclops* (*Microcyclops*) *varicans.*—Herbst, 1959:65–66, figs. 29–31. (Brazil).

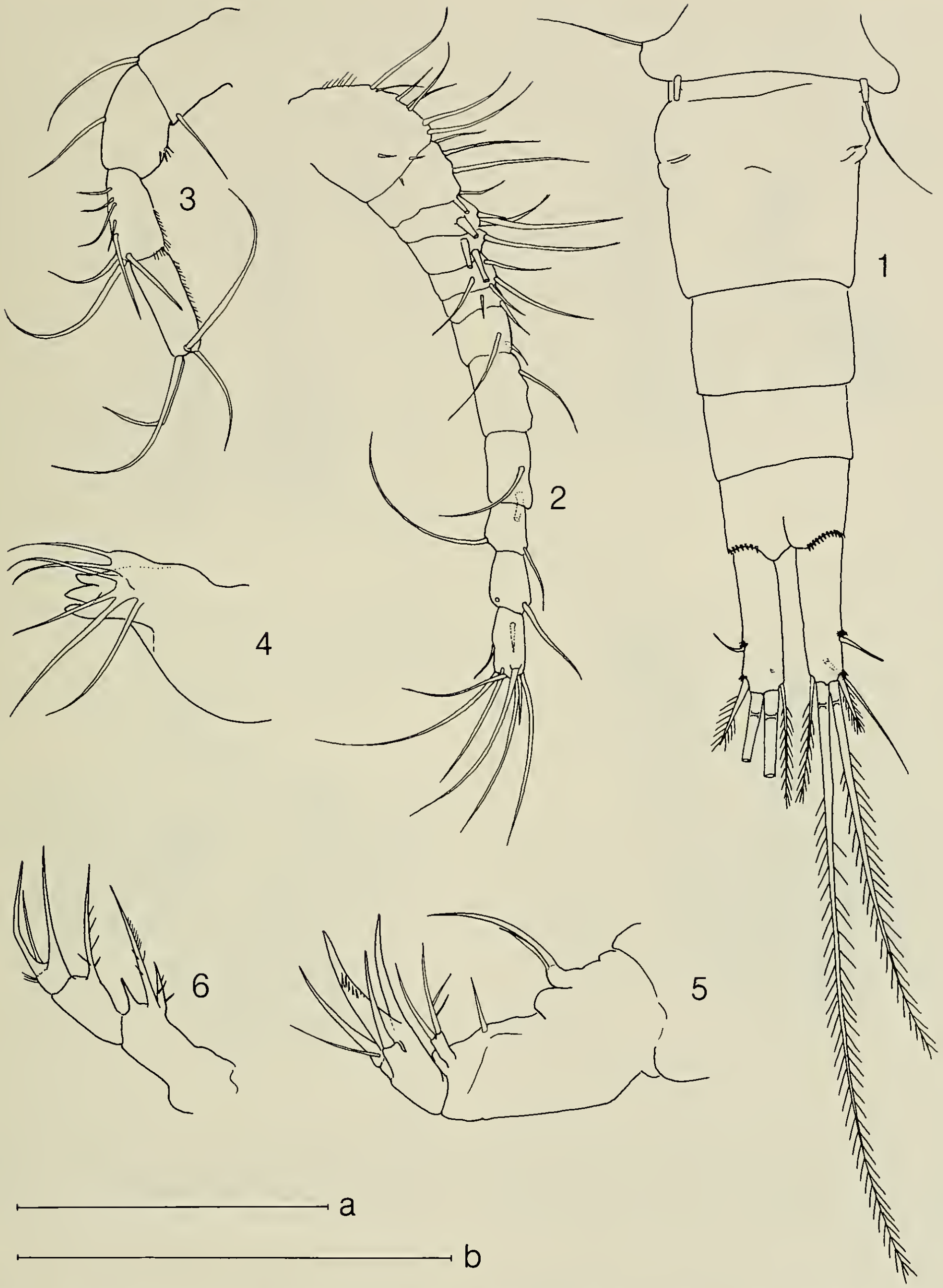
*Material examined.*—Honduras, La Ceiba, all dissected on slides, stained, and mounted in glycerine jelly: USNM 222298, 1 female (Marsh's No. 4259, labelled "eggbearing"), collected 19 Mar 1916; USNM 222299, 2 females (Marsh's Nos. 4277 and 4280, labelled "eggbearing") and 1 female (Marsh's No. 4283), collected 27 Sep 1916. All are labelled "*C. cubanensis*" on the slides but "*Cyclops ceibaënsis*" in Marsh's card file, and correspond to the description of *C. ceibaënsis.* Marsh does not indicate whether collections were made from one or several ponds.

Slides numbered 4281 and 4282, also indicated in the card file as being *C. ceibaënsis,* are not present in the collection. Although No. 4277 was labelled "ant. abd. ft.", only the antennule and antenna can now be located on the slide. Two copepodites (Marsh's Nos. 4278 and 4284) were also listed in Marsh's card file under *C. ceibaënsis,* but labelled only as "*Cyclops*" on the slides. No. 4278 is partly dissected and the abdomen cannot be located on the slide. The caudal rami of specimen No. 4284, which is mounted whole, are very short. Since both are early copepodite stages (II or III), they cannot with certainty be assigned to *M. ceibaensis.*

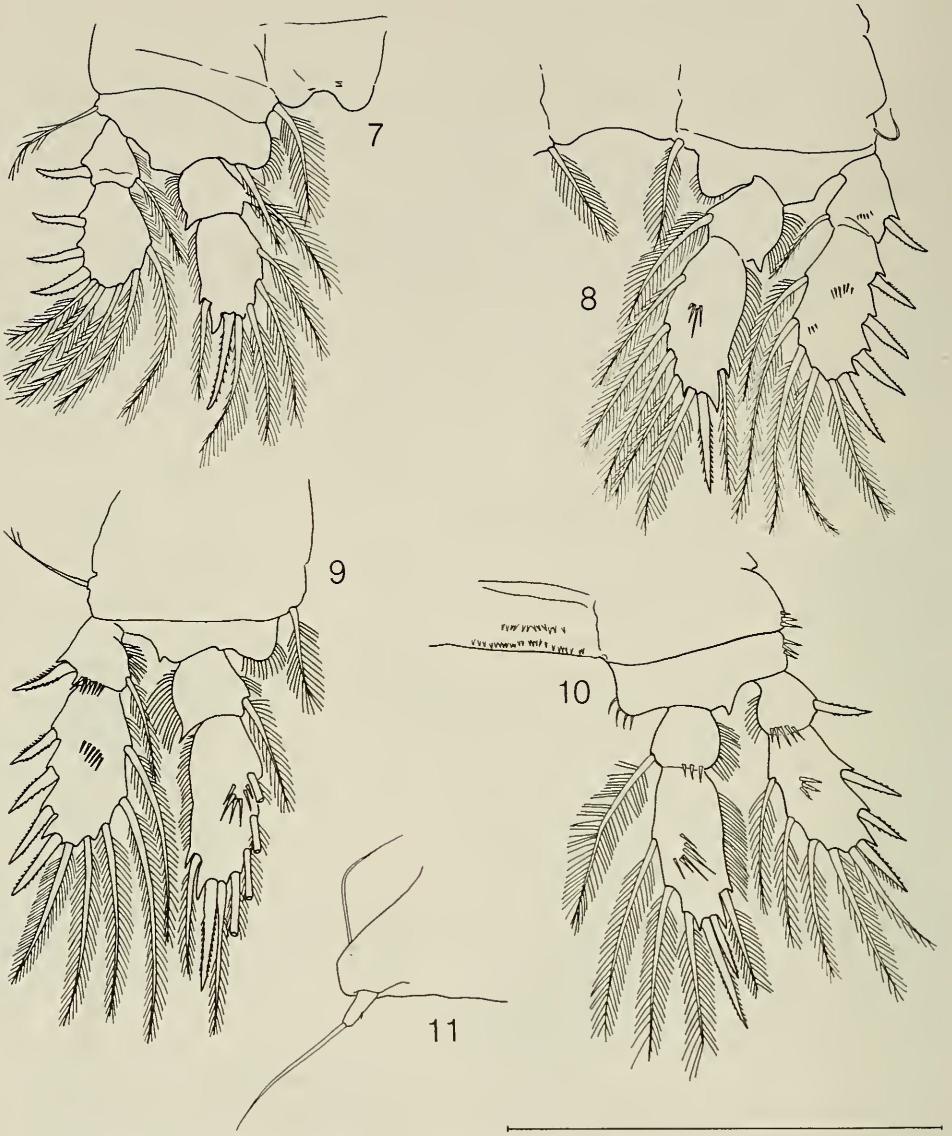
Slide No. 4280 contains the most complete specimen, which was used for the present diagnosis and figures. The slide contains, dissected: cephalothorax with antenna and some mouthparts attached; both antennules, separated; 1 maxilla; 1 maxilliped; legs 1, paired, having 3 external spines on exopod segment 2; 1 pair of legs having 4 external spines on exopod segment 2; 1 isolated leg with 3 external spines on exopod segment 2; 1 right and 1 left leg, attached one above the other, with 4 and 3 external spines on exopod segment 2 respectively; and abdomen with legs 5.

Since 1 pair and 1 other leg (not leg 1) have 4 external spines on exopod segment 2, the spine formula of 3,3,4,3 given by Marsh for *M. ceibaënsis* is impossible. Marsh's notes several times indicate confusion (which will be understood by anyone who has dissected a small copepod!) as to the dissections and therefore the armature of the swimming legs. The true spine formula is then 3,4,4,3, which is normal for the genus. The formula of 3,4,4,3 was also given by Smith and Fernando (1978) for Cuban specimens ascribed to *M. ceibaensis.* Assuming that Marsh dissected legs 3 and 4 together, a conclusion supported by the 2 strong terminal spines on endopod 2 of the supposed leg 4, the pair of legs with 4 external spines on exopod 2 are therefore legs 2, and all 4 legs can be figured.

*Female.*—Abdomen (Fig. 1) of 4 segments, length 193 μm. Anterior third of gen-



Figs. 1–6. *Microcyclops ceibaensis,* Marsh's No. 4280, eggbearing female, La Ceiba, Honduras: 1, Abdomen and legs 5, ventral; 2, Antennule; 3, Antenna; 4, Maxillula; 5, Maxilla; 6, Maxilliped. Scale a, Fig. 1; scale b, Figs. 2–6; scales = 100 μm.



Figs. 7–11. *Microcyclops ceibaensis*; Figs. 7–10, Marsh's No. 4280, eggbearing female, La Ceiba, Honduras: 7, Leg 1; 8, Leg 2; 9, Leg 3; 10, Leg 4. Fig. 11, Marsh's No. 4259, female, La Ceiba, Honduras, Leg 5. Scale = 100 μm.

ital somite broadened, greatest width about equal to length; shape of seminal receptacle not distinguishable. Anal somite with spinules on posteroventral border. Caudal rami about 3.8× longer than broad, bearing 4–5 spinules anterior to insertions of lateral and outer subterminal setae; lateral seta inserted at posterior fifth of ramus. Inner margins of rami smooth. Relative lengths of caudal setae as in Fig. 1 and Table 1.

Antennule (Fig. 2) shorter than cephalothorax, of 12 articles; no hyaline lamella distinguishable on terminal articles. Antenna, maxillula, maxilla and maxilliped as in

Figs. 3–6 respectively. Mandible not examined. Legs 1–4 (Figs. 7–10 respectively) with endopods and exopods of 2 articles; spine formula 3,4,4,3. Inner extension of basipod 2 of leg 1 with strong spine. Connecting lamellae of legs 1–3 without conspicuous ornamentation; lamella of leg 4 with 2 parallel rows of spinules on anterior surface. Exopods 2 of legs 2–4 each with group of 3–6 spinules on anterior surface. Endopod 2 of leg 4 about 2× longer than broad; inner terminal spine about 1.6× longer than outer (Table 1). Free article of leg 5 (Figs. 1, 11) slightly tapering distally, about 3.5× longer than broad, with minute spinule at midlength of inner margin and 1 long smooth terminal seta. 1 long seta inserted anterolaterally to free article of leg 5. Leg 6 not visible.

Comparative measurements of Marsh's 3 most complete specimens appear in Table 1. The seminal receptacle and leg 6 are not visible on these specimens.

Table 1.—Measurements from Marsh's specimens of *Microcyclops ceibaensis,* deposited in the National Museum of Natural History. Abbreviations: CR, caudal ramus; P4, leg 4; enp2, second (terminal) article of endopod. *Indicates specimen turned slightly laterally.

| Specimen no. | 4280 | 4259 | 4283 |
|---|---|---|---|
| Cephalothorax, length | 330 μm | — | — |
| Abdomen, length | 193 | 296 | 296 |
| Genital segment, length | 90 | 90 | 94 |
| Genital segment, width | 90 | 90 | 100 |
| CR, length | 73 | 96* | 76 |
| CR, width | 19 | 17* | 20* |
| Antennule, length | 220 | 215 | — |
| P4 enp2, length | 50 | 55 | 54 |
| P4 enp2, width | 24 | 24 | 23 |
| P4 enp2, outer terminal spine | 24 | 23 | 23 |
| P4 enp2, inner terminal spine | 40 | 40 | 36 |
| CR, setae: Lateral | 20 | 18 | 15 |
| Dorsal | 73 | 42 | 65 |
| Inner terminal | 55 | 48 | 50 |
| Inner median terminal | 275 | 300 | 280 |
| Outer median terminal | 173 | 180 | 165 |
| Outer terminal | 31 | 29 | 28 |

## Discussion

A. The synonymy of *Microcyclops ceibaensis* (Marsh) and *M. diversus* (Kiefer): Kiefer (1935) cited as diagnostic features of *M. diversus* the length/width ratios of the caudal ramus and of the endopod 2 of leg 4; the proportions of the terminal spines of the latter article; leg 5 with its "kleines, aber gut ausgeprägtes Dörnchen"; and the shape of the seminal receptacle. He also noted two horizontal rows of spinules on the connecting lamella of leg 4. As may be seen from Tables 1 and 2, the reported ranges of variation in total length and proportions of caudal rami and 4th legs for most characters of *M. diversus* are similar to those of *M. ceibaensis.* The proportions of leg 5, with its tiny spinule on the inner ventral margin, the spinules on the anterior surface of leg 4 endopod 2, and the two parallel rows of spinules on the anterior surface of the basal lamella of leg 4 are also features shared by both species. Kiefer later (1936) commented on several similarities between *M. diversus* and *M. ceibaënsis,* but since Marsh had provided neither exact measurements of *ceibaënsis,* the correct spinal formula nor a description of the connecting lamella of the 4th legs, Kiefer was unable to form a definite opinion as to the synonymy of these species.

A useful diagnostic character in many cyclopoid copepod genera is the shape of the seminal receptacle. Unfortunately Marsh (1919) was unable to see this feature in his material, and it is not visible on any of his specimens. However, the forms of the seminal receptacle reported for different populations of *M. diversus* vary so much (Figs. 12–16) that its value as a diagnostic character in this case is dubious. Fig. 17 shows the shape of the receptacle of a specimen from São Paulo, Brazil, ascribable to *M. ceibaensis.* Dussart and co-workers' reasons for considering *M. diversus* as distinct from *M. ceibaensis* appear to be the spine for-

Table 2.—Measurements of female specimensfrom different populations of *Microcyclops ceibaensis.* Abbreviations: CR, caudal ramus; P4, leg 4; enp2, second (terminal) article of endopod; L:W, ratio of length to width. *Indicates measurement made from author's figure.

| Record | Total length (mm) | CR L:W | P4 enp2 L:W | P4 enp2 Terminal spines inner : outer | P4 enp2 Length of enp2: inner term. spine |
|---|---|---|---|---|---|
| Honduras (1) | — | 3.8–5.6:1 | 2.0–2.35:1 | 1.56–1.73:1 | 1.25–1.50:1 |
| Uruguay (2) | 0.96–1.0 | 3.76–4.27:1 | 2.09–2.43:1 | 1.26–1.41:1 | 1.85–1.97:1 |
| Haiti (3) | 0.54–0.60 | 4.0:1 | 2.38:1 | 1.61–1.80:1 | 1.19–1.35:1 |
| Cuba (4) | 0.60–0.65 | about 5:1 | about 3:1 | 1.6:1* | 1.4:1* |
| Venezuela (5) | 0.88 | 4.5:1 | 2.2:1 | 1.4:1 | 1.9:1 |
| Brazil (6) | 0.92 | 5.2:1 | 2.97:1 | 1.44:1 | 1.44:1 |
| Brazil (7) | 0.75–0.76 | 3.62–3.72:1 | 2.21–2.31:1 | 1.52–1.58:1 | 1.43–1.75:1 |
| Costa Rica (8) | — | 3.4:1* | 2.0:1* | 1.8:1* | 1.2:1* |

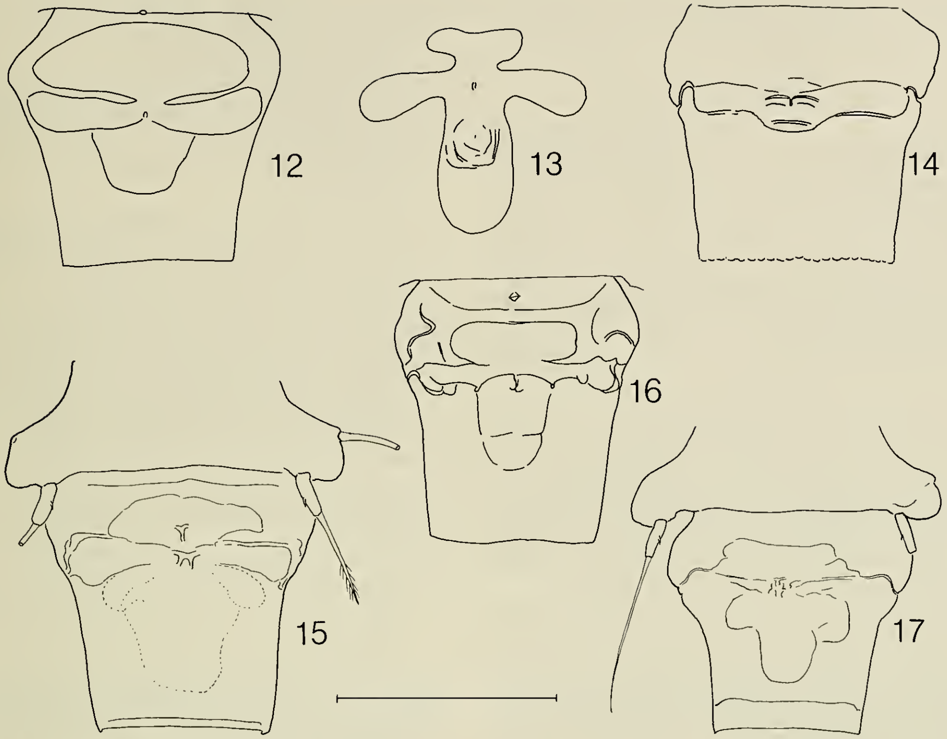
(1) Marsh (1919), measurements presented in this article; (2) Kiefer (1935); (3) Kiefer (1936); (4) Fernando and Smith (1978); (5) Dussart (1984) and specimen from Camaguan, Venezuela; (6) Herbst (1959); (7) 3 specimens from Rio Una do Prelado, State of São Paulo, lent by C. E. F. da Rocha; (8) Collado et al. (1984).

mulae, following Marsh's erroneous description; and the form of the seminal receptacle in specimens from geographically distant populations ascribed either to *M. diversus* (Dussart 1984) or to *M. ceibaensis* (Collado et al., 1984), though they state that the species are "difficult to separate" (Collado et al., 1984). Although the shape of the receptacle is not distinguishable in the present specimens, it is my opinion that the reported variability of this character in these forms is such as to diminish its taxonomic utility. *Microcyclops diversus* should be considered a synonym of *M. ceibaensis.*

*Microcyclops ceibaensis* as presently defined is at least a very variable species. Its records include freshwater ponds and lakes and one river in Brazil, Costa Rica, Cuba, Haiti, Honduras, Uruguay, and Venezuela. A record by Osorio Tafall (1941) from Lake Pátzcuaro, Mexico, is dubious, since no figures were furnished. Most records seem to be from the littoral zone. Löffler's (1958) characterization of *M. diversus* as a pelagic species in cold polymictic lakes seems based on Harding's record from the Peruvian plateau (Harding 1955); though this may not in fact be *M. ceibaensis,* as discussed below.

B. Notes on some South American records of *Microcyclops* spp.: Harding (1955) reported that specimens ascribed to *M. diversus* from Peru lacked a spine on the inner extension of basipod article 1 of leg 1. The neotropical species *M. anceps* (Richard, 1897), and its subspecies *M. anceps pauxensis* Herbst, 1962 (=*M. anceps minor* Dussart, 1984); *M. finitimus* Dussart, 1984, known from Venezuela and French Guiana (Dussart 1983); and *M. crassipes* (O. Sars, 1927) from South Africa have also been reported as lacking this spine. However, Harding's fig. 68 clearly shows two rows of spinules on the connecting lamella of the 4th leg, a diagnostic character shared by *M. ceibaensis* and *M. finitimus.* It is possible that Harding's specimens from Lakes Umayo and Arapá refer to the latter species.

Herbst (1959) described a *Cyclops* (*Microcyclops*) *varicans* from the State of São Paulo, Brazil, with two rows of spinules on the leg 4 lamella and leg 4 endopod article 2 2.82–3.24× longer than wide. *Microcyclops varicans* lacks the former character and the terminal article of leg 4 endopod is shorter (Dussart 1969; Gurney 1933). The placement of the inner spinule of leg 5 of Herbst's specimen "neben der langen Endborste" is similar to *varicans,* but Herbst's specimens are probably referable to *M. finitimus* or to *M. ceibaensis.*



Figs. 12–17. Seminal receptacles of *Microcyclops*: 12–13, *M. diversus,* Uruguay: 12, After Fig. 10 of Kiefer (1935); 13, After Fig. 13 of Kiefer (1935); 14, *M.* cf. *diversus* and *ceibaensis,* Haiti, after Fig. 68 of Kiefer (1936); 15, *M. diversus,* Camaguan, Venezuela, coll. 13 Oct. 1981, from specimen lent by Dr. B. H. Dussart; 16, *M. ceibaensis,* Costa Rica, after Fig. 28 of Collado et al. (1984); 17, *M. ceibaensis,* Rio Una do Prelado, State of São Paulo, Brazil, coll. 7 June 1984, from specimen lent by Dr. C. E. F. da Rocha. Scale = approximately 100 μm.

Herbst (1959) also described a *Cyclops* (*Microcyclops*) spec. from São Paulo with caudal rami 5.19× longer than wide, and remarked on the similarity of this form to *M. diversus.* In view of the reported variation of the length of the caudal ramus in *M. ceibaensis,* Herbst's specimen should be referred to this species.

C. The *Microcyclops varicans* Group in South and Central America: Several species of *Microcyclops* with a spinule at or near the midpoint of the inner surface of leg 5 have been recorded from South and Central America and some Caribbean islands. These include *M. varicans varicans* (Sars, 1863), *M. v. subaequalis* (Kiefer, 1928), *M. elongatus* (Lowndes, 1934), as well as *M. ceibaensis* and *M. finitimus.* As discussed above, *M. finitimus* lacks a spine at the inner corner of basipod 2 of leg 1 and should therefore be considered part of the *M. anceps* group (Dussart 1983, 1984). Both subspecies of *M. varicans* have a relatively short caudal ramus (3.5–4.5× longer than broad), and lack spinules on the connecting lamella of leg 4. *Microcyclops elongatus* is distinguished by its very long caudal rami (5–6× longer than broad); a row of spinules above the lateral seta of the caudal ramus, reaching to the midpoint of the dorsal and ventral surfaces of the ramus; and spinules on the anterior face of the terminal articles of the endopods of legs 2–4 borne on a "definite scale" (Lowndes 1934).

## Acknowledgments

I am grateful to Dr. Bernard H. Dussart for lending a specimen, and for providing a prepublication draft of the article by Collado et al.; to Dr. Carlos Eduardo F. da Rocha for lending specimens; and to Dr. Thomas E. Bowman for helpful comments on the manuscript.

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99(1), 1986, pp. 79–83

# A NEW GENUS AND SPECIES OF INTERSTITIAL SIGALIONIDAE AND A REPORT ON THE PRESENCE OF VENOM GLANDS IN SOME SCALE-WORM FAMILIES (ANNELIDA: POLYCHAETA)

Paul S. Wolf

*Abstract.*—*Metaxypsamma uebelackerae,* a new interstitial polychaete genus and species of the family Sigalionidae, is described from the northern Gulf of Mexico. *Metaxypsamma uebelackerae* differs from other known sigalionids in lacking notopodia and elytra, but these represent neotenic features coincident with an adaptation to an interstitial habitat. The similarities in the structure of the piercing-type jaws and associated venom glands of the Sigalionidae, Polynoidae, Polyodontidae, Pholoididae, and Pisionidae are discussed, and these are compared with two other scale-worm families, Eulepethidae and Aphroditidae, both of which lack piercing-type jaws and venom glands.

During 1975–1981, the U.S. Bureau of Land Management (now Minerals Management Service) funded several projects designed to characterize the fauna of the outer continental shelf along the northern Gulf of Mexico. In 1979, Barry A. Vittor & Associates, Inc., Mobile, Alabama, was funded by MMS to produce a taxonomic guide designed to standardize the identifications of polychaetes collected during these BLM projects (Uebelacker and Johnson 1984). *Metaxypsamma uebelackerae,* n. gen., n. sp., was discovered among the material examined during the preparation of a chapter to be included in this publication. At that time, *M. uebelackerae* was considered a potential new family (Wolf 1984). The species is described herein as a neotenic, interstitial member of the family Sigalionidae.

While examining *M. uebelackerae,* an internal canal was found in each jaw. This raised the question of why an internal canal was present except perhaps to channel a fluid in or out through the large fang. Larger sigalionids were then examined, and a large gland (colored white in preserved material) was found associated with each jaw. This is probably a venom gland. This has led to the inclusion here of a report of the presence of venom glands in families heretofore not known to have such glands.

## *Metaxypsamma,* new genus

Family B, Genus A, Wolf 1984:60-1.

*Type-species.*—*Metaxypsamma uebelackerae,* new species.

*Gender.*—Feminine.

*Diagnosis.*—Body slender, with up to 24 segments. Prostomium with single median antenna arising frontally, lateral antennae lacking. Two pairs eyes present. Peristomium or tentacular segment achaetous, with tentaculophores directed anteriorly, each bearing dorsal and ventral tentacular cirrus. Pair of smooth digitiform palps emerging ventral to tentaculophores. Elytra lacking but low, fleshy mounds, each bearing 2–4 long, slender, knobbed papillae, present on segments 2, 4, 5, 7, continuing on alternate segments. Parapodia uniramous, with single internal aciculum. Setae as compound falcigers with short, serrate, unidentate blades. Proboscis eversible, muscular, with 2 pairs of chitinous, piercing-type jaws and distal papillae; venom glands present, adhering to ventrolateral plates of each jaw.

*Etymology.*—The generic name is derived from the Greek *metaxy,* between, and *psammos,* sand, referring to the interstitial habitat of the type-species.

*Remarks.*—*Metaxypsamma uebelackerae* at first appears to differ considerably from other members of Sigalionidae since it lacks notopodia and, instead of elytra, it has paired mounds of papillae. Cazaux (1968:531–534) describes the larval nectochaete I and II stages of *Pholoe synophthalmica* Claparède, 1868. He shows the nectochaete I stage as lacking notopodia and, instead of elytra, there are paired mounds of papillae. The nectochaete II develops notopodia but still retains the mounds of papillae, which are very similar to those of *Metaxypsamma.* It is apparent then, that *Metaxypsamma uebelackerae* is a neotenic sigalionid.

Among adult sigalionids, *Metaxypsamma* is most similar to *Pholoe* in lacking lateral antennae, in having an achaetous tentacular segment, in being of rather small size with few segments, in lacking branchiae, in having compound falcigers with short nonarticulate blades, and in lacking compound spinigers.

*Metaxypsamma uebelackerae,* new species
Fig. 1

Family B, Genus A, Wolf 1984:60-3, figs. 60-1, 60-2a–e.

*Material examined.*—FLORIDA: SOFLA Sta 5A, 26°45.70′N, 84°00.13′W, coarse sand, 91 m, Aug 1981, 3 paratypes, including 1 female (USNM 86845).—SOFLA Sta 5G, same location and date, 3 paratypes (USNM 86844).—MAFLA Sta 2426G, 28°57′59.4″N, 85°23′00.2″W, fine sand, 82 m, Feb 1978, 1 specimen, 1 slide (USNM 89582).—Sta 2748, 27°37.2′N, 83°53.5′W, coarse sand, 50 m, Jul 1978, Holotype, female (USNM 86846).—Sta 2958J, 25°40′N, 83°50′W, medium fine sand, 120 m, Feb 1977, 1 specimen.—Sta 2958I, same location, Aug 1977, 1 female.—Sta 2959H, 25°40′N, 83°05′W, silty-very fine sand, 60 m, Aug 1977, paratype, ripe male (USNM 97801).

*Description.*—Length to 2.5 mm, width to 0.5 mm, including parapodia, to 0.24 mm, excluding parapodia. Complete specimens with 21–24 segments. Segmentation distinct although intersegmental furrow present only on every other segment beginning at posterior margin of segment 9 and continuing to anterior margin of pygidium (Fig. 1a, c).

Prostomium bilobed with median antenna arising terminally between lobes (Fig. 1a); 2 pairs of eyes arranged trapezoidally; palps smooth, digitiform, emerging beneath prostomium; tentaculophores directed anteriorly, without setae or acicula, with dorsal and ventral tentacular cirrus, similar to median antenna in size and shape. Facial tubercle lacking.

Dorsum without elytra but with paired fleshy mounds bearing long, filiform papillae located above parapodia of segments 2, 4, 5, 7 and alternate segments thereafter (Fig. 1a, b). Anterior 5–6 mounds each with 2 papillae, following ones with 3–4 papillae.

Beginning on segment 2, ventrum with 2 pairs of globular papillae per segment on either side of midline just posterior to parapodia; beginning on segment 9, alternate segments with additional midventral papilla (Fig. 1c).

Ventral (buccal) cirri of segment 2 twice as long as following ventral cirri. Parapodia uniramous, highly contractile, each supported by single, pointed aciculum; parapodial stylodes and papillae lacking (Fig. 1a, b). Setae compound, unidentate falcigers only, about 6–7 per parapodium, 2 above aciculum in single row, 4–5 below aciculum in 2 rows. Falciger blades with minute teeth along concave margin; blades of anterior segments somewhat longer than those of following segments and with shorter marginal teeth (Fig. 1d, e).

Pygidium with 2 pairs of filiform anal cir-

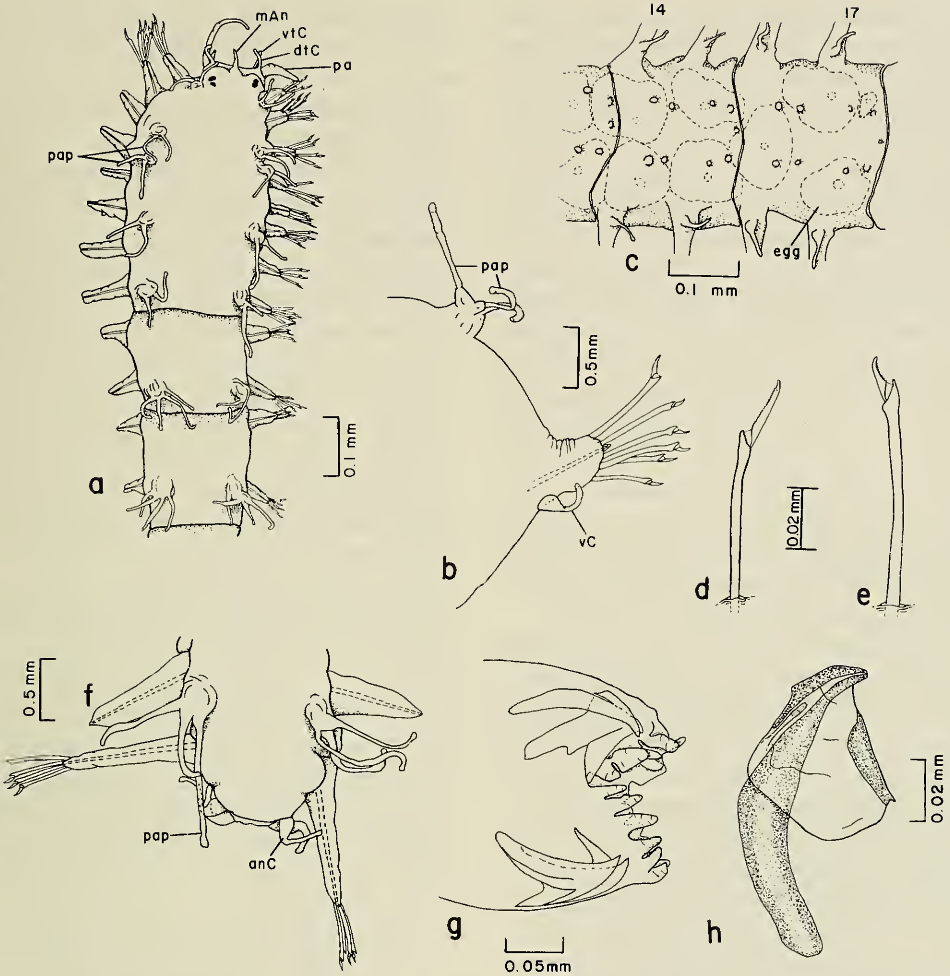

Fig. 1. *Metaxypsamma uebelackerae*: a, Anterior end, dorsal view; b, Parapodium from segment 9, posterior view; c, Segments 14–17, ventral view; d, Neuroseta from segment 2; e, Neuroseta from segment 9; f, Posterior end, dorsal view; g, Distal end of dissected proboscis, lateral view; h, Dorsal left jaw, inside lateral view. anC, anal cirrus; dtC, dorsal tentacular cirrus; mAn, median antenna; pa, palp; pap, papilla; vC, ventral tentacular cirrus (Figs. a, b, d–f from Wolf, 1984:Figure 60-2a–e).

ri located lateral to terminal anus; cirri about half as long as dorsal papillae (Fig. 1f).

Proboscis eversible, muscular, with 2 pairs of chitinous, piercing-type jaws and distal circle of 9 pairs of papillae (Fig. 1g). Each jaw with a broad plate located ventrolateral to long stem, with internal canal extending to tip of large tooth (Fig. 1h). Venom gland not observed.

*Remarks.*—Three mature females, including the holotype, were collected. The diameter of the largest egg was about 128 μm. About 30 eggs were present in the holotype from segment 9 to the pygidium (Fig. 1c). One ripe male contained large amounts of sperm from setiger 10 to the end of the body.

A peculiar phenomenon was noted for *M. uebelackerae,* namely the presence of intersegmental furrows on alternate segments beginning on the posterior margin of segment 9 (Fig. 1a, c). Coincident with this alternate arrangement of the furrows is the arrangement of the midventral papilla and the paired mounds of papillae dorsally. I then examined several undescribed species of *Pholoe* and found the intersegmental furrows on alternate segments, also, except that beginning on segment 23 the furrows are found on every segment. Segment 23 is also where elytra appear on every segment. I also examined larger sigalionids (*Sthenelais* sp. and *Psammolyce ctenidophora*) and found the intersegmental furrows on every segment even in the region where elytra are present on alternate segments. This arrangement was also observed in *Pholoides bermudensis* (Pholoididae), two species of *Pisione* (Pisionidae), and several species of Polynoidae and Polyodontidae. In *Pholoides bermudensis,* however, the furrows are faint along the entire body.

The significance of the segmental arrangement of the furrows is not possible to assess here, since histological sectioning would be necessary to determine whether or not what appears externally to be reduced segmentation is actually the case internally. Such resources were not available to the author.

The morphological adaptations of *M. uebelackerae* afford an interesting comparison with *Pholoe swedmarki* Laubier (1975: 671–678), an interstitial sigalionid from Bermuda. *Pholoe swedmarki* has notopodia, but they are reduced with few notosetae, whereas *M. uebelackerae* has lost its notopodia completely. *Pholoe swedmarki* has retained its elytra; *M. uebelackerae* has replaced them with paired mounds each bearing long, flexible papillae. Both species have somewhat reduced tentacular cirri. In *P. swedmarki* the dorsal tentacular cirri are longer than the median antenna and the ventral cirri are much smaller and of a different shape than the dorsal ones. In *M. uebelackerae,* the dorsal and ventral tentacular cirri are similar to each other and to the median antenna in size and shape. *Pholoe swedmarki* has up to 27 segments; *M. uebelackerae* has up to 24. *Pholoe swedmarki* measures up to 1.6 mm by 0.4 mm while *M. uebelackerae* measures up to 2.5 mm by 0.5 mm.

Both species are considered to be interstitial worms, but the neotenic *M. uebelackerae* exhibits the more derived conditions, i.e., the loss of elytra, loss of notopodia, and reduction in the number of segments, even though it is a slightly larger species. It is body width, however, that determines the minimum diameter of the interstitial space an animal may inhabit (Westheide 1984:265). It is suggested here that *M. uebelackerae* has, through the loss of elytra, gained a functionally narrower body width than *P. swedmarki.* This could enable the former to invade smaller interstitial spaces than the latter.

*Etymology.*—The species is named in honor of Ms. Joan Uebelacker who, as senior editor of "Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico" (Uebelacker and Johnson 1984), edited every chapter and, therefore, is largely responsible for the success of those volumes. Her editorial and scientific efforts are gratefully acknowledged and deeply appreciated.

*Distribution.*—Gulf of Mexico, off Florida, 50–120 meters.

## Observations on Scale-worm Jaws and Venom Glands

The jaws of three other sigalionids, *Sthenelais* sp., *Psammolyce ctenidophora, Pholoe* sp., and *Ehlersileanira incisa* were also examined. In all these specimens, the basic structure and appearance of the jaws were the same including the presence of an internal canal and a large, white, spongy, glandular mass of tissue adhering to the dorsal side of the large, ventrolateral plate of each jaw. This glandular mass leads into the internal canal within the fang of the jaw. This white mass is here interpreted to be a venom gland. A venom gland could not be found in *Metaxypsamma uebelackerae,* perhaps because of its minute size, but its presence is suggested by what appears to be a small duct and a volume of cellular material within the internal canal of each jaw.

The jaws of other scale-worm families were also examined: Polyodontidae (*Polyodontes lupinus* and *Eupanthalis tubifex*), Polynoidae (*Lepidasthenia* sp.), Pholoididae (*Pholoides bermudensis*), Eulepethidae (*Grubeulepis* sp.), and Aphroditidae (*Aphrodita* sp.). The polynoid and pholoidid jaws are very similar in shape to that of the sigalionids and have venom glands associated with their jaws.

The polyodontid jaw differs in that its ventrolateral plate is fused to the concave margin of the main fang, and this plate is dentate along its outer edge. These jaws have a venom gland adhering to the dorsal side of the plate, but it appears smaller and less developed relative to the large size of the animal and its jaws, as compared to the large gland found in the Sigalionidae, Polynoidae, and Pholoididae.

The Eulepethidae and Aphroditidae do not possess piercing-type jaws. Their jaws consist of broad, chitinous plates which do not have any associated venom glands.

The jaws of the Pisionidae (*Pisione* sp.) were also examined and found to be remarkably similar to the sigalionid jaw. A venom gland, located as in the sigalionids, leads into an internal canal that extends to the tip of the fang.

If the above described glands do indeed produce venom, the question remains as to how the venom is released. Glycerids, according to Gibbs and Bryan (1980:205), release venom through a series of lateral pores located on the main fang of the jaw. No such pores were found associated with the jaws of the scale-worms examined. The internal canal does extend to the very tip of the main fang, but there did not appear to be an open pore at the tip.

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# *GLOSSOTHELEPUS,* A NEW GENUS OF THELEPINAE (POLYCHAETA: TEREBELLIDAE) FROM THE GULF OF CALIFORNIA, MEXICO

P. A. Hutchings and C. J. Glasby

*Abstract.*—A new genus of Thelepinae, *Glossothelepus,* is described from deep water off Mexico, with the type species *G. mexicanus,* n. sp. The genus is closely related to *Decathelepus* Hutchings and *Rhinothelepus* Hutchings from Australia, and *Telothelepus* Day from South Africa.

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While examining material in the collections of the Allan Hancock Foundation, an undescribed genus was found. Dr. Kristian Fauchald had already separated this material, recognizing it as a new genus. We are thankful to Dr. Fauchald for allowing us to describe the new genus, which extends the distribution of those genera of Thelepinae with expanded tentacular lobes.

## *Glossothelepus,* new genus

*Diagnosis.*—Expanded tentacular lobe with numerous buccal tentacles; dorsal buccal lobe T-shaped, and thickened. Numerous sessile simple branchial filaments on segments 2 and 3. Notopodia from segment 3, continuing for at least 23 segments. Notosetae smooth-tipped, narrow-winged, broad-bladed capillaries. Neurosetae from setiger 7, arranged in single rows, avicular.

*Type species.*—*Glossothelepus mexicanus.*

*Etymology.*—The generic name is a combination of the Greek 'glossos,' a tongue, and 'thelepus' and refers to the expanded glandular tentacular lobe.

## *Glossothelepus mexicanus,* new species
Fig. 1

*Holotype.*—AHF Poly 1449, posteriorly incomplete, 10 mm length, 1.2 mm maximum width, 23 setigers, Sta P51–59 (N15136-F3205): 25°31′5″N, 109°31′5″W; 9 fms. Paratypes: 1 spec. USNM 98572 posteriorly incomplete, 15 mm length, 2.5 mm maximum width, 20 setigers, Sta 496-36 (F3115): 23°21′55″N, 109°24′40″W: 80 fms, mud; 1 spec. AM W 199659 posteriorly incomplete, 20 mm length, 2 mm maximum width, 20 setigers, Sta 1732-49 (F3101): 23°24′45″N, 109°23′50″W to 23°24′30″N, 109°24′00″W; 50 fms; sand and mud. All material from Fraile Bay, Gulf of California, Mexico.

*Description.*—Body pale yellow, stout, with long golden setae. Prostomium with expanded tentacular lobe with convoluted margins, dorsally T-shaped, thickened, almost papillate, from which some tentacles arising (Fig. 1a); ventrally forming elongate upper lip (Fig. 1b). Large numbers of grooved buccal tentacles of 2 types; few, thick, slightly bulbous ones resembling those found in Polycirrinae, and more numerous thin ones. Eye spots absent.

Ventrum of peristomium thickened, slightly ridged, with maximum width in anterior-posterior axis, forming discrete glandular pad. Segment 2 wedge-shaped laterally, connected ventrally by very narrow strip, almost completely hidden by peristomium and thickened ridge of segment 3. Anterior lateral margins of segments 2 and 3 slightly thickened, glandular, but not forming discrete lateral folds. Ventrum of setigerous segments 1–8 slightly more glandular than subsequent segments, also slight-

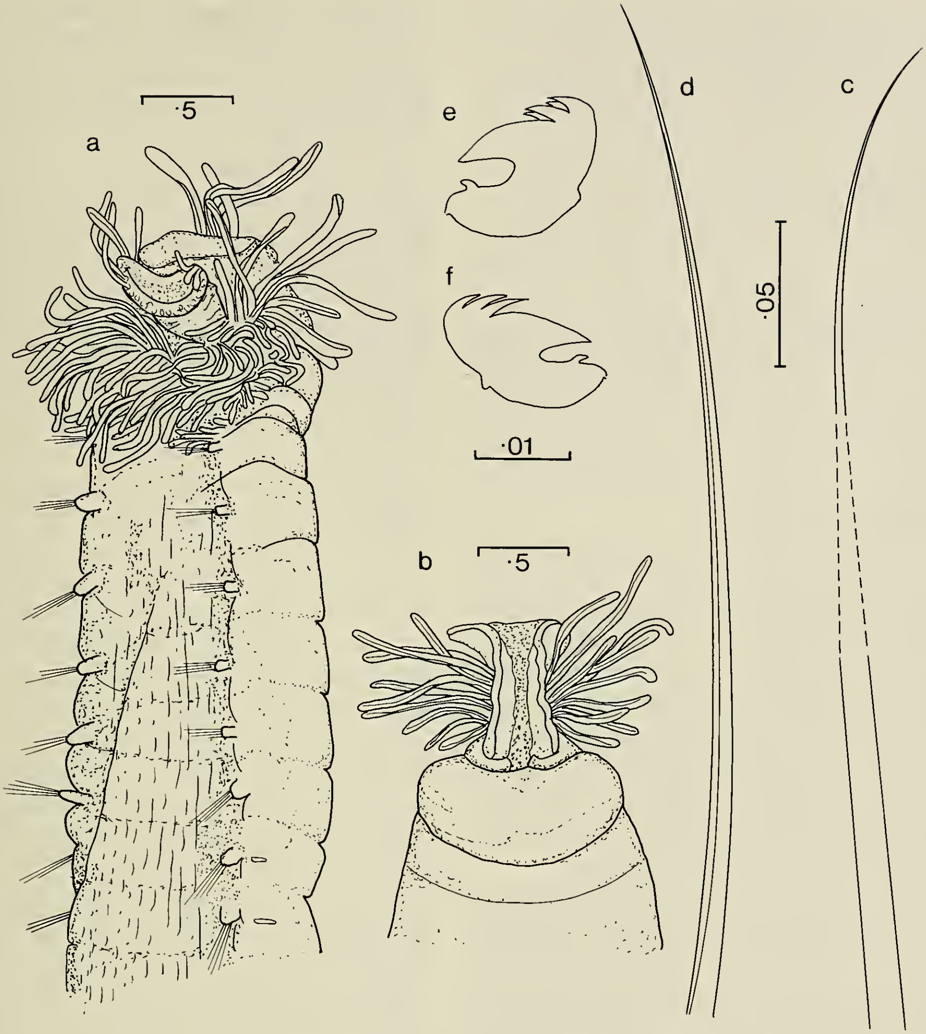

Fig. 1. *Glossothelepus mexicanus*: a, Holotype, head end, dorsolateral view; b, Head end, ventral view; c, d, Paratype (AM) long and short notosetae respectively; e, f, Paratype (AM), uncini from setiger 8 and setiger 19, respectively. Scales in mm.

ly granular in appearance. Thin medial ventral glandular stripe occurring along rest of body; stripe segmented, each segment having an additional intrasegmental fissure. Segmentation becoming more distinct posteriorly. Dorsum appearing slightly reticulate, especially anteriorly.

Branchiae consisting of numerous sessile filaments on segments 2 and 3. Each branchia consisting of laterally arranged group of sessile filaments with distinct medial gap. Segment 2 with approximately 20 filaments on each side arranged on arc-shaped thickened ridge, more laterally arranged than those on segment 3. Segment 3 with about 15 filaments on each side.

Notosetae from segment 3, continuing for at least 23 segments. First pair of notosetae inserted at angle, in contrast to others. Notopodia elongate, flattened, rectangular podia with setae arranged longitudinally. Notosetae golden, long, arranged in 2 tiers, short broad-bladed, narrow-winged capillaries and longer wingless capillaries, both with fine tips (Fig. 1c, d). Tips of setae under high magnification appearing slightly fuzzy.

Neurosetae from setiger 7, uncini arranged in single rows on long tori, on slightly raised glandular strip extending across body to medial ventral groove; uncini only occurring along part of ridge. Posteriorly uncinial tori becoming slightly elevated. Uncini minute, avicular with strongly crested head; dental formula MF: 6–10:∞, with teeth arranged in 2 arcs above main fang; hooked dorsal button and rounded prow consistent throughout (Fig. 1e, f).

*Variation.*—The two paratypes exhibit slight variations from the holotype. The paratype lodged in the Australian Museum is in poor condition but is lightly pigmented like the holotype, whereas the USNM paratype is very darkly pigmented, with setigers 1–3 having even darker pigmentation across the ventrum. This paratype exhibits marked lateral expansion from setigers 5–7, the body then resumes original width, which is far more marked than in the holotype.

*Discussion.*—Within the subfamily Thelepinae to which this species clearly belongs, because of its sessile, simple branchial filaments, avicular uncini arranged in single rows throughout and the characteristically Thelepinae like uncini, the setiger on which the noto- and neurosetae begin is considered to be an important generic character (Hutchings and Glasby in press). No existing described genus in the subfamily has notosetae beginning on segment 3 and neurosetae on setiger 7, and for this reason, this species is described in the new genus *Glossothelepus.* Within the Thelepinae, at least two distinct groups can be recognised, one group of genera with a compact prostomium, the other group with an expanded tentacular lobe. *Glossothelepus* clearly belongs to this latter group, which also includes *Telothelepus* Day, 1955, *Rhinothelepus* Hutchings, 1974, and *Decathelepus* Hutchings, 1977. Currently, *Glossothelepus, Telothelepus,* and *Decathelepus* are monospecific genera, and *Rhinothelepus* is represented by two species. All these genera except *Glossothelepus* are currently only known from shallow intertidal areas. With the discovery of *Glossothelepus* from deep water off Mexico, the geographical distribution of these apparently closely related genera is expanded from South Africa (*Telothelepus*) and Australia (*Rhinothelepus* and *Decathelepus*) to Mexico. One may speculate that the development of an expanded tentacular lobe is an advanced character in the Thelepinae and these four genera are closely related to each other, and that additional deep-water related genera may occur in the South Pacific and Indian Ocean. An alternative hypothesis is that these genera with an expanded tentacular lobe have risen independently several times from the parent stock of Thelepinae. This seems unlikely, as *Glossothelepus* very closely resembles *Rhinothelepus* and *Decathelepus* in all major body characteristics except for the setiger on which the uncini begin. One may further speculate on the evolutionary significance of uncini beginning on setiger 6 in *Rhinothelepus,* setiger 10 in *Decathelepus* and on the first abdominal segment in *Telothelepus,* and on setiger 7 in *Glossothelepus.* It would be very interesting to observe the feeding behavior in these genera, since presumably the uncini are used to retain the animal in its burrow.

*Etymology.*—The name given by Dr. Fauchald has been retained and refers to the geographical location where the animal was collected.

*Habitat.*—Deep water, in sand and muddy substrata.

*Distribution.*—Gulf of California, Mexico.

## Acknowledgments

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# NEW RECORDS OF *MIMILAMBRUS WILEYI* WILLIAMS, 1979 (CRUSTACEA: DECAPODA: BRACHYURA), WITH NOTES ON THE SYSTEMATICS OF THE MIMILAMBRIDAE WILLIAMS, 1979, AND PARTHENOPIDAE MACLEAY, 1838, SENSU GUINOT, 1978

Peter K. L. Ng and Gilberto Rodríguez

*Abstract.*—The family Mimilambridae was established by Williams (1979) to receive his new species *Mimilambrus wileyi.* The species is herein reported from several localities in Venezuela. The characters of *Mimilambrus* fit well within the definition of the subfamily Parthenopinae, family Parthenopidae MacLeay, 1838 (sensu Balss 1957) (equivalent to Guinot's (1978) Parthenopoidea). There is agreement in many morphological details, such as in the ventral spines, fingers and dentition of the chelipeds, and the form of the second male pleopod. Some characters like the ischio-meral articulation of the chelipeds and the articulation of segments 3 to 5 of the male abdomen, show a primitive condition. A comparison of the structures associated with respiration shows that the peculiar arrangement of afferent and efferent channels in *Mimilambrus* is merely a continuation of a trend already found in the more typical parthenopids. Placing this genus in a family of its own is thus unwarranted, and it should instead be included as a rather specialized genus with the rest of the parthenopids in the superfamily Parthenopoidea MacLeay, 1838, sensu Guinot, 1978.

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*Mimilambrus wileyi* Williams, 1979, was described from two males and one female collected at Tobago, West Indies, and was placed by Williams in a new monotypic family, Mimilambridae, close to the family Parthenopidae MacLeay, 1838, sensu Balss, 1957. Guinot (1977a, 1978a, b, 1979), in her revision of Brachyuran classification, elevated the Parthenopidae to superfamily status. Bowman and Abele (1982) subsequently elevated the Mimilambridae to its own superfamily, Mimilambroidea, probably in accordance with the superfamilial method of classification proposed by Guinot (1977a, b, 1978a).

Williams (1979) suggested that his new family was intermediate between the traditional "oxyrhynchan" families Majidae and Parthenopidae (sensu Balss 1957), and the traditional "oxystomatan" families Leucosiidae and Calappidae. The current evidence, however, suggests that both the Oxystomata and Oxyrhyncha, are in fact heterogeneous groups, and not 'good' taxa (Guinot 1977a, 1978a, b, 1979; Stevcić and Gore 1980). Within this context, a reexamination of the family Mimilambridae is of particular interest.

During the study of samples taken on the Venezuelan coast, several specimens of *Mimilambrus wileyi* were collected. Opportunity was taken to evaluate the characters used by Williams (1979) to differentiate his new family from the Parthenopidae sensu Balss, 1957. To this end, we have examined four American parthenopoids: *Parthenope agona* (Stimpson, 1871), *Platylambrus serratus* (H. Milne Edwards, 1834), *Leiolam-*

*brus nitidus* (Rathbun, 1901) and *Heterocrypta tomasii* da Costa, 1959; and five Indo-Pacific ones: *Daira perlata* (Herbst, 1790), *Daldorfia horrida* (Linnaeus, 1758), *Cryptopodia fornicata* (Fabricius, 1781), *Rhinolambrus longispinis* (Miers, 1879), and *Platylambrus echinatus* (Herbst, 1790). We have also used morphological data available in the literature whenever appropriate. The systematics of the Parthenopoidea sensu Guinot, 1978a, b, are also briefly discussed in relation to several other characters. The material cited is deposited in the reference collection of the Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, and the Zoological Reference Collection (ZRC) of the Department of Zoology, National University of Singapore.

### *Mimilambrus wileyi* Williams, 1979

*Mimilambrus wileyi* Williams, 1979:400, Figs. 1–5.

*Parthenope* sp., Rodríguez, 1980:294, Fig. 70, Pl. 31A.

*Material.*—Punta Arenas de Pariche, Golfo de Cariaco, 10°32′N, 64°12′W, 12 Jul 1959; Luis R. Salazar: 1 male, cl. 26.3 mm, cb. 28.6 mm, exploratory fishing with shore net, shallow water (IVIC).—Between Margarita Island and the Venezuelan mainland, 8 km west of Isla Coche, 10°46′N, 62°50′W: 1 male, cl. 14.8 mm, cb. 16.2 mm, 9 fathoms (IVIC).—Paraguaná Península, north of Punto Fijo, 11°40′N, 70°10′W, 4 Mar 1982, G. Kremer & M. Bevilacqua: 1 male, cl. 29.7 mm, cb. 33.7 mm, 1 ovigerous, 1 spent female, cl. 25.6 and 30.5 mm, cb. 28.1 and 32.0 mm, respectively, between 10 and 17 fathoms (IVIC). (cb. measured at base of postero-lateral spines in all cases.)

### Discussion

Our material agrees closely with Williams' (1979) original description. The eggs of our ovigerous female have a mean diameter of 0.32 mm (n = 15, largest 0.34, smallest 0.31 mm). The present records extend the range of the species to the north coast of South America and show that it is not an uncommon species.

The superfamily Parthenopoidea (essentially the Parthenopidae of Balss (1957) with the exclusion of the Eumedoninae Miers, 1879) has been subjected to considerable scrutiny recently. Their origins are poorly understood, and they appeared rather suddenly in the Middle Eocene (Glaessner 1969), some 45 million years ago. Most classifications have included them in the Oxyrhyncha, for they, like the majids and hymenosomatids, "have a general elongate-triangular, narrow fronted carapace and incomplete orbits which contrast strongly with the rest of the brachygnathous crabs" (Rice 1980:311). Acceptance of this systematic arrangement, however, is not unanimous. Flipse (1930) for instance, thought that the parthenopids were transitional between the Oxyrhyncha and the Cyclometopa. Guinot (1977a, b, 1978a, b), in her comprehensive review of Brachyuran systematics, dismantled the Oxyrhyncha, and elevated the Parthenopidae MacLeay, 1838, to their own superfamily, with the exclusion of the subfamily Eumendoninae Miers, 1879. Otherwise, they were essentially the Parthenopinae of Alcock (1895), Rathbun (1925), and Balss (1957). She recognized four groups within the Parthenopoidea: 1, With only the thoracic sternal sutures 4/5 and 5/6 interrupted and having the III B type of endophragmal skeleton (e.g., *Daldorfia* Rathbun, 1904). 2, With all the thoracic sternal sutures interrupted and having the III C type of endophragmal skeleton (e.g., *Parthenope* Weber, 1795). 3, Containing the genera *Daira* de Haan, 1833, and *Dairoides* Stebbing, 1920 (=*Asterolambrus* Sakai, 1938). 4, Containing the 'Parthénoxystomien' group (Guinot 1967a, 1978b), with the genera *Aethra* Leach, 1816, *Hepatus* Latreille, 1802, *Hepatella* Smith, 1869, *Osachila* Stimpson, 1871, and *Actaemorpha* Miers, 1878 (sensu Guinot 1967a, 1978b).

A new genus, *Sakaila* Manning & Holthuis, 1981, was subsequently included in Guinot's "Parthénoxystomien" group. Although she did not designate these groups as separate families, it may prove worthwhile to recognize each of these four groups as such, i.e., the families Daldorfidae, Parthenopidae s. s., Dairidae, and Aethridae respectively. All further references to these families in this paper will be used as defined above.

Guinot (1967b, 1977a, 1979) has also provided indications that the parthenopoids may have evolved from some xanthoid-like stock. In fact, the genera *Daira* and *Dairoides* are almost perfect intermediates for linking the xanthoids with the Daldorfidae and Parthenopidae s. s. The larval characters also suggest that the parthenopoids evolved from some xanthoid stock via the more primitive portunoid families (sensu Guinot 1978a, b) (Rice 1980, 1983) or that both the parthenopoids and portunoids evolved from the same xanthoid stock (Ng 1983).

The subfamily Eumedoninae Miers, 1879, formerly placed in the family Parthenopidae sensu Balss, 1957, is almost certainly not closely affiliated with the true parthenopoids, but is probably closer to the Xanthoidea (Serène, Tran, and Nguyen 1958), and may be related to (Serène 1968) or part of the Pilumnidae Samuelle, 1819, sensu Guinot, 1978 (Ng 1983). Recent work on the larvae of the eumedonine *Echinoechus pentagonus* (A. Milne Edwards, 1878) lends support to Ng's (1983) suggestion that the Eumedoninae be removed from the Parthenopoidea and affiliated with the Pilumnidae instead.

The family Parthenopidae s. s. forms a sharply defined and presumably monophyletic group, well characterized by the shape of the carapace and chelipeds. *Mimilambrus wileyi* shares with this family the following characters: heterotrematous gonopore arrangement (Guinot 1977a, b, 1978b, 1979; Saint Laurent 1980), carapace with frontal region narrow (the general outline is semicircular in *Mimilambrus* and several other genera, but more usually triangularly elongate or pentagonal), orbits distinct and complete, cardiac and gastric regions so deeply marked off as to make the dorsal surface of the carapace trilobed, pseudorostrum (sensu Stevcić and Gore 1980) simple (obscurely trilobed in *Mimilambrus* and some other species), second article of antennae small, short, not fused with the epistome or front, palp of the third maxilliped articulated at the antero-internal angle of the merus, chelipeds vastly longer and more massive than the ambulatory legs, and the second male pleopods relatively short.

Several characters that have been regarded as characteristic of the Mimilambridae are also not as definitive as they may initially appear. Williams (1979) gives diagnostic generic value to the articulation of segments 3 to 5 of the male abdomen. These segments do show a rather primitive condition in *Mimilambrus* since the articulation, although ankylosed, is still present as a thin line. In all parthenopoids, segments 3 to 5 are ankylosed (Flipse 1930; Ng 1983), but there is some variability as to whether the sutures are still distinct or not. In *Parthenope agona,* the sutures are still visible near the midline of the abdomen, while in *Platylambrus serratus,* they are completely absent. In the supposedly primitive *Daira* and *Dairoides,* the sutures are still relatively distinct. Whether the segments 3 to 5 are ankylosed or free is itself an important clue to the cohesiveness of the taxa, and also provides valuable information about their affinities. The ankylosed segments in all the members of the Parthenopoidea as recognized by Guinot (1978a, b) (including *Mimilambrus*) not only lends support to the exclusion of the Eumedoninae, in which all the segments are free, but also suggests that the parthenopoids have close phylogenetic links with the Portunoidea (sensu Guinot 1978a, b), as well as the more primitive xanthoids, like the Carpiliidae Ortmann,

1893. This relationship has in fact, already been suggested through the studies of their larvae (Rice 1980, 1983; Ng 1983). Williams (1979) also regards the first male pleopod as characteristic, but although it is certainly unusual, it could have been easily derived from ancestral parthenopid structures. In fact, *Cryptopodia concava* Stimpson, 1871 (Gore and Scotto 1979) and *Pseudolambrus triangula* (Stimpson, 1860) (Garth 1958) have very similar appendages, but their long subterminal spines are less well developed and the lateral hairs are still abundant.

The most important character that differentiates *Mimilambrus wileyi* from most Parthenopidae is probably the position and structure of the afferent channels which are located inside the buccal cavity, and the efferent channels, which are fused and discharge at the anteromedial part of the endostome. As a consequence of the reorganization of these respiratory channels, the exognath of the third maxilliped is completely concealed behind the endognath, and the anterior part of the carapace is narrow and spoutlike, implanted at a sharper angle in relation to the upper surface of the carapace. In this respect it resembles the frontal areas of some Leucosiidae which have similarly structured respiratory channels. The structure of the mouthparts is clearly an adaptation to a fossorial or semi-fossorial mode of life.

Burrowing activities differ greatly in various groups of crabs. The majids usually do not burrow into the substrate, whereas many catometopans tend to form permanent burrows in the sand. In contrast, many species of the traditional oxystomatan families Leucosiidae and Calappidae and many cyclometopans which inhabit sandy or gravelly substrata have burrowing habits. Their burrows, however, are never permanent channels in the sand but merely temporary excavations. Each of these different habits is associated with different morphological traits. In parthenopids, the crab is actually embedded in the sand (Schäfer 1950). The chelipeds are flexed to the underside of the anterolateral regions, with the fingers, which are flat and bend downwards and inwards, fitting closely at each side of the buccal cavity. The internal surfaces of the chelipeds are channeled and glossy. There is thus produced on each side of the crab, between the chelipeds and carapace, a ventral channel which communicates with the afferent aperture located at the base of the chelipeds. Since the back of the crab is covered with sand, the teeth on the internal margins of the merus of the cheliped, and those of the anterior part of the carapace, act as a coarse sieve placed at the orifice of these accessory channels.

In the most generalized condition, only these "exostegal channels" (Garstang 1897a, b) exist, and there are no accessory ridges or other structures on the pterygostomial regions to act as afferent channels. This condition is found in the genus *Cryptopodia* H. Milne Edwards, 1834 (A. Milne Edwards 1878, pl. 29, fig. 1a, 2a). In many parthenopids, there are usually ridges that delimit the afferent channels. In *Platylambrus serratus* for instance, there is a sinuous, crenulate ridge that runs transversely across the pterygostomial and distal subbranchial regions. In its distal part this ridge is provided with long hairs, which together with similar hairs on the anterior border of the coxa, basis and ischiomerus and third maxilliped, form a funnel-like entrance to the afferent aperture at the base of the cheliped. In *Heterocrypta,* there is a submarginal ridge that, starting at the suborbital region, runs parallel to the margin, and forms with it a channel that is lined with hairs. This channel is joined by a second channel that runs perpendicularly to the first, and ends at the base of the chelipeds. In *Heterocrypta tommasii,* the channels communicate with the upper surfaces of the carapace through an hepatic notch located at the junction of the two channels.

In *Solenolambrus* Stimpson, 1871 (Rathbun 1925), *Mesorhoea* Stimpson, 1871 (A. Milne Edwards 1878, pl. 29, fig. 5a, 6a) and *Aulacolambrus* Paulson, 1875 (Flipse 1930), there is on each pterygostomial region, a sharp, elevated and crenulate crest that runs from the antero-external angle of the buccal area to the base of the chelipeds, separating the concave pterygostomial region from the subhepatic region, which is also concave and channellike. When retracted, the extremity of the hands of the chelipeds covers the pterygostomial regions, forming the afferent passages. In the very rare genus *Tutankhamen* Rathbun, 1925, there are ridges similar to those of *Solenolambrus,* which extend from the antero-external angle of the buccal area to the base of the chelipeds, but the structure is more complex because the channels are shorter and deeper, bordered by a laminar expansion of the hepatic and anterior branchial margin above, and by a parallel lamina having an emargination near the beginning of the branchial region below (A. Milne Edwards 1878).

In *Leiolambrus* A. Milne Edwards, 1878, the exognath of the third maxilliped is partly concealed behind the endognath; the merus and ischium of the endognath are bordered by long, arched hairs which form with the hairs on the pterygostomial region, a ventral covering to the afferent channels. *Mimilambrus* has a similar arrangement, but the exognath is completely concealed beneath the endognath, and the pterygostomial ridge is more prominent, particularly in its distal part.

The efferent channels show a similar tendency towards a rearrangement within the buccal cavity. In *Aethra* Leach, 1816 (Guinot 1967a) and some parthenopids, the efferent channels are located on each side of the buccal frame, forming with the margin of the first maxilliped two separate sinuses. In *Parthenope agona, Platylambrus serratus, Leiolambrus nitidus,* and *Heterocrypta tommasii,* the anterior endostomial crests are sinuous, forming two adjacent openings that are separated by a medial endostomial septum, but in fact discharging near the midline of the concave epistome. A last step in what Guinot (1966:747) has called "la tendence des Parthenopidae vers le type oxystomien" is seen in *Mesorhoea,* with "the two efferent channels meeting at the middle of the endostome, which has there a triangular projection, and a deep notch in its vertical, laminiform wall" (Rathbun 1925: 546). In *Mimilambrus,* a similar arrangement is found. The efferent respiratory channels empty through a common anterior median opening, into the concave epistome, which also has a ciliated notch.

Williams (1979) has noted that the last pair of ambulatory legs of *Mimilambrus* is similar in shape to that of the calappid *Acanthocarpus alexandri* Stimpson, 1871, and its structure suggests that *Mimilambrus* is probably a more active burrower than most of the other parthenopids (with the possible exception of *Mesorhoea*). Its more fossorial habits could easily explain why its mouthparts have evolved convergently with the leucosiids and calappids, which spend their daylight hours almost completely buried in sand or silt.

Stevcić and Gore (1980), in summarizing the known characters of the Parthenopidae and Mimilambridae, also noted that whereas the Parthenopidae have antennules folding slightly obliquely, *Mimilambrus* has them folding almost vertically. The folding of the antennule, however, appears to be a very variable character in the Parthenopidae, and appears to be dependent on the width of the pseudorostrum. In *Parthenope agona,* they are distinctly oblique, whereas in *Leiolambrus nitidus,* they are almost vertical. The presence of small antennae, with the peduncles in the orbital hiatus can also be found in many Parthenopidae.

In our comparative studies of the Parthenopoidea with the Mimilambridae, we also examined several other characters that are common to both. Of the genera dealt

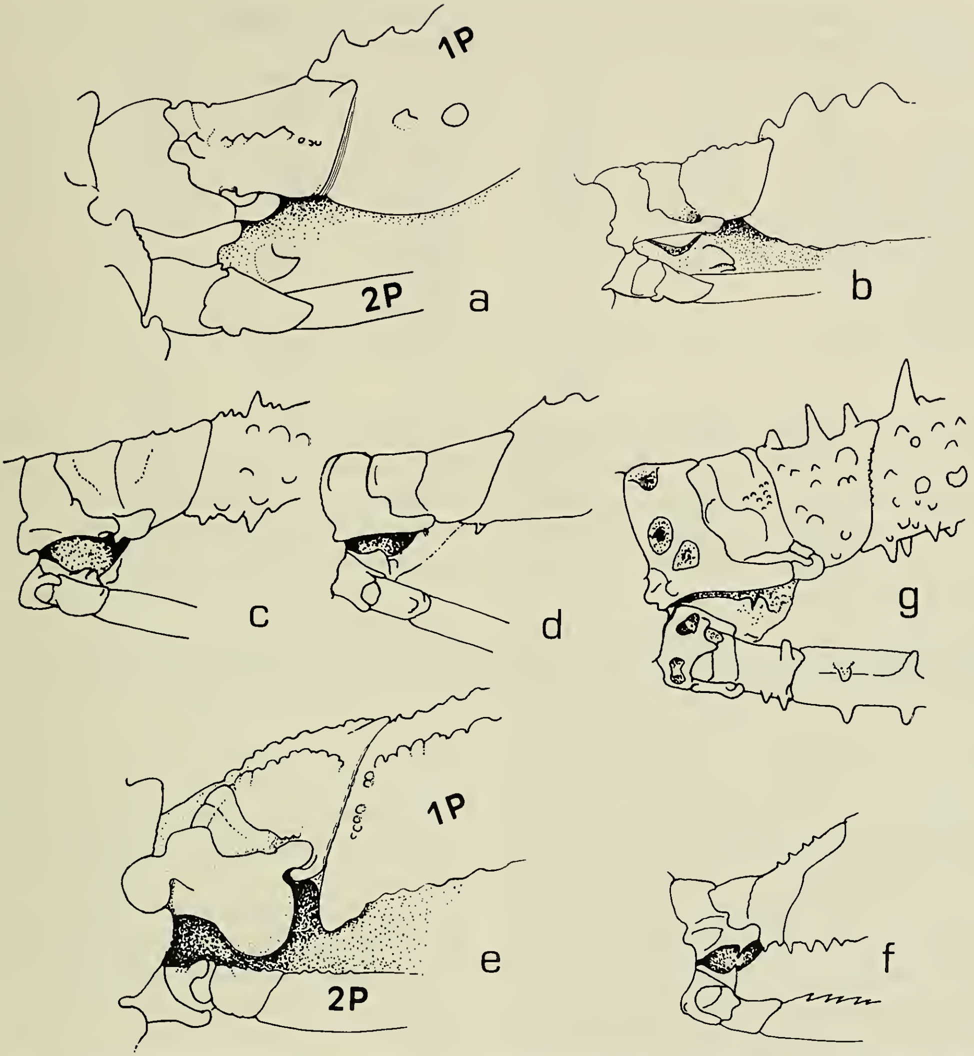

Fig. 1. Ventral view of Parthenopidae and *Mimilambrus,* showing locking mechanism of chelipeds: a, *Mimilambrus wileyi*; b, *Platylambrus serratus*; c, *Platylambrus echinatus*; d, *Rhinolambrus longispinis*; e, *Leiolambrus nitidus*; f, *Cryptopodia fornicata*; g, *Daldorfia horrida.* 1P, Left cheliped; 2P, Second pereopod.

with, the only daldorfid is *Daldorfia*; *Daira* and *Dairoides* are dairids, *Aethra* the only aethrid, all the others being parthenopids. These characters will now be discussed systematically.

1. *Ventral spines.*—These spines are located at each side of the sternum, near the bases of the chelipeds. When the chelipeds are moved backwards, the respective spine locks against the ischio-meral articulation and prevents any further displacement backwards of the appendage (Fig. 1).

These spines have the same position in *Mimilambrus* (Fig. 1a) and *Parthenope agona, P. hyponca* (Stimpson, 1871), *P. ornatus* (Flipse, 1930, Fig. 24), *Platylambrus*

Table 1.—Inclination (in degrees) of the fixed finger and dactylus in some parthenopids and in *Mimilambrus wileyi*. Minimum and maximum values are given in parentheses.

| | | Fixed finger | | Dactylus | |
|---|---|---|---|---|---|
| | n | Left | Right | Left | Right |
| *Platylambrus serratus* | 4 | 38 (30, 43) | 38.5 (34, 43) | 15 (10, 21) | 7 (2, 10) |
| *Platylambrus echinatus* | 4 | 18 (16, 22) | 18 (11, 26) | 1.5 (0, 5) | 3 (0, 6) |
| *Rhinolambrus longispinis* | 1 | 28 | 19 | 8 | 3 |
| *Leiolambrus nitidus* | 5 | 18 (17, 20) | 20.6 (17, 25) | 0 | 0 |
| *Cryptopodia fornicata* | 5 | 9.5 (6, 15) | 9.5 (8, 13) | 3 (2, 4) | 1.5 (1, 2) |
| *Daldorfia horrida* | 2 | 12 (11, 13) | 11.5 (11, 12) | 8.5 (8, 9) | 6 (4, 8) |
| *Mimilambrus wileyi* | 5 | 20.6 (14, 26) | 14 (5, 20) | 0.6 (−10, 10) | 4 (−9, 10) |

*serratus* (Fig. 1b), *P. pourtalesii* (Stimpson, 1871) (Rathbun 1925) and *Heterocrypta tommasii.* In *Solenolambrus typicus* Stimpson, 1871, and *S. portoricensis* Rathbun, 1924 (both Rathbun 1925) the position of the ventral spine is occupied by a row of tubercles instead. In *Leiolambrus nitidus,* the sternum is smooth, but the merus of the chelipeds has a triangular tooth on the anteroproximal angle which accomplishes a similar function (Fig. 1e). Flipse (1930, fig. 40) shows a similar acute spine on the merus of *Daldorfia semicircularis* (Flipse 1930). *Daldorfia horrida* (Fig. 1g) however, lacks such an acute spine but has two blunt teeth in place of the ventral spine. The ventral spines of *Rhinolambrus longispinis* (Fig. 1d) and *Platylambrus echinatus* are both reduced to blunt tubercles. In *P. echinatus* (Fig. 1c), the antero-proximal angle has a blunt tooth which opposes the ventral tubercle. This tooth is absent in *R. longispinis.* The ventral spine of *Cryptopodia fornicata* (Fig. 1f) is quite well developed and opposes another sharp spine on the antero-distal angle of the coxa. The chelipeds are consequently much less mobile when compared to the other parthenopids and daldorfids. The chelipeds of *Daira* are extremely mobile, with only a very small tubercle located far back behind the sternum, and no opposing spine or tubercle on any part of the cheliped.

2. *Fingers of chelipeds.*—In most parthenopoids, the fingers of the chelipeds are bent downwards, and the dactylus bent inwards in a very characteristic way. To evaluate this character, we measured, in material available to us, (a) the angle formed by the fixed finger with the longitudinal axis of the cheliped (relative downward inclination), and (b) the angle formed by the dactylus with the transverse axis of the cheliped (inward inclination) (Table 1). The fixed finger is bent downwards in *Platylambrus serratus, P. echinatus, Rhinolambrus longispinis, Leiolambrus nitidus, Cryptopodia fornicata, Daldorfia horrida,* and *Mimilambrus wileyi.* The inclination of the dactylus in *Platylambrus serratus* is always inwards, but tends to be straight in *Cryptopodia fornicata* and *Platylambrus echinatus,* and in *Leiolambrus nitidus,* it is in line with the palm of the cheliped. That on *Mimilambrus wileyi* shows considerable variation, with the inclination being either inwards or outwards.

3. *Dentition of the chelipeds.*—*Mimilambrus wileyi* shows dimorphic asymmetry in the dentition of the chelipeds (Fig. 2i–l); the occlusive surface of the cheliped on one side (the crusher) has a double row of teeth that coalesce side-by-side to form molariform crushers (Fig. 2j, l). The cheliped of the other side (the cutter) has two rows of broad, thin shearing teeth over the occlusive surface of the dactylus, and a row of similar teeth on the occlusive surface of the fixed finger (Fig. 2i, k). Additionally, the fixed finger has a lateral row, arched dorsally in the middle, bearing eight triangular teeth. Some variability is displayed in our material of *Mimilambrus.* In the male specimen

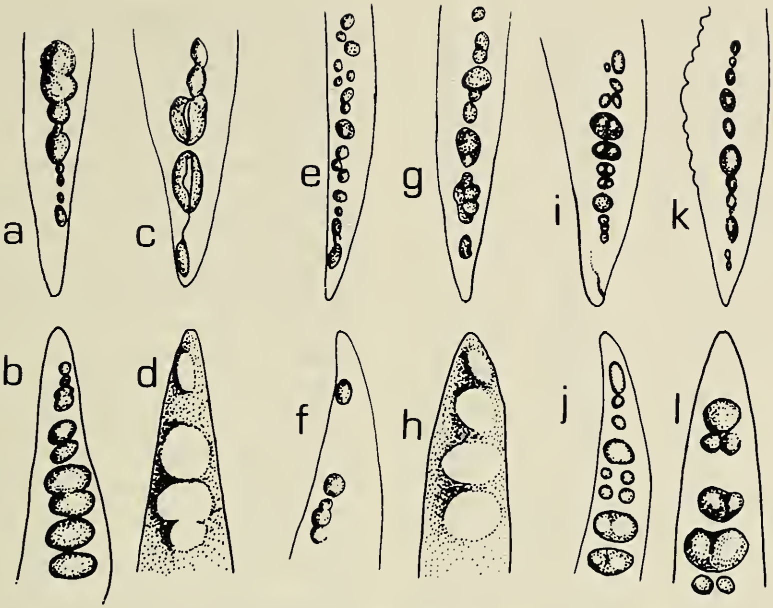

Fig. 2. Dentition of chelipeds in American Parthenopidae and in *Mimilambrus*: a, b, c, d, *Platylambrus serratus*; e, f, g, h, *Leiolambrus nitidus*; i, j, k, l, *Mimilambrus wileyi*. a, e, i, Dactylus of left cheliped; c, g, k, Fixed finger of left cheliped; b, f, j, Dactylus of right cheliped; d, h, l, Fixed finger of right cheliped.

from Golfo de Cariaco (cl. 26.3 mm) and Paraguaná (cl. 29.7 mm), the molariform crushers have distinct and acute cusps, and the lateral row of teeth of the cutter cheliped are very prominent and convex, being sharp and distinct. In other specimens, the teeth of the crusher cheliped have coalesced to form single, oblong molars, the lateral row of the cutter cheliped is less convex and prominent, with smaller teeth.

A similar dimorphic asymmetry is found in the members of the Parthenopidae. In *Parthenope agona* and *Platylambrus serratus* (Fig. 2a–d), there are two molar crushers on the fixed finger, but the cusps of the proximal one still have the cups discernible, and the cutter cheliped has a row of shearing teeth on both fingers and an additional oblique row of tubercles on the lateral surface of the fixed finger. *Heterocrypta tommasii* has three molars with indiscernible cusps on the fixed finger of the crusher cheliped, with crenulations on the dactylus, and there is no lateral row of tubercles on the fixed finger of the cutter cheliped. The chelar dentition of *Leiolambrus nitidus* (Fig. 2e–h) shows a greater resemblance to that of *Mimilambrus* (Figs. 2e, i). The crusher cheliped of *Leiolambrus* has four molars without distinct cusps, diminishing in size distally on the fixed finger, while the dactylus is almost devoid of teeth except for a distal protuberance. The cutter cheliped has an indistinct double row of shearing teeth on the dactylus, some of which are fused to form molars. The lateral row of tubercles over the fixed finger is weak, with only minute granules.

The parthenopoids from the Indo-Pacific, *Cryptopodia fornicata* (Fig. 3m–p), *Rhinolambrus longispinis* (Fig. 3i–l), *Platylambrus echinatus* (Fig. 3e–h), and *Daldorfia horrida* (Fig. 3a–d) also show heterochely, with a distinct crusher and cutter cheliped. The crusher cheliped of *Daldorfia* is almost twice the size of the cutter, and the fixed finger has one very massive molar running through most of its length, without cusps, and slightly depressed medially (Fig. 3c). The dactylus bears a row of three strong,

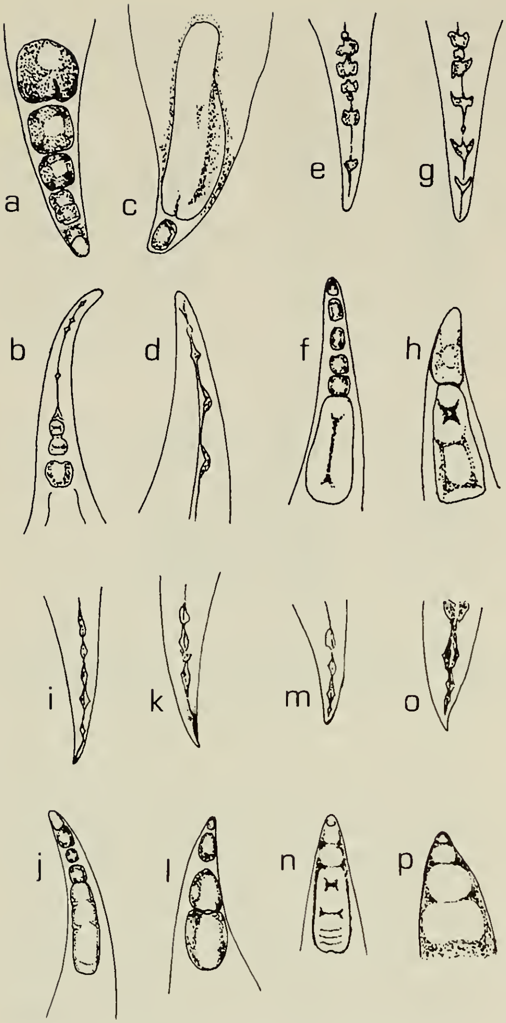

Fig. 3. Dentition of chelipeds in Indo-Pacific Parthenopoidea: a, b, c, d, *Daldorfia horrida*; e, f, g, h, *Platylambrus echinatus*; i, j, k, l. *Rhinolambrus longispinis*; m, n, o, p, *Cryptopodia fornicata*. a, e, i, m, Dactylus of left cheliped; c, g, k, o, Fixed finger of left cheliped; b, f, j, n, Dactylus of right cheliped; d, h, l, p, Fixed finger of right cheliped.

coniform molars (Fig. 3a). The crusher cheliped of *Cryptopodia* is slightly less well developed than that of *Daldorfia,* but the molars on both fingers appear confluent (Fig. 3n–p). *Platylambrus echinatus* has two, almost confluent molars on the fixed finger of the crusher cheliped which have low cusps (Fig. 3h) that occlude on a larger molar on the dactylus (Fig. 3f). The crushing apparatus of *Rhinolambrus longispinis* is quite close to *Platylambrus serratus,* with two large molars on the fixed finger (Fig. 3l) and a row of smaller ones on the dactylus (Fig. 3j), but their cusps are rather lower.

The crushing chelipeds are clearly associated with molluscivorous diets, and the form of the crushing and cutting chelipeds of *Mimilambrus* falls within the range of variation observed in the Parthenopidae s. s. The chelipeds of the Parthenopidae (including *Mimilambrus*) and the Daldorfidae however, show some minor, but distinct differences. In the daldorfids, heterochely is much more pronounced, and the crushing chelipeds have very much stronger and larger molariform teeth than the parthenopids.

4. *Ischio-meral articulation of chelipeds.*—Guinot (1968) has stressed the importance of this articulation in the phylogeny of the Brachyura. In *Mimilambrus wileyi,* the ischio-meral articulation is still mobile, and the two articles are joined together by an arthrodial membrane. This character is commmonly found in the family Majidae (sensu Guinot 1978), and has been regarded by Guinot (1968) as primitive. In the Daldorfidae and Parthenopidae s. s., this character is rather variable, with a tendency towards ankylosis and total disappearance of the articulation and the arthrodial membrane. In *Platylambrus serratus, P. echinatus, Rhinolambrus longispinis,* and *Cryptopodia fornicata,* no arthrodial membrane is present, and movement of the two articles is at best very slight. In the genus *Mesorhoea* Stimpson, 1871, *Daldorfia horrida, Leiolambrus nitidus,* and *Parthenope agona,* there is a thin arthrodial membrane, but movement of the articles is still very restricted. In *Daira,* the arthrodial membrane is present, but it is thin, and the two main articles remain, for all purposes, immobile.

5. *Second male pleopod (P2).*—The P2 of all very primitive crabs (Dromiidae, Dynomenidae, and Homolidae) are long and whiplike, the cup is absent, and the basal portion of the flagellum cannot be differ-

entiated. In some groups, e.g. in the superfamily Xanthoidea (sensu Guinot 1978a, b), both long and short P2s can be found, and Ng (1983) has suggested that the long P2 represents the plesiomorphous condition.

In the Parthenopoidea, the morphology of the P2 is slightly more homogeneous (Fig. 4). An examination of the material deposited in our collections, and the figures of these appendages that are available in the literature reveal that there are approximately three main types within the superfamily. In the following list, we give the ratio of the flagellum to the total length of the appendage (f/a).

(A) Flagellum long and whiplike f/a > 0.4.

*Aethra scruposa* (Linnaeus, 1764) (Guinot 1967a, fig. 40).
*Daldorfia horrida* (Linnaeus, 1758).
*Daira perlata* (Herbst, 1790).
*Dairoides margaritatus* (Stebbing, 1920) (Guinot 1967b, fig. 14).

(B) Flagellum short, in the form of a spike, sometimes with basal cup, ratio f/a between 0.2 and 0.4.

*Parthenope macrochelos* (Herbst, 1790) (Monod 1956, fig. 861).
*P. agona* (Stimpson, 1871).
*Platylambrus pourtalesii* (Stimpson, 1871) (Williams 1965, fig. 252C).
*P. fraterculus* (Stimpson, 1871) (Williams 1965, fig. 252D).
*P. echinatus* (Herbst, 1790).
*Rhinolambrus longispinis* Miers, 1879.
*R. massena* (Roux, 1830) (Monod 1956, fig. 856).
*Cryptopodia fornicata* (Fabricius, 1781).
*C. concava* Stimpson, 1871 (Gore and Scotto 1979, fig. 5I).
*Leiolambrus nitidus* (Rathbun, 1901).
*Solenolambrus typicus* Stimpson, 1871 (Gore and Scotto 1979, fig. 9C).

(C) Flagellum very short, forming a cuplike structure, ratio f/a < 0.2.

*Platylambrus serratus* (H. Milne Edwards, 1834).

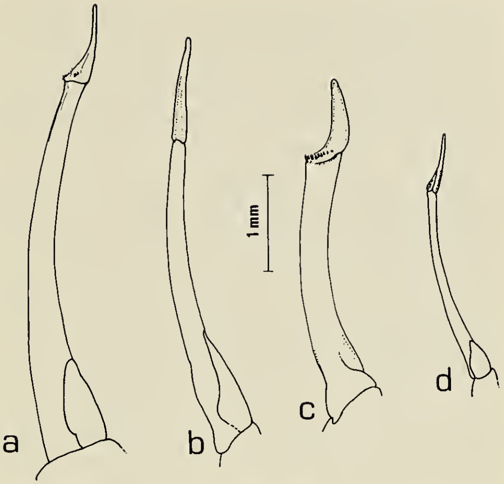

Fig. 4. Second male pleopod: a, *Platylambrus serratus*; b, *Parthenope agona*; c, *Mimilambrus wileyi*; d, *Leiolambrus nitidus*.

*Heterocrypta maltzami* Miers, 1881 (Monod 1956, fig. 867).
*H. granulata* (Gibbs, 1850) (Williams 1965, fig. 252E).
*Thyrolambrus erosus* (Miers, 1879) (Guinot 1967a, fig. 37).

All the genera with an f/a > 0.4 belong to the families Dairidae, Aethridae, and Daldorfidae, whereas genera with f/a < 0.4 constitute the Parthenopidae s. s. *Mimilambrus wileyi* belongs to the second group of P2 type, since its f/a is 0.22 with the flagellum relatively short, spikelike, with a fairly well developed basal cup, i.e., the Parthenopidae group.

Also, as mentioned earlier, the genera *Daira* and *Dairoides* or their allies probably gave rise to the main line of the parthenopids, and their male abdominal segments 3 to 5 are ankylosed, with the sutures still present, and their P2s are of the first group, i.e., with the flagellum long and whiplike. There is thus a very good chance that the evolutionary trend of the P2 observed in the Xanthoidea (Ng 1983) is also true for the Parthenopoidea.

In summary, some of the characters of *Mimilambrus,* such as the articulation of the male abdominal segments 3 to 5, and the ischio-meral articulation of the chelipeds appear to be rather primitive. The structures of the afferent and efferent channels, on the other hand, are advanced and specialized. The vertically folding antennules and form of the crusher cheliped of *Mimilambrus* finds an analogue in *Leiolambrus,* with their mouthparts and afferent channels also quite similar. The very unusual mouthpart arrangement of *Mimilambrus* with its medial efferent opening is not unique to it, but can also be found in *Mesorhoea.* The only unusual character of *Mimilambrus* seems to be the free chelar ischio-meral joints with an anthrodial membrane, which appears to be a plesiomorphous condition. In the more primitive parthenopoids like *Daira,* these joints are tightly appressed, but still distinct. The genera *Mesorhoea* and *Leiolambrus* also have the two joints distinct, but basically immobile. The condition of the ischio-merus in *Mimilambrus* suggests that it may be a fairly primitive and specialized species. Presumably, the genus represents an early offshoot of the main parthenopoid stock. The respiratory adaptations could be explained by convergent evolution, and are unlikely to have been derived from similarly advanced structures like those on *Leiolambrus* and *Mesorhoea.* Placing *Mimilambrus* in a family (and superfamily) of its own is, therefore, unwarranted since it shares far too many common characters with the Parthenopidae s. s., and should instead be regarded merely as a rather specialized genus in the family.

## Acknowledgments

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# DESCRIPTIONS OF TWO NEW SPECIES OF *HYLODES* FROM THE ATLANTIC FORESTS OF BRAZIL (AMPHIBIA: LEPTODACTYLIDAE)

W. Ronald Heyer and Reginald B. Cocroft

*Abstract.*—Analysis of available advertisement calls and morphology indicates that *Hylodes babax* and *H. lateristrigatus* occur at Santa Teresa, Espírito Santo, Brazil, and that several new species are present within the *Hylodes lateristrigatus* species cluster. We have adequate materials for description of two of these: *H. charadranaetes* from Teresópolis, Rio de Janeiro, and *H. phyllodes* from Boracéia, São Paulo.

This study was begun to determine the nomenclatural status of the smaller species of *Hylodes* that occurs at Boracéia, São Paulo, Brazil. This interest was stimulated by a forthcoming summary of the frogs of Boracéia (Heyer, Rand, Cruz, Peixoto, Nelson, in prep.). In an effort to use the proper names for the *Hylodes,* it became apparent that we would have to evaluate data previously published on species from elsewhere in its range. W. C. A. Bokermann and Eugênio Izecksohn are involved in a long-term revision of the genus *Hylodes* (Bokermann, pers. comm.). At their suggestion (Bokermann, pers. comm.), we report our data and conclusions to facilitate work on the Boracéia fauna.

Two names have been used in the literature for the smaller *Hylodes* from Boracéia and/or Paranapiacaba: *glabrus* (as *Elosia glabra,* Bokermann 1967a) and *lateristrigatus* (as *Elosia lateristrigata,* Cochran 1955). Heyer (1982) demonstrated that *H. lateristrigatus* did not apply to the species from Paranapiacaba, and questioned whether *glabrus* was the correct name for the Paranapiacaba species. Izecksohn and Gouvêa (1983) conclude that *Elosia glabra* Miranda-Ribeiro, 1926, is a senior synonym of *E. pulchra* Lutz, 1951. Through the courtesy of Professor Antenor Leitão de Carvalho, we were able to borrow and examine the holotype of *Elosia glabra,* and we agree with their conclusion. The Boracéia/Paranapiacaba species is clearly a *lateristrigatus* group member. *Hylodes glabrus* is not, since it lacks the diagnostic dorsolateral light stripe, so this name can not be applied to the Boracéia/Paranapiacaba populations. Based on proximity of localities in the same block of the Serra do Mar, Paranapiacaba and Boracéia would be expected to have the same species of *Hylodes.*

The purposes of this report are: (1) to summarize data we have analyzed on the advertisement calls and external adult morphology of *Hylodes*; and (2) to describe new species for those populations lacking names and for which we have adequate materials for description.

## Variation in Calls and Morphology of Geographic Samples of the *lateristrigatus* Group

Heyer (1982) proposed informal species clusters for *Hylodes* based on external morphology. We follow that system, recognizing that the groupings are ones of convenience and may not be monophyletic. With the exclusion of *glabrus* from this group, the following names pertain to the *lateristrigatus* group: *Hylodes babax* Heyer, 1982; *Hylodes lateristrigatus* (Baumann, 1912); *Hylodes magalhaesi* (Bokermann, 1964); *Hylodes ornatus* (Bokermann, 1967b); *Hylodes otavioi* Sazima and Bokermann, 1982; *Hylodes*

Table 1.—Advertisement call characteristics of members of the *Hylodes lateristrigatus* group.

| Population | Call duration (s) | #Notes/ call | Note duration (s) | #Notes/s | Dominant frequency (Hz) | Frequency modulation of notes |
|---|---|---|---|---|---|---|
| *H. babax* | 0.2–0.5 | 4–8 | 0.04–0.05 | 16–17 | 4290–5420 | |
| *H. lateristrigatus* | 1.3–1.6 | 12–13 | 0.05–0.07 | 8–9 | 3700–4300 | +, ↑ |
| *H. magalhaesi*[a] | 1.0 | 26 | 0.02–0.03 | 20–25 | 1400–3000 | +, ↑ |
| *H. otavioi*[b] | 2.0 | 6–15 | 0.09–0.10 | 8 | 3800–5200 | — |
| *H. regius* | 1.7 | 22–32 | 0.02–0.03 | 14–19 | 5200–6300 | +, ↑ |
| Boracéia | | | | | | +, ↑ |
| (*H. phyllodes*) | 1.0–2.1 | 12–20 | 0.05–0.06 | 8–11 | 4100–5700 | |
| Paranapiacaba[c] | | | | | | +, ↑ |
| (*H. phyllodes*) | 1.8–3.0 | 15–32 | 0.03–0.05 | 10–13 | 5400–6000[d] | |
| Santa Teresa A | | | | | | + (weak), ↑ |
| (*H. lateristrigatus*) | 2.4 | 19 | 0.05–0.06 | 8 | 3100–3900 | +, ↑ |
| Santa Teresa B | | | | | | |
| (*H. babax*) | 0.6–0.8 | 10–12 | 0.03–0.05 | 14 | 3500–4900 | +, ↑ |
| Teresópolis | | | | | | |
| (*H. charadranaetes*) | 1.1–1.3 | 2–4 | 0.06–0.17 | 2–4 | 4300–5500 | +, ↑↓ |

[a] Data from Bokermann 1964.

[b] Data from Sazima and Bokermann 1982.

[c] Data from Bokermann 1964, 1967.

[d] Published figures indicate dominant frequency range of 4200–5700 Hz.

*regius* Gouvêa, 1979; *Hylodes vanzolinii* Heyer, 1982.

*Calls.*—Advertisement calls are known for all named members of the *Hylodes lateristrigatus* group except for *ornatus* and *vanzolinii.* It is likely that *vanzolinii* is voiceless (Heyer 1982). In addition to advertisement calls from the type localities of the remaining named species, call data are available for the *lateristrigatus* group from Boracéia, São Paulo; Paranapiacaba, São Paulo; two species from Santa Teresa, Espírito Santo; and a second species (in addition to *lateristrigatus*) from Teresópolis, Rio de Janeiro. Few recordings are available for most of these species; for the following comparisons, the number of calls analyzed ranges from three calls from one individual from the Santa Teresa B population to ten calls from two individuals of *Hylodes charadranaetes.* Field observations (Heyer, pers. obs.), however, indicate that call characteristics in *Hylodes* are consistent within populations, so these samples are considered to be representative.

None of the calls are identical when the major call features are compared (Table 1). In the two instances of sympatry (Santa Teresa and Teresópolis), the calls differ strikingly. At Teresópolis, *lateristrigatus* and the second species (*Hylodes charadranaetes* n. sp., see below) differ by at least an order of magnitude in number of notes per call and number of notes per second. The two forms are also differentiated in terms of note duration, dominant frequency channel, and frequency modulation within notes (Table 1). The two forms from Santa Teresa differ strikingly in call duration, number of notes per call, and number of notes per second; the broadcast channel and note duration are also distinctive, though they show some overlap (Table 1). The distinctiveness of the calls of the two forms at Santa Teresa and Teresópolis is consistent with species level differentiation.

Most two-way comparisons of populations for which call data are available demonstrate the same degree of differentiation observed in the sympatric pairs (Table 1). Certain two-way comparisons are not as distinctive, and each is discussed.

1) *Hylodes babax*-Santa Teresa B. None of the major call characteristics (Table 1) differ markedly between the two samples, although the calls are distinct in duration, number of notes per call, and number of notes per second. When tapes of these calls are played one after the other, the calls sound distinctive to the human ear, but it is not possible to tell whether the differences are due to recording (i.e., equipment, distance from specimen, etc.), individual, or species differences.

2) *Hylodes lateristrigatus*-*H. otavioi.* These calls differ somewhat in call duration, broadcast channel, and note duration. Comparison of audiospectrograms indicates more similarities than differences between calls. The call data can not be unambiguously used to determine whether distinct species are involved.

3) *Hylodes otavioi*-Boracéia and Paranapiacaba. These calls differ slightly in terms of number of notes per call and distinctively in note duration. Comparison of audiospectrograms indicates a different note structure for *H. otavioi*; the notes of the Boracéia and Paranapiacaba populations have a simpler and more vertical appearance on the audiospectrograms. Furthermore, there is no indication of pairing of notes in *H. otavioi,* which occurs in the other two populations. We believe these differences are indicative of species level differentiation.

4) *Hylodes lateristrigatus*-Santa Teresa A. The calls differ only in call duration and number of notes per call; this simply indicates a longer call. The broadcast channel, though somewhat distinctive, is overlapping. Comparison of audiospectrograms of the calls shows them to be very similar in other structural components. The differences between calls are more of the level expected for geographic variation than for species level differentiation.

5) Boracéia-Paranapiacaba. The calls differ somewhat in each of the major call characteristics (Table 1) but each characteristic shows some overlap. If the data from Bokermann's (1964, 1967a) figures are used rather than the values he presents in the text, the broadcast channels are identical. Comparison of audiospectrograms indicates that two features are shared by these two populations alone. First, there is noticeable frequency modulation within the call, which begins at a higher frequency and ends at a lower frequency. Other known *lateristrigatus* group members have either no noticeable frequency modulation of the call or an increase in frequency after the first one or two notes of the call. Second, the calls from the Boracéia population tend to have paired notes given at the end of the call. Bokermann's (1964, 1967a) audiospectrograms suggest the same pattern, though not as strongly as do the Boracéia audiospectrograms. We interpret the Boracéia and Paranapiacaba calls to represent the same species.

*Morphology.*—Within the *lateristrigatus* group, *H. ornatus, H. regius,* and *H. vanzolinii* are distinctive in size and/or pattern (see Heyer 1982). The remaining populations are strikingly similar in morphology. The two forms occurring at Teresópolis differ mostly in size, with subtle pattern differences (Heyer 1982). There is a much smaller size difference between the two forms from Santa Teresa (adult males 32.7–33.6 mm SVL versus 36.7–37.1 mm SVL) and we can find no other differences. In order to examine the morphological variation among populations of the *lateristrigatus* group that are similar in appearance, a discriminant function analysis was performed. Although samples were limited, the results are instructive. Because only males were available for the Santa Teresa A and B forms, the analysis is limited to males. The variables measured and used in the analysis were: SVL, head length, head width, vertical tympanum diameter, eye diameter, eye-nostril distance, internarial distance, width of third finger disk, width of fourth toe disk, hand length, femur length, tibia length, and foot length. Initially, three samples were

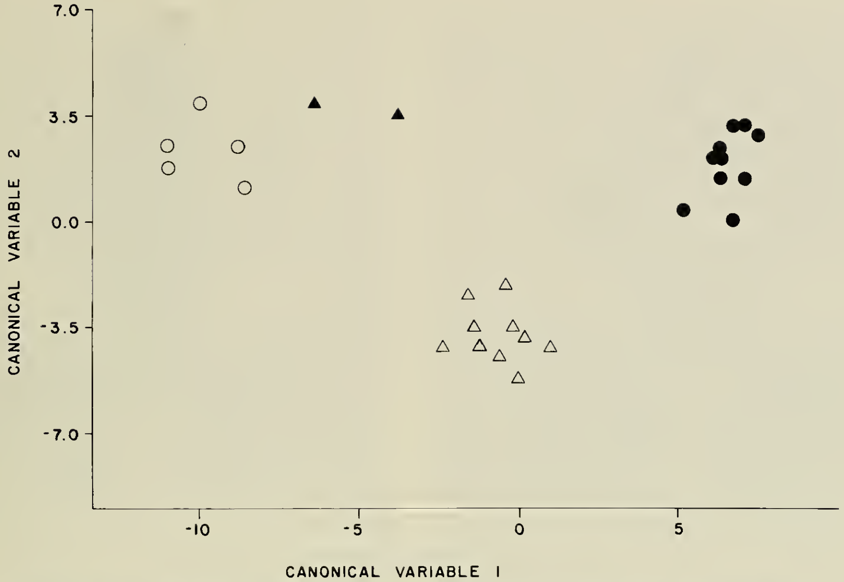

Fig. 1. Discriminant axis plot of males of four samples of the *Hylodes lateristrigatus* group. Triangles = Teresópolis, solid triangles = Santa Teresa B, circles = *lateristrigatus,* solid circles = Boracéia.

used for the preformed groups: *lateristrigatus* (two males from Teresópolis and one from Correias), Teresópolis, and Boracéia. These three groups were separated by the discriminant function analysis. The canonical variable coefficient results were used to plot four additional specimens on the plot of the first two canonical variables. Prior to the analysis, we were unable to differentiate morphologically the *lateristrigatus* males from the two Santa Teresa A males. The two Santa Teresa A males were adjacent to the *lateristrigatus* males when plotted, and the two Santa Teresa B males were closest to the Santa Teresa A males. Next, four preformed groups were analyzed: *lateristrigatus* (five males from Correias, Teresópolis, and Santa Teresa), Boracéia (ten males), Teresópolis (ten males), and Santa Teresa B (two males). There is 100% discrimination of cases among these groups. The plot of the first two canonical variables accounts for 95% of the total dispersion, and best separates the groups along the first canonical variable, which is size related (Fig. 1). In fact, the Boracéia, Santa Teresa B, and *lateristrigatus* groups are only differentiated on the first axis and the Santa Teresa B and *lateristrigatus* groups are very close to each other, even in size. Only the Teresópolis group is distinctive along the second canonical variable axis. The variable with the highest loading on this axis is the width of the third finger disk (20.4; the next highest value, −9.2, is for eye-nostril distance). Comparison of specimens indicates that the finger disk size does not allow visual discrimination of the Teresópolis specimens from the other samples. The morphological analyses indicate that: (1) the males of Santa Teresa A and *lateristrigatus* form a single morphological group; (2) the Santa Teresa B group is very similar to the *lateristrigatus* group; and (3) the four groups are quite similar, differing principally in size.

There are too few specimens to perform a meaningful discriminant function analysis on external morphology between *H. babax* and Santa Teresa B males. Direct comparisons indicate similarities in size, pattern, and color. There is overlap in male size (*babax* 30.6–32.6 mm SVL, Santa Teresa B

32.0–33.6 mm SVL). The belly patterns of boldly contrasting dark and light mottling are similar. The undersides of the femurs are red in life for both samples (Peter Weygoldt, pers. comm. for Santa Teresa B specimens), a condition recorded only from these two samples and *H. regius.* We do not believe the available data support recognition of Santa Teresa B as a species distinct from *H. babax.* We do point out, however, that differences in call parameters (noted above) and pattern (the lateral stripes are more distinct in the Santa Teresa specimens) exist in the few individuals at hand, and encourage additional call and morphological samples to be gathered to understand the nature of the differences observed.

Combining the available advertisement and morphological data with previously published analyses, we recognize the following species in the *lateristrigatus* group: *babax* (including Santa Teresa B), *lateristrigatus* (including Santa Teresa A), *magalhaesi, ornatus, otavioi* (more information is needed to clarify the specific status of *otavioi* relative to *lateristrigatus*), *regius, vanzolinii,* a new species for the populations from Boracéia and Paranapiacaba, a new species for the second species from Teresópolis, and a new species for an Itatiaia population which is morphologically distinct, but for which only one adult and no call recordings are available. The two new species for which adequate samples are available are described in the following section.

### *Hylodes phyllodes,* new species
Fig. 2

*Holotype.*—MZUSP 59934, male, from Brazil: São Paulo; Boracéia, 23°38′S, 45°50′W. Collected by W. Ronald Heyer, 6 Dec 1976.

*Paratopotypes.*—MZUSP 1700–1702, 1704–1706, 1708–1711, 1714, 1716–1721, 3308, 3527, 3529, 4040–4043, 4143, 23050–23053, 23561, 23678–23697, 36874, 37573–37585, 37678–37687, 37701–37703, 37712-37717, 38854, 56497; USNM 129156–129158, 243480–243506.

*Diagnosis.*—*Hylodes phyllodes* has a light stripe from the eye to the groin, distinct at least posteriorly; *H. vanzolinii* lacks such a stripe. The dorsum of *H. phyllodes* lacks the distinct light spots found in *H. regius. Hylodes phyllodes* is larger (males 27.5–31.4 mm SVL, females 29.0–35.5 mm SVL) than *ornatus* (males and females 23.2–26.1 SVL) and smaller than *lateristrigatus* (males 36.7–39.2 mm SVL) and *otavioi* (males and females31.4–34.0 mm SVL). *Hylodes phyllodes* differs consistently from *babax, charadranaetes,* and *magalhaesi* in advertisement call characteristics. In life, *H. phyllodes* lacks the brick red color on the under surface of the legs found in *H. babax.* The variegated belly of *H. phyllodes* never consists of a bold pattern of distinct light spots on a dark ground which is found in some individuals of *H. magalhaesi. Hylodes phyllodes* is smaller than *charadranaetes* (males to 34.7 mm SVL, females to 37.7 mm SVL) and has a more slender body form. Male *H. phyllodes* differ from all other known male *Hylodes* in having nuptial thumb spines.

*Description of holotype.*—Snout truncate from above, protruding in profile; canthus rostralis sharp; lores vertically concave in cross section; tympanum distinct, large, diameter about ⅔ diameter of eye; vomerine teeth in two small transverse patches between and on line drawn across posterior edges of choanae, separated by less than length of one vomerine tooth patch; vocal slits present, near angle of jaw on each side; vocal sacs paired, lateral, inflated; finger lengths I ≃ II < IV < III; middle of thumb with scattered small whitish spines in small ovate area on inner and dorsal surface; dorsal texture finely etched, few scattered warts posteriorly, dorsal surfaces of legs with series of longitudinal ridges; weak fold from eye to groin; throat and belly smooth, under surfaces of thighs smooth anteriorly, areolate posteriorly; finger and toe tips with disks, disks about twice as broad as digit imme-

Fig. 2. Holotype of *Hylodes phyllodes* (MZUSP 59934, a male): dorsal and ventral views.

diately behind disk, finger and toe disks about equal size, upper surface of disks with pair of scutes; fingers fringed, most extensively on fingers III and IV; toes extensively fringed; subarticular tubercles moderate sized, rounded; inner oval metatarsal tubercle about twice as large as pungent, rounded outer metatarsal tubercle; extensive tarsal fold-flap extending ⅞ distance of tarsus, continuous distally with toe fringe on outer side of first toe; no metatarsal fold; outer tarsus and sole of foot smooth.

SVL 29.2 mm, head length 10.2 mm, head width 8.9 mm, eye-nostril distance 2.1 mm, femur 13.1 mm, tibia 14.4 mm, foot 14.5 mm.

Dorsum almost uniformly dark brown (fine bronze and gray mottle under microscope) with faint darker mid-dorsal pin stripe with small whitish dots spaced along stripe; upper limbs tan with narrow brown cross bands; flank a blending of dorsal and ventral patterns with distal ⅓ of eye-groin fold whitish and distinct; continuation of dorsal color as dark canthal stripe, rest of face lighter brown and white mottle, lightest under eye and continuing under tympanum to shoulder; mid-ventral brown stripe from almost tip of chin through chest to anteriormost belly; rest of throat and belly mottled brown and white; under limbs mottled with brown and pigmentless areas; posterior surfaces of thighs indistinctly mottled darker and lighter browns.

*Variation.*—Males range from 27.5–31.4 mm SVL, females 29.0–35.5 mm SVL.

In preservative, the dorsum ranges from brown to brassy brown with various markings, including an irregular mid-dorsal light stripe with almost regularly spaced small darker brown (than dorsum) spots, or a series of short dark mid-dorsal dashes, or dorsum scattered with small dark brown spots, or series of mid-dorsal large light blotches, or big darker brown blotches on a lighter brown background, or almost uniform with a series of faint light mid-dorsal dots; pair of dark round or U-shaped spots, one on each side of anus; upper limbs distinctly to indistinctly crossbarred brown on tan; flank with dark brown (almost black) band behind eye across tympanum just to or above arm, fading to mottled brown and white, ranging to flank almost uniformly dark.

In life, iris copper to yellow, darker on sides forming black band with pupil; dor-

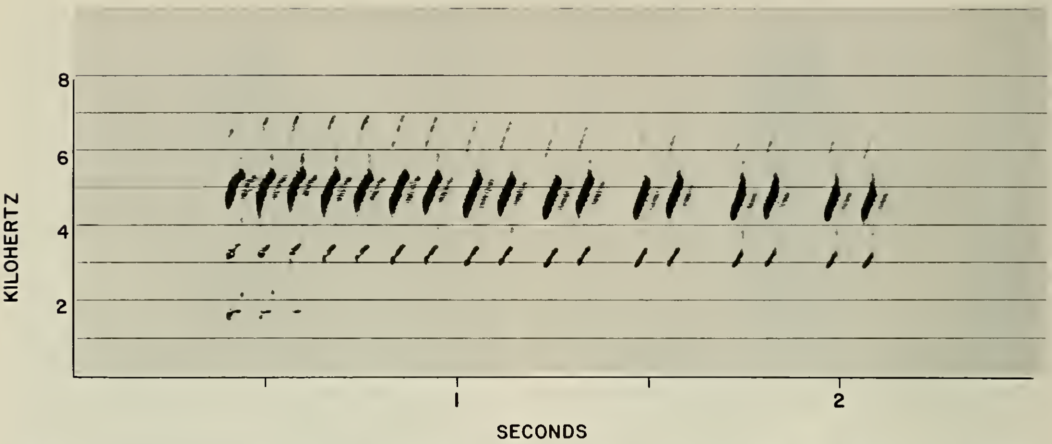

Fig. 3. Advertisement call of *Hylodes phyllodes.* From specimen MZUSP 59934, Brazil, São Paulo, Boracéia. Recorded 6 December 1976, air temperature 20.4°C.

sum olive to dark and light brown; light stripes cream, copper, yellow, yellow-gold, or gold; flanks dark brown; upper limbs dark and light brown with or without red cast; groin yellow or not; throat and belly opalescent, bright opalescent yellow, or yellow to golden with variable brown spotting, distinct or not; under limbs colorless to dirty greenish yellow.

*Advertisement call.*—Calls given sporadically, call duration 1.05–2.10 s; 12–20 notes per call given at rate of 8–11 per s; notes given at regular intervals at beginning of call, usually given in pairs at end of call; note duration 0.05–0.06 s; individual notes not pulsed, but weakly pulsatile; calls slightly frequency modulated, beginning higher, ending lower; calls not noticeably intensity modulated; fundamental frequency about 1500–2200 Hz; dominant frequency (=third harmonic) range at beginning of call 4300–5700 Hz, at end of call 4100–5300 Hz, call with harmonic structure (Fig. 3).

*Etymology.*—From the Greek *phyllo* (leaf) and *oides* (like) in allusion to the difficulty of visually distinguishing the frogs from leaves on or near the ground along streams during the day.

*Referred specimens.*—Brazil: São Paulo; Caminho do Mar km 47 (very near Paranapiacaba), MZUSP 10216, Ilha de São Sebastião, MZUSP 9973–9974, 51669, Ilha dos Búzios, MZUSP 23952–23955, São Sebastião, MZUSP 58717.

## *Hylodes charadranaetes,* new species
Fig. 4

*Holotype.*—MZUSP 60648, male, from Brazil: Rio de Janeiro; Alto do Soberbo, near Teresópolis, 22°26'S, 42°59'W. Collected by Ronald I. Crombie, Maria Christina Duchène, and W. Ronald Heyer, 10 Dec 1977.

*Paratopotypes.*—MZUSP 60649–60669, USNM 245894–245915, collected from Brazil: Rio de Janeiro; 2–5 km NE junction BR 116 and Teresópolis bypass on various dates by various collectors.

*Diagnosis.*—*Hylodes charadranaetes* has a light stripe from the eye to the groin, distinct at least posteriorly; *H. vanzolinii* lacks such a stripe. The dorsum of *H. charadranaetes* lacks the distinct light spots found in *H. regius. Hylodes charadranaetes* is larger (males 31.3–34.7 mm SVL, females 31.9–37.7 mm SVL) than *ornatus* (males and females 23.2–26.1 mm SVL) and smaller than *lateristrigatus* (males 36.7–39.2 mm SVL). *Hylodes charadranaetes* differs consistently from *babax, magalhaesi, otavioi,* and *phyllodes* in advertisement call characteristics. In life, *H. charadranaetes* is not brick red

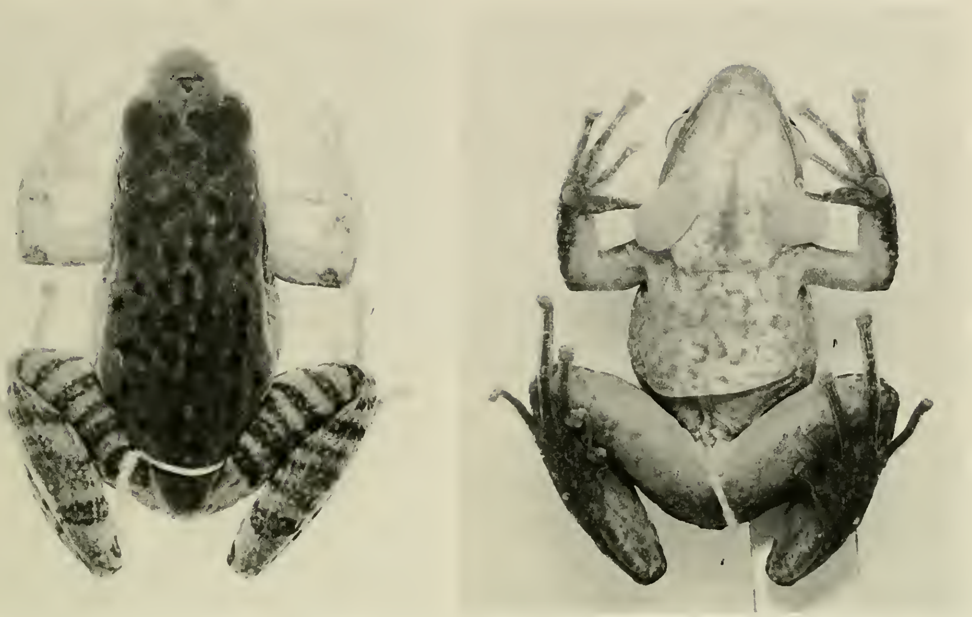

Fig. 4. Holotype of *Hylodes charadranaetes* (MZUSP 60648, a male): dorsal and ventral views.

on the under surface of the legs as is *H. babax*. The variegated belly of *H. charadranaetes* never consists of a bold pattern of distinct light spots on a dark ground such as found in some individuals of *H. magalhaesi. Hylodes charadranaetes* is more robust than *H. otavioi, phyllodes,* and *babax* and is somewhat larger than either *phyllodes* (males to 31.4 mm SVL, females to 35.5 mm SVL) or *babax* (males to 33.6 mm SVL). Male *H. charadranaetes* differ from male *H. phyllodes* in lacking nuptial thumb spines.

*Description of holotype.*—Snout subovoid from above, protruding in profile; canthus rostralis sharp; lores almost vertical in cross section; tympanum large, diameter greater than ½ diameter of eye; vomerine teeth in two small patches, separated by about length of one tooth patch, lying on line between posterior portions of choanae; vocal slits present, near angle of jaw; vocal sacs paired, lateral, inflated; first, second, and fourth fingers subequal, third longest; thumb lacking nuptial asperities; dorsal texture finely etched, few scattered warts posteriorly; fold from eye over tympanum to groin, upper legs with series of longitudinal ridges; throat and belly smooth, under surfaces of thighs smooth anteriorly, areolate posteriorly; finger and toe tips with disks, disks about ½ again as broad as digit immediately behind disk, finger and toe disks about same size, upper surface of disks with pair of scutes; fingers fringed, developed into extensive flaps on fingers III and IV; toes with extensive fringes produced into flaps; subarticular tubercles moderate, rounded; inner ovate metatarsal tubercle twice size of rounded outer metatarsal tubercle; extensive tarsal fold extending ⅞ distance of tarsus, continuous distally with fringe on outer side of first toe; no metatarsal fold; outer tarsus and sole of foot smooth.

SVL 34.4 mm, head length 12.2 mm, head width 10.4 mm, eye-nostril distance 2.6 mm, femur 16.2 mm, tibia 17.3 mm, foot 15.8 mm.

Dorsum variegated tan and light brown with field of darker brown spots almost regularly arranged in rows; upper limbs tan with narrow brown cross bands; dark brown spot on either side of anus; dark canthal

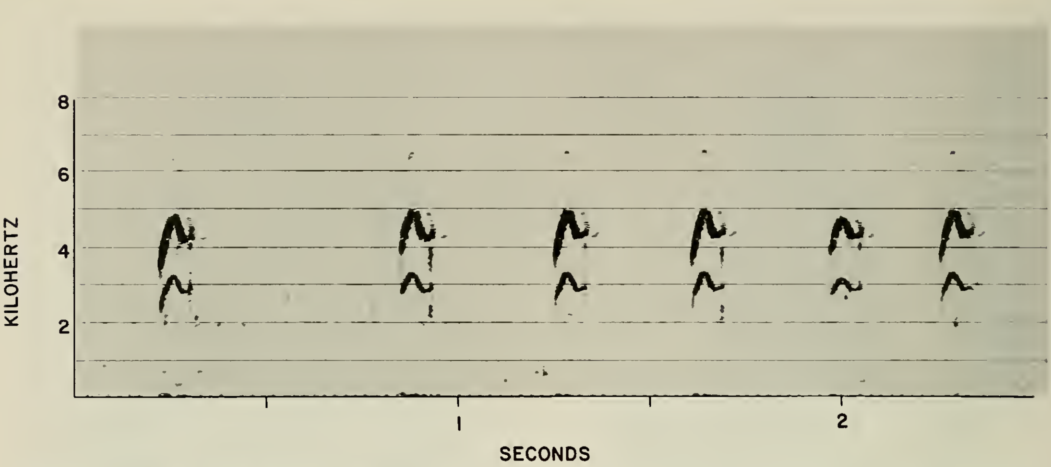

Fig. 5. Advertisement call of *Hylodes charadranaetes*. From specimen USNM 245909, Brazil, Rio de Janeiro, near Teresópolis. Recorded 8 December 1977, air temperature 21.2°C.

stripe extending anteriorly past nostril to about ½ way to tip of snout, below canthal stripe light with scattering of brown melanophores, becoming lighter under eye and continuing as light stripe to under middle of tympanum; flank a blending of dorsal and ventral patterns with light stripe highlighting eye-groin fold; throat and belly variegated white and tan, tan mid-throat stripe; under arm with scattering of white pigment, under legs variegated tan and pigmentless areas; posterior thigh mottled tan and dark brown.

*Variation.*—Males range from 31.3–34.7 mm SVL, females 31.9–37.7 mm SVL.

Variable number of dorsal spots, sometimes definitely arranged in rows; few specimens with faint row of small light dots mid-dorsally; light lip stripe continuing to shoulder in some specimens; eye-groin fold more or less distinctly highlighted by white stripe, white always distinct in groin area; degree of ventral mottling ranging from mostly white with few tan markings to equal amounts of white and tan or brown vermiculation.

In life, iris bronze; lip stripe cream; eye-groin stripe tan anteriorly, cream posteriorly, belly ranging from white, coppery white, coppery, to yellow, colors on belly same as those on front of thighs and ventral calves; posterior surface of thighs with faint red wash (belly colors noted for several individuals; other color description based on USNM 245908).

*Advertisement call.*—Calls given sporadically, call duration 1.1–1.3 s; 2–4 notes per call given at rate of 2–4 notes per s; note duration 0.06–0.17 s; notes not noticeably pulsed; each note frequency modulated, rising then falling; calls not noticeably frequency or intensity modulated; fundamental frequency range about 1000–1500 Hz, dominant frequency (third harmonic) range 4300–5500 Hz; calls with harmonic structure (Fig. 5).

*Etymology.*—From the Greek *charadra* (bed of mountain stream) and *naetes* (inhabitant), referring to the habitat of the species.

## Discussion

*Hylodes phyllodes* is the only *Hylodes* with nuptial spines. As expected, these spines occur only in male *H. phyllodes.* The nuptial spines in *H. phyllodes* likely serve a function different from the thumb spines occurring in the related genus *Crossodactylus,* where they occur in both sexes (a rare condition in frogs).

Maxson and Heyer (1982) presented data on relationships among certain populations

Table 2.—Cross reaction of certain *Hylodes* to albumin antisera against *Hylodes pulcher* and *Megaelosia goeldi* from Maxson and Heyer (1982). Values are in immunological distance units.

| Species tested | Anti-*Hylodes pulcher* | Anti-*Megaelosia goeldi* |
|---|---|---|
| *Hylodes charadranaetes* | 37 | 49 |
| *Hylodes lateristrigatus*—Teresópolis | 40 | 56 |
| *Hylodes lateristrigatus*—Santa Teresa | 42 | 51 |
| *Hylodes phyllodes* | 60 | 49 |
| *Hylodes* sp.—Brejo de Lapa | 108 | 86 |
| *Hylodes* sp.—Eugenio Lefêvre | 39 | 71 |

of *Hylodes,* most without specific names, based on immunological microcomplement fixation analysis of albumin. The data for the *lateristrigatus* species cluster are repeated (Table 2), with the names recognized in this paper. The specimen from Brejo da Lapa represents the undescribed new species from Itatiaia. The specimen from Eugênio Lefêvre was not recorded and its morphology is not distinctive; it may be from a population of *H. magalhaesi,* but recordings will probably be required for certain identification. The molecular data are consistent with our recognition of *lateristrigatus* from both Teresópolis and Santa Teresa and support the distinctiveness of the other species recognized in this paper.

## Acknowledgments

Dr. Peter Weygoldt (Albert-Ludwig-Universität, Freiburg) kindly provided data on the Santa Teresa specimens that he collected, including call recordings and color notes. Ronald I. Crombie provided assistance in suggesting names for the new species. George R. Zug provided a thorough review of the manuscript.

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# THE STATUS OF THE INDO-WEST PACIFIC CARDINALFISHES *APOGON AROUBIENSIS* AND *A. NIGROFASCIATUS*

John E. Randall and Ernest A. Lachner

*Abstract.*—*Apogon aroubiensis* Hombron and Jacquinot (1853) from Malaysia was named from a single 6 cm specimen which is not extant. It was described and illustrated as having four closely spaced black stripes on the side of the body and 12 pectoral fin rays. This nominal species cannot be equated to any apogonid fish known today. The species of *Apogon* most authors have identified as *A. aroubiensis* is *A. nigrofasciatus* Lachner which is known from the Red Sea and the western Pacific to French Polynesia. It is characterized as follows: five broad uniform dark brown stripes on body, the midlateral stripe ending in a dark spot at caudal base; no narrow short stripe extending posteriorly from upper margin of orbit; pectoral rays 14; gill rakers 20–24; least bony width of interorbital space 5.25–6.0 in head; last anal-fin ray not elongate, its length 2.55–4.0 in head. *Apogon nigrofasciatus* has been confused with *A. angustatus* (Smith and Radcliffe), *A. cookii* Macleay, *A. fasciatus* (Shaw), *A. novemfasciatus* Cuvier, and *A. taeniophorus* Regan. These five valid dark-striped species are differentiated from it in our discussion.

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*Apogon aroubiensis* was described by Hombron and Jacquinot (1853:31, pl. 1, fig. 1) from a single specimen nearly 6 cm in length collected at Aroub, Malaysia. The color was given as silvery green with four black stripes; the fins were green with a broad brown border; the pectoral fin ray count was 12. Their illustration, reproduced herein as Fig. 1, shows the four black stripes closely spaced on the side of the body with no stripe dorsally or ventrally; very broad dark margins are evident on the second dorsal, anal, caudal, and pelvic fins.

Jordan and Seale (1906:241, fig. 35) recorded a dark-striped species of cardinalfish from Apia and Pago Pago in the Samoa Islands as *Amia aroubiensis*. However, it is clearly different from the *A. aroubiensis* of Hombron and Jacquinot. The illustration of the Samoan fish shows five black stripes—three broad ones on the side and a narrow one dorsally and ventrally; there are no dark borders on any fins.

Radcliffe (1911:250, pl. 22, upper figure) recorded 125 specimens of the same cardinalfish as that of Jordan and Seale as *Amia aroubiensis* from 50 localities in the Philippines and Celebes collected by the U.S. Bureau of Fisheries steamer *Albatross* in 1908 and 1909. He placed *Apogon fasciatus*, as identified in *Fische der Südsee* by Günther (1873:19), in part, in the synonymy of *A. aroubiensis*, specifically citing the broad-striped "variety" of figure A of Günther's plate 20. He pointed out that the true *Apogon fasciatus* is the fish described by White (1790:268, fig. 1) (actually Shaw in White) from Port Jackson (now Sydney), New South Wales. Since Shaw's type has not been found, Lachner (1953:439, pl. 35 A) designated a neotype (USNM 59972, 80.5 mm SL) collected at "Port Jackson" by D. G. Stead. Radcliffe (1911:249) had already provided a description of this fish and illustrated it on pl. 22 (lower figure, though obviously retouched).

1.

Fig. 1. Holotype of *Apogon aroubiensis,* Aroub, Malaysia (after Hombron and Jacquinot 1853).

Günther (1873) included *Apogon fasciatus* Quoy and Gaimard (1825:344) in his synonymy; however, this is a secondary homonym of *Apogon fasciatus* (Shaw). We have examined the holotype of Quoy and Gaimard's *A. fasciatus* (MNHN 853, 54 mm SL); it is a specimen of *A. novemfasciatus* Cuvier (in Cuvier and Valenciennes, 1828).

McCulloch (1915:118) reported two specimens as *Amia fasciata aroubiensis* from Murray Island, Torres Strait and one from Suva, Fiji. He was followed by Marshall (1964:127).

Fowler (1928:157) used the name *Amia aroubiensis* for what he believed to be the same species as Jordan and Seale (1906), listing their reference in his synonymy, and recording Bishop Museum specimens from Tubuai, Nuku Hiva, and Raiatea.

Weber and de Beaufort (1929:302) erroneously placed *A. aroubiensis* in the synonymy of *A. novemfasciatus* Cuvier.

Fowler and Bean (1930:53) reported on the same material from the Philippines and East Indies as Radcliffe; they listed the 104 lots by *Albatross* collection number, locality, date, and gave the lengths of the specimens.

In his treatment of the fishes of the Phoenix and Samoan Islands, Schultz (1943:95) cited the Jordan and Seale reference and one lot of their material as *Apogon aroubiensis*; he recorded an additional specimen from Tutuila.

Lachner (1953:466) described *Apogon nigrofasciatus* from 132 specimens in 26 lots from the Marshall Islands, seven specimens from Guam, five from Western Samoa, and one from Tubuai, Austral Islands. He distinguished his new species from what he regarded as its closest relative, *A. aroubiensis,* principally by its narrower dark stripes.

Randall (1955:71) recorded 17 specimens of *A. nigrofasciatus* from Onotoa, Gilbert

Islands (Kiribati). Noting the similarity to *A. aroubiensis* as defined by Lachner, he wrote, "It is possible that these two forms are merely subspecies of one wide-ranging species."

In 1978 the senior author noticed the discrepancy in color pattern of the illustration and description of *A. aroubiensis* by Hombron and Jacquinot and the fish the above authors have identified as this species. He wrote M. L. Bauchot of the Muséum National d'Histoire Naturelle to request a loan of the holotype of *A. aroubiensis* if extant. She sent a specimen of what was listed as the type, but it proved to be *A. kallopterus* Bleeker, a very different species of cardinalfish. Clearly an error had been made and another fish substituted for the type. Much searching by Bauchot and associates failed to yield the true type of *A. aroubiensis,* and it must be presumed lost.

There is little chance that *A. aroubiensis* Hombron and Jacquinot is the same as the species later authors identified with this name. Not only is the color pattern different, but the pectoral-fin ray count of 12 given by Hombron and Jacquinot does not match the count of 14 that is consistently found in *A. nigrofasciatus.* These authors gave a count of 12 for the pectoral-fin rays of another species of *Apogon* they described as new, *Apogon nigromaculatus.* This nominal species is now regarded as a synonym of *Sphaeramia orbicularis* (Cuvier) which has 12 pectoral-fin rays. It might also be mentioned that the misnamed *A. aroubiensis* is a clear-water fish usually found on well-developed coral reefs, hence a Malaysian locality for it would not be expected. It therefore seems more likely that the true *A. aroubiensis* is a valid species that has not been correctly reported since the original description in 1853. Nevertheless, we recommend that it be regarded as a doubtful species until material which conforms to the original description and figure is found.

Recent collections of fishes in the western Pacific have failed to yield any broad-striped specimens of the species that has been misidentified as *A. aroubiensis,* but numerous lots of *A. nigrofasciatus* have been taken from the Philippines, New Guinea, and Indonesia, largely by Victor G. Springer and associates of the National Museum of Natural History. It would seem that *A. nigrofasciatus* has completely replaced the once abundant *A. "aroubiensis."* A close examination of the color pattern of recent material of *A. nigrofasciatus,* however, has revealed that the pale interspaces have a slight dark pigmentation in a zone next to the adjacent dark stripe on each side. We now conclude that specimens initially preserved in alcohol, as was the *Albatross* material from the Philippines and East Indies, maintain the full dark pigmentation of the stripes in preservative, whereas specimens placed in formalin largely lose the dark edges of the stripes, thus giving a pattern of dark and light bands of about equal width.

We present below a description of *A. nigrofasciatus,* followed by discussion of related or confused species and distribution. Key characters to many of the species of the dark striped "*A. fasciatus*" group are given in Radcliffe (1911) and Lachner (1953). Proportional measurements based on more than 30 specimens are rounded to the nearest 0.05.

Specimens examined are deposited in the Australian Museum, Sydney (AMS); British Museum (Natural History), London [BM(NH)]; Bernice P. Bishop Museum, Honolulu (BPBM); Muséum National d'Histoire Naturelle, Paris (MNHN); J. L. B. Smith Institute of Ichthyology, Grahamstown (RUSI); and National Museum of Natural History, Washington, D.C. (USNM). The lengths given of specimens in Material Examined are standard lengths (SL) in millimeters.

### *Apogon nigrofasciatus* Lachner
Figs. 2, 3

*Apogon nigrofasciatus* Lachner, in Schultz and collaborators, 1953:440, 446, fig. 81,

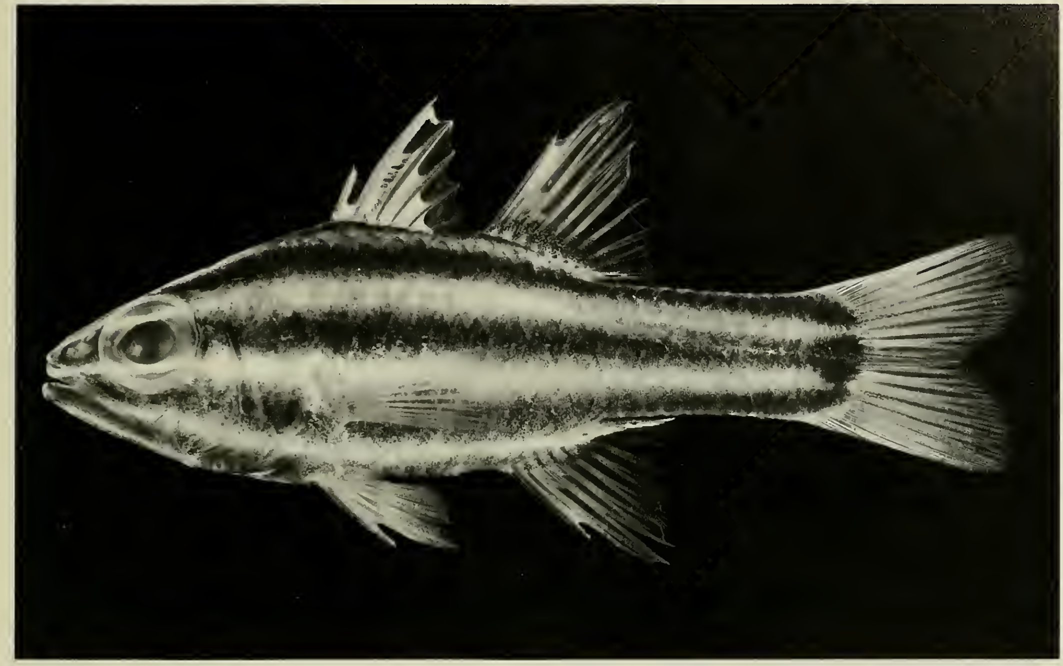

Fig. 2. *Apogon nigrofasciatus,* BPBM 8003, 51 mm SL, Enewetak, Marshall Islands.

pl. 37, D, E (type locality, Bikini, Marshall Islands).

*Description.*—Dorsal-fin rays VII-I,9; anal-fin rays II,8; pectoral-fin rays 14 (rarely 13); lateral line complete, the pored scales 24 or 25 (usually 25) (3 additional pored scales posterior to base of hypural plate); gill rakers 20 to 24 ($\bar{x} = 21.6$); mouth terminal, oblique, the maxilla reaching to or slightly beyond a vertical through posterior edge of pupil; a broad band of villiform teeth in jaws, and a narrow band on vomer and palatines; anterior preopercular margin smooth; posterior preopercular margin serrate (the edge with a series of close-set, small spinules); margin of subopercle smooth; body depth 2.7–3.1 in SL; head length 2.4–2.55 in SL; least bony width of interorbital space 5.25–6.0 in head; first dorsal spine very small, about 20 to 35% length of second dorsal spine, which in turn is about 35 to 50% length of third dorsal spine; third dorsal spine 1.85–2.1 in head; first dorsal soft ray longest, 1.35–1.6 in head; last anal-fin ray not prolonged, its length 2.55–4.0 in SL; caudal fin slightly forked, lobes rounded; pectoral fins 1.45–1.7 in head; pelvic fins reaching beyond anus, sometimes to or slightly posterior to origin of anal fin, longest ray 1.6–1.75 in head. Color in alcohol: pale brown with five uniform dark brown stripes, first narrow, middorsal on nape and along base of dorsal fins, extending broadly onto base of second dorsal fin except for last ray; second dark stripe beginning narrowly on dorsal part of snout, passing along upper edge of eye, enclosing anterior part of lateral line, and ending at upper base of caudal fin; third dark stripe from side of snout, through eye, along center of side of body to mid-caudal base where it is slightly enlarged and darker, thus appearing as an elliptical spot within stripe; fourth stripe from side of maxilla, along lower edge of eye, enclosing pectoral base, and passing to lower caudal fin base; fifth stripe narrow (often faint in preservative), passing from mandible

Fig. 3. Underwater photo of *Apogon nigrofasciatus* taken in the Red Sea off Jeddah, Saudi Arabia.

through pelvic fin base, along lower abdomen, and ending as a band basally in anal fin; second to fourth dark stripes as broad or broader than pale interspaces (distinctly broader if initial preservative was alcohol); ends of second and fourth stripes may converge slightly toward posterior end of midlateral stripe on caudal base, or even join with it (but not extending out onto fin); some dusky pigment anteriorly and basally in spinous dorsal fin; dark stripe at base of second dorsal and anal fins, that of dorsal not set off from base by unpigmented band, except narrow clear zone on last one or two membranes (dark basal band of second dorsal and anal fins more heavily pigmented on mature males than females); faint dusky midlateral streak on caudal fin. In life dark stripes are dark brown to black, suffused with red, lower stripe and anterior part of third and fourth stripes often mainly red; slight enlargement and intensification of black pigment to form spot at caudal fin base at end of midlateral body stripe; another darker area within fourth dark stripe anterior to pectoral fin base; pale interspaces white, sometimes pale yellowish or greenish yellow; edges of fin spines and rays light red, membranes clear (except where noted above as dusky or black).

*Remarks.*—*Apogon nigrofasciatus* is mainly a coral reef inhabitant. It has been taken in the depth range of 1 to 45 m. It rarely occurs in less than 2 meters, however.

Based on available material, this species exhibits a disjunct distribution. It is found throughout the islands of Oceania except the Hawaiian Islands, Easter Island, the Pitcairn Group, and the Marquesas. (The Bishop Museum specimen from Nuku Hiva reported by Fowler, 1928, as *Amia aroubiensis* has been lost. Extensive rotenone collec-

Table 1.—Gill-raker counts of four dark-striped species of *Apogon*.

| | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|---|---|
| *A. angustatus* | | | 14 | 26 | 6 | 1 | | |
| *A. cookii* | 17 | 32 | 33 | 3 | | | | |
| *A. nigrofasciatus,* Marshall Islands | | | | | 4 | 18 | 21 | 3 |
| Other Pacific localities | | | | 7 | 36 | 48 | 17 | 1 |
| Red Sea and Gulf of Aden | | | | | 3 | 18 | 27 | 6 |
| *A. taeniophorus* | 21 | 43 | 41 | | | | | |

tions by the senior author and associates in these islands failed to yield any *A. nigrofasciatus*.) In the western Pacific, *A. nigrofasciatus* ranges from Wakayama Prefecture, Honshu (Masuda et al. 1975) to the Capricorn Group of the southern Great Barrier Reef (Russell 1983). It probably occurs throughout Indonesia and New Guinea. It has been reported (as *Apogon* sp.) by Allen and Steene (1979) from Christmas Island in the eastern Indian Ocean. It is unknown from the rest of the Indian Ocean but is present in the Red Sea where it is among the more common apogonids on coral reefs.

The largest specimen of *A. nigrofasciatus* examined, USNM 142290, from Bikini, measures 73 mm SL.

Lachner (1953:470) noted that *A. nigrofasciatus* from islands in Oceania attains a larger average size than individuals from the East Indies and Philippines. This is still apparent from the additional material we have examined. He also found that the gill-raker counts were higher in the Marshall Islands than in the Philippines. Our additional counts reveal Marshall Island material typically higher than all other Pacific localities combined, though the two sets of counts are broadly overlapping (Table 1). We found no difference between the counts of specimens from western Pacific localities and those of islands of Oceania other than the Marshalls, and have combined these two sets of data. Specimens of *A. nigrofasciatus* from the Red Sea also show higher gill-raker counts than those from Pacific localities other than the Marshall Islands.

*Apogon nigrofasciatus* has been confused by some authors with *A. novemfasciatus* Cuvier. The latter, however, is easily distinguished by two sectors of its midlateral stripe which are darker and slightly enlarged—one behind the gill opening and one in the middle of the body. Also the second and fourth stripes converge toward the midlateral stripe well out on the caudal fin (see Jordan and Seale 1906: fig.36).

The three dark-striped, Indo-Pacific species most often confused with *A. nigrofasciatus* are: *A. cookii* Macleay (1881), of which *A. melanotaenia* Regan (1905) and *A. robustus* (Smith and Radcliffe in Radcliffe, 1911) are junior synonyms; and *A. angustatus* (Smith and Radcliffe in Radcliffe, 1911); and *A. taeniophorus* Regan (1908), of which *A. fasciata stevensi* (McCulloch, 1915) and *A. saipanensis* (Fowler, 1945) are junior synonyms.

Fowler was unable to locat the type specimens of his *Lovamia saipanensis* for Lachner, so the latter regarded it as a valid species (Lachner 1953:439). Fraser (in Böhlke 1984), however, placed it in the synonymy of *A. novemfasciatus*. Except for a diagonal dark stripe on the abdomen (which Fowler attributed to the blackish peritoneum showing through the body wall), the color pattern of Fowler's figure of *A. saipanensis* resembles *A. taeniophorus,* not *A. novemfasciatus.* The second and fourth dark stripes do not converge on the caudal fin and the midlateral stripe is uniform in width and pigmentation. We made counts of 14 pectoral rays and 18 for the gill rakers of the holotype of

Fig. 4. *Apogon cookii,* BPBM 20834, 75 mm SL, Gulf of Aqaba, Red Sea.

*A. saipanensis.* On the basis of the color pattern and these counts we place *A. saipanensis* in the synonymy of *A. taeniophorus.*

*Apogon cookii* (Fig. 4) may be distinguished from *A. nigrofasciatus* by nearly always having 15 pectoral rays (Fraser 1974, Table 1), by its lower gill-raker counts (Table 1 herein), its broader interorbital space (bony width 4.15–5.1 in head, compared to 5.25–6.0 for *A. nigrofasciatus*), and in color. Adults have a narrow dark stripe extending posteriorly from the upper edge of the orbit, often to below the second dorsal fin. Also the dark band in the second dorsal fin is separated from the base by a narrow whitish band. Grant (1982: pl. 130) illustrated *A. cookii* in color (as *A. novemfasciatus*). This species occurs in very shallow water, generally less than 2 m. Although usually found on rocky substrata, as under ledges in tidepools, it may also be seen in seagrass beds or around small coral heads.

*Apogon taeniophorus* (Fig. 5) has the same pectoral-ray count of 14 as *A. nigrofasciatus*; however, it is completely separable by its low gill-raker counts (Table 1). It also has a broad interorbital space, the least bony width 4.5–5.35 in head. It is very similar in color to *A. cookii,* differing in lacking a distinct dark spot in the midlateral stripe at the caudal fin base. Its spot, if it can be distinguished at all, is elliptical, only slightly broader than the stripe, and at best slightly darker. By contrast, the caudal base spot of *A. cookii* is distinctly larger than the stripe width, round or nearly round, and darker than the stripe. The narrow dark stripe extending posteriorly from the upper orbit is not as well developed as on *A. cookii. Apogon taeniophorus* is also a species of shallow water of variable habitat from surge chan-

Fig. 5. *Apogon taeniophorus,* BPBM 16045, 58 mm SL, Guadalcanal, Solomon Islands.

nels of exposed reefs to rock or debris in mud-bottom harbors.

*Apogon angustatus* (Fig. 6) usually has 14 pectoral rays. Its gill-raker counts are lower than those of *A. nigrofasciatus* but do not provide complete separation (Table 1). The last anal rays of this species are elongate, thus the distal border of the fin is distinctly concave; the length of the last anal ray is contained 1.75–2.65 times in the head length, compared to 2.55–3.8 for *A. nigrofasciatus.* The dark stripes of *A. angustatus* are narrower than the whitish interspaces; they are blackish at Indian Ocean localities and yellowish brown at islands of Oceania (on these Pacific fish the black spot at the caudal fin base is therefore more conspicuous). *Apogon angustatus* has been collected on coral reefs in the depth range of 6 to 40 meters.

Mention should be made of *Apogon fasciatus* (Shaw) since some authors have placed *A. aroubiensis* in the synonymy of, or as a subspecies of this species. *Apogon fasciatus* is now regarded as a senior synonym of *A. quadrifasciatus* Cuvier. It has the short post-ocular dark stripe from the upper edge of the orbit as in *A. cookii* and *A. taeniophorus,* but lacks a well developed dark stripe below the midlateral stripe (though this was mistakenly added to the illustration in Radcliffe 1911: pl. 22). The anus is black. The gill rakers range from 18–22; the neotype has 22.

*Material examined.—Apogon angustatus*: In addition to the holotype of *Amia angustata* Smith and Radcliffe, we have examined USNM material from Borneo and the Trobriand Islands, and two MNHN and 40 BPBM specimens, 21–78 mm, from the Pitcairn Group, Tuamotu Archipelago, Society Islands, Line Islands, Palau Islands, New Caledonia, New Guinea, Seychelles, and Mauritius. Also we have examined ten RUSI specimens from Natal, 23–63 mm.

*Apogon cookii*: We have examined the syntypes of *Apogon cookii* Macleay (AMS I.16307-001, 6: 35.5–63) from the Endeav-

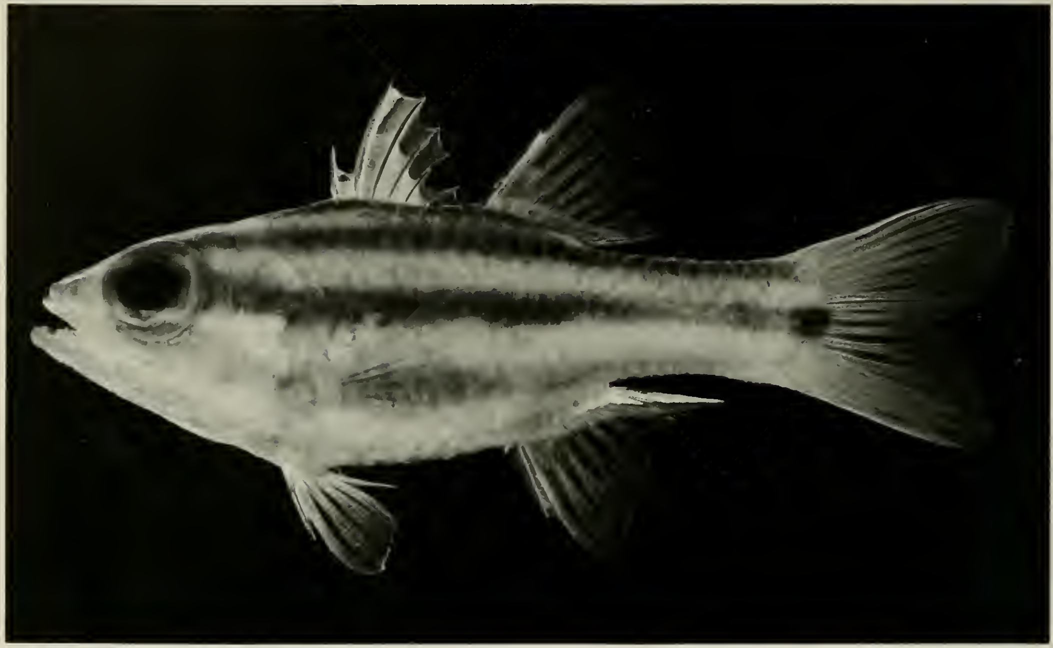

Fig. 6. *Apogon angustatus,* BPBM 6946, 71 mm SL, Tahiti, Society Islands.

or River, northern Queensland and the holotype of *Apogon robustus* (Smith and Radcliffe) from Jolo, Philippines. Also 100 BPBM and USNM specimens from the following major localities: New Caledonia, Great Barrier Reef, Taiwan, Western Australia, SE India, Seychelles, Natal, Tanzania, Kenya, and the Red Sea.

*Apogon nigrofasciatus*: In addition to the type specimens as listed by Lachner (1953) and the USNM material given by *Albatross* field numbers in Fowler and Bean (1930), we have examined specimens from the following localities: TUAMOTU ARCHIPELAGO: Mangareva, BPBM 13558, 2: 49–56.8 mm. Rangiroa, BPBM 10258, 48 mm; BPBM 25224, 57.2 mm. SOCIETY ISLANDS: Tahiti, BPBM 10283, 2: 26–54.2 mm. Moorea, MNHN 1984-118, 3: 32.2–52.5 mm; BPBM 11969, 7: 40.5–53 mm. Raiatea, BPBM 1674, 48 mm; BPBM 1675, 46 mm. RAPA: BPBM 17268, 2: 55.7–69.6 mm. AUSTRAL ISLANDS: Tubuai, BPBM 794, 65 mm; BPBM 795, 62 mm. COOK ISLANDS: Aitutaki, BPBM 5612, 11: 33–52.1 mm. FIJI: Viti Levu, USNM 176632, 2: 54–59 mm. VANUATU (NEW HEBRIDES): Espiritu Santo, USNM 262508, 2: 37–47 mm. Efate, BPBM 5615, 55.5 mm. LOYALTY ISLANDS: Uvéa, BPBM 27071, 61.4 mm. NEW CALEDONIA: BPBM 11466, 46.2 mm. GREAT BARRIER REEF: Hook Island, BPBM 15556, 4: 33.4–51 mm. Yonge Reef, MNHN 1978-588, 51 mm. SOLOMON ISLANDS: Guadalcanal, BPBM 5695, 41 mm; BPBM 15578, 2: 29–34.2 mm; BPBM 16157, 3: 32.5–41 mm; USNM 262511, 46 mm. NEW IRELAND: USNM uncat., 17: 32–48 mm. NEW GUINEA: Bagabag Island, USNM 262709, 31: 18–52 mm. Massas Island, BPBM 262612, 6: 19–48.5 mm. Louisade Archipelago, USNM 262710, 36: 30–59 mm. Madang, BPBM 15761, 44.2 mm. Ninigo Islands, BPBM 30345, 29: 31.2–46.8 mm; USNM 262426, 15: 16–49 mm. Hermit Islands, USNM 261037, 32: 20–29.5 mm. INDONESIA: Ambon, BPBM 19312, 3: 35–53.7 mm. Banda Islands, USNM 262706, 13: 29–42 mm. Kai Islands, USNM

262704, 12: 30–47 mm. Bali, BPBM 30181, 3: 42.5–49 mm. PHILIPPINES: Siquijor Island, BPBM 30210, 29: 31.2–46.8 mm; USNM 260967, 75: 15–49 mm. Apo Island, BPBM 30344, 24: 28.7–48 mm; USNM 262375, 3: 42–51.5 mm. Palawan, USNM 262369, 17: 38–46 mm. Negros, BPBM 28585, 2: 49–51.5 mm; BPBM 30343, 67: 29–48.9 mm; USNM 262366, 16: 13.5–48 mm. Balicasag Island, USNM 260963, 19: 32–51 mm. Cebu, USNM 262383, 15: 13.5–47 mm. Mactan Island, USNM 262374, 10: 24–48 mm. TAIWAN: BPBM 23302, 33 mm; BPBM 23369, 36.5 mm. RYUKYU ISLANDS: Ishigaki, BPBM 8697, 5: 45–64.5 mm. PALAU ISLANDS (BELAU): BPBM 7423, 60.6 mm; BPBM 9808, 2: 44–47 mm. CAROLINE ISLANDS: Truk, BPBM 9062, 42.2 mm. MARSHALL ISLANDS: Enewetak, BPBM 8003, 5: 49–63 mm; BPBM 8220, 44.2 mm; BPBM 8254, 2: 56–56.2 mm; BPBM 8256, 4: 44.5–59.3 mm; BPBM 8288, 54.5 mm; BPBM 29142, 15: 38.5–71 mm. GULF OF ADEN: MNHN 1977-639, 4: 48.5–52 mm; MNHN 1977-642, 57 mm; MNHN 1977-643, 54 mm. RED SEA: MNHN 1952-95, 52 mm. Gulf of Aqaba, BPBM 13397, 3: 35–52.2 mm; BPBM 18370, 3: 51.3–65 mm; MNHN 1977-815, 62 mm; MNHN 1977-816, 52.5 mm; USNM 212777, 12: 37.7–61 mm; USNM 212782, 21: 17.0–62 mm; USNM 213612: 35 mm.

*Apogon taeniophorus*: We have examined the syntypes of *A. taeniophorus* Regan from the Maldives BM(NH) 1908.3.23.90–92, 3: 43–77 mm SL, and the holotype of *A. saipanensis* (Fowler) from the Marianas (ANSP 71588, 22 mm SL). In addition, we have seen specimens listed by Lachner (1953) from the Marshall Islands and Marianas as *Apogon robustus,* and 128 BPBM specimens, 19–92.5 mm, from the following major localities: Pitcairn Group, Society Islands, Austral Islands, Rapa, Cook Islands, Line Islands, Gilbert Islands (Kiribati), Marshall Islands, Minami Tori Shima (Marcus Island), Taiwan, Indonesia, Fiji, Solomon Islands, New Britain, SW Thailand, SW India, Seychelles, Tanzania, Natal, Gulf of Aden, and the Red Sea.

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# *HADOCERAS TAYLORI,* A NEW GENUS AND SPECIES OF PHREATIC HYDROBIIDAE (GASTROPODA: RISSOACEA) FROM SOUTH-CENTRAL TEXAS

Robert Hershler and Glenn Longley

*Abstract.*—*Hadoceras taylori,* a new genus and species of Hydrobiidae, Littoridininae, is described from three localities in Real County, Texas. This phreatic species may well range throughout the southern portion of the Edwards Plateau and into northern Mexico. The detailed morphological description provided for this species includes aspects of the shell, operculum, pallial cavity, digestive system, and reproductive system of both sexes. Generic separation of *Hadoceras* from similar-shelled late Tertiary *Orygoceras* is warranted by both morphological and ecological considerations. A suite of unique characters, including the uncoiled, horn-like shell and concentric operculum with ventral process, separates *Hadoceras* from other known phreatic littoridinines of south-central Texas and northern Mexico.

Taylor's (1974) discovery of living phreatic snails from Roaring Springs, Texas referable to *Orygoceras* Brusina, 1882, a genus previously known only as late Tertiary fossils from Idaho and southeastern Europe, ranks as a particularly exciting event in the recent history of freshwater malacology. The uncoiled, horn-like shell of *Orygoceras* is highly unusual among gastropods (Rex and Boss 1976) and the systematic placement of this genus has long been debated (Taylor 1974). Taylor (1974) concluded that living *Orygoceras* is a hydrobiid (Prosobranchia: Rissoacea), but did not describe this species. His morphological study was necessarily limited as he collected a single live specimen, and various aspects of anatomy, including details of the male and female reproductive system critical to the systematic assessment of rissoacean snails, were not dealt with.

As part of an ongoing survey and systematic study of phreatic gastropods of south-central Texas (see Hershler and Longley, 1986) we collected more than 20 live *Orygoceras* sp. (including a number of adults) from Roaring Springs and two other springs in Real County, Texas. We describe this snail as *Hadoceras taylori,* a new genus and species of Hydrobiidae; provide a detailed morphological description of this taxon, including aspects of the male and female reproductive systems; and discuss the systematic relationships of *Hadoceras,* emphasizing comparisons with other members of the diverse phreatic hydrobiid fauna of south-central Texas and northern Mexico.

*Localities.*—*Hadoceras taylori* was collected during May 22–24, 1985 from the following three springs (see Fig. 1): a) Roaring Springs (unnamed on USGS topographic sheets), about 7.6 miles W of Camp Wood (water temperature 21.0°; conductivity 319.2 ymHOS; 5/23); b) Unnamed spring in South Prong Canyon, 6.6 miles W of Camp Wood (temperature 21.0°; conductivity 415.0 ymHOS; 5/23); and c) Unnamed spring at Jo Jan Van Camp, 9 miles N of Vance. All three springs are moderate-sized rheocrenes, with numerous orifices. They occur in the Nueces River drainage in the region where the southern edge of the Edwards Pla-

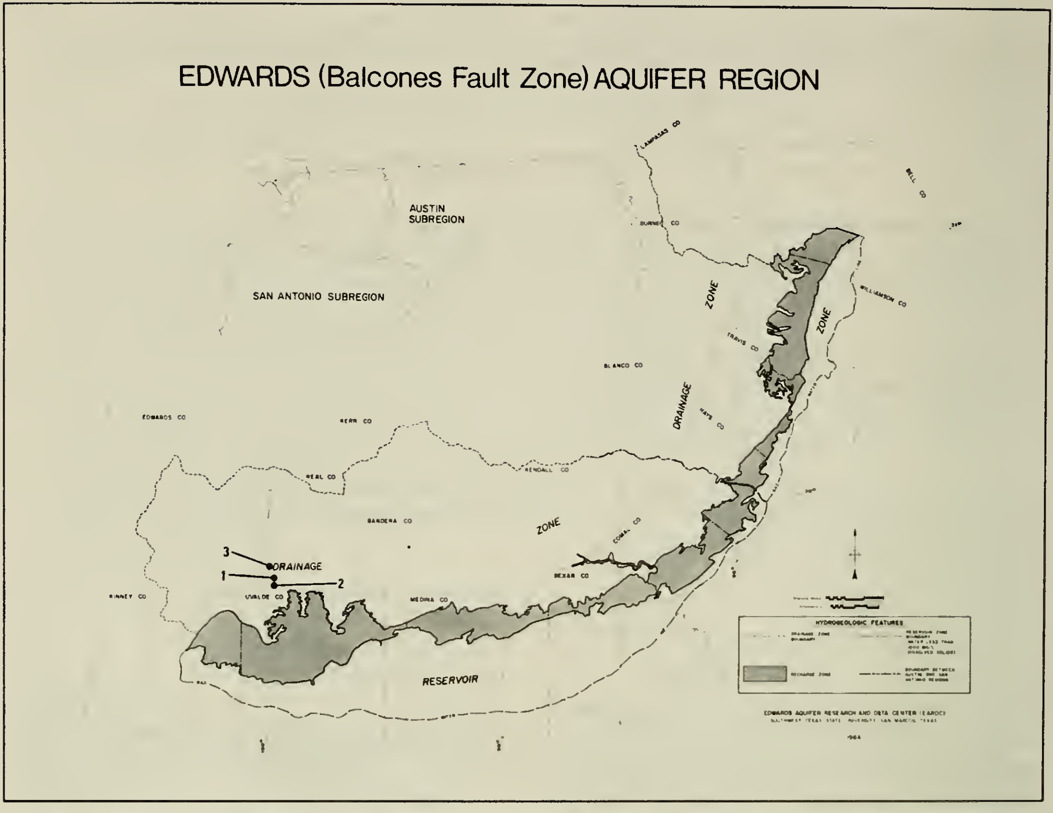


Fig. 1. Map of the Edwards (Balcones Fault Zone) Aquifer Region showing the three localities from which *Hadoceras taylori* were collected. The localities are Roaring Springs (1), an unnamed spring in South Prong Canyon (2), and an unnamed spring at Jo Jan Van Camp (3).

teau gives rise to the well-dissected Hill Country. The water-bearing unit feeding the springs is probably the Trinity group of lower Cretaceous limestone (Ashworth 1983).

*Methods.*—Three methods were used to collect *H. taylori* and other phreatic organisms at these localities. Sections of PVC pipe capped with fine (64 $\mu$) mesh netting at one end were placed overnight in spring orifices to filter the water stream emerging from underground. Cotton gauze was placed overnight in the orifices to serve as an artificial colonization substrate for these organisms. Finally, sediments in the uppermost sections of the spring runs were sifted using a fine hand sieve.

Methods of morphological study are those of Hershler and Longley (1986). Usage of body surface references follows that of Fretter and Graham (1962). All morphological data presented are from individuals collected from Roaring Springs. Unless otherwise indicated, unrelaxed preserved specimens (initially fixed in formalin) were used for anatomical study. A total of six individuals was dissected.

### Family Hydrobiidae
### Subfamily Littoridininae
### *Hadoceras,* new genus

*Orygoceras* Brusina, 1882 (in part):33.

*Diagnosis.*—Shell (Figs. 2–4) minute (maximum dimension, less than 2.8 mm),

Fig. 2. Holotype (USNM 849000) of *Hadoceras taylori* (shell width, 2.37 mm).

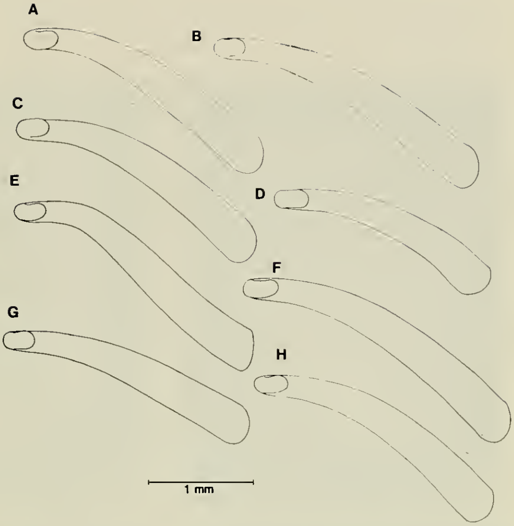
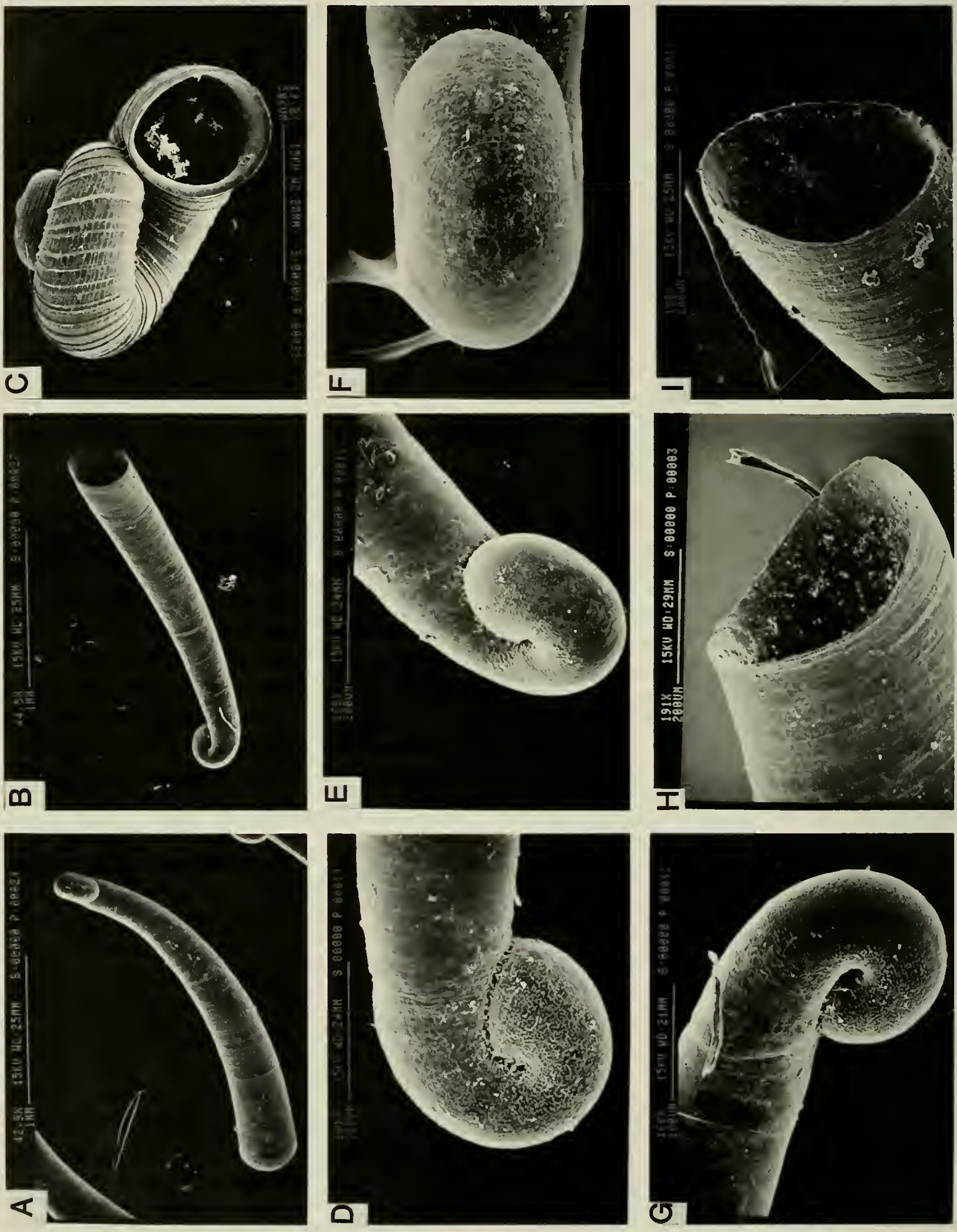


Fig. 3. Camera lucida drawings of shell outlines of *H. taylori,* including the holotype (A) and paratypes (D–H, USNM 849001). Note the variation in translation rate along the coiling axis.

colorless, transparent, horn-like in shape with uncoiled teleoconch and simple aperture (Fig. 4B, H, I). Protoconch with pitted microsculpture (Fig. 4D), teleoconch with strong collabral growth lines (Fig. 4H). Operculum (Fig. 5) concentric, with a large, peg-like, non-calcareous process on ventral surface. Animal unpigmented and without eyespots (Figs. 6, 7). Ctenidium absent (Fig. 7). Intestine (In) with loop on right side of style sac (Fig. 10) and coil in roof of pallial cavity (Figs. 6, 7). Central tooth of radula trapezoidal in shape, with a single pair of basal cusps arising from lateral angles (Figs. 8, 9). Pallial gonoducts (Pr, Ag, Fig. 6) displaced ventrally. Gonads consisting of non-lobed mass, occupying 20–25% of total body length. Pallial portion of prostate less than 20% of prostate length; anterior vas deferens exiting from anterior tip of prostate (Fig. 10C). Penis simple, without lobes or specialized glands (Fig. 10B). Capsule gland (Cg) with two tissue sections and terminal opening (Cga, Fig. 11). Albumen gland (Ag) loops posteriorly (around bursa (Bu)), with posterior tip joining oviduct (Ov, Fig. 11); sperm duct (Sdu) issuing from this juncture and connecting with anterior portion of spermathecal duct (Sd). Seminal receptacle absent; spermathecal duct and capsule gland opening jointly (Cga).

*Remarks.*—The morphological groundplan of *Hadoceras* clearly indicates that it is a member of the Hydrobiidae (see family definition in Davis 1979) and the presence of a spermathecal duct suggests placement in the Littoridininae (see Davis et al. 1982; Hershler 1985). Apart from its shell form, unique among hydrobiids, character-states distinguishing *Hadoceras* from other littoridinines include the concentric operculum with ventral process, unusual ventral displacement of the pallial gonoducts, and combination of minute adult size and simple penis.

There is little doubt that European *Orygoceras,* which has been considered as either an uncoiled valvatid or planorbid (Wenz 1938–44; Papp 1962), is distinct from *Hadoceras.* The shells of the former are not only much larger (to 10 mm) than those of *Hadoceras,* but also differ in form, having a much larger whorl expansion rate, non-circular aperture, and (often) macrosculptural de-


A
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velopment. The inferred habitat of European fossil *Orygoceras* is lacustrine (Taylor 1974), as opposed to the phreatic habitat of *Hadoceras*. A similar set of arguments suggests generic distinction of *Hadoceras* from the Idaho fossil *Orygoceras*, which are as large as those from Europe, and are similarly found in ancient lake bed deposits (Dall 1924; Yen 1944; Taylor 1966).

*Type species.*—*Hadoceras taylori* (by original designation).

*Etymology.*—From the Greek words *Hades* and *keras*, meaning the god of the underworld and a horn, respectively, and referring to the subterranean habitat and horn-like shell of this genus. Gender neuter.

*Distribution.*—*Hadoceras taylori* occurs in phreatic habitats associated with Cretaceous limestone aquifers in Real County, Texas. Davis (1983) reports fresh shells referable to this species from Williamson County, and it is likely that the species ranges throughout limestone aquifers in the southern edge of the Edwards Plateau. In addition, live specimens of what appears to be the same species were collected by the senior author from groundwater outlets in the Cuatro Cienegas Basin, northeastern Mexico (Hershler 1985). Fossil shells in the 2–3 millimeter range representing possibly a second *Hadoceras* sp. were collected by W. Pratt from an archaeological site in the Las Vegas Wash (Nevada) northeast of Henderson. The shells were radiocarbon dated as 400 years B.P. and the inferred fossil habitat at the site is a marshy spring area (W. Pratt, pers. comm. 1985).

*Habitat.*—The collection of living *H. taylori* by placing nets into groundwater outlets, nets that cannot be entered by crenobiontic organisms, demonstrates that this species does occur in the phreatic environment. It is also apparent from collections taken from the upper spring runs that the species also inhabits this epigean habitat. We do not concur with the assertions of Taylor (1974) and Davis (1983) that *H. taylori* is necessarily interstitial in habit. The Cretaceous limestone aquifers in south-central Texas are extremely porous, with openings ranging upwards in size to large caverns (Brune 1975), and there is no reason to suspect that the species is limited to interstitial habitats. The presence of much larger phreatic organisms in these aquifers, including vertebrates, attests to the use of non-interstitial habitats (Longley 1981).

*Associated fauna.*—Phreatic organisms collected with *H. taylori* include another phreatic hydrobiid, *Phreatodrobia* sp. (Fig. 4C), as well as diverse crustaceans, including isopods, amphipods, and copepods.

### *Hadoceras taylori*, new species

Figs. 1–12

*Orygoceras* sp. Taylor, 1974:93.

*Description.*—Shell: For 8 (fresh) adult shells, height and width ranged from 0.946–1.81 and 2.00–2.03 mm respectively (Table 1). The thin shell is transparent when fresh, but has an opaque, white aspect in older specimens. The protoconch has 1.0–1.12 whorls, a diameter of about 0.32 mm, and coils in the same plane as the beginning of the teleoconch (Fig. 4A, F). The junction between the protoconch and teleoconch is quite noticeable (Fig. 4D), often due to a sudden increase in diameter of the generating curve, or sudden change in direction of coiling at the beginning of the teleoconch. The teleoconch typically gently curves away from and down the coiling axis with only a slight whorl expansion, producing the horn-

←

Fig. 4. Scanning electron micrographs of shells of *H. taylori* (A, B, D–I) and *Phreatodrobia* sp. (C). The protoconch is shown from above (D), below (G), and from the side (F, 300×). The aperture is shown from above (H, inner lip to the right) and below (I, inner lip above).

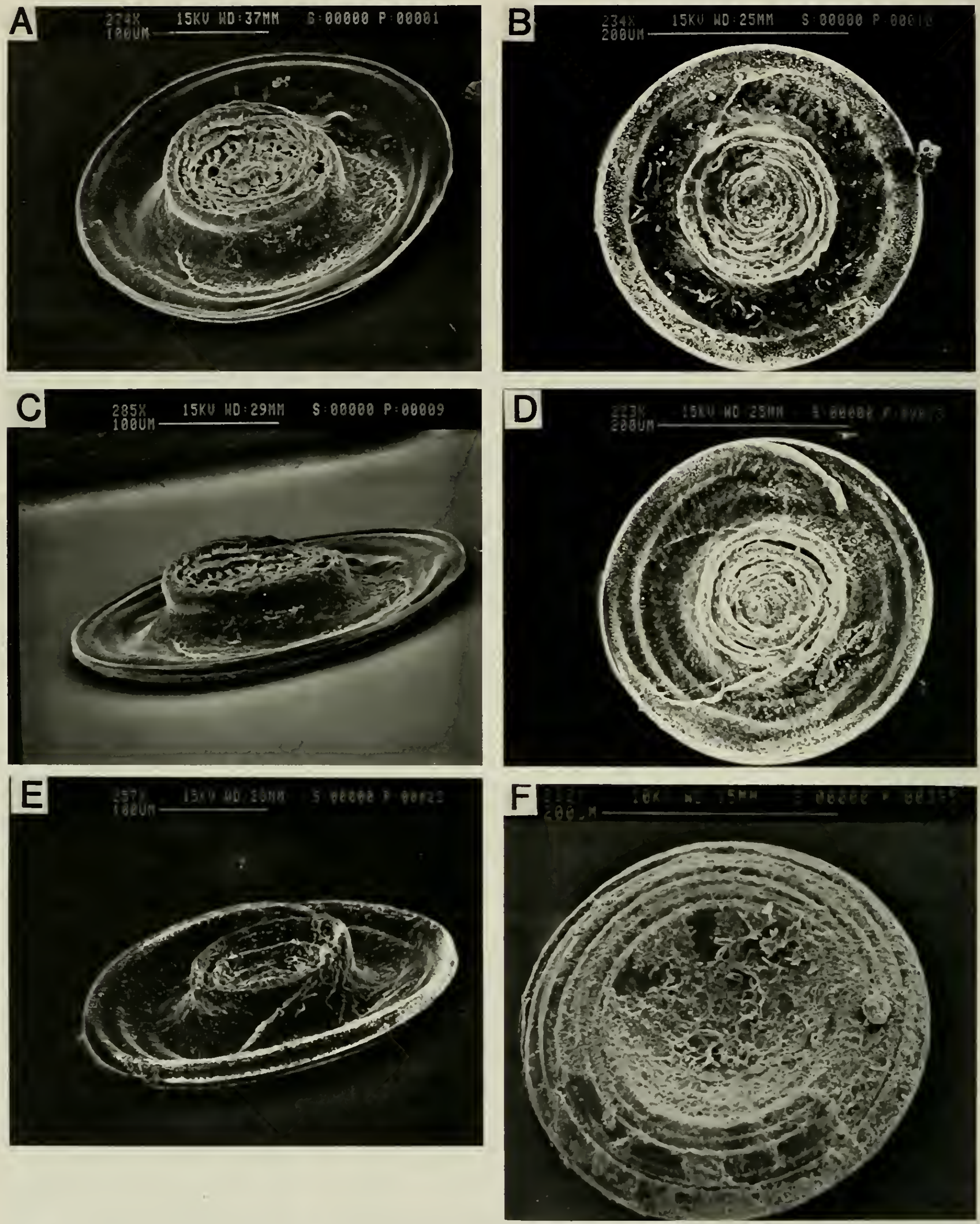

Fig. 5. Scanning electron micrographs of the operculum of *H. taylori* showing the ventral (A–E) and dorsal (F) aspects.

like shell shape, but the rate and nature of whorl translation vary, as seen in Fig. 3 and reflected in the above data. Note that the teleoconch may initially translate slightly above the protoconch, or suddenly dip down the coiling axis. The teleoconch does not coil in a single plane, but is somewhat bowed (towards the viewer in Fig. 3). The aperture, while near-circular (diameter of 0.35 mm), does not lie in a single plane as the inner lip is rather advanced. While not noticeably flared, the aperture is sometimes slightly expanded at the outer lip (Fig. 4H). The teleoconch growth lines are especially pronounced at the aperture.

*Operculum.*—The horny operculum is near-circular (Fig. 5B, D, F), with a typical diameter of 0.31 mm. The ventral process, centrally located, occupies a good portion of the operculum area. When viewed dorsally, this central region appears depressed (Fig. 5F). The portion of the operculum peripheral to the ventral process is also thickened and somewhat curved in the ventral direction (Fig. 5C, E). Of the 7–8 operculum whorls, which are arranged in near-concentric circles, the earliest 4 are located in the area occupied by the ventral process. Note that the distal end of the ventral process is concave, reflecting the progressive increase in process height from the first to fourth whorl. After the fourth whorl the process height then quickly decreases to the level of the peripheral portion of the operculum.

*General anatomy.*—A set of anatomical data obtained from each of 4 specimens (2 males, 2 females) is given in Table 2. While lacking melanin pigment, the body of the snail does have black, spherical granules typically concentrated in 3 areas: on the right side of the digestive gland, where it covers the stomach and ventral to the gonad (Fig. 6A); and on the left side of the style sac (not figured). Apart from the red-pink color seen in the buccal mass and foot (due to hemoglobin), yellow-green color of the prostate (Pr), and yellow color of the ovary (Ova), the only other color visible in the animals is in the stomach, style sac and intestine, where the food contents and faecal pellets appear brown.

Table 1.—Shell height and width (mm) for the eight adult specimens of *Hadoceras taylori* shown in Fig. 4.

| | Shell height | Shell width |
|---|---|---|
| Holotype | 1.20 | 2.37 |
| Paratype | 1.82 | 2.15 |
| Paratype | 1.12 | 2.00 |
| Paratype | 0.95 | 2.44 |
| Paratype | 1.81 | 2.41 |
| Paratype | 1.34 | 2.17 |
| — | 1.20 | 2.63 |
| — | 1.27 | 2.06 |

The illustration of the head in Fig. 7 is based on examination of a single, somewhat damaged live specimen in a partly contracted state. In a more typical live individual the snout (Sn) is probably less squat and the tentacles (Tn) more elongate, as illustrated by Taylor (1974, fig. 1). Terminal setae on the tentacles, figured by Taylor (1974, fig. 1), were not visible in the contracted specimens examined. The inner base of the tentacles has a dense concentration of clear, crystalline granules (Fig. 7).

As seen in Fig. 6, the pallial gonoducts (Pr, Ag) are situated more ventrally than is typical of hydrobiids (and prosobranchs in general), and actually lie over the oesophagus. The functional necessity for such a shift may be the need to accommodate the large kidney and intestinal loop on the style sac that lie dorsal to the gonoducts. This space constraint is also reflected in the unusual narrow nature of both gonoducts.

*Pallial cavity.*—The contents of the pallial cavity, which occupies 21–26% of the total body length, are shown in Fig. 7. While no trace of the ctenidium is seen, the large osphradium (Os), occupying 27–34% of the pallial cavity length, is found in its usual position. The intestine (In) makes a large, U-shaped loop that fills much of the pos-

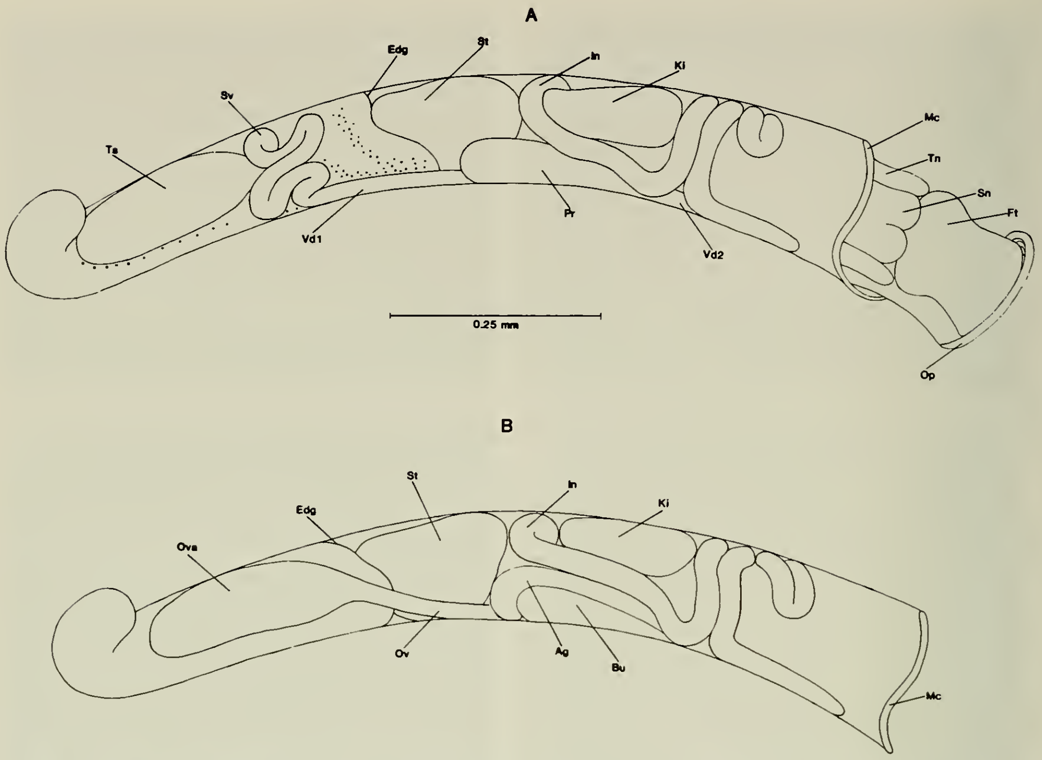

Fig. 6. Male (A) and female (B, minus the head/foot) *H. taylori,* viewed from the right lateral aspect. Ag, albumen gland; Bu, bursa copulatrix; Edg, anterior end of the digestive gland; Ft, foot; In, intestine; Ki, kidney; Mc, mantle collar; Op, operculum; Ov, oviduct; Ova, ovary; Pr, prostate; St, stomach; Sv, seminal vesicle; Tn, tentacle; Ts, testis; Vd1, posterior vas deferens; Vd2, anterior vans deferens.

terior portion of the pallial cavity roof, the loop actually bending back upon itself when the pallial cavity roof is viewed in its normal curved orientation (Fig. 6), and not flattened out as in Fig. 7. The anus is situated within 0.06 mm of the mantle edge. The pericardium (Pc) is rather small and narrow, whereas the kidney (Ki) is enlarged, with a simple, non-fleshy opening.

*Digestive system.* —The radula of *H. taylori* is shown in Figs. 8 and 9. The generalized cusp formulae, based on examination of scanning electron microscope photographs of 4 radulae, are as follows: central, 4(5)-1-4(5)/1-1; lateral, (4–6)-1-5; inner marginal, 17–21; outer marginal, 15–16. The width of the central tooth is about 0.0097 mm. Note that the central cusps of the central and lateral teeth are enlarged relative to other cusps on these teeth. Also note the relatively large basal cusps on the central teeth and the well-excavated basal process. The shape of the cusps on the central teeth varies from hoe-like (Fig. 8B) to dagger-like (Fig. 8D).

The oesophagus (Oes) coils once immediately upon exiting from the head/foot mass (Fig. 7). The two stomach chambers (Ast, Pst) are poorly differentiated externally (Fig. 10A) and there is no caecal appendix. Two solid masses of digestive gland exit from the single opening of the stomach (Odg). The digestive gland lacks noticeable tubular swellings. The stomach is typically only slightly longer than the narrow style sac (Sts). Note that the intestine (In) exits from the left side of the style sac very close to where the latter joins the stomach.

*Male reproductive morphology.*—The seminal vesicle (Sv) exits from the anterior tip of the testis and consists of a tight mass of several coils, measuring about 0.2 by 0.2 mm, that fills the space between the testis and stomach. The prostate (Pr), which is 5 times as long as wide, overlies a portion of the anterior stomach chamber. Note that the vas deferens (Vd1) enters the prostate near its mid-line, which is considerably posterior to the end of the pallial cavity (Fig. 10C). The anterior vas deferens (Vd2) exits from the tip of the prostate as a thickened tube, which then travels 0.6–0.7 mm anteriorly in the pallial cavity roof before turning back posteriorly to enter the "neck" and travel a similar distance to the base of the penis (Pn, Fig. 7).

The penis (Fig. 10B) coils counter-clockwise in a tight fashion, on the "neck" behind the snout. While lobes are absent, both edges of the penis have small folds, although the folds end on the inner edge at two-thirds of the penis length from the base. The vas deferens does not coil greatly in the penis and is eversible at the penis tip. The single penis examined from a living individual (shown in Fig. 10B) lacked cilia, although columnar epithelia were seen along both edges. Single large spherical granules occur along the proximal two-thirds of the penis.

*Female reproductive morphology.*—Large, spherical oocytes were seen in the posterior portion of the ovary of several specimens. Note that the anterior end of the ovary (Ova) abuts the posterior end of the stomach (St, Fig. 6B). The oviduct (Ov) exits from the anterior end of the ovary and disappears to the left side of the bursa and pallial oviduct (Bu, Ag, Fig. 6B).

The pallial oviduct (Cg + Ag, Fig. 11) is unusually narrow along its entire length. The anterior section of the capsule gland is twice as long (but much narrower) as the posterior section, and clear rather than white. The albumen gland, which is thin, clear, tubular, and decidedly non-glandular; extends posteriorly to slightly overlap the stomach, and then loops anteriorly with its length slightly overlapping the right side of the bursa (Bu, Figs. 10B, 11). Although egg capsules were not found, we suspect that the species is oviparous and not ovoviviparous.

The oviduct (Ov) has a single, swollen coil on the left side of the bursa. The coil has a pink sheen and is the probable site of sperm storage, given the absence of a seminal receptacle. Just anterior to this coiled section, the oviduct opens into the albumen gland, the connection being difficult to recognize as the terminal portion of the albumen gland is extremely fragile and easily ruptured. The sperm duct (Sdu) issuing from this point is very narrow relative to the coiled oviduct, and extends anteriorly, looping back to the right side of the spermathecal duct (Sd) to enter the pallial cavity roof and finally join

Table 2.—Measurements (mm) of organs and structures for four specimens of *Hadoceras taylori*. M = male, F = female.

| Specimen | 1 (M) | 2 (M) | 3 (F) | 4 (F) |
|---|---|---|---|---|
| Shell width | 2.54 | 2.51 | 2.51 | 2.57 |
| Body length | 2.04 | 1.92 | 1.96 | 2.26 |
| Snout length | 0.16 | 0.14 | 0.18 | 0.12 |
| Tentacle length | 0.16 | 0.14 | 0.18 | 0.14 |
| Pallial cavity length | 0.42 | 0.41 | 0.51 | 0.59 |
| Osphradium length | 0.14 | 0.14 | 0.14 | 0.16 |
| Osphradium width | 0.089 | 0.079 | 0.10 | 0.12 |
| Stomach length | 0.36 | 0.34 | 0.34 | 0.36 |
| Stomach width | 0.22 | 0.22 | 0.22 | 0.24 |
| Style sac length | 0.30 | 0.20 | 0.28 | 0.32 |
| Style sac width | 0.10 | 0.10 | 0.11 | 0.10 |
| Gonad length | 0.44 | 0.38 | 0.50 | 0.51 |
| Gonad width | 0.16 | 0.16 | 0.14 | 0.20 |
| Prostate length | 0.50 | 0.50 | — | — |
| Prostate width | 0.10 | 0.12 | — | — |
| Pallial prostate length | 0.10 | 0.08 | — | — |
| Penis length | 0.20 | 0.18 | — | — |
| Pallial oviduct length | — | — | 0.87 | 0.83 |
| Pallial oviduct width | — | — | 0.18 | 0.10 |
| Bursa length | — | — | 0.42 | 0.59 |
| Bursa width | — | — | 0.12 | 0.14 |

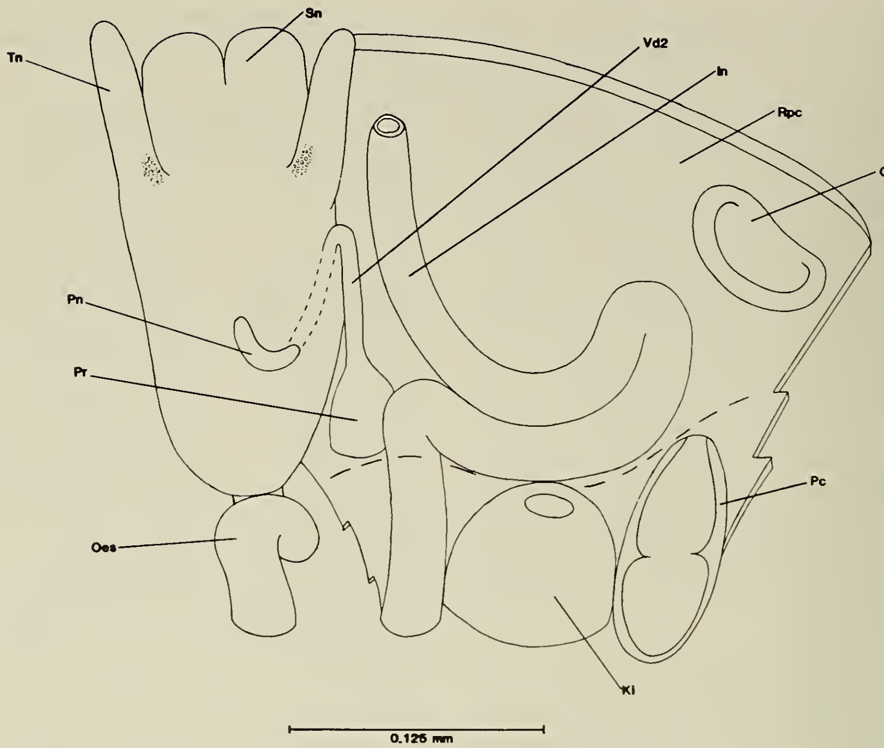

Fig. 7. Head and contents of the pallial cavity of *H. taylori.* The length of the pallial cavity roof has been cut along the extreme left side and then flattened out to the right. The dashed line indicates the posterior end of the pallial cavity. The posterior portion of the prostate has been removed. In, intestine; Ki, kidney; Oes, oesophagus; Os, osphradium; Pc, pericardium; Pn, penial attachment area; Pr, prostate, Rpc, roof of pallial cavity; Sn, snout; Tn, tentacle; Vd2, anterior vas deferens.

the spermathecal duct (Osdu) in the anterior portion of the pallial cavity. The bursa (Bu) is white and very solid (compared to the pallial oviduct). While the main body of the bursa is pear-shaped, it narrows anteriorly and then swells to form a vestibule (just anterior to the end of the pallial cavity), which then gives rise to the narrower spermathecal duct. The spermathecal duct is tightly appressed to the capsule gland, and the wide common opening of the two (Cga) is located anterior to the anus and close to the mantle edge.

*Holotype.*—USNM 849000 (Figs. 2, 3A).

*Paratypes.*—USNM 849001 (Figs. 3D–H), UF 67466.

*Type locality.*—Roaring Springs, Real County, Texas.

*Etymology.*—Named after Dwight W. Taylor, in recognition for his discovery of this species and immense contributions to the study of western American freshwater molluscs.

## Systematic Relationships among Phreatic Littoridinines

With the description of *H. taylori* the known phreatic littoridinine fauna of south-central Texas and northeastern Mexico totals five genera and six species. A comparison between *Hadoceras* and the other four genera, involving 21 characters, is given in

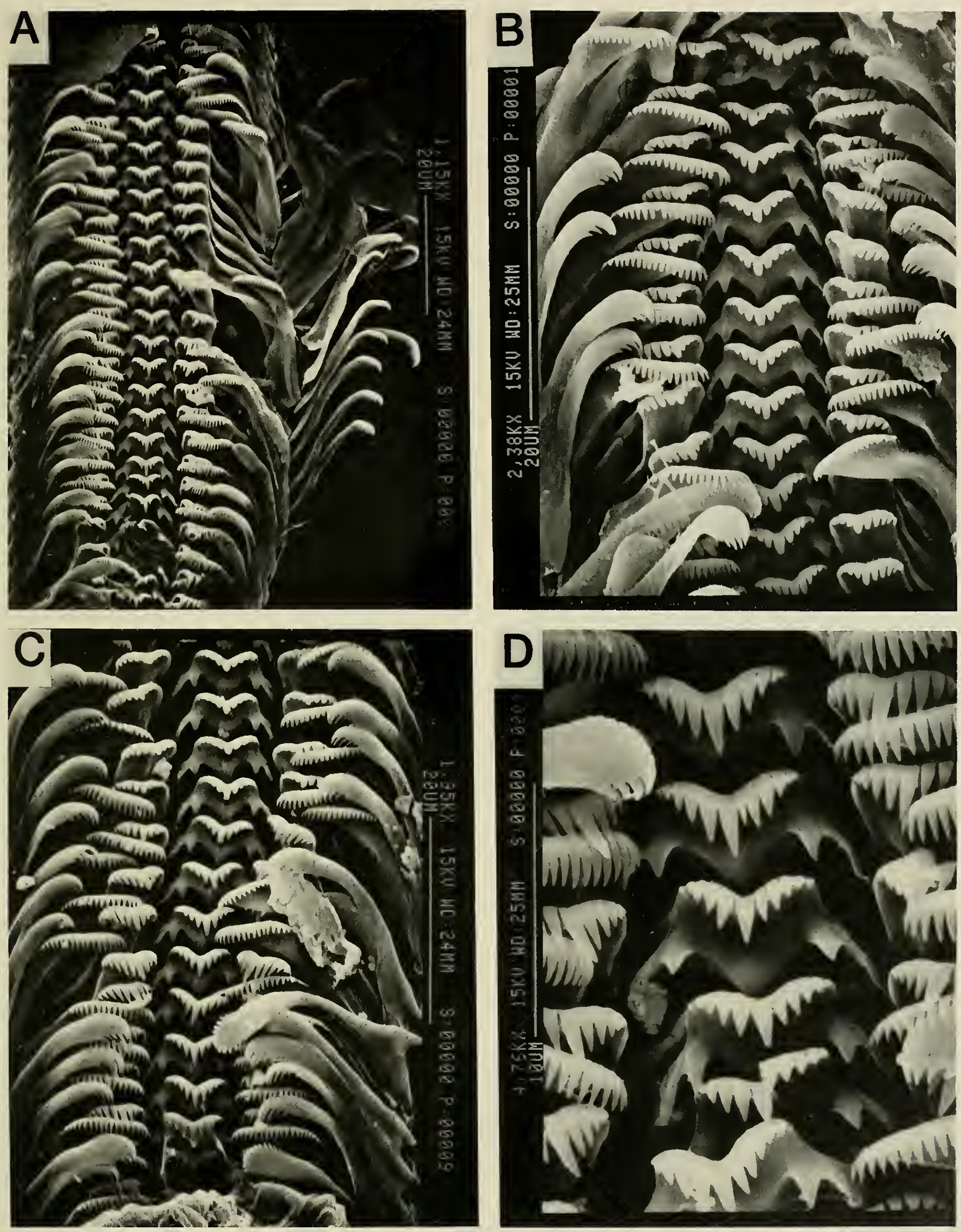

Fig. 8. Scanning electron micrographs of radulae of *H. taylori*. A–C, Sections of the radular ribbon; D, Close-up of central teeth.

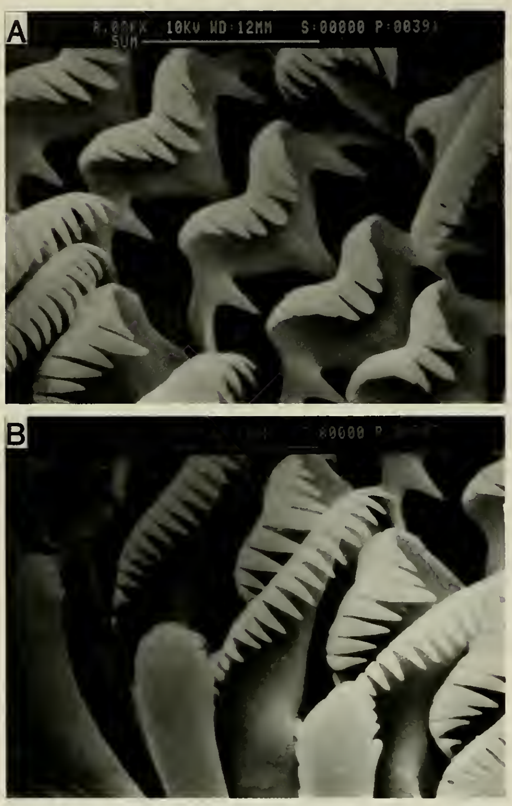

Fig. 9. Scanning electron micrographs of radulae of *H. taylori.* A, Close-up of central teeth; B, Close-up of lateral, inner marginal and outer marginal teeth.

Table 3. A phenogram, based on simple averaging of percent differences among generic pairs, is shown in Fig. 12.

The most similar pair, linking at 33% difference, are *Paludiscala* and *Coahuilix,* both endemic to the Cuatro Cienegas Basin, Mexico. The similarity between these genera extends to details of the anterior portion of the female reproductive system, with both taxa having a large-sized bursa (but no seminal receptacle) ventral to the pallial oviduct, and a sperm duct travelling from the right side of the bursa to enter the posterior portion of the albumen gland. While differing in features involving shell form (*Coahuilix,* planispiral; *Paludiscala,* elongate-conic), nature of the openings of the spermathecal duct and capsule gland (separate vs. fused), and site of sperm storage (albumen gland proper vs. albumen gland pouch), the two taxa are probably part of the same local radiation and perhaps should even be considered congeneric. *Stygopyrgus* and *Balconorbis,* both occurring in the Edwards (Balcones Fault Zone) Aquifer in south-central Texas, link at 48% difference and have rather dissimilar groundplans of the anterior portion of the female reproductive system. We have speculated (Hershler and Longley 1986) that *Balconorbis* may belong to the *Paludiscala-Coahuilix* group, despite differences in characters such as protoconch microsculpture type, as its arrangement of the anterior portion of the female reproductive system is derivable (involving loss of the bursa) from that of the latter group. In *Stygopyrgus* the oviduct loops on the left side of the albumen gland, and enters the anterior end of this gland, with the spermathecal duct arising from this juncture and then receiving the duct of the seminal receptacle well into the pallial cavity. This unique arrangement, coupled with the mammiform penial glands seen in this genus (versus bulbous apocrine glands in the above three genera), suggests that *Stygopyrgus* belongs to a second radiation of phreatic littoridinines.

*Hadoceras* differs from the other four genera by 57–68% of the characters considered and has a number of unique character-states, including the horn-like shell, concentric operculum with ventral process, intestinal loop on the right side of style sac, lack of penial lobes, and ventral displacement of the pallial gonoducts. The anterior portion of its female reproductive system does not closely resemble the arrangements seen in either of the other genera considered: note the unusual nature of the albumen gland, which is slender, non-glandular, and loops around the periphery of the bursa, and the elongate sperm duct, which joins the spermathecal duct well into the pallial cavity. Given the diversity of unique character-states seen in *Hadoceras,* we conclude that

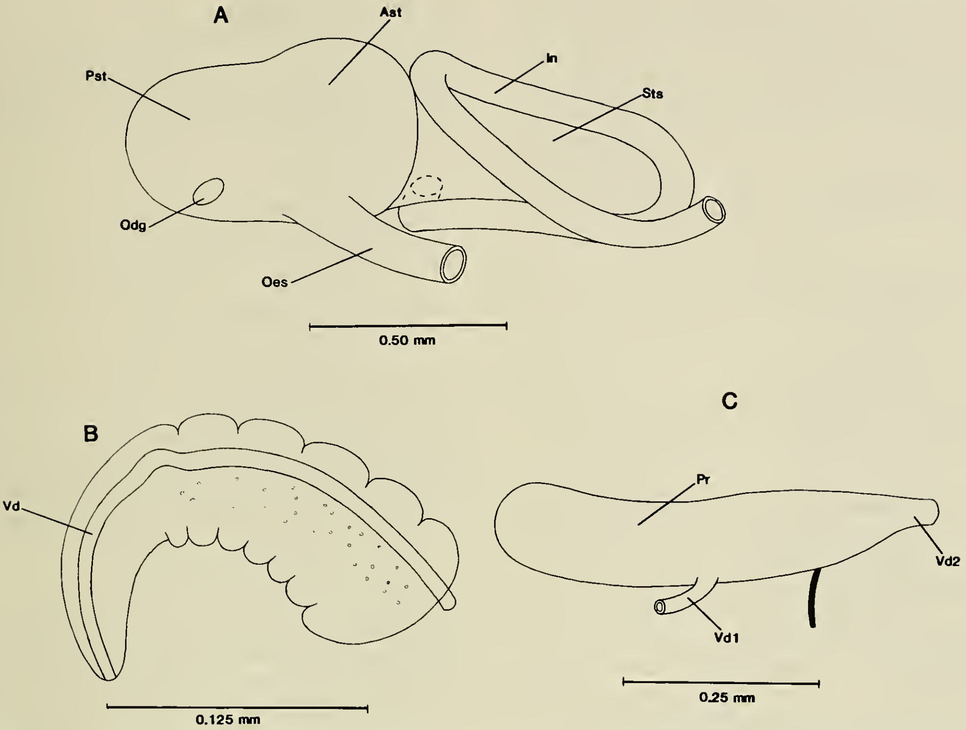

Fig. 10. Stomach (A), penis (B), and prostate (C) of *H. taylori.* The right aspect is shown in A and B, and the ventro-right lateral aspect shown in C. The dark, curving line in C indicates the posterior end of the pallial cavity. Ast, anterior stomach chamber; In, intestine; Odg, opening of digestive gland; Oes, oesophagus; Pr, prostate; Pst, posterior stomach chamber; Sts, style sac; Vd, vas deferens; Vd1, posterior vas deferens; Vd2, anterior vas deferens.

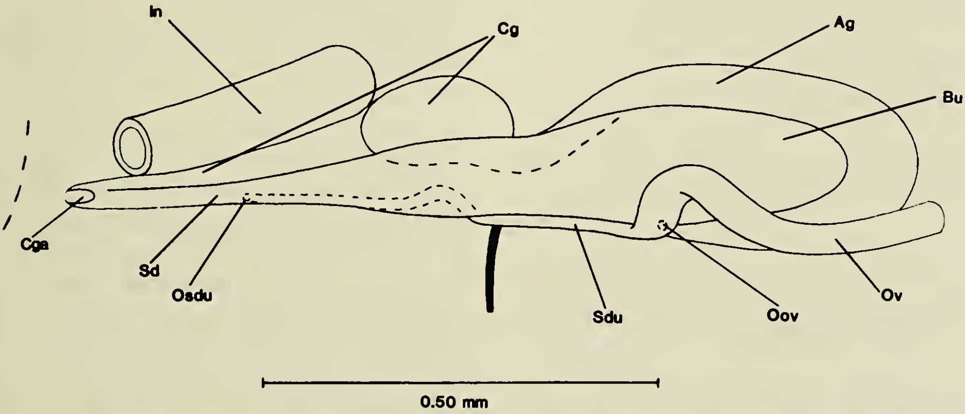

Fig. 11. Left lateral aspect of the anterior portion of the female reproductive system. The posterior portion of the intestine (In) has been removed. The thick curving line indicates the posterior end of the pallial cavity while the dashed line (to the left) indicates the mantle edge. Ag, albumen gland; Bu, bursa copulatrix; Cg, capsule gland; Cga, common opening of the capsule gland and spermathecal duct; In, intestine; Oov, opening of the oviduct into the albumen gland; Ov, oviduct; Osdu, opening of the sperm duct into the spermathecal duct; Sdu, sperm duct; Sd, spermathecal duct.

Table 3.—Comparison of phreatic littoridinine genera involving 21 characters. B = *Balconorbis,* S = *Stygopyrgus,* P = *Paludiscala,* C = *Coahuilix,* and H = *Hadoceras.* Data for genera other than *Hadoceras* are from Hershler (1985) and Hershler and Longley (1986).

| | Genus | | | | |
|---|---|---|---|---|---|
| Character | B | S | P | C | H |
| Shell | | | | | |
| 1. Maximum dimension >2.0 mm (0, 1) | 0 | 0 | 1 | 0 | 1 |
| 2. Shell form: | 0 | 1 | 1 | 0 | 2 |
| a) planispiral (0) | | | | | |
| b) elongate-conic (1) | | | | | |
| c) horn-like (2) | | | | | |
| 3. Protoconch microsculpture: | 0 | 1 | 1 | 1 | 1 |
| a) spiral lines (0) | | | | | |
| b) punctate (1) | | | | | |
| 4. Teleoconch sculpture: | 0 | 0 | 1, 2 | 2 | 2 |
| a) spiral lines (0) | | | | | |
| b) collabral costae (1) | | | | | |
| c) absent (2) | | | | | |
| Operculum | | | | | |
| 5. Operculum concentric (0, 1) | 0 | 0 | 0 | 0 | 1 |
| 6. Operculum with ventral process (0, 1) | 0 | 0 | 0 | 0 | 1 |
| Nonreproductive anatomy | | | | | |
| 7. Ctenidium present (0, 1) | 0 | 0 | 1 | 0, 1 | 0 |
| 8. Intestinal loop on style sac (0, 1) | 0 | 0 | 0 | 0 | 1 |
| 9. Intestinal loop in pallial cavity roof (0, 1) | 1 | 1 | 0 | 1 | 1 |
| Reproductive morphology | | | | | |
| 10. Pallial gonoducts displaced ventrally (0, 1) | 0 | 0 | 0 | 0 | 1 |
| 11. Number of penial lobes: | 1 | 2 | 1 | 1 | 0 |
| a) 0 (0) | | | | | |
| b) 1 (1) | | | | | |
| c) 2 (2) | | | | | |
| 12. Position of lobe(s): | 0 | 1 | 0 | 0 | — |
| a) outer curvature of penis (0) | | | | | |
| b) inner curvature (1) | | | | | |
| 13. Penial gland type: | 0 | 1 | 0 | 0 | — |
| a) apocrine (0) | | | | | |
| b) mammiform (1) | | | | | |
| 14. Anterior coil of oviduct: | 0 | 1 | 2 | 2 | 1 |
| a) ventral to pallial oviduct (0) | | | | | |
| b) on left side of pallial oviduct (1) | | | | | |
| c) absent (2) | | | | | |
| 15. Oviduct opens into: | 0 | 2 | 1 | 1 | 0 |
| a) posterior tip of albumen gland (0) | | | | | |
| b) posterior section of albumen gland (1) | | | | | |
| c) anterior end of albumen gland (2) | | | | | |
| 16. Albumen gland with posterior loop (0, 1) | 1 | 0 | 0 | 0 | 1 |
| 17. Bursa copulatrix present (0, 1) | 0 | 0 | 1 | 1 | 1 |
| 18. Seminal receptacle present (0, 1) | 0 | 1 | 0* | 0 | 0 |
| 19. Openings of spermathecal duct and capsule gland: | 0 | 0 | 0 | 1 | 0 |
| a) fused (0) | | | | | |
| b) separate (1) | | | | | |
| 20. Number of capsule gland tissue sections: | 0 | 0 | 1 | 0 | 0 |
| a) 2 (0) | | | | | |
| b) 3 (1) | | | | | |
| 21. Capsule gland opening muscularized (0, 1) | 0 | 1 | 0 | 1 | 0 |

* Secondarily-derived seminal receptacle present.

this genus represents yet another separate phreatic invasion within the Littoridininae. Epigean littoridinines having either a simple penis, or a penis having mammiform or apocrine glands are known from Texas and northern Mexico (see Hershler 1985) and represent possible ancestors of the three phreatic radiations mentioned above. Further study of the diverse epigean littoridine fauna of the region will be necessary, however, before the above phylogenetic speculations can be tested.

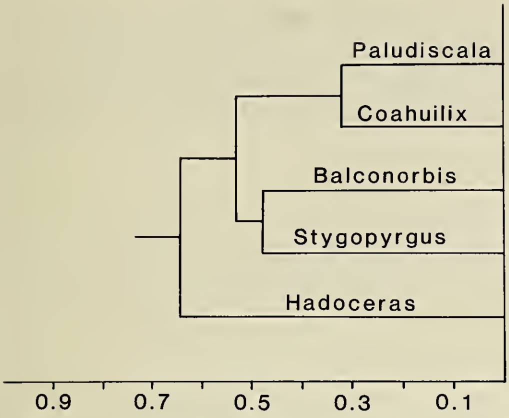

Fig. 12. Phenogram showing similarities among *Hadoceras* and other phreatic littoridinines from Texas and northeastern Mexico. Data used to generate the phenogram are given in Table 3.

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# A NEW SPECIES OF *HELMINTHOGLYPTA* (GASTROPODA: PULMONATA: HELMINTHOGLYPTIDAE) FROM SAN DIEGO COUNTY, CALIFORNIA

Richard L. Reeder and Walter B. Miller

*Abstract.*—*Helminthoglypta montezuma* is described from California. The species differs from its nearest consubgeners in having densely granulose shell sculpture. Relationships within the genus are discussed.

Henry A. Pilsbry's magnificent compilation of information on the western land snail genus *Helminthoglypta* Ancey, 1887 (Pilsbry 1939), has remained the most complete and authoritative reference to date for workers studying this genus. Anatomical data are lacking for many species and subspecies listed, however, and their systematic position may therefore be incorrect. During the period 1956–1964, the late W. O. Gregg and the second author conducted a series of field explorations in southern California for the express purpose of collecting from known populations of *Helminthoglypta* in the region, and using the material for comparative morphological study. In the process, new populations were discovered and some were found to be undescribed species. One such new species from Montezuma Valley in San Diego County is described below.

### Helminthogyptidae Pilsbry, 1939
### *Helminthoglypta* Pilsbry, 1939
### *Helminthoglypta montezuma,* new species
Figs. 1, 2

*Description of holotype.*—Shell small, depressed, helicoid, umbilicate, with umbilicus contained about 8 times in diameter of shell. Color light brown with pale, chestnut band on rounded shoulder. Aperture nearly round, with peristome thickened, only slightly reflected, expanded slightly more at columellar insertion. Embryonic shell of 1½ whorls, smooth. Post-embryonic whorls with radial growth wrinkles, covered with such dense numbers of minute papillae as to appear granulose. Papillae tend to be in descending spiral rows on second and third whorls, randomly distributed on later whorls and continuing strongly on to base of shell and into umbilicus. Diameter 17.4 mm, height 10.1 mm, diameter of umbilicus 2.2 mm, number of whorls 4¾.

*Reproductive anatomy of holotype.*—The genital system is typical of the genus, with an atrial sac having a dart sac at its proximal end, the latter structure being relatively small. There are two mucous glands with mucous bulbs, the ducts of which unite to form a single duct before entering the atrial sac. The spermatheca is spherical and the spermathecal duct bears a diverticulum of moderate length. The penis has a short, narrow lower chamber and a longer, wider, double-walled upper chamber of uniform diameter. The lumen of the upper penis expands broadly in its lower half. The penis forms a continuous tube with the epiphallus which is of moderate length and bears an epipallic caecum at its proximal end, also of moderate length. The penial retractor muscle attaches to the epiphallus. Measurements of distinctive organs are as follows:

| | |
|---|---|
| Penis | 11.4 mm |
| Epiphallus | 12.3 mm |
| Epiphallic caecum | 9.1 mm |
| Spermathecal duct | 24.0 mm |
| Spermathecal diverticulum | 18.6 mm |

Fig. 1. Shell of holotype of *Helminthoglypta montezuma* (SBMNH 33917). Dorsal, apertural, and umbilical views. Diameter 17.4 mm.

*Variation in paratypes.*—A total of 19 adult and 15 juvenile shells was examined. The largest adult paratype is 19.6 mm in diameter and 11.0 mm in height, and the smallest 14.2 mm and 8.1 mm respectively. All of the shells exhibit the characteristic granulose condition and narrow umbilicus. Five reproductive anatomies were examined; all exhibited the same cylindrical shape of uniform diameter, and the same upper and lower penis.

*Disposition of type material.*—Holotype: Santa Barbara Museum of Natural History no. 33917. Paratypes: The Academy of Natural Sciences of Philadelphia no. 359265; U.S.N.M. no. 842310; W. B. Miller collection nos. 4302, 4306 and 7490; R. L. Reeder collection no. 685; H. L. Fairbanks collection no. 459.

*Type locality.*—San Diego County, California; in rocks among oaks along north side of Montezuma Valley Road from 1.0–2.0 road miles east of junction with San Felipe Road; 33°13.0′N, 116°35.5′W; elevation 1040 m (3440 ft.).

*Discussion.*—The anatomy of *H. montezuma* clearly indicates that the species belongs in the nominate subgenus. Its nearest consubgeneric relatives are *H. thermimontis* Berry, 1953, *H. waltoni* Gregg and Miller, 1976, and *H. milleri* Reeder, 1985. It differs from all three in that it has densely granulose shell sculpture while the others are only moderately papillose. It is also consistently smaller than the other species, with a maximum diameter ranging from 14.2 to 19.6 mm while the smallest of the others is 21.8 mm for *H. thermimontis.* Its umbilicus, likewise, is narrower, ranging from 2.1 to 2.8 mm, while the others range from 3.2 to 4.3 mm. Its anatomy, while similar to that of the other three, does have certain distinctive features involving the shape of the penis. In *H. waltoni* the upper penis is decidedly club-shaped. In *H. thermimontis,* the upper penis is cylindrical for most of its

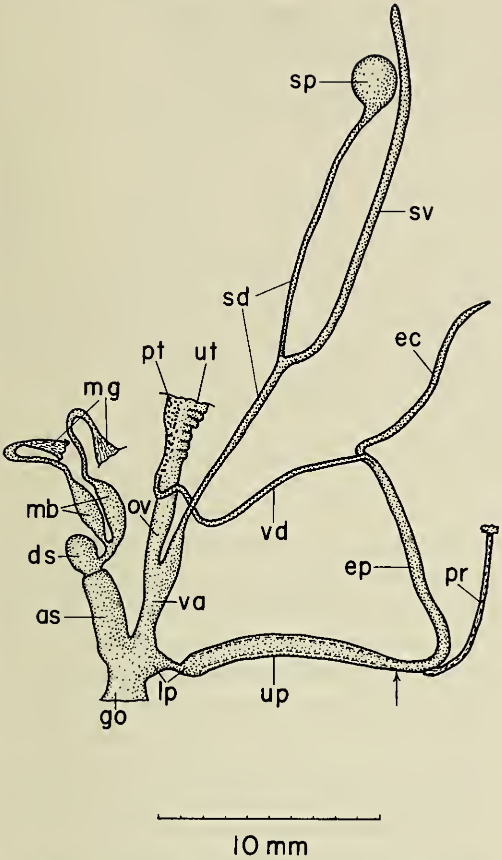

Fig. 2. Portion of reproductive system of *Helminthoglypta montezuma* Reeder and Miller, showing diagnostic characters. Drawing made from projection of stained whole mount, #4302-DT; arrow shows junction of upper penis and epiphallus. as—atrial sac; ds—dart sac; ec—epiphallic caecum; ep—epiphallus; go—genital orifice; lp—lower part of penis; mb—mucous gland bulbs; mg—mucous gland membranes; ov—oviduct; pr—penial retractor muscle; pt—prostate; sd—spermathecal duct; sp—spermatheca; sv—spermathecal diverticulum; up—upper part of penis; ut—uterus; va—vagina; vd—vas deferens.

length and then tapers to the smaller initial diameter of the venturi-shaped lower penis; the venturi portion is extremely narrow. In *H. montezuma,* the upper penis is cylindrical for all of its length, joining a lower penis of equal initial diameter. In *H. milleri,* the upper and lower penes have essentially the same characteristics as in *H. montezuma* except that the venturi portion is consistently wider.

*Helminthoglypta montezuma* is currently known only from the type locality in Montezuma Valley. Vegetation at this locality consists primarily of *Quercus dumosa, Quercus agrifolia, Cercocarpus betuloides, Rhus ovata, Artemesia tridentata, Photinia arbutifolia, Adenostoma fasciculatum, Berberis pinnata,* and *Symphoricarpos* sp.

*Etymology.*—This species is named for Montezuma Valley, California, where it lives.

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We are indebted to the late Wendell O. Gregg for providing some of the specimens and information used in preparation of this description, and to Susan J. McKee for photographs and excellent assistance in the laboratory. Thanks also to The University of Tulsa for support of field work and to The University of Arizona for providing laboratory facilities.

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# TWO SPECIES OF *UROCOPIA,* PLANKTONIC POECILOSTOMATOID COPEPODS OF THE FAMILY UROCOPIIDAE HUMES AND STOCK, 1972

Gayle A. Heron and David M. Damkaer

*Abstract.*—Since the original description of the bathypelagic copepod *Urocopia singularis* Sars, 1917, there have been only two other records of this species. New material from the eastern North Pacific Ocean has led to additional morphological details of the female and the first description of the male. A second poecilostome species, *Sinoculosapphirina deeveyae* Boxshall, 1981, is now considered to be in the genus *Urocopia.*

The bathypelagic genus *Urocopia* was based by Sars (1917) on two female copepods collected in the North Atlantic Ocean during the 1913 cruise of the ARMAUER HANSEN. Sars (1917:3) placed this genus in the family Lichomolgidae because of the morphology of the oral appendages, but he stated that the copepods "differed essentially from other known Lichomolgidae." Humes and Stock (1972) included the family Urocopiidae in the superfamily Lichomolgoidea when they revised the family Lichomolgidae. In Humes and Stock's key to the families (1972:122), the distinguishing characters of Urocopiidae are the 3-segmented exopods of legs 1 and 2 and endopod of leg 4, and leg 5 without a free segment. The family Lichomolgidae was separated on the basis of leg 4 endopod being 2-segmented, 1-segmented, reduced to a small knob, or absent.

There are characters in both families Urocopiidae and Lichomolgidae that resemble those of some species of *Sapphirina* J. V. Thompson, 1829, but this genus may be separated by the 1-segmented leg 5. Additional distinctive characters of *Sapphirina* species are two anterior cuticular lenses, a conspicuously depressed body with epimeral plates expanded laterally, and the lamelliform caudal rami.

An unpublished record of *Urocopia singularis* from off Oregon and California in the eastern North Pacific Ocean (Olson 1949) was later published and corroborated with a record from the Bering Sea (Minoda 1971). The following new records from the eastern North Pacific further characterize the geographical range of *U. singularis.*

Collections were made in 1964 and 1965 from the BROWN BEAR, former research vessel of the Department of Oceanography, University of Washington, with a specially-designed plankton net (mesh aperture 110 μm) which accompanied a deep water-bottle cast (Heron and Damkaer 1978).

The rare specimens of *Urocopia singularis* from the BROWN BEAR cruises and the loan of slides prepared by J. B. Olson have enabled us to supplement the published morphological details, as well as to describe the male. Figures were drawn with the aid of a Wild M2O[1] drawing tube. The slide of the male *Urocopia singularis* from which the male appendages were illustrated, was prepared by W. K. Peterson in 1965 with methyl blue stain and Turtox CMC mounting medium. The stain Solophenyl

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1. Collection data.

| | Date | Depth (m) | Location | Length | | |
|---|---|---|---|---|---|---|
| | | | | ♀ (mm) | ♂ (mm) | ♂ V(mm) |
| | | | Previous records | | | |
| Sars | VII 13 | 700–600 | 59°35.0'N, 20°40.0'E | 2 (1.90) | | |
| Olson | 25 V 39 | 800–0 | 44°46.0'N, 128°22.0'W | 1 (1.97) | | |
| | 13 VI 39 | 800–0 | 35°42.0'N, 124°19.5'W | | 1 (1.28) | |
| Minoda | 13 VI 61 | 883–743 | 56°23.0'N, 174°38.0'E | 1 (2.10) | | |
| | | | New Records | | | |
| *BROWN BEAR* | | | | | | |
| Cruise | | | | | | |
| 344 | 4 V 64 | 2600–0 | 45°29.3'N, 126°58.0'W | | | 1 (1.08) |
| | 28 V 64 | 4310–0 | 47°49.2'N, 144°57.7'W | | 1 (1.05) | |
| 368 | 10 VIII 65 | 2700–0 | 45°22.0'N, 128°36.0'W | 1 (2.25) | 1 (damaged) | |
| | 13 VIII 65 | 2000–0 | 45°20.6'N, 134°56.5'W | | 1 (1.29) | |
| | 14 VIII 65 | 4250–0 | 45°17.5'N, 139°09.6'W | 1 (2.28) | | |

blue 2RL, dissolved in lactic acid, was used to study the other specimens (English and Heron 1976).

The collection data for previous records and the new records of *Urocopia singularis* are shown in Table 1.

Specimens collected from the BROWN BEAR described in this report, except the 10 VIII 65 male and female, have been deposited in the Crustacea collection of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. The Olson male and female, mounted on slides, have also been deposited in the National Museum of Natural History.

### Poecilostomatoida Kabata, 1979
### Urocopiidae Humes and Stock, 1972
### *Urocopia* G. O. Sars, 1917

*Sapphoncaea* Minoda 1971:46.
*Sinoculosapphirina* Boxshall 1981:307.

*Diagnosis.*—Body cyclopiform, elongate. Urosome in female 5-segmented, in male 6-segmented. Caudal ramus elongate, lamellar. Rostrum absent. First antenna 6-segmented; incomplete sutures between segments 1 and 2 or 2 and 3. Second antenna 4-segmented, sexually dimorphic; terminal segment of female with stout claw and 2 short apical setae; in male, length of terminal segment and width of claw reduced, outer apical seta very long.

### Key to the Species of *Urocopia*

#### Females

1. Length 1.90–2.28 mm; caudal ramus length approximately equal to that of 3 preceding segments combined .................. *U. singularis*
– Length 3.50 mm; caudal ramus length approximately equal to that of 3 preceding segments plus genital segment combined ....... *U. deeveyae*

### *Urocopia singularis* G. O. Sars, 1917
Figs. 1–4

*Urocopia singularis* G. O. Sars, 1917:3–11, figs. 1–15.—Lysholm and Nordgaard, 1921:29.—Humes and Stock, 1972:329, 330, fig. 183.—Gotto, 1979:6, 11, 13, fig. 26.

*Sapphoncaea moria* Olson, [MS], 1949:112, pl. 27, figs. 3–11; pl. 28, figs. 1–12.—Minoda, 1971:46, 47, pl. 4, figs. 1–12.

*Material examined.*—2 ♀♀, 3 ♂♂ (1 damaged), 1 ♂V; eastern Pacific (see Table). The

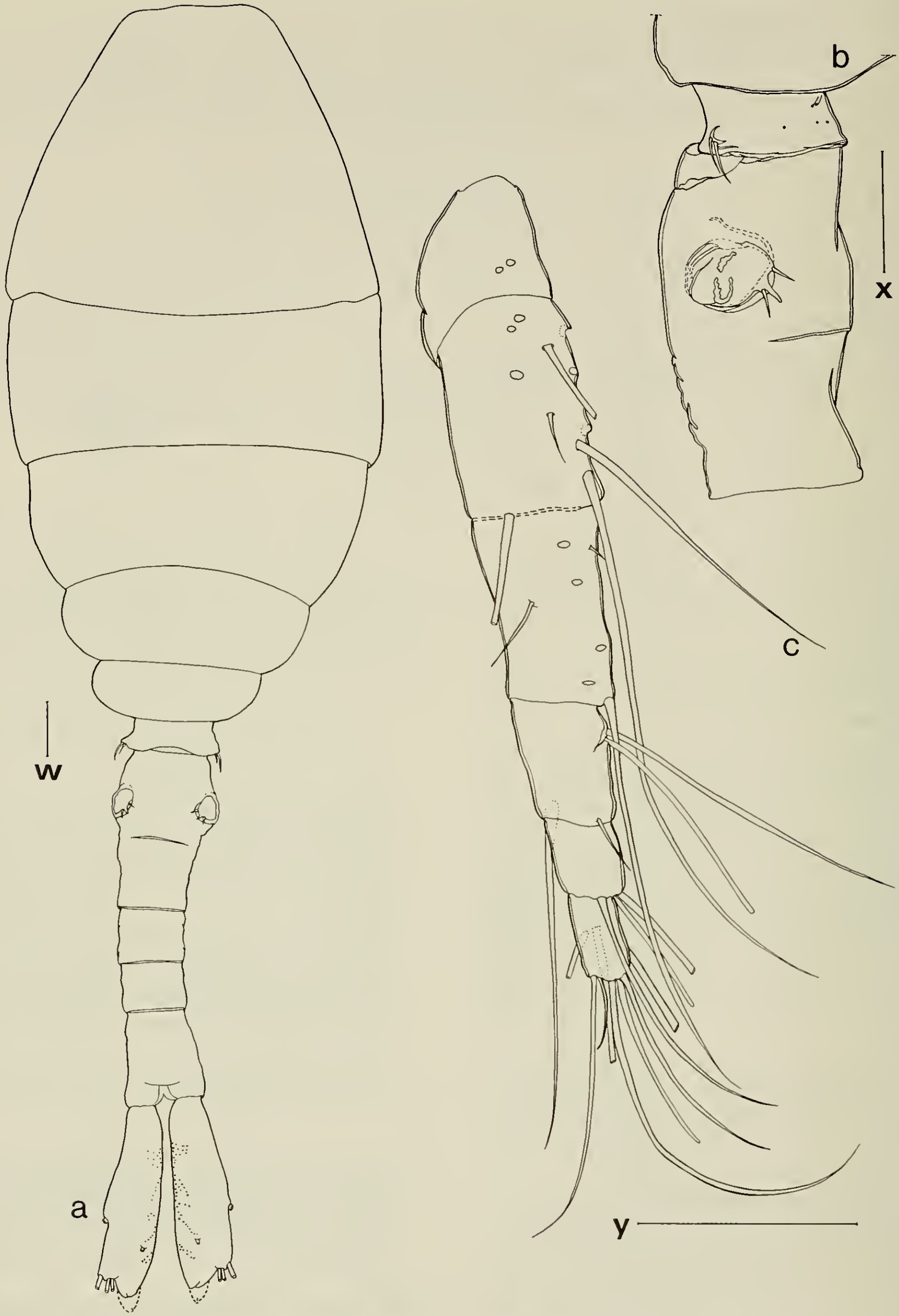

Fig. 1. *Urocopia singularis* Sars, female: a, Habitus, dorsal (w); b, Segment of leg 5 and genital segment, lateral (x); c, First antenna, right ventral (y). Each scale bar equals 0.10 mm.

male of this species is described for the first time.

*Female.*—Lengths of two females 2.25 and 2.28 mm. Prosome relatively robust compared to slender urosome (Fig. 1a). Ratio of length of prosome to that of urosome 1.2: 1. Pediger 1 delimited from cephalosome dorsally by suture. Between segment of leg 5 and genital segment a pronounced ventral intersegmental sclerite (Fig. 1b).

Genital segment shorter than length of caudal ramus. Genital areas located dorsolaterally anterior to middle of segment; lamellar fringe forming dorsal transverse line on one female. Each genital area with 2 setae, posteriormost adjacent to sclerotized prong extending from operculum and overlying 2 pores, anteriorly and posteriorly. Surfaces of genital segment and 3 postgenital segments with slightly crenulate appearance.

Caudal ramus elongate, dilated in area of lateral seta, terminating in inner tapered protuberance (that of smaller female twice as protuberant, shown by dashed line on Fig. 1a); minute spinules on inner and dorsal surfaces. Setae broken or missing; based on hyaline circles of insertion (and those of male and stage V male specimens), a lateral, a dorsal, and three short terminal setae present. Innermost terminal seta absent.

Rostrum absent. First antenna (Fig. 1c) 6-segmented, with partly coalesced suture between segments 2 and 3. Most setae broken or missing; based on hyaline circles of insertion, armament formula may be: 2; 11; 7; 3, 1 esthete; 2, 1 esthete; 7, 1 esthete.

Second antenna (Fig. 2a) 4-segmented; inner seta on first and second segments, 2 inner setae on short third segment, and stout claw plus 2 apical setae on fourth segment.

Labrum (Fig. 2a) incised into 2 rounded, posteroventral lobes; inner third of each lobe delimited with thinner chitin; intricate sclerotization pattern extending from apex of incision.

Mandible (Fig. 2b) with 2 outer setose elements followed by denticulate ridge; terminating in spiniform lash; inner row of spinules on concave edge of blade.

First maxilla (Fig. 2c) with row of short, minute spinules on outer anteroventral corner; 4 setae on anterior half of segment; minute spinules on 2 longest setae, the terminal and antepenultimate. Single apodeme, remarkably long, extending from base of segment.

Second maxilla (Fig. 2d) 2-segmented; first segment with rugose ventral surface. Second segment bearing 2 elements on inner surface; shorter element barbed, distalmost element spinose and longer than terminal lash. Terminal lash, with vertical row of setules near base, carrying ventral row of setules adjacent to 3 or 4 triangular, inwardly-directed teeth.

Maxilliped (Fig. 2e) 3-segmented. First segment with short, minute spinules on inner surface. Second segment with inner and distal patches of minute spinules plus 2 inner setae. Third segment bearing 2 inner setae near base and terminating in barbed claw.

Legs 1–4 with trimerous rami. Spines with wide, serrate, hyaline flange. Minute spinules on posterolateral margins of coxae. First and second segments of leg 4 endopod with anterior digital projection overlapping base of wide, flat setae. Leg armament: see Table 2.

Leg 5 (Fig. 1b) represented by 2 posterolateral setae inserted on short pedicel.

Leg 6 (Fig. 1b) probably represented by 2 setae and prong on posterodorsal margin of genital operculum.

*Male.*—Lengths of two males 1.05 and 1.29 mm. Body compact, length of prosome approximately twice that of urosome (Fig. 3a, b). Pediger 1 delimited from cephalosome by dorsal suture. Urosome (Fig. 3c) 6-segmented. Anal segment and caudal ramus with rows and patches of minute spinules on dorsal and ventral surfaces. Caudal ramus showing remarkable sexual dimor-

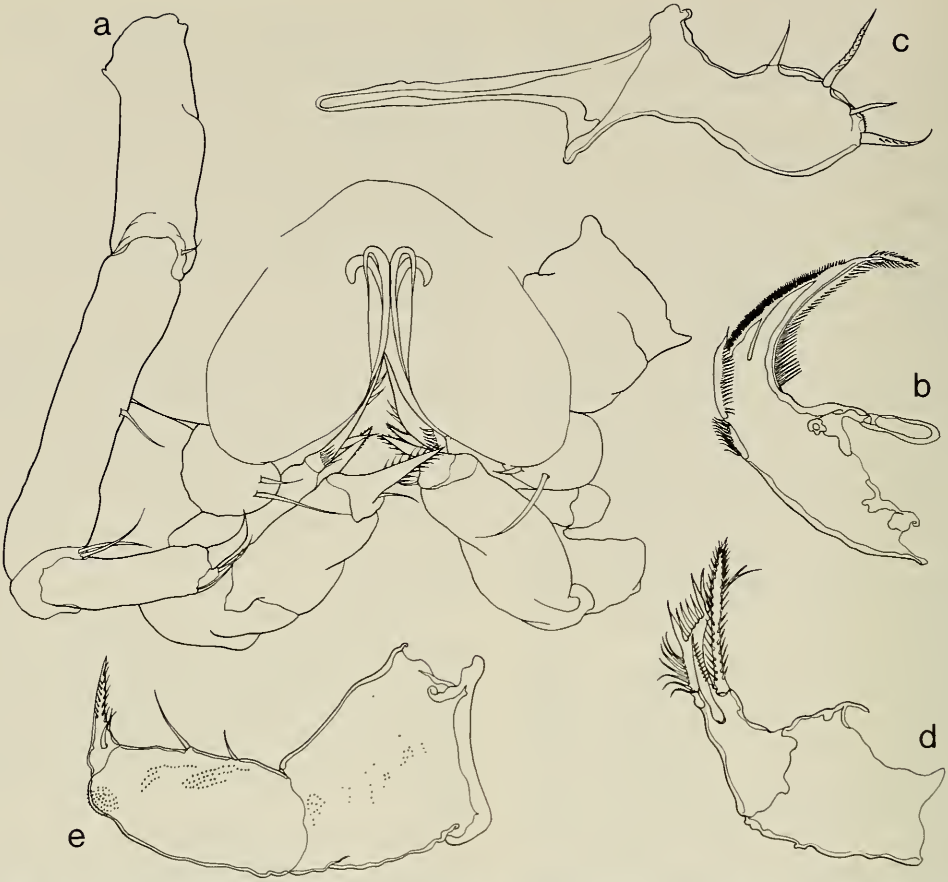

Fig. 2. *Urocopia singularis* Sars, female: a, Second antenna and oral area, ventral (y); b, Mandible, right (y); c, First maxilla, right (y); d, Second maxilla, right (y); e, Maxilliped, right (y).

phism; terminal protuberance of female developed as articulated, blunt outgrowth, possibly the modification of innermost terminal seta.

Rostral area, mandible, first maxilla, and second maxilla similar to those of female.

First antenna with line of coalescence between segments 2 and 3 scarcely discernible; several setae and esthetes longer than those of female, posterior esthete reaching as far as coxa of leg 1.

Second antenna (Fig. 3d) segments resem-

Table 2. Leg armament.

| | | | Endopod | | | | | Exopod | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | | | 1 | 2 | | 3 | | |
| Leg | Coxa | Basis | Si | Si | Si | St | Se | Se | Si | Se | Si | St | Se |
| 1 | 1 | 1 | 1 | 1 | 4 | 1 | I | I | 1 | I | 4 | I | III |
| 2 | 1 | 1 | 1 | 2 | 3 | II | I | I | 1 | I | 5 | I | III |
| 3 | 1 | 1 | 1 | 2 | 2 | II | I | I | 1 | I | 5 | I | III |
| 4 | 1 | 1 | 1 | 1 | – | II | – | I | 1 | I | 5 | I | II |

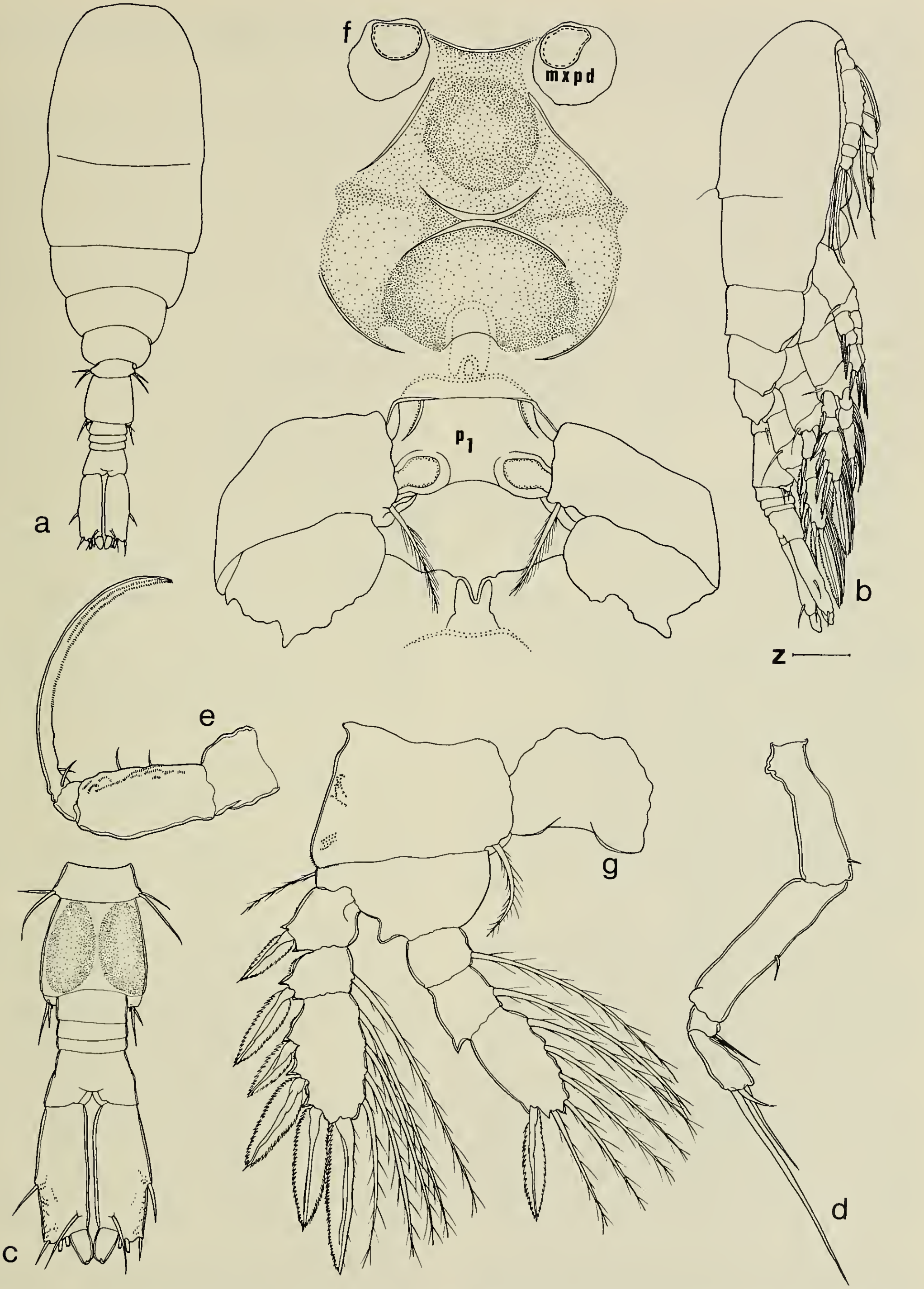

Fig. 3. *Urocopia singularis* Sars, male: a, Habitus, dorsal (w); b, Habitus, lateral (z); c, Urosome, dorsal (x); d, Second antenna, right (y); e, Maxilliped, right (y); f, Area between maxillipeds and first legs, ventral (y); g, Leg 1, anterior (y).

bling those of female in general form; armament formula similar, but structure differing on fourth segment, with reduced claw and increased length of 2 setae, 1 longer than second segment.

Maxilliped (Fig. 3e) 4-segmented; second segment with two inner setae and patches of short spinules; third segment short and unarmed. Terminal claw bearing 2 proximal setae and 2 inner rows of minute spinules. Distinct sclerotized band between bases of maxillipeds. Area between maxillipeds and first pair of legs (Fig. 3f) protruding ventrally as anterior and posterior lobes, separated by 2 constrictive sclerotized bands.

Legs 1–4 (Figs. 3g; 4a, b, c) segmented as in female, with same armament formula.

Leg 5 (Fig. 3c) similar to that of female, except relatively longer setae.

Leg 6 (Fig. 3b, c) probably represented by posterolateral flap on ventral surface of genital segment, bearing 2 setae and sclerotized prong similar to those of female.

*Stage V male.*—One specimen, 1.08 mm, resembles a mature male, including the articulated, blunt outgrowth on the caudal ramus and the rows of minute spinules on ventral surfaces of anal segment and caudal ramus (Fig. 4d). This stage lacks the third postgenital urosome segment of the adult male.

Without dissection most oral appendages appear similar to those of the mature female. Hyaline setae of leg 5 and the caudal ramus appear to be more transparent and fragile than those of the adults.

*Remarks.*—Most setae of leg 5 and caudal ramus were broken or missing on all specimens. Setae which were not damaged appeared to be hyaline with sclerotized support only in the proximal half, to that point where many of the setae were broken.

Despite the omission of some swimming leg armament and slight differences in interpretations of details and illustrations of oral appendages, there seems little question that Olson's, Minoda's, and our specimens, all of similar size, are the same species as *Urocopia singularis* described by Sars (1917).

When Olson (1949:113) listed the armament pattern of the swimming legs of *Sapphoncaea moria,* he inadvertently omitted a terminal spine on all exopods and endopods. All armament, including terminal spines, was on his illustrations, except 1 seta from the second segment of the female leg 3 endopod, the long terminal spine, 2 outer spines on the exopod, and 1 of the terminal spines on the endopod of female leg 4. Olson stated that this missing armament was present on his male specimen and he considered the armament formula to be similar to that of the female. Minoda (1971:47) identified a female specimen as *Sapphoncaea moria,* but his illustrations and formula omitted a seta on the second segment of leg 3 endopod and a spine from each exopod segment of leg 4. He also omitted a terminal spine of each swimming leg rami in the armament formula of swimming legs, although these spines were included on the illustrations.

### *Urocopia deeveyae* (Boxshall, 1981), new combination

*Sinoculosapphirina deeveyae* Boxshall, 1981:307–311. figs. 1a–h, 2a–e (2 ♀♀, 3.50 mm).

*Material examined.*—The paratype female (USNM 173941) with legs dissected and mounted on a slide.

Legs 1–4 have the same armament formula as *U. singularis,* but relative lengths of spines differ. The proximal spine of the third exopodal segment of legs 1–3 is relatively shorter for *U. singularis* as is also the outer terminal spine of leg 4 endopod.

*Remarks.*—The swimming legs and leg 5 of *Sinoculosapphirina deeveyae* are similar to those of *Urocopia singularis.* The lack of cuticular lenses and the presence of unsegmented leg 5 indicate that it is more closely related to Urocopiidae than to Sapphirinidae. The 6-segmented first antenna of *Uro-*

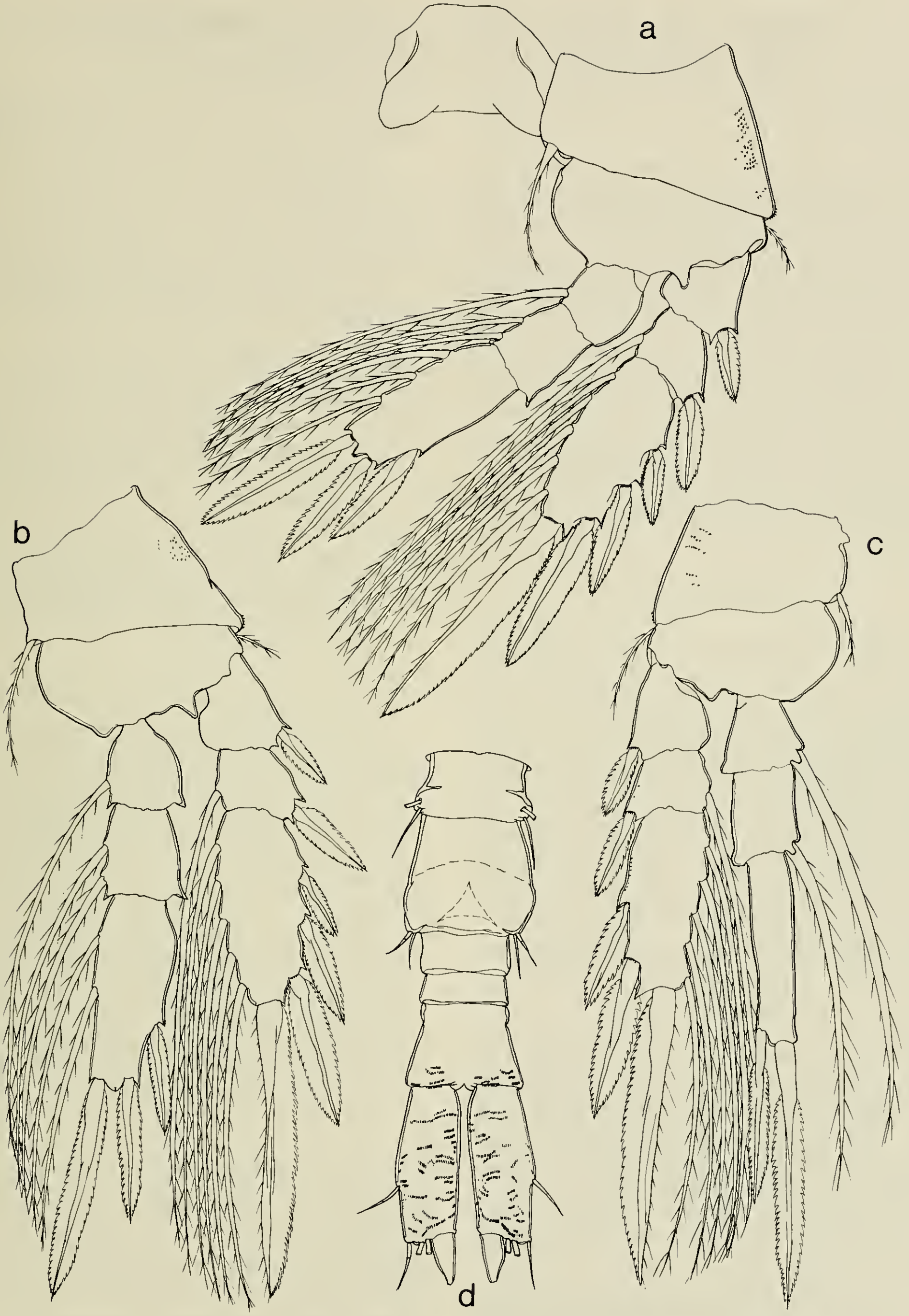

Fig. 4. *Urocopia singularis* Sars, male: a, Leg 2, anterior (y); b, Leg 3, anterior (y); c, Leg 4, anterior (y). Copepodid V, male: d, Urosome, ventral (x).

*copia singularis* has an incomplete suture between segments 2 and 3. Rather than 5-segmented, there is the possibility of an incomplete articulation on the long second segment of the first antenna of *Sinoculosapphirina deeveyae.* Although Boxshall described the second antenna as being 5-segmented, his illustration appears to have four segments with a strong terminal claw. The second antenna of the superfamily Lichomolgoidea Humes and Stock (1972:122) was defined as being either 4-segmented or 3-segmented by a fusion of the last two segments. Humes and Stock (1973:329) noted that Sars had mistakenly regarded the terminal claw as a fifth segment when he described the second antenna of *Urocopia singularis.*

## Acknowledgments

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# SUBSPECIES OF THE GLAUCOUS GULL, *LARUS HYPERBOREUS* (AVES: CHARADRIIFORMES)

Richard C. Banks

*Abstract.*—Current writings treat the Holarctic Glaucous Gull, *Larus hyperboreus,* either as a monotypic species or as having two or three subspecies; if divided, birds of Canada, Greenland, and Europe are considered to be of the nominate subspecies. This study shows that there are four subspecies, the birds of Canada and Greenland being separable from those of Europe; the name *L. h. leuceretes* Schleep, 1819, based on a Greenland bird, is available for the former. Alaskan birds (*L. h. barrovianus*) are relatively dark on the mantle, those of Canada and Greenland are pale, those of Europe and western Asia are dark, and those of Siberia (*pallidissimus*) are very pale. From the small Alaskan birds there is an increase in size to the east around the Holarctic to very large birds in Siberia. The Alaskan and Canadian populations intergrade in extreme northwestern Canada. Nonbreeding Glaucous Gulls along the Pacific coast of North America are of the Alaskan form, *barrovianus*; those east of the Rockies, previously referred to as *barrovianus* or *hyperboreus,* are all *leuceretes* or, in the western plains states, from the intergrade area.

The nature and extent of geographic variation in the Holarctic Glaucous Gull, *Larus hyperboreus,* and the nomenclatural recognition of this variation have been a matter of dissent since the species was first divided in the late 19th century. Authorities writing in the last two decades have considered the species to be either monotypic or composed of two or three subspecifically distinct populations. Authors who recognize subspecies have not agreed on the application of names or on the boundaries of the named populations.

A request for subspecific identification of a wintering specimen prompted a reexamination of the series of this species in the National Museum of Natural History (USNM), the American Museum of Natural History (AMNH), and the Academy of Natural Sciences of Philadelphia (ANSP), and some individual specimens borrowed from other institutions (see Acknowledgments), as well as the taxonomic literature of the species. This has allowed the identification of some of the sources of earlier disagreement, and revealed that geographic variation is more complex than has been recognized. I believe that four populations are recognizable at the subspecific level.

## Taxonomic History

The name *Larus glaucus* Brünnich, 1764, was used for the Glaucous Gull until the early part of the 20th century. The American Ornithologists' Union (A.O.U. 1908), citing a manuscript by C. W. Richmond (apparently never published), noted that *Larus glaucus* of Brünnich is preoccupied by *Larus glaucus* Pontippidan, 1763, a synonym of *Larus canus* Linnaeus, 1758, and that the next available name is *Larus hyperboreus* Gunnerus, 1767. The latter has been the accepted specific name ever since.

Ridgway (1886) described *Larus barrovianus* as an Alaskan species of gull that was smaller and darker than the related North Atlantic *L. glaucus.* The name *barrovianus* was applied to Bering Sea birds by Taczanowski (1893), but was synonymized with *glaucus* by Saunders (1896). Dwight (1906) thought that the size difference between *barrovianus* and *glaucus* was insufficient for the recognition of the former, and although he did not comment on the color difference he also placed *barrovianus* in the synonymy of *glaucus.* After 1908, *barrovianus* was carried in the synonymy of *hyperboreus,* even by Ridgway (1919). Oberholser (1918), however, proposed recognition of *barrovianus* as a subspecies of *hyperboreus,* emphasizing the color difference, and attributed to it a breeding range in "Alaska and the territories of Yukon and western Mackenzie." In a stinging rebuff, Dwight (1919) reemphasized the weakness of the characters used by Ridgway and Oberholser; the latter repeated his argument (Oberholser 1919) only to have it rebutted again (Dwight 1925). Despite support for the recognition of *barrovianus* by Bishop (1927), that form was not recognized in compendia by the A.O.U. (1931) or Peters (1934).

Portenko (1939), on the basis of a statement in a letter from Herbert Friedmann that "the characters given concerning the colouring of the mantle [of the type of *barrovianus*] . . . do not hold for other specimens from the same region," believed that the type of "*barrowianus*" was a hybrid between *L. hyperboreus* and *L. glaucescens* and not "identical with the pale coloured Glaucous Gulls from the Arctic shores of N.E. Asia and N.W. America." Portenko (1939) proposed the name *L. h. pallidissimus* for the birds of eastern Asia, primarily on the basis of their paler mantle color relative to birds of Europe and western Asia but noting also their larger size. Portenko had a similarly pale bird from Ellesmere Island, and presumed that the range of *pallidissimus* extended from Siberia eastward across arctic America at least to that island. Thus the Alaskan birds, first described as smaller and darker, were incorporated into a subspecies based on pallor and large size.

Witherby (in Witherby et al. 1941:112) noted that *pallidissimus* had been described, but stated that "specimens from Amur and Alaska do not appear to me to differ from European examples." Bird and Bird (1941) examined the same specimens as Witherby had and suggested that Portenko had merely renamed *barrovianus*; they also were unable to find characters to divide the species in any part of its range, and considered *hyperboreus* to be monotypic.

Rand (1942) supported the earlier views of Oberholser and Bishop that *barrovianus* was subspecifically distinct from *hyperboreus,* without mentioning *pallidissimus.* Two subspecies, *L. h. hyperboreus* and *L. h. barrovianus* were recognized by the A.O.U. (1945). However, Hellmayr and Conover (1948:261) continued to follow Dwight in denying recognition of *barrovianus.* They used only the binomial *Larus hyperboreus* for the birds in North America, but in a footnote commented that "this form is replaced by *L. h. pallidissimus*" on the arctic coast of Asia. They were equivocal on the validity of the latter, but stated that "birds from Greenland, Arctic America, and Alaska are not separable from those of northern Europe."

Dement'ev (in Dement'ev and Gladkov 1951) recognized two subspecies, *hyperboreus* from eastern Canada, Greenland, northern Europe, and extreme western Asia, and "*barrowianus*" from eastern Asia, Alaska, and Canada east to Ellesmere Island. In this, he essentially followed Portenko's division of the species but considered *pallidissimus* a synonym of *barrovianus,* rejecting Portenko's claim that the latter was based on a hybrid. He reinterpreted Friedmann's statement to Portenko (see above), as had Bird and Bird (1941), as indicating that the type of *barrovianus* was merely atypical and that the gulls from arctic America are "in fact extremely light." He also noted that the east Siberian birds are larger than Atlantic ones, and assumed that Alaskan ones agreed with those in Siberia in this respect. Dement'ev stated, however, that (p. 562) "the boundary lines of the range in America remain completely obscure . . ." and further that the identity of American birds with those of Siberia "is still unproved, although quite likely."

The A.O.U. (1957) continued to recognize *barrovianus* as an Alaskan form and *hyperboreus* as the single other subspecies, extending from western Canada around the Holarctic to and including Siberia. Walrus Island, in the Pribilofs, was mentioned in the breeding range of both forms. Gabrielson and Lincoln (1959) followed the treatment by the A.O.U. but included Walrus Island and St. Matthew Island in the range only of *hyperboreus.* They indicated that the latter populations might belong to *pallidissimus,* which they had not fully evaluated.

Todd (1963:363) discussed the difference of opinion on the validity of *barrovianus* as distinct from *hyperboreus.* He noted an average color difference, but also that individual specimens from eastern and western Canada were "scarcely to be distinguished in general coloration." He further remarked that "the western birds of this species run smaller, sex for sex, than those from the East." However, he agreed with Dwight (1906, 1925) that the degree of size difference was insufficient for the recognition of subspecies. Ingolfsson (1970) similarly considered *L. hyperboreus* as monotypic.

Vaurie (1965:475) recognized three subspecies, with *barrovianus* restricted to "coasts and islands of Alaska . . . to about Franklin Bay in northwestern Mackenzie." He considered birds from central Mackenzie eastward through North America and Europe "to about the Taimyr Peninsula" in Siberia to be nominate *hyperboreus.* To *pallidissimus* he gave the range from the Taimyr Peninsula to the tip of the Chuckchi Peninsula, including Anadyrland, Wrangel Island, and the Pribilofs. He considered *barrovianus* to be small and dark, with a slender bill, and *pallidissimus* to be paler in adult and immature plumages than *hyperboreus.* Portenko (1973) followed in recognizing these three subspecies, as did Glutz von Blotzheim and Bauer (1982) and Cramp (1983).

Several clues in this historical summary suggest that a pattern of variation in *L. hyperboreus* has been overlooked. Bishop (1927) noted that individuals of *hyperboreus* from Siberia (actually Portenko's later named *pallidissimus*) wander to Alaska, and suggested that such vagrants may have influenced Dwight's conclusions about the validity of a small, dark Alaskan subspecies. Portenko (1939) recognized, on the basis of one specimen from Ellesmere Island, that eastern Canadian birds are paler than European birds, as are Siberian birds. Both Portenko and Dement'ev (1951) were misled by Friedmann's letter to Portenko into thinking that Alaskan birds were also pale, despite Oberholser's (1918, 1919) statements to the contrary. Dement'ev (1951) noted that Siberian birds were larger than European ones, and Todd (1963) commented on increasing size to the east across Canada.

An additional clue to the reason for disagreement on the recognition of subspecies in North America is found in AMNH birds marked "Dwight ref. spec.," individuals that apparently formed the basis for Dwight's concept of various populations. A Greenland bird (AMNH 64142, unsexed, 2 Aug 1893, badly stained ventrally and soiled dorsally) and one from Sable Island, Nova Scotia (AMNH 358035, male, 22 Feb 1895) seem typical of their populations in size and color. However, the reference specimen from Pt. Barrow, Alaska (AMNH 358051, female, 5 Sep 1897) is not an adult bird; it has a black band on the bill and some brown mottling in the wing and tail feathers. Both age and date indicate that it is not a breeding bird. Although it is the size of other Alaska specimens, it is very pale on the mantle,

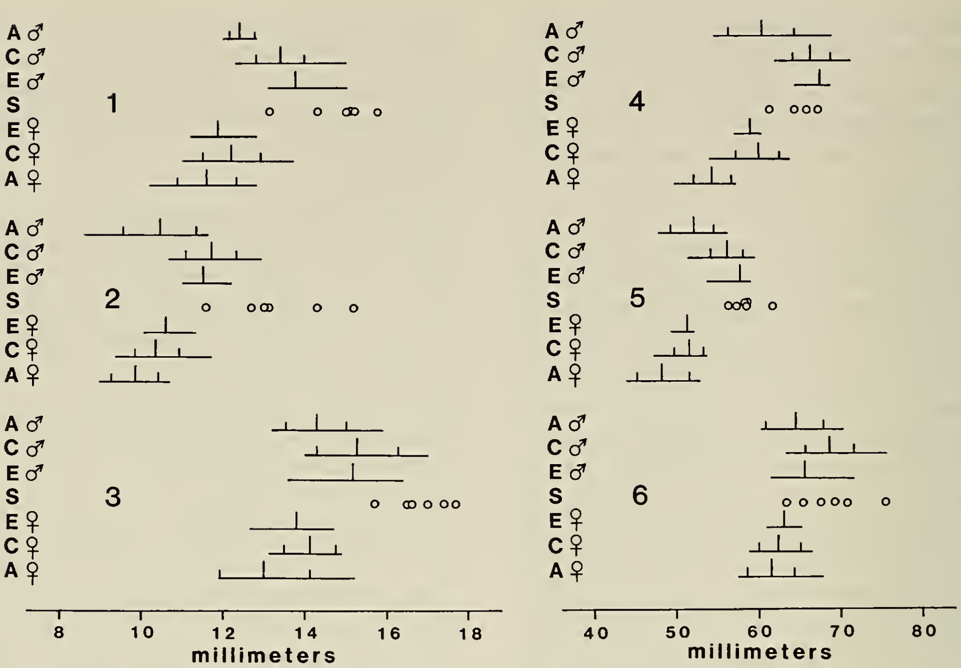

Fig. 1. Range of measurements in populations of the Glaucous Gull: 1, Depth of upper mandible; 2, Depth of lower mandible at gonys; 3, Width of upper mandible; 4, Length of culmen; 5, Length of lower mandible; 6, Length of tarsus. Horizontal line represents the range, the longer vertical line the mean, and the shorter vertical lines one standard deviation to either side of the mean. Individual measurements are plotted for the Siberian birds, which are not separated by sex, because of the small sample size.

even paler than the other two reference specimens. That reference specimen is probably why Dwight adamantly refused to recognize a dark-mantled Alaskan population.

## Methods of the Present Analysis

Sexed birds in the adult, gray-mantled plumage, taken mainly in the breeding season, were divided into subsets related to geographic origin—Alaska, eastern Canada and Greenland, Europe, and eastern Asia. The color of the mantle was judged in relative terms as pale or dark and was related to the Munsell (1929–1942) color system. Six measurements were made on each bird: 1) depth of the upper mandible at the anterior point of its lateral feathering; 2) depth of the lower mandible at the gonys; 3) length of the unfeathered culmen; 4) length of the lower mandible from the point of its lateral feathering; 5) width of the bill at the point of lateral feathering on the upper mandible; and 6) length of the tarsus. Several of these measurements are not standard, but are self-explanatory. The culmen length measurement (3) approaches "length of total culmen" more nearly than "length of exposed culmen" of Baldwin et al. (1931). These measurements were designed to show the "massiveness" of the bill. Wing and tail length were not measured, because extensive wear on many specimens renders them unreliable.

Color comparisons were also made on the few downy young available, and on birds in the first-year brown streaked plumage. Color comparisons are not possible in the "second-year" fully white ("*hutchinsii*") plumage. Measurements of birds in other than adult plumage were used for identification purposes after analysis had shown that the four samples represented separable populations.

## Results

Consideration of both color and size (Fig. 1) of birds from their breeding grounds indicates that four populations of *Larus hyperboreus* are distinguishable. Birds from the mainland of Alaska and nearby islands have relatively dark mantles and are small, the latter especially noticeable in the bill. Those of the eastern Canadian archipelago and Greenland have considerably larger bills and are paler on the mantle. European birds have similarly large bills but are darker on the mantle. Birds from Siberia and some islands in the Bering Sea are very large, with massive bills, and are very pale on the mantle. Thus, Siberian and eastern Canadian/Greenland birds are similar in their pale color (Munsell N 8.5–9/0), as noted by Portenko (1939), but differ in size of bill. Alaskan and European populations differ from the other two in being darker (Munsell N 7.5–8/0), and differ from one another in size of the bill. The relative color differences of the mantles of the adult birds are evident also in overall coloration of both downy young and first-year birds.

In general, there is a trend of increasing size in all bill measurements and in tarsal length (Fig. 1) eastward from Alaska around the Holarctic to Siberia, with the result that the largest and smallest populations are adjacent (but separated by the Bering and Chuckchi Seas and Bering Straits). There are reversals or interruptions in the trend in several instances; European birds are smaller than expected if the trend were a smooth cline. This may be an artifact of the small samples of European and Siberian birds or it may indicate that European birds are in fact only slightly different in size from those of Canada and Greenland. The trend of increasing size around the Holarctic can only provisionally be considered a true cline because too few populations, each from a large area, are considered.

## Systematic Treatment

### *Larus hyperboreus barrovianus*
### Ridgway, 1886

*Larus barrovianus* Ridgway, 1886:330.

*Holotype.*—USNM 88913, adult male, Point Barrow, Alaska, 4 Aug 1882. This specimen has some feathers of the neck, back and rump edged with brown; a few are edged with black that looks rather like oiling. The tail is also discolored at the tip. These markings may be what Friedmann was referring to in his letter to Portenko (see above). One other Point Barrow bird (USNM 93304) is similarly but less extensively marked.

*Breeding range.*—Coasts and islands of Alaska from Bristol Bay north to Kotzebue Sound and Point Barrow, and eastward on the Alaskan north coast. I have not examined specimens of *barrovianus* from east of Point Barrow.

*Discussion.*—If the species' range is continuous across the northern coast of Canada, as indicated by Godfrey (1966) but not by Snyder (1957), *barrovianus* probably intergrades with the next form between the Mackenzie River Delta and Franklin Bay. A worn, pale bird (AMNH 119090) from the Mackenzie River Delta is intermediate in three of the six measurements. Manning et al. (1956) commented that birds from western Canada are smaller than those in the east and in Greenland, although specimens from the Mackenzie Delta show less approach to *barrovianus* in color than in size. Henri Ouellet (pers. comm., 1985) noted that specimens in the National Museum of Canada from Mackenzie Delta, Anderson River, and Harrowhy Bay are closer to *barrovianus* in size and closer in average coloration of the mantle to *leuceretes,* and emphasized that Canadian birds are not uniform in color; an occasional dark-mantled bird may occur anywhere from Banks Island east to Baffin Island.

A number of Alaskan specimens and nonbreeding birds from the Pacific coast of North America are extensively dark on the primaries, perhaps a result of hybridization with the Glaucous-winged Gull, *Larus glaucescens,* or the Herring Gull, *L. argentatus* (Ingolfsson 1970:357–358; Strang 1977). Some very large birds from Alaska seem to be nonbreeding vagrant *pallidissimus* from Siberia, as suggested by Bishop (1927).

*Larus hyperboreus leuceretes* Schleep, 1819

*Larus leuceretes* Schleep, 1819:314.

*Holotype.*—Schleep (1819) mentioned three young birds from unspecified localities but based most of his description on an adult from Greenland in the collection of Herr Benicke of Schleswig. The range of the species was given as Greenland, Iceland, and Spitsbergen. Hellmayr and Conover (1948: 260) accepted the Greenland adult as the type, noting, however, that it is probably lost.

*Breeding range.*—Northern Canada eastward from Franklin Bay, Mackenzie, the Canadian archipelago, south in Hudson Bay to the Belcher Islands and on the Atlantic coast to northern Labrador (Hopedale), Greenland, probably Iceland.

*Discussion.*—Ridgway (1919), Dwight (1925), and Hellmayr and Conover (1948) gave extensive synonymies for *L. hyperboreus,* from which a name applicable to the Canada-Greenland population, here recognized as an entity for the first time, must be chosen. The earliest available and appropriate name seems to be *Larus leuceretes* Schleep, 1819, based on specimens from Greenland, Iceland, and Spitzbergen, of which an adult bird from Greenland is considered to be the type (Hellmayr and Conover 1948:260). Meyer (footnote in Schleep 1819) indicated that *leuceretes* was a synonym of *Larus giganteus* Temm., but the latter name seems to be, at least in part, a synonym of *L. marinus* Linnaeus (Saunders 1896; Ridgway 1919; Dwight 1925). Schleep (1819) contrasted *leuceretes* with *glaucus* by noting that the mantle of the former was "hellgraulichweiss" as opposed to "hellblaugrau" in *glaucus.* He also noted that the tarsus of *leuceretes* was slightly longer, and the bill was similar in form to that of *glaucus* but proportionately larger. In a table, Schleep further compared both *leuceretes* and *glaucus* to *L. marinus.* It is clear that he distinguished his Greenland bird from European specimens of *glaucus* (now *hyperboreus*).

My sample from the Canada-Greenland population included birds from Coronation Gulf, Baffin Island, and various islands in the northern Canadian archipelago, as well as from Greenland. Most are definitely breeding birds, but a few September specimens (Cornwallis Island) may have moved some distance from their nesting area.

Icelandic birds are provisionally placed with *leuceretes,* although the situation is far from clear. Ingolfsson (1970) has shown that Glaucous Gulls in Iceland now interbreed freely with Herring Gulls; recent specimens would be difficult to interpret on the subspecific level. I have examined only three older specimens from Iceland. A male (AMNH 745238, June, year not specified) is pale on the mantle like birds from eastern Canada and Greenland. In most measurements this bird falls into the range of the latter population, but it is in the zone of overlap with European birds in three measurements; in depth of the upper mandible it matches only the small Alaskan birds. A female (AMNH 745239, 9 Sep 1898) is not fully adult but matches European birds best in mantle color. Most of its measurements are in the overlap zone. The third specimen (AMNH 745241, female, 30 Nov 1823) is the type of *Larus minor* Brehm = *Larus medius* Brehm, names now carried in the synonymy of *L. hyperboreus.* It is less than fully adult, having a slight dark ring on the bill and some brown in the crown. There is too much dark color on the primaries to be typical of *hyperboreus,* and the bird appears to be very small. In most measurements it fits with Canadian or Alaskan series, but the depth of the upper mandible is less than in any other specimen I measured. It is slightly paler on the mantle than European birds, but not quite as pale as Greenland specimens. I am not convinced that the bird is an example of *hyperboreus,* although it is too large to be an Iceland Gull, *L. glaucoides.* It may be a hybrid between these two species.

### *Larus hyperboreus hyperboreus* Gunnerus, 1767

*Larus hyperboreus* Gunnerus, in Leems 1767:226.

*Holotype.*—Probably none extant, the name based on birds from northern Norway (Ridgway 1919; Hellmayr and Conover 1948; A.O.U. 1957).

*Breeding range.*—Northern Europe from Jan Mayen and Spitzbergen east along the coast and islands of the U.S.S.R. to the Taimyr Peninsula (Vaurie 1965).

*Discussion.*—My breeding sample of this population is small, only six birds, but wintering adults from Europe, presumed to represent this subspecies on geographic grounds, are similar in all characters. It is possible that some birds from Greenland stray to Europe in winter, and that the presence of paler Greenland birds with the darker European ones has given the impression of a wider range of variability in the European population than is evident from the examination of breeding birds alone.

### *Larus hyperboreus pallidissimus* Portenko, 1939

*Larus hyperboreus pallidissimus* Portenko, 1939:226.

*Holotype.*—Male, settl. Naukan, Chukotski Peninsula (female paratype from settl. Uelen), in collection of L. Portenko, now presumably in the Leningrad Museum.

*Breeding range.*—Arctic Siberia from about the Taimyr Peninsula eastward to the tip of the Chuckchi Peninsula, Wrangel Island, St. Matthew Island, and Walrus Island in the Pribilofs (Vaurie 1965; Portenko 1973).

*Discussion.*—An unsexed bird from Diomede Island, Jul 1881 (USNM 97255) is pale on the back like *pallidissimus,* but is in the size range of *barrovianus.* The Diomedes would be a reasonable place for intergradation of the two subspecies, if they do intergrade. I also consider a male from Cape Lisburne, Alaska, 1 Aug 1897 (USNM 745279) to be intermediate; it is as large as typical *pallidissimus* but the mantle color is dark like that of *barrovianus.*

### Nonbreeding Distribution in North America

Glaucous Gulls are inclined to wander extensively in the nonbreeding season, and movement to the east or west into the breeding range of another subspecies has been responsible, I believe, for some of the misunderstanding of geographic variation in the species. One bird from Point Barrow, Alaska, taken 5 Oct 1897 (AMNH 358049) is typical of the Siberian breeding population, *pallidissimus,* in both color and size. This bird was formerly in Dwight's collection and, if considered by him to be representative of the Barrow breeding population, may have been partly responsible for his (1906, 1919, 1925) rejection of Ridgway's name for the smaller, darker Alaskan form. Oberholser (1918) placed this bird with *barrovianus,* presumably on geographic grounds. A bird from Unalaska Island in the Aleutians (USNM 230781, 9 Jun 1911) is typical of *pallidissimus* in size but is in the all white plumage.

Several Alaska and Yukon birds appear to represent postbreeding or nonbreeding birds from the more eastern *leuceretes.* A bird from Tolugak Lake, Alaska (USNM 435222, 11 Jun 1949) in the all white plumage has measurements more similar to Canadian birds than to Alaskan ones. Juvenile birds from Bettles, Alaska (USNM 298495, 11 Oct 1924) and Old Crow, Yukon (USNM

469302, 28 Nov 1957) are both paler than typical juveniles from farther west in Alaska. As noted previously, Dwight's reference bird from Point Barrow (AMNH 358051, 5 Sep 1897) is pale dorsally, and another immature bird from there (USNM 93301, 15 Sep 1882) is also pale. These may all represent wanders from a more eastern, perhaps intermediate, population.

Most of the birds that move southward in the winter are young, in the all white plumage or some combination of that and a brown streaked plumage. For these birds color comparison is impossible and subspecific identification must be from measurements alone. No one measurement will suffice to separate the forms, although there is little or no overlap in most mensural characters of Siberian and Alaskan birds. A series or set of measurements, however, should indicate at least a strong probability of the breeding population from which a properly sexed specimen has been derived.

Glaucous Gulls appear somewhat infrequently in winter in Hawaii, more regularly along the Pacific coast of Canada and the United States to southern California and Baja California (Devillers et al. 1971), inland south to Texas and the Gulf coast, and on the Atlantic coast to Florida and, rarely, Bermuda. Pacific coastal birds have generally been referred to *barrovianus* when a subspecific determination has been made, and all west coast and Hawaiian birds that I have examined are indeed of that subspecies. A bird taken in Seattle, Washington (USNM 163899, 12 May 1896) was referred to *barrovianus* by Oberholser (1918) but to *hyperboreus* in distinction to *barrovianus* by Jewett et al. (1953). That identification to the larger form suggested that it might be a vagrant from the Siberian population, but measurements indicate that it is *barrovianus*. Devillers et al. (1971) mentioned an extremely large Glaucous Gull from the Salton Sea, California. I have examined that male bird (SBCM 33216), which is white with extensive brown mottling, and find that it, too, is best considered *barrovianus* although its measurements ovelap those of *leuceretes*.

When subspecific identification has been reported, Atlantic coast specimens have been called *hyperboreus*. Those that I have examined should be referred to *leuceretes*, here separated from the European *hyperboreus*. A Bermuda specimen (AMNH 783759, female, collected by D. Wingate, 18 Dec 1964) is a young bird, and its measurements are rather small, especially the depth of the lower mandible, but it best fits with *leuceretes*. Stevenson and Atherton (1984) have recently reviewed Florida records of *L. hyperboreus*, and noted that some specimens from that state are small.

Bailey and Niedrach (1965) reported two specimens of Glaucous Gull from Barr, Colorado, in the Denver Museum of Natural History, under the subspecific name *barrovianus*. Allan R. Phillips kindly provided measurements of these birds, taken to my specifications, and noted that both are in a brown mottled "first year" plumage. A male (DMNH 18800, 1 Apr 1938) is in the overlap zone of Alaskan and Canadian birds in three measurements but resembles Alaskan birds in culmen length and width and depth of the upper mandible. A female (DMNH 18799, 28 Mar 1938) equals or exceeds Canadian birds in all measurements except that of upper mandible width, leading one to wonder if it is missexed. If it were a male, two measurements would be those of Canadian birds, two of Alaskan, and two in the overlap zone. Asked for an impression of bill massiveness relative to Barrow, Alaska, birds in the DMNH collection, Phillips (in litt.) reported that the Colorado birds' bills were "heavier than most." With this information, and considering probably minor differences in measuring techniques, I suggest that both birds are from a population in western Canada that is in the intergrade zone.

One specimen of Glaucous Gull has been reported from Kansas (Rintoul 1984) and two from Oklahoma (Anderson 1971; Ports 1976), all without subspecific identification. All three are in immature plumage with much brown mottling, and all are referred to *leuceretes* on the basis of measurements (KSTC B-1406, female, Cheyenne Bottoms, Barton Co., Kansas, 6 Mar 1967; UOMZ 7175, male, Salt Fork, Arkansas River, Alfalfa Co., Oklahoma, 5 Feb 1971; UOMZ 7913, male, Lake Hefner, Oklahoma Co., Oklahoma, 27 Dec 1974).

Another bird (MCZ 33036, 17 Dec 1880) is claimed as a specimen record for both Oklahoma (Sutton 1967) and Texas (Oberholser 1974); it was taken on the Red River, which separates the states. Oberholser (1918, 1974) considered this bird to be *barrovianus.* The bird is labelled as a male, and if this sex determination is correct I agree with Oberholser's identification. However, the depth of the upper mandible is less than in any male *barrovianus* that I measured and I suspect that the specimen is actually a female, in which case the measurements place in the low range of *leuceretes.* It may represent the population where the two subspecies intergrade. Ragsdale (1881) commented that the bird had been dead for six weeks before he obtained it; when and by whom the sex was determined is not indicated.

A specimen from Gainesville, Cook Co., Texas (MCZ 32371; date unknown) was allotted to *L. h. hyperboreus* by Oberholser (1918, 1974). I refer this unsexed bird to *leuceretes.* A bird found dead at the Hagerman National Wildlife Refuge, Grayson Co., Texas, by Karl Haller is also *leuceretes.*

One other Texas specimen (WWF 1357, Mustang Island, Neuces Co., 10 Apr 1967) has also been listed as an example of *L. h. barrovianus* (Oberholser 1974). This bird was reexamined by R. G. McCaskie, who believed it to be an albinistic Herring Gull, *L. argentatus.* I have also studied this specimen and agree that it is a Herring Gull. Although its culmen length is within the range of *L. h. barrovianus,* all other measurements are too small for any subspecies of *hyperboreus.* A similar all-white-plumaged specimen from Louisiana (LSU 130496, female, 2 mi NNE Chalmette, St. Barnard Par., 28 Feb 1982) is also probably an albino, most likely of *argentatus,* rather than any form of *hyperboreus.* However, a partly gray-backed, nearly adult plumaged bird (LSU 103495, female) taken at the same time and place as the last is an example of *L. h. leuceretes.*

It thus appears from the specimen record now available that Alaskan Glaucous Gulls (*barrovianus*) move to the south only along the Pacific coast, and not into the inland states. All specimens from east of the Rocky Mountains represent the Canadian population, *leuceretes,* although some seem to be from the western portion of the breeding range of that subspecies where intergradation with *barrovianus* presumably occurs.

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# THE SYSTEMATICS OF THE GENUS *PACHYSTACHYS* (ACANTHACEAE)

Dieter C. Wasshausen

*Abstract.*—In 1847, Nees von Esenbeck described the genus *Pachystachys* with a single species, *P. riedeliana,* from Brazil. Later that same year, he published six additional species including *P. coccinea* (Aublet) Nees, a species that has long been confused with *P. riedeliana.* Although the two species are superficially similar, they can readily be separated by the longer, linear calyx segments of *P. coccinea.* Recent field activities in South America have shown that in number of species and in morphological diversity, the genus reaches its zenith in Amazonian Peru. Nine new taxa are currently proposed, whereas four of Nees' six species are reduced to synonymy. The genus is characterized by a prominent terminal spike of flowers with large, ringent, two-lipped corollas and two stamens that are about as long as the corolla, having equal, deeply sagittate anthers. Several species (*P. coccinea, P. spicata*) have been observed to be hummingbird pollinated, and the inflorescences of two additional species (*P. ossolaea, P. puberula*) are extensively covered with ants. However, floral morphology appears to preclude myrmecophily as a factor in the pollination system of the red-flowered rain-forested species of *Pachystachys.* All taxa have been studied in depth, including their pollen morphology, and analytical keys to the species have been prepared to facilitate the identification of the 12 species recognized in this treatment. The data from pollen morphology show only slight variation in the pollen of species of *Pachystachys* and support the retention of the genus in Bremekamp's (1938) tribe Odontonemeae subtribe Graptophyllinae.

The genus *Pachystachys* Nees is a Neotropical genus of 12 species. A member of the subfamily Acanthoideae (=Imbricatae Lindau, 1893), these plants occur along edges of the lowland rainforest at relatively low elevations (below 1000 meters) from the West Indies southward to Peru and Bolivia and eastward to French Guiana and Amazonian Brazil.

Members of *Pachystachys* are perhaps best known for their ornamental beauty, and many may be found in botanical gardens throughout the warmer regions of the world. Their prominent terminal spikes with bright red flowers are an impressive sight when the showy inflorescences reach full anthesis, and these shrubs or subshrubs are highly prized in the garden.

Recent field activities in South America have shown that in number of species and in morphological diversity, the genus reaches its zenith in Amazonian Peru. Since attempts to determine specifically the material from these collections proved unsatisfactory, I have decided to present a basic revision of the genus.

## History

In 1847, Nees von Esenbeck described the genus *Pachystachys* with a single species, *P. riedeliana,* from Amazonian Brazil. Later that same year in de Candolle's *Prodro-*

*mus* he published six additional species including *P. coccinea,* originally described as *Justicia coccinea* by Aublet in his "Histoire des plantes de la Guiane francoise" in 1775.

A second epithet, *Justicia spicata,* published by Ruiz & Pavon (Fl. Peruv. & Chil. Prodr. 1798) and based on one of their own collections from Peru, was cited by Nees in his second publication in synonymy under *P. riedeliana.* Unfortunately, this earlier epithet (1798) has priority over *riedeliana* (1847), and therefore *P. spicata* becomes the correct name for this species.

No further additions were made to the genus until 1947, when Carlos Rizzini described *P. albiflora* from Brazil. This species, collected in Acre, is synonymous with *P. lutea* from nearby Amazonian Peru.

## Morphology

The plants are suffrutescent and climbing and are between 1 and 3 meters tall, with relatively large, entire or undulate, petiolate leaves. Their prominent terminal flowering spikes are often large and conspicuous, with variously shaped and colored bracts and with bright red, pinkish-red or white corollas. The large, showy corollas are ringent, slenderly obconic, curved, and two-lipped. The upper lip is usually erect or recurved, narrow and bilobed, whereas the lower lip is three-lobed, the lobes spreading, subequal, oblong or ovate. There are two fertile stamens; these are about as long as the upper corolla lip and are attached near the base of the corolla tube. Both anthers are deeply sagittate, with the sacs equal and muticous at the base. The pollen of *Pachystachys* is the typical tricolporate, subprolate pollen characteristic of the tribe Odontonemeae. Here each colpus is flanked on either side by a pseudocolpus of approximately equal length. The colpi rarely fuse at one or both poles, whereas the pseudocolpi converge and are fused into three pairs just below the poles. The surface is commonly reticulate. While the pollen is slightly variable, the variation does not appear to be taxonomically significant.

The red floral colors seem to suggest that the flowers are largely adapted to hummingbird-pollination, and indeed this is what I have personally observed in several of the species. Furthermore, nectar appears to be secreted by a cushion-like nectary which surrounds the base of the ovary. Another interesting phenomenon that I have observed is that the inflorescences of most specimens of *Pachystachys,* as well as certain species of *Aphelandra* and *Ruellia,* are extensively covered with ants and homopterous insects. It appears that the ants feed on the honeydew exudate produced by the armored scales and in return protect the plants from other indiscriminate feeders.

Like most Acanthaceae, these taxa are of extreme local distribution in undisturbed forests and are rarely collected in secondary growth. There is no doubt in my mind that, as more field work is being undertaken in relatively uninhabited areas of Peru, additional taxa will be discovered. Furthermore, the genus appears to be well suited for reproductive biology studies, especially pollinator relationships and seed dispersal.

## Taxonomy

*Pachystachys* Nees in Mart. Fl. Bras. 9:99. 1847. Type species: *Pachystachys riedeliana* Nees.

Herbaceous or suffrutescent plants; leaves large, petioled; spikes terminal, dense; bracts conspicuous, herbaceous; bractlets small or none; flowers borne in terminal spike of verticillasters consisting of 3 or 4 flowers each; calyx 5-parted, the segments relatively short; corolla ringent, slenderly obconic, curved, 2-lipped, upper lip narrow, 2-lobed at tip, lower lip 3-lobed, lobes subequal, oblong or ovate; stamens 2, about as long as corolla, attached near base of its tube; anthers deeply sagittate, basal lobes muticous, equal; staminodes, if present, rudimentary; capsule 4-seeded.

## Key to the Species of *Pachystachys*

1. Corolla white; bracts bright yellow or orange yellow ........................ *P. lutea*

*1.* Corolla red, crimson, pinkish-red or pink; bracts green, yellowish-green, green with purple at tips or brownish red ........................ 2

2. Bracts 3–4.5 cm long ........................ 3

3. Bracts elliptic-ovate, 15–17 mm wide ........................ *P. longibracteata*

*3.* Bracts oblanceolate, 6–8 mm wide ........................ 4

4. Leaf blades oblong to ovate, 8–8.5 cm wide; spikes 6–10 cm long; bracts 7–8 mm wide, terminated by mucro about 1 mm long, principal veins not prominent ........................ *P. schunkei*

*4.* Leaf blades elliptic to oblong, 11–14.5 cm wide; spikes 19–20 cm long; bracts 6–7 mm wide, not terminated by mucro, three principal veins prominent ........................ *P. fosterii*

*2.* Bracts less than 3 cm long ........................ 5

5. Bracts brownish-red, lanceolate, 0.8 cm long, 1.5 mm wide ....*P. badiospica*

*5.* Bracts green, yellowish-green or green with purple at tips, lanceolate, oblanceolate, ovate or narrowly elliptic, 1.5–2.8 cm long, 6–18 mm wide .. 6

6. Corolla 3.5–4 cm long ........................ 7

7. Bracts yellowish-green, membranous, sparingly glandular-pilose; corolla pink, upper lip erect ........................ *P. incarnata*

*7.* Bracts dark-green, not membranous, densely puberulous; corolla crimson, upper lip recurved ........................ *P. puberula*

*6.* Corolla 5–7.5 cm long ........................ 8

8. Calyx segments narrowly triangular, 3 mm long, 1 mm wide . *P. spicata*

*8.* Calyx segments lanceolate, 5–10 mm long, 0.5–1.5 mm wide ..... 9

9. Calyx 9–12 mm long, segments 8–10 mm long; corolla pink, pinkish-red or orange-red ........................ 10

10. Bractlets minute, 2 mm long, 0.4 mm wide, glabrous; bracts narrowly ovate, 2.2–2.5 cm long ........................ *P. roseus*

*10.* Bractlets 11 mm long, 1.25 mm wide, pilose; bracts broadly elliptic, 1.7 cm long ........................ *P. killipii*

*9.* Calyx 5.5–7 mm long, segments 5 mm long; corolla bright red or crimson ........................ 11

11. Bracts green with purple at tip; corolla puberulous and glandular punctate, upper lip 2-lobed, lobes obtuse, 1.5 mm long, 1.2 mm wide ........................*P. ossolaea*

*11.* Bracts green; corolla rather sparingly pubescent with minute spreading hairs (hirtellous), upper lip emarginate, lobes 1 mm long, 0.5 mm wide ........................ *P. coccinea*

### *Pachystachys lutea* Nees, DC. Prodr. 11:320. 1847

*Justicia lutea* Ruiz & Pavon ex Schult. Mantissa 1. 146. 1822, nom. nud. *Pachystachys albiflora* Rizzini, Bol. Mus. Nac. Rio de Janeiro 8: 24, pl. 7. 1947.

Erect, lax shrub 1.5–2.5 m tall; stem slender, subterete, brownish, glabrous, the nodes more or less tumid; leaf blades subsessile, oblong-lanceolate, 8.5–18 cm long and 2–5 cm wide, acuminate at apex, gradually narrowed from below middle to a rounded, clasping base, 1 cm wide in larger leaves, entire or undulate, membranous, glabrous except for puberulent midrib, cystoliths numerous and prominent both above and below; inflorescence consisting of terminal, solitary spike 6–10 cm long, rachis densely puberulous; bracts densely imbricate, bright yellow or orange-yellow, ovate, 1.5–2 cm long, 1–1.5 cm wide (terminal bracts somewhat smaller, basal ones larger), short-acuminate at apex, subcordate at base, glandular-pilose, especially so along upper margins; bractlets lanceolate-spatulate to elliptic, 9–12 mm long, 3.5–4 mm wide, acuminate, glandular-pilose along margins; calyx campanulate, 9–10 mm long, segments linear-lanceolate, 7–9 mm long and 1–1.1 mm wide near base, sparingly puberulous and ciliate; corolla white, 5.5 cm long, tube curved, 3 mm wide at base, narrowed to 1.75 mm at 5 mm above base, thence gradually enlarged to 8.5 mm at throat, pilose and glandular-punctate, upper lip erect, lanceolate, 1.8 cm long, 5–5.5 mm wide near base, gradually narrowed to 1 mm at tip, sparingly pilose, minutely 2-lobed, lobes obtuse, lower lip ovate, undulate, sparingly pilose, 3-lobed, lateral lobes 3.5 mm long, 2 mm wide, obtuse or rounded, middle lobe 3.5 mm long, 2.5 mm wide, obtuse or rounded; stamens attached near base of corolla tube, filaments 5 cm long, sparingly puberulous, anthers bright green, 5 mm long, deeply sagittate, basal lobes muticous; pollen grains 53 $\mu$m long, 45 $\mu$m wide, tricolporate, each colpus flanked by 2 pseudocolpi, tectum almost complete, psilate-punctate (Fig. 1); staminodes none; ovary glabrous; capsule clavate, 13 mm long, 5 mm broad, 2.75 mm thick, glabrous; retinacula 2 mm long, slightly curved, tip flattened, obtuse; seeds 2, brownish, cordate, flattened, about 4.5 mm long and 4 mm broad, glabrous.

*Material.*—PERU: San Martín: Lamas, *Matthews 1538* (syntype K); On trail from Lamas to San Antonio E of Río Chupiseña, *Belshaw 3500* (NY, UC, US); Pongo de Cainarachi, Río Cainarachi, 230 m, *Klug 2655* (NY, US); Juanjui, 400 m, *Klug 3838* (NY, US); Prov. Mariscal Cáceres: Dtto. Tocache Nuevo: Quebrada de Huaquisha, 500–600 m, *Plowman, Schunke & Rury 11389* (F, US); Quebrada de Cañuto, ca. 500 m, *Schunke-Vigo 12083* (NY, US); Quebrada de Saule Chico, *Schunke-Vigo 4346* (F, NY, US); Between Uchiza and Puerto Huicte, 500–600 m, *Ferreyra 4410* (US, USM); Fundo Melódia, road to Shunté, 800 m, *Schunke-Vigo 7436* (US); Huánuco: Chicolaya, *Tafalla 345* (syntype G, MA); Prov. Tingo María: Vicinity of Tingo María, 650–700 m, *Ferreyra 6772* (US, USM): 625–1100 m, *Allard 21622* (US); Junín: Near La Merced, *Soukup 2531* (US); Cuzco: Prov. La Convención: Hda. Luisiana, 620 m, *Dudley 11525* (NA). BRAZIL: Acre: Varadouro S. Luiz, *Kuhlmann 728* (R, holotype of *P. albiflora* Rizz.).

At edge of ravines in dense forests, sometimes saxatile on very steep dry cliffs, usually found on banks of streams at elevations between 230 and 1100 meters. This native of Peru is often found in cultivation in greenhouses.

### *Pachystachys longibracteata* Wasshausen, sp. nov.
Figs. 1, 2

Suffrutex; caules subquadrangulares, glabri; lamina foliorum elliptica, acuminata, basi angustata in petiolum amplectens, glabra; spicae solitariae, terminales, rhachidi puberula; bracteae grandes, viridae, elliptica-ovatae, 15–17 mm latae, apice acuminatae vel obtusae; bracteolae lineari-lanceolatae; calycis segmenta anguste triangularia; corolla coccinea vel scarlatina, puberula, labio inferiore oblongo, lobo medio conduplicato apice curvato, lobis lateralibus leviter rotundatis.

Shrub 1–3 m high; stems subquadrangular, glabrous; leaf blades elliptic, to 35 cm long and 13 mm wide, acuminate at apex, narrowed from about middle to rounded, clasping base 2–3 cm wide in larger leaves,

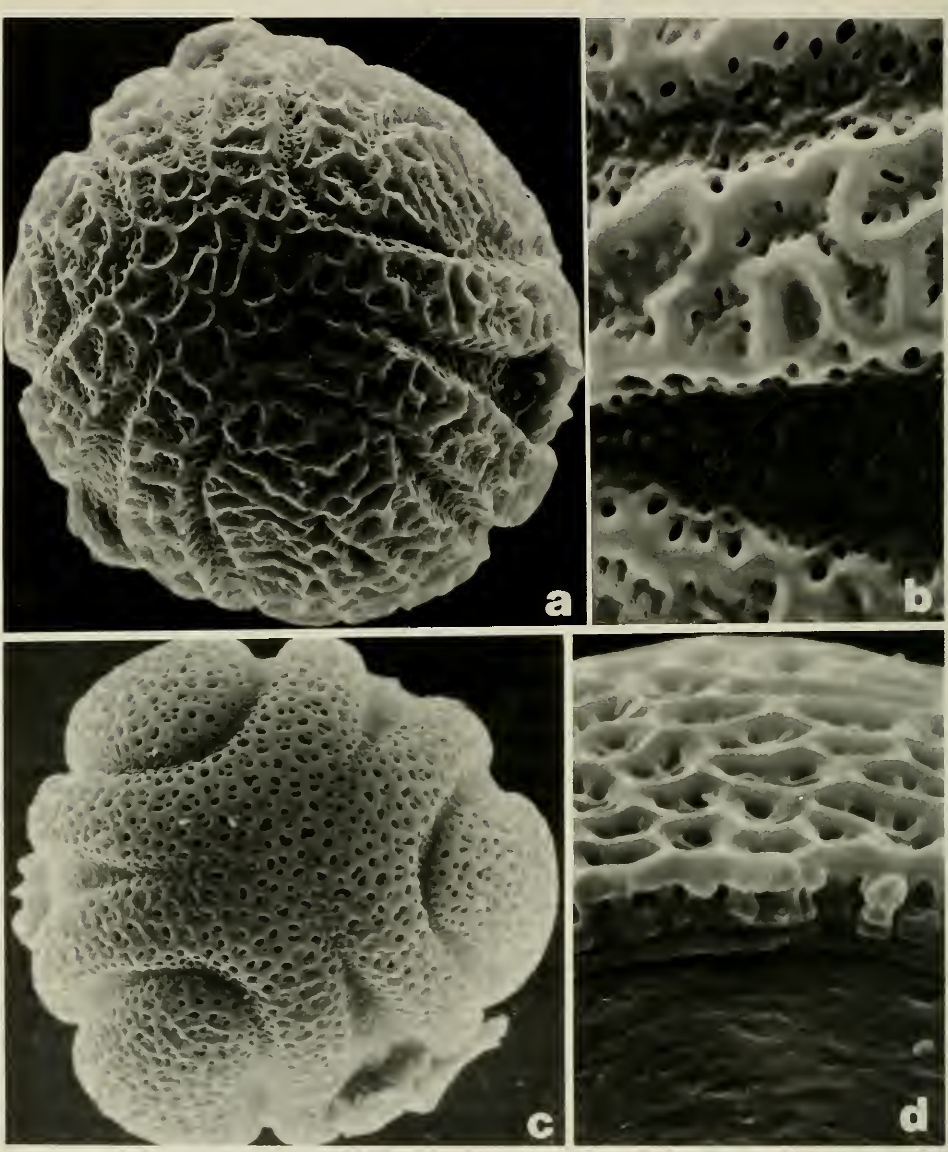

Fig. 1. SEM photomicrographs of *Pachystachys* pollen. A–B, *Pachystachys lutea* (*Mennega 71-136*); C–D, *Pachystachys longibracteata* (*Killip & Smith 28725*). A, Polar orientation, ×1800; B, Portion of surface, including colpus at ×4600; C, Polar orientation, ×1700; D, Surface view of reticulate form of fractured grain, ×6600.

entire or undulate, glabrous, cystoliths numerous, about 0.25 mm long; petioles to 7 cm long, glabrous; inflorescence to 23 cm long, internodes, bracts, calyx, and ovary densely but minutely puberulent; bracts green, elliptic-ovate, 3–4.5 cm long and 15–17 mm wide, acuminate to obtuse at apex, narrowed at base to short winged petiole; bractlets linear-lanceolate, to 17 mm long and 3 mm wide; calyx 2–3 mm long, segments narrowly triangular; corolla scarlet, sparingly and minutely puberulent, 6 cm

Fig. 2. A–E, *Pachystachys longibracteata* (*Killip & Smith 27866*). A, Flowering spike; B, Leaf blade; C, Bract and calyx; D, Corolla and exserted stamens and style; E, Corolla expanded, showing attachment of filaments.

long, 3 mm broad at base, narrowed to 2 mm at 5 mm above base, and then gradually narrowed to 8 mm at throat, lobes minutely ciliate, those of lower lip oblong, about 13 mm long, 6 mm broad, two lateral rounded at top, middle conduplicate and curved at tip, upper lip 2 cm long, 4 mm at base, gradually narrowed to small, bilobed tip about 1 mm broad; filaments glabrous, anthers about 4 mm long; pollen grains 58 $\mu$m long, 40 $\mu$m wide, tricolporate, each mesocolpium flanked by two colpoid streaks, membrane densely granular, sexine suprareticulate, reticulation heterobrochate (Fig. 1); style glabrous, persistent after fall of corolla; capsule wanting.

*Type.*—PERU: Loreto: Puerto Arturo, lower Río Huallaga below Yurimaguas, ca. 135 m, *Killip & Smith 27866* (holotype US; isotype NY).

*Additional specimens.*–PERU: Loreto: Santa Rosa, lower Río Huallaga below Yurimaguas, ca. 135 m, *Killip & Smith 28725* (NY, US); Yurimaguas, lower Río Huallaga, ca. 135 m, *Killip & Smith 28055* (US); Shitari, near Isla Santa María, Yurimaguas, 150–180 m, *Ferreyra 10159* (US, USM).

Occasional in dense forest at elevations of 135–180 meters.

This species is well marked and distinguished by its densely puberulous inflorescence and large leaf blades with their bases clasping the petiole and the unusually broad or short lobes of the lower lip of the corolla.

### *Pachystachys schunkei* Wasshausen, sp. nov.

Fig. 3

Suffrutex; caules subquadrangulares, bruneoli, puberuli; lamina foliorum oblonga vel ovate, acuminata, basi angustata in petiolum amplectens, glabra; spicae terminales, bifurcatae, aliquanto breves, rachidi dense puberula; bracteae viridae, oblanceolatae, acuminatae et minute mucronatae; bracteolae linear aristatae; calycis segmenta lanceolata, puberula, ciliolata; corolla coccinea, glabra, tubo leviter curvato, labio superiore recurvato bilobato, labio inferiore 3-lobato, lobis obovatis, lobo medio conduplicato.

Shrub 2–3 m tall; stem subquadrangular, brownish, puberulous; leaf blades oblong to ovate, 19–22 cm long and 8-8.5 cm wide, acuminate at apex, gradually narrowed from below middle to a rounded, clasping base 1.5 cm wide in larger leaves, entire or undulate, thin, glabrous, shining, cystoliths inconspicuous; petioles 3–8.5 cm long, glabrous; inflorescence consisting of terminal, bifuricate spike 6–10 cm long, rachis densely puberulous; bracts green, oblanceolate, 3.5–4 cm long, 7–8 mm wide, acuminate, terminated by mucro about 1 mm long, gradually narrowed at base and attenuate, densely gladular pilose without, minute eglandular hairs intermixed with glandular ones, principal veins not prominent; bractlets linear-aristate, about 2 cm long, 1 mm wide, pubescence similar to that of bracts; calyx campanulate, 4.5 mm long, segments lanceolate, 4 mm long and 1 mm wide near base, acuminate, densely puberulous and ciliate; corolla vivid red, 5–5.5 cm long, tube slightly curved, 4 mm wide at base, narrowed to 2 mm at 5 mm above base, thence gradually enlarged to 6.5 mm at throat, glabrous, upper lip recurved, oblong to narrowly lanceolate, 1.4 cm long, 2.5 mm wide just below middle, gradually narrowed to 1.5 mm at tip, minutely 2-lobed, lobes obtuse, lower lip 3-lobed, lobes spreading, obovate, rounded at tip, lateral pair 13 mm long, 6 mm wide, middle lobe 9 mm long and 4.5 mm wide, conduplicate; stamens attached near middle of corolla tube, filaments 3 cm long, sparingly and inconspicuously puberulous, anthers 4 mm long, deeply sagittate, basal lobes muticous; staminodes none; ovary puberulous; capsule wanting.

*Type.*–PERU: San Martín: Prov. Mariscal Cáceres: Dtto. Tocache Nuevo, Quebrada de Santa Rosa de Cachiyacu, 500–700 m, *Schunke-Vigo 7597* (Holotype US).

Occasional in tall forest.

*Discussion.*—*Pachystachys schunkei* is perhaps nearest in relationship to *P. fosteri,* another new species from Peru, but differs markedly in that the latter species has leaf blades elliptic to oblong, 11–14.5 cm wide, spikes 19–20 cm long, and prominently veined bracts 6–7 mm wide, not terminated

Fig. 3. A–D, *Pachystachys schunkei* (*Schunke-Vigo 7597*); E–I, *Pachystachys badiospica* (*Schunke-Vigo 2714*). A, Habit; B, Bract, bractlets and calyx; C, Corolla and exserted stamens and style; D, Corolla expanded, showing attachment of filaments; E, Habit; F, Bract and bractlets; G, Calyx; H, Corolla closed; I, Corolla expanded, showing attachment of filaments.

by a mucro. In contrast, *H. schunkei* has leaf blades oblong to ovate, 8–8.5 cm wide, spikes 6–10 cm long, and bracts not prominently veined, 7–8 mm wide, terminated by a mucro about 1 mm long.

### *Pachystachys fosteri* Wasshausen, sp. nov.
Fig. 4

Suffrutex; caules subquadrangulares, bruneoli, glabri; lamina foliorum elliptica vel oblonga, acuminata, basi angustata in petiolum amplectens, glabra; spicae terminales, bifurcatae, 19–20 cm longae, rachidi dense puberula; bracteae viridae, oblanceolatae, acuminatae, glanduloso-puberulae, venis 3 principalibus prominentibus; bracteolae lineares, puberulae; calycis segmenta lanceolata, puberula; corolla scarlatina, puberula, labio superiore erecto et recurvato bilobato, labio inferiore trilobato, lobis obovatis, lobo medio conduplicato et retuso.

Shrub 2–3 m tall; stem subquadrangular, brownish, glabrous; leaf blades elliptic to oblong, 33 cm long and 11–14.5 cm wide, acuminate at apex, gradually narrowed from below middle to a rounded, clasping base 2 cm wide in larger leaves, entire or undulate, glabrous, cystoliths numerous, especially below; petioles 3–9 cm long, glabrous; inflorescence terminal, consisting of bifuricate spike 19–20 cm long, rachis densely puberulous; bracts green, oblanceolate, 3.3 cm long, 6–7 mm wide, acuminate at apex, gradually narrowed at base and attenuate, densely glandular puberulous without, ciliate, three principal veins prominent; bractlets linear, 2.3 cm long, 1 mm wide, densely glandular-puberulous and ciliate; calyx campanulate, 6 mm long, segments lanceolate, 4.5 mm long and 1 mm wide near base, acuminate, densely puberulous and ciliate; corolla scarlet, 5 cm long, tube slightly curved, 3–3.5 mm wide at base, narrowed to 2 mm at 4 mm above base, thence gradually enlarged to 8 mm at throat, puberulous and occasionally interspersed with minute glands, upper lip erect and recurved, oblong to narrowly lanceolate, 1.2 cm long, 2.5 mm wide just below middle, gradually narrowed to 1.5 mm at tip, minutely 2-lobed, lobes obtuse, lower lip 3-lobed, lobes spreading, obovate, lateral pair 12 mm long, 5 mm wide, rounded at tip, middle lobe 9 mm long and 6–6.5 mm wide, conduplicate and retuse at tip; stamens attached near middle of corolla tube, filaments 3.5 cm long, sparingly puberulous, anthers 4.7 mm long, deeply sagittate, basal lobes muticous; staminodes none; ovary densely tomentose; capsule wanting.

*Type.*—PERU: Huánuco: Pachitea; Puerto Inca, 2–5 km E of town, 250–300 m, *Foster 8686* (holotype US).

Occasional, along forest trails.

*Discussion.*—Named in honor of the collector, Robin B. Foster, in recognition of his valuable contributions to our knowledge of Peruvian botany. The major differences between *Pachystachys fosteri* and *P. schunkei,* its nearest relative, are described under the discussion of the latter species.

### *Pachystachys badiospica* Wasshausen, sp. nov.
Figs. 3, 5

Suffrutex; caules subquadrangulares, brunneoli, glabri; lamina foliorum elliptica vel ovata, acuminata, basi angustata in petiolum amplectens, glabra; spicae terminales, solitariae vel bifurcatae, rachidi dense puberula; bracteae badiae lanceolatae, mucronulatae, extus dense glanduloso-pilosae; bracteolae lanceolatae; calycis segmenta subaequalia, lanceolata, parce glanduloso-pilosa; corolla coccinea, parce pilosa, tubo leviter curvato, labio superiore erecto, bilobato, labio inferiore trilobato, lobis lateralibus oblongis, obtusis, lobo medio retuso; antherae rubrae.

Shrub 1–2 m tall; stem subquadrangular, brownish, glabrous; leaf blades petiolate, elliptic to ovate, 15–26 cm long and 5.5–11.5 cm wide, acuminate at apex, narrowed from

Fig. 4. A–E, *Pachystachys fosteri* (*Foster 8686*); F–I, *Pachystachys rosea* (*Vargas C, 23159*). A, Habit; B, Bract and bractlets; C, Calyx; D, Corolla and exserted stamens and style; E, Corolla expanded, showing attachment of filaments; F, Habit; G, Bractlets and calyx; H, Corolla and exserted stamens and style; I, Corolla expanded, showing attachment of filaments.

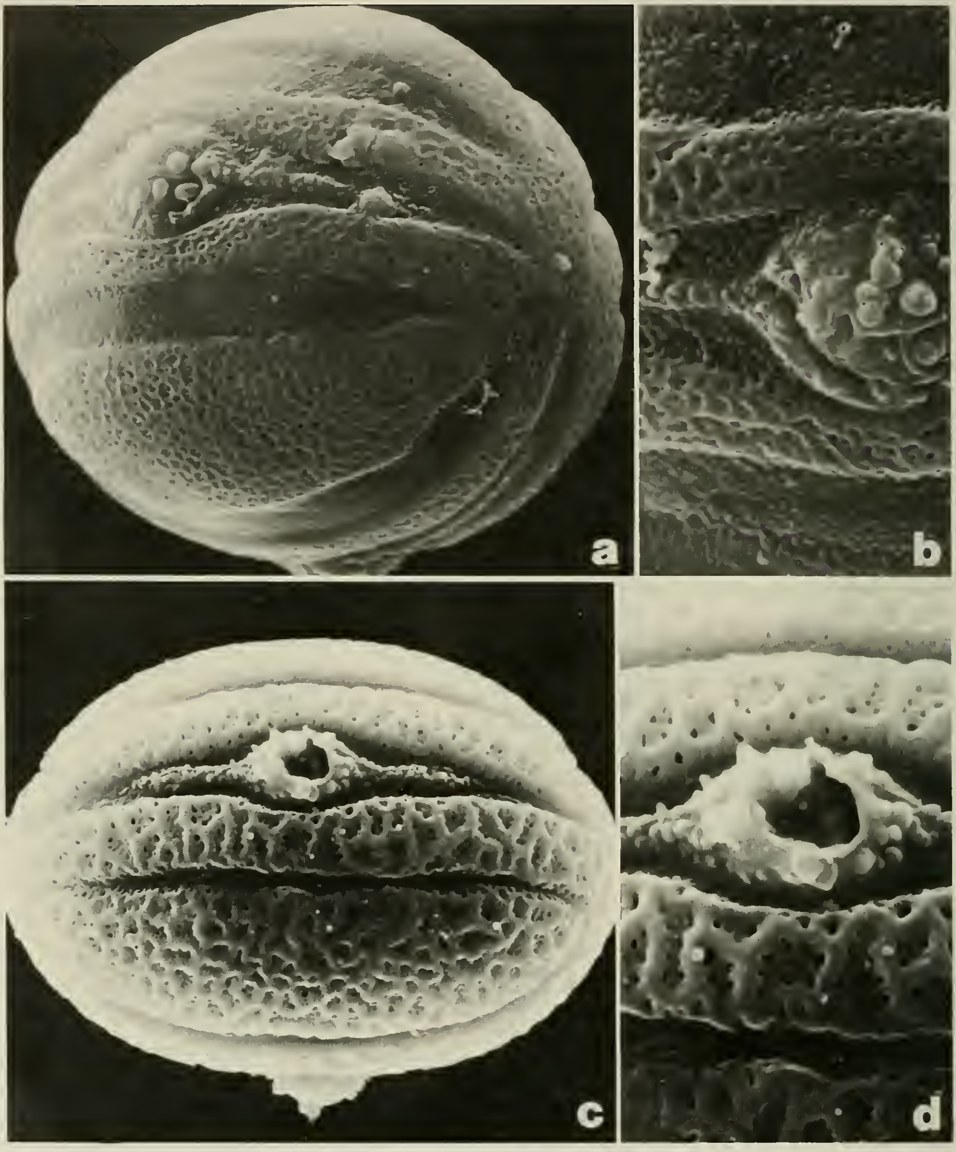

Fig. 5. SEM photomicrographs of *Pachystachys* pollen. A–B, *Pachystachys badiospica* (*Schunke-Vigo 2714*); C–D, *Pachystachys incarnata* (*Killip & Smith 28926*). A, Equatoiral view, × 1700; B, Portion of surface, including pore at × 3000; C, Equatorial view, × 2000; D, Portion of surface, including pore at 3700.

below middle to rounded, clasping base 15 mm wide in larger leaves, moderately firm, entire or undulate, upper surface dark-green, nitid, lower surface paler green, glabrous, cystoliths numerous and conspicuous both above and below; petioles 2–6 cm long, canaliculate, glabrous; inflorescence consisting of solitary or bifuricate, terminal spike 10–16 cm long, rachis densely glandular puberulous; bracts brownish-red, lanceolate, 8 mm long, 1.5 mm wide, mucronulate at apex, densely glandular-pilose without, minute eglandular hairs intermixed with glandular ones; bractlets lanceolate, 6.5 mm long, 1.25 mm wide, pubescence similar to that of bracts; calyx deeply 5-parted, 15 mm long, segments lanceolate, subequal, sparingly glandular-pilose, posterior segment 9 mm long, 1 mm wide, anterior pair 13 mm long, 1.5 mm wide, lateral pair 12 mm long, 1.25 mm wide; corolla red, 5 cm long, sparingly pilose, tube slightly curved, 5 mm wide at base, narrowed to 3 mm at 5 mm above base, thence gradually enlarged to 18 mm at throat, upper lip erect, oblong to narrowly lanceolate, 1.5 cm long, 4 mm wide, minutely 2-lobed, lobes obtuse, lower lip ovate, 1 cm long, 3-lobed, lateral lobes oblong, 7 mm long, 3 mm wide, obtuse or rounded, middle lobe 8 mm long, 6 mm wide, retuse; stamens attached near base of corolla tube, filaments 2.7 cm long, sparingly puberulous, anthers red, 4.5 mm long, deeply sagittate, basal lobes muticous, pollen grains 50 μm long, 41 μm wide, tricolporate, each mesocolpium with two colpoid streaks, tectum almost complete, psilate-punctate (Fig. 5); staminodes none; ovary glabrous; capsule clavate, long-stipitate, 2 cm long, puberulous, 2-seeded, solid basal portion about 1 cm long, seed-bearing cavity 8 mm broad, seeds flattened, orbicular, 7 mm long and broad, muricate, retinacula 3 mm long, slightly curved, tip flattened, obtuse.

*Type.*—PERU: JUNÍN: Satipo, *Ridoutt s.n.* (holotype US; isotype USM).

*Additional specimens.*—PERU: Loreto: Prov. Coronel Portillo, Dtto. Iparia, Bosque Nacional de Iparia, along Río Ucayali in the vicinity of Iparia, 300 m, *Schunke V. 2714* (US). JUNÍN: road between Santa Clara and Satipo, *Ridoutt s.n.* (US, USM).

In openings and along the edge of dense, humid forests.

*Discussion.*—This species is readily distinguished by its narrow, brownish-red, lanceolate, glandular-pilose bracts, bractlets, and calyx segments. It is not very closely allied to any of the known species of *Pachystachys.*

### *Pachystachys incarnata* Wasshausen, sp. nov.
Figs. 5, 6

Frutex, caules erecti, teretes, brunneoli, glabri; lamina foliorum elliptica vel ovata, acuminata, basi angustata in petiolum amplectens, membranacea, nitida, glabra; spicae terminales, rachidi dense puberula; bracteae dense imbricatae, stramineae, ovatae, mucronulatae, parce glanduloso-pilosae; bracteolae lineari-lanceolatae, puberulae; calyx campanulatus, segmenta lanceolata, puberula; corolla rosea, puberula, tubo leviter curvato, labio superiore erecto, bilobato, labio inferiore trilobato, lobis patulis, lobis lateralibus oblongis vel anguste ovatis, rotundatis, lobo medio obovato, conduplicato et retuso.

Erect shrub about 2 m tall; stem terete, brownish, glabrous; leaf blades elliptic to ovate, 20–25 cm long and 7.5–8.2 cm wide, acuminate at apex, gradually narrowed from below middle to a rounded, clasping base 1 cm wide in larger leaves, entire or undulate, membranous, nitid and dark-green above, much lighter-green below, glabrous, cystoliths numerous and prominent both above and below; petioles 2–3 cm long, minutely puberulous; inflorescence consisting of terminal, solitary spike 13 cm long, rachis densely puberulous; bracts densely imbricate, yellowish-green, ovate, 2 cm long, 1.4 cm wide, mucronulate at apex, gradually narrowed and cuneate at base, sparingly glandular-pilose, especially near apex; bractlets linear-lanceolate, 11 mm long, 1.25 mm wide, puberulous and ciliate, bearing few glandular trichomes near apex; calyx campanulate, 12 mm long, segments lanceolate, 10 mm long and 1 mm wide near base, acuminate, puberulous and ciliate; corolla pink, 4 cm long, puberulous, tube slightly curved, 4 mm wide at base, narrowed to 1.8 mm at 5 mm above base, thence gradually enlarged to 6.5 mm at throat, upper lip erect, oblong to narrowly lanceolate, 1.2 cm long, 3.5–4 mm wide near base,

Fig. 6. A–D, *Pachystachys incarnata* (*Killip & Smith 28926*); E–G, *Pachystachys killipii* (*Killip & Smith 2661*). A, Habit; B, Bractlets and calyx; C, Corolla and exserted stamens; D, Corolla expanded, showing attachment of filaments; E, Habit; F, Bractlets and calyx; G, Corolla and exserted stamens and style.

gradually narrowed to 1 mm at tip, minutely 2-lobed, lobes obtuse, lower lip 3-lobed, lobes spreading, lateral pair oblong to narrowly ovate, 15 mm long, 5 mm wide, rounded at tip, middle lobe obovate, 12 mm long and 4.5 mm wide, conduplicate and retuse, minutely lobulate on one side; stamens attached near base of corolla tube, filaments 4 cm long, minutely puberulous, anthers 5 mm long, deeply sagittate, basal lobes muticous; pollen grains 46 μm long, 28 μm wide, tricolporate, each mesocolpium with two colpoid streaks, tectum almost complete, psilate-punctate (Fig. 5); staminodes none; ovary puberulous; capsule wanting.

*Type.*—PERU: Loreto: Santa Rosa, lower Río Huallaga below Yurimaguas, ca. 135 m, *Killip & Smith 28926* (holotype US; isotype NY).

Occasional in dense forest.

*Discussion.*—*Pachystachys incarnata* superficially resembles *P. lutea* Nees. However, in *P. lutea,* the corolla is white, 5.5 cm long, the bracts bright yellow or orange-yellow, and the leaf blades are oblong-lanceolate, 8.5–18 cm long and 2–5 cm wide. In *P. incarnata,* the corolla is pink, only 4 cm long, the bracts yellowish-green, and the leaf blades are elliptic to ovate, 20–25 cm long and 7.5–8.2 cm wide.

### *Pachystachys puberula* Wasshausen, sp. nov.
Figs. 7, 8

Suffrutex; caules subquadrangulares, brunnei, glabri; lamina foliorum oblonga vel ovata, breviter acuminata, basi angustata in petiolo amplectens, atrovirens et nitida, glabra; spicae terminales, solitariae, rachidi subtiliter puberula; bracteae laxe imbricatae, atrovirens, late ovatae, obtusae et apiculatae, basi angustatae ad petiolos brevialatae; calyx campanulatus, segmenta anguste triangularia, dense puberula; corolla carminea, puberula, tubo leviter curvato, labio superiore erecto et recurvato, bilobato, labio inferiore trilobato, lobis obovatis, patulis, lobo medio conduplicato apice obtuso.

Shrub 2–5 m tall; stem subquadrangular, dark-brown, glabrous; leaf blades very dark-green and glossy, oblong to ovate, 15–28 cm long and 7.5–13.5 cm wide, short-acuminate at apex, gradually narrowed from below middle to a rounded, clasping base 1 cm wide in larger leaves, entire or undulate, glabrous, cystoliths numerous, especially below; petioles 3–8 cm long; inflorescence consisting of solitary, terminal spike 7–15 cm or more long, rachis finely puberulous; bracts rather loosely imbricate, dark-green, broadly ovate, 1.5–2.5 cm long, 10–18 mm broad (terminal bracts somewhat smaller, basal ones larger), rounded and apiculate at apex, narrowed at base to short-winged petiole, densely puberulous; bractlets lanceolate, about 4 mm long and 1.2 mm broad, densely puberulous; calyx campanulate, 3.5 mm long, segments narrowly triangular, about 2 mm long and 1 mm wide at base, acuminate, densely puberulous; corolla crimson, 3.5–4 cm long, tube slightly curved, 3.5–4 mm wide at base, narrowed to 2 mm at 7 mm above base, thence gradually enlarged to 7 mm at throat, puberulous, upper lip erect and recurved, lanceolate, 1.5 cm long, 3.5 mm wide near base, gradually narrowed to 1 mm at tip, minutely 2-lobed, lobes obtuse, lower lip 3-lobed, spreading, lobes obovate, rounded at tip, lateral ones 12 mm long, 6 mm broad, middle lobe 15 mm long and 5.5 mm broad, conduplicate, obtuse at tip; stamens attached near base of the corolla tube, filaments 3.5–4.3 cm long, glabrous, anthers 3.8–4 mm long, deeply sagittate, basal lobes muticous; pollen grains 52 μm long, 35 μm wide, tricolporate, each mesocolpium flanked with two colpoid streaks, tectum almost complete, psilate-punctate (Fig. 8); staminodes none; ovary puberulous; capsule wanting.

*Type.*—PERU: San Martín: Prov. Martín: Puente Colombia, 24 km S of Tarapoto,

Fig. 7. A–D, *Pachystachys puberula* (*Wasshausen & Encarnación 1023*). A, Habit; B, Calyx; C, Corolla and exserted stamens and style; D, Corolla showing attachment of filaments.

350–550 m, *Wasshausen & Encarnación 1023* (holotype US, isotypes USM, US-2).

*Additional specimens.*—PERU: San Martín: Prov. Lamas: trail San José de Sisa-Agua Blanca, 380–400 m, *Ferreyra 7946* (US, USM); between Agua Blanca and Desquito, 600–800 m, *Ferreyra 7963* (US, USM); Prov. San Martín: Tarapoto, 830 m, *Woytkowski 35110* (US); Juan-Guerra, Tarapoto, *Ule 6489* (G, K); near Tarapoto, *Spruce 3974* (K); Pucayacu, 11 km S of Tarapoto, 200–250 m, *Ferreyra 7730* (US, USM); Granja El Porvenir, 25 km S of Tarapoto, 400–500 m *Ferreyra 17855* (US, USM); Pucacaca, *Plowman 6016A* (GH, US); Dtto. Shapaja: Shapaja, 264 m, *Schunke-Vigo 9815* (MO); 1–4 km S of Shapaja, ca. 300 m, *Belshaw 3133* (UC, US); Puente Colombia, 200–250 m, *Ferreyra 17545* (US, USM); Prov. Huallaga: between Bellavista and Baños, 200–300 m, *Ferreyra 4731* (US, USM); between Juanjui and Tingo de Saposoa, 200–300 m, *Ferreyra 4793* (US, USM); near Bellavista, 250–300 m, *Ferreyra 10099* (US, USM); Prov. Mariscal Cáceres: vicinity of Juanjui, 300–400 m, *Ferreyra 4498* (US, USM); *4538a* (US, USM).

Distributed in open places and along margins of trails in lowland rainforest.

*Discussion.*—*Pachystachys puberula* is distinguished from *P. spicata* in that the corollas of the former species are 3.5–4 cm long, the upper corolla lip is recurved and 3.5 mm broad near base, the lower corolla lip lobes are obovate with the lateral ones 12 mm long and 6 mm broad and the bracts are broadly ovate, 10–18 mm broad, narrowed and apiculate at apex. In *P. spicata* the corollas are 5–7 cm long, the upper corolla lip is erect and 6.5 mm broad near base, the lower corolla lip lobes are linear with the lateral ones 17–24 mm long and 4 mm broad and the bracts are ovate-lanceolate, 7–11 mm broad, acuminate at apex.

### *Pachystachys spicata* (R.&P.) Wasshausen, comb. nov.

*Justicia spicata* Ruiz & Pavón, Fl. Peruv. & Chil. Prodr. 1:8. pl. 9. 1798. *Pachystachys riedeliana* Nees in Mart. Fl. Bras. 9:99. 1847. *P. latior* Nees in DC. Prodr. 11: 320. 1847. *P. asperula* Nees in DC. Prodr. 11:320. 1847.

Suffrutescent, erect, simple or sparingly branched plant 1–5 m tall; stem glabrous, terete or with upper portions subquadrangular; leaves petioled, blades oblong, elliptic or broadly oblanceolate, 15–27 cm long and 7–11 cm wide, acute to acuminate, tip itself usually blunt, gradually to rather abruptly narrowed at base, glabrous, firm, margins entire, costa and lateral veins (9–12 pairs) rather prominent; petioles 2.5–7 cm long, glabrous; spikes solitary, terminal, 12–22 cm long, rachis finely puberulous; bracts imbricate, green, ovate-lanceolate, 1.5–2.5 cm long, 7–11 mm broad, terminal bracts somewhat smaller, basal ones larger, acuminate, narrowed at base, short-petiolate, both surfaces puberulous, lower surface more densely so, bearing additional glandular hairs; bractlets narrowly linear, about 3 mm long and 0.5 mm broad, sparingly puberulous; calyx campanulate, 4.5 mm long, segments narrowly triangular, about 3 mm long and 1 mm wide at base, acuminate, sparingly hirtellous; corolla scarlet, becoming orange-red with age, 5.5–7 cm long, glabrous to sparingly hirtellous, tube curved, 4 mm wide at base, gradually enlarged to 8 mm at throat, upper lip erect, lanceolate, 6.5 mm broad near base, gradually narrowed to 1.5 mm at tip, 2-lobed, lobes obtuse, 1 mm long and wide, lower lip 3-lobed, lobes spreading, linear, rounded at tip, middle lobe 17 mm long and 3 mm broad, lateral ones 17–24 mm long and 4 mm broad; stamens attached near base of corolla tube, filaments yellow, about 5 cm long, puberulous, anthers yellow, 7 mm long, deeply sagittate, basal lobes muticous; pollen grains 61 μm long, 35 μm wide, tricolporate, each mesocolpium with two colpoid streaks, membrane densely granular, sexine suprareticulate, reticulation heterobrochate (Fig. 8); staminodes rudimentary, puberulous; ovary glabrous; capsule clavate, 16 mm long, 5 mm broad, 4.5 mm thick, glabrous; retinacula 3 mm long, slightly curved, tips flattened, obtuse; seeds 4, brownish, cordate,

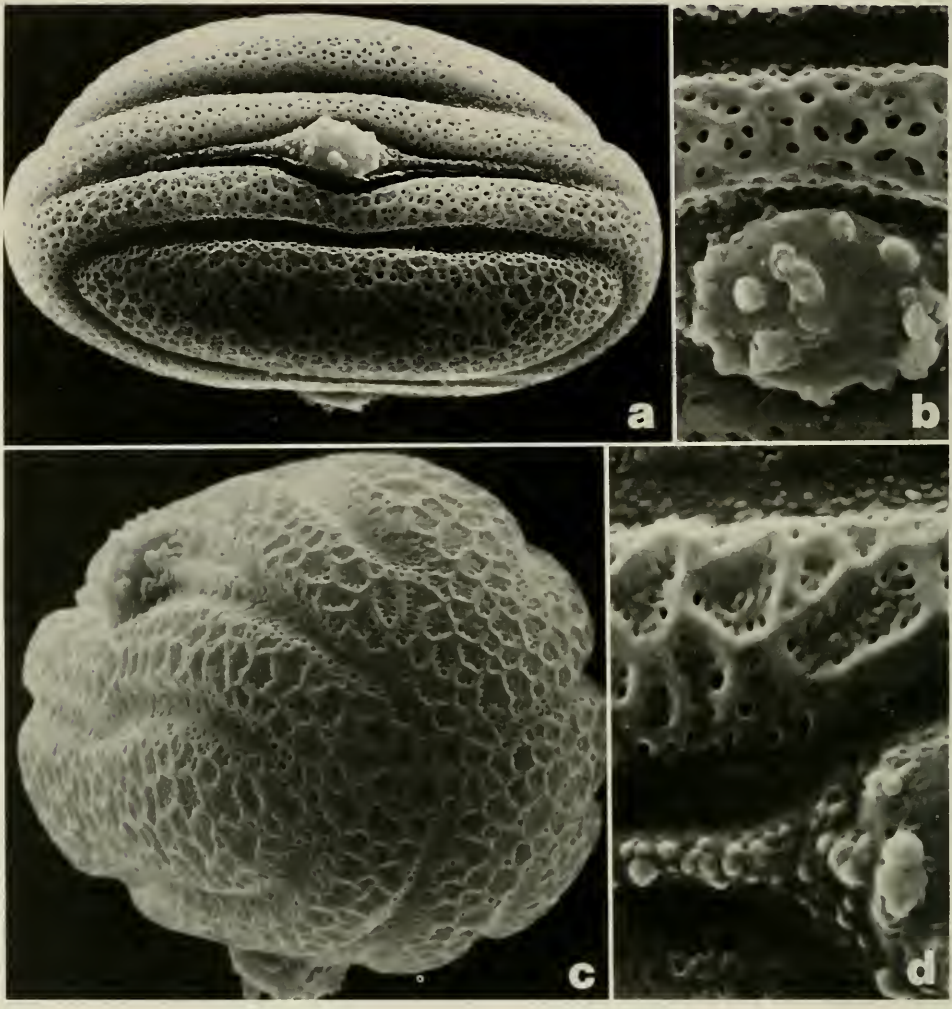

Fig. 8. SEM photomicrographs of *Pachystachys* pollen. A–B, *Pachystachys puberula* (*Wasshausen & Encarnación 1023*); C–D, *Pachystachys spicata* (*Calderón 2826*). A, Equatorial view, ×1400; B, Portion of surface, including pore at ×4000; C, Polar orientation, ×1800; D, Portion of surface, including pore at 4400.

flattened, 5.5 mm long, 4 mm wide, glabrous, muricate.

*Material.*—CUBA: Oriente: Monte Verde, *León 3832* (NY); Santiago, banks of Cañas River, El Cobre, *Clemente 5885* (NY, US); Sierra Maestra, Finca la Philanthropia, *Ekman 15697* (NY, S, US); Sierra Maestra, Loma del Gato, banks of Cañas River, *Clement 562* (NY), La Perla to Santa Ana, 660 m, *Shafer 8592* (NY, US). JAMAICA: Westmoreland: Bluefields Mountains, 650 m, *Britton & Hollick 1975* (NY). Manchester: Mandville, *Smith s.n.* (US). Clarendon: 1 m NW of Rock River, 165–230 m, *Proctor 32842* (NY). St. Catherine: Bog Walk, *Crawford 814* (NY). St. Mary: Castelton district, 150 m, *Harris 11933* (NY, US); Metcalf district, Constant Spring to Annatto Bay, *Britton 825* (NY). St. Andrew: Manning Hill, 380 m, *Powell 778* (NY, US); Stoney Hill, *Smith s.n.* (US). Portland: vicinity of Mill Bank, 200–300 m, *Maxon &*

*Killip 202* (US); vicinity of Windsor, 150–175 m, *Maxon & Killip 271* (NY, US); Blue Hole, *Fosberg 59422* (US); near Long Bay, 15 m, *Gentry 28287* (MO, NY). Without exact locality: *Fredholm 3229* (US). LESSER ANTILLES: Guadeloupe: Sainte Rose, *Quentin 1936* (P, US); Trois-Rivieres, *Stehlé 1855* (US). Dominica: Carib Reserve, *Hodge 3307* (US); Geneva, *Nicolson 2172* (US); between Fond Baron Estate and Pichelin, *Ernst 1591* (US); Lisdara, *Hodge 2326* (GH, NY); road to Morne Plat Pays, *Gillis 8118* (FTG, US); Portsmouth, *Hodge 847* (NY, US); Salybia, *Hodge 846* (GH); along Stewart's River near its mouth on Grand Bay, *Eggers 641* (C), *Wilbur et al. 8027* (US). Martinique: Balata to Trivoli, 250 m *Stehlé 5742* (US); La Gracée, *Rodriguez 3622* (US). St. Vincent: along Chateaubelair River, 300–400 m, *Morton 5104* (US); 160 m, *Smith & Smith 981* (NY). Grenada: Mt. Pleasant, 500 m, *Miller 160* (US). TRINIDAD: Caura River Valley, *Britton & Hazen 1203* (NY, US); E of Sangre Grande near Cunapi River, *Crosby 4* (DUKE, US); edge of Aripo Savannah, *Howard 10350* (NY, US); Arima Valley Road, North Range, 150–600 m, *Cowan & Simmonds 1221* (US); 15.8 km above Arima, *Harriman 17598* (OSH, US); Maracas waterfall, 160 m, *Kallov B152* (NY). Without exact locality: *Lockhart s.n.* (K, holotype of *P. asperula* Nees); 1877–80, *Fendler 534* (BM, NY); 1874, *Kuntze 598* (NY, US); 1889, *Broadway 3435* (US). GUYANA: Without exact locality: *Parker s.n.* (K, holotype of *P. latior* Nees). COLOMBIA: Meta: Río Duida, Mt. Macarena, 330 m, *Gilliard s.n.* (NY); Llanos Orientales, Villavicencio to Guayuriba, 600 m, *Garcia-Barriga 18944* (AMES). El Valle: Las Juntas, on the Río Dagua, *Lehmann 1887* (US); Cisneros, 300–500 m, *Killip 35590* (US). ECUADOR: Esmeraldas: Río Santiago at Concepción, 30 m, *Holm-Nielsen et al. 25976* (AAU). Manabí: Balao, *Eggers 14135* (US); Olmedo, 100 m, *Haught 3484* (NY, US). Guayas: 3 km E of Olon, 75–190 m, *Dodson & Thien 1660* (US); 2–4 km E from Recinto Olon, *Gentry 10045* (MO, US). Los Ríos: near Quevedo, Canton Vinces, ca. 50 m, *Mexia 6609* (US). El Oro: between Santa Rosa and La Chorita, 0–100 m, *Hitchcock 21116* (NY, US). Pichincha: Santo Domingo, 570 m, *Dodson & Thien 1626* (US); Río Blanco below confluence with Río Toachi, 300 m, *Harling 4490* (S, US); Patricio Pilar, 45 km S of Santo Domingo, 400 m, *Holm-Nielsen 16017* (AAU). Chimborazo: base of Volcán Chimborazo, 900 m, *Spruce s.n.* (K). Pastaza: Shiguacocha, ca. 5 km E of Puerto Sarayacu, *Lugo 3852* (GB, US). Without exact locality: *Pearce s.n.* (K); *Gilmartin 367* (US). PERU: Amazonas: Prov. de Bagua: Río Marañon opposite Quebrada Miraná, 425–450 m, *Wurdack 2010* (NY, US, USM). San Martín: Prov. Moyobamba: Moyobamba, *Mathews 1537* (K). Prov. Lamas: along Río Mayo, *Spruce 4872* (K); Lamas, 600–800 m, *Ferreyra 17333* (US, USM); between Tabalosos and Lamas, ca. 500 m, *Belshaw 3414* (K, NY, UC, US). Prov. Huallaga: Saposoa, 200–300 m, *Ferreyra 4614* (US, USM); 350 m, *Sagastegui 6837* (US). Prov. Mariscal Caceres: Juanjui, *Sandeman 35* (K); Dtto. Tocache Nuevo: Quebrada Cachiyacu de Huaquisha, ca. 500–600 m, *Schunke-Vigo 12515* (US); Quebrada de Saule Chico, *Schunke-Vigo 4349* (NY, US); Fundo "Curare Land," propriedad de José-Schunke V., 500–525 m, *Schunke-Vigo 10951* (MO, US). Loreta: Prov. Maynas: San Antonio, on Río Itaya, ca. 110 m, *Killip & Smith 29426* (NY, US); Soledad, on Río Itaya, ca. 110 m, *Killip & Smith 29683* (NY, US); Caballococha, *Williams 2367* (US); below mouth of Río Ucayali, 130 m, *Gentry et al. 29999* (MO, US); Río Nanay, *Torres 0224* (AMAZ, US). Prov. Alto Amazonas: Pumayacu, between Balsapuerto and Moyabamba, 600–1200 m, *Klug 3219* (NY, US). Prov. Coronel Portillo: bank of Río Neshuya, km 61 on Federico Basache road, *Encarnación 672* (US). Huánuco: Prov. Leoncio Prado: Dtto. Rupa Rupa: Tingo María, *Plowman 7565* (US); *Asplund 13218* (S); 600–700 m, *Ferreyra*

*2278* (US, USM); 650 m, *Wasshausen & Tovar 1260* (US, USM); E of Tingo María, 700–800 m, *Schunke-Vigo 10518* (US). Junín: Prov. Tarma: La Merced, ca. 650 m, *Macbride 5565* (F, NY, US); Río Seco, 15 km from La Merced, *Soukup 2494* (US); Río Negro, 800 m, *Woytkowski 5814* (MO, US); Río Perené, Colonia Perené, 600 m, *Killip & Smith 25228* (US); Río Paucartambo Valley, near Perené Bridge, 700 m, *Killip & Smith 25380* (US). Ayacucho: Prov. La Mar: Hda. Luisiana, 640 m, *Wasshausen & Encarnación 639* (US, USM). Cuzco: Prov. La Convención: 3 km NE of Hda. Luisiana and Río Apurimac, 660 m, *Dudley 11450* (NA); 4 km E of San Francisco de Apurimac, 750 m, *Wasshausen & Encarnación 518* (US, USM). Prov. Paucartambo: Hda. Villa Carmen, 540 m, *Vargas 14701* (CUZ, US); Dtto. Cosñipata: 9 km N of Pilcopata, 600 m, *Wasshausen & Encarnación 580* (US, USM); Valley de Cosñipata, between Mitiana and Keros, ca. 800 m, *Scolnik 866* (NY). Prov. Quispicanchis: Marcapata Valley, 1200 m, *Herrera 1170* (US). Madre de Dios: Río Acre: Seringal Auristella, *Ule 9808b* (G, K). Without exact locality: *Ruiz & Pavon s.n.* (MA, holotype of *Justicia spicata* Ruiz & Pavon; F, photo); 1878, *Martinet s.n.* (P). BOLIVIA: Pando: W bank of Río Madeira, opposite Abuña, *Prance et al. 5695* (INPA, NY, US); 2 km above Ribeirão, *Prance 6499* (INPA, NY, US); Nicolas Suarez, ca. 30 km SW of Cobija on road to Naraueda, ca. 250 m, *Sperling & King 6607* (NY, US). El Beni: junction of Rivers Beni and Madre de Dios, *Rusby 1099* (NY, US). La Paz: Mapiri, *Bang 1555* (NY, US); 750 m, *Buchtien 1472* (US). Prov. S. Yungas: basin of Río Bopi, San Bartolome, 750–900 m, *Krukoff 10236* (NY, US); Bopi River Valley, 650 m, *White 646* (NY). Cochabamba: Prov. Chapare, Todos Santos, 300 m, *Steinbach 429* (NY, US). Without exact locality: *Pearce s.n.* (K). BRAZIL: Amazônas: Borba, *Riedel s.n.* (LE, holotype of *P. riedeliana* Nees; frag. GRZ); Parati, *Traill s.n.* (K); Río Acre, Seringal São Francisco, *Ule 9898* (K); *9809* (K); Bôca do Acre, Ríos Purus & Acre, track from São Paulo to Terra Firme, Río Purus, opposite Bôca do Acre, *Prance et al. 2582* (INPA, NY); Manacapuru, *Spruce 1622* (K); Namorado Novo, watershed between Río Curuquetê and Río Madeira at Abuña, *Prance et al. 14677* (INPA, NY, US). Rondônia: Río Jamari-Cachoeira de Sta. Cruz, *Pires & Martin 9957* (UB, US); basin of Río Madeira, 4 km N of Mutuparaná, *Prance et al. 5470* (INPA, NY, US); S bank of Río Madeira, 2 km above Mutuparaná, *Prance et al. 5670* (INPA, NY, US); São Lourenço cassiterite mine, ca. 20 km NW of Río Madeira, across from Mutuparaná, *Calderón et al. 2826* (US). Acre-Amazônas: municipío de Boca do Acre, vicinity of Río Iaco, *Cid & Nelson 2730* (INPA, NY). Acre: near mouth of Río Macauhan (tributary of Río Yaco), *Krukoff 5376* (NY); *5547* (NY). Pará: 1908, *Bakar s.n.* (US); Tauá, *Spruce 266* (K); Pôrto do Igarapé Mururetena, S. Miguel do Guamá, *Black 56-18888* (INPA, US).

Edge of lowland rainforest, margins of thickets, along trails or river banks at elevations between 150 and 700 meters. West Indies southward to Bolivia and eastward to Amazonian Brazil (Amazônas, Rondônia, Acre and Pará).

*Discussion.*—Leonard (1953:291) first noted that *Pachystachys spicata* (*P. riedeliana*) has often been confused with *P. coccinea* (Aublet) Nees of French Guiana and northern Amazonian Brazil. He further states: "Although the two species are superficially similar, they can readily be separated by the longer, linear calyx segments of *P. coccinea.*"

Only one chromosome count has been obtained for a species of *Pachystachys,* that by Takizawa (1957), for *P. spicata,* reported by him as *Justicia coccinea,* of n = 16.

### *Pachystachys rosea* Wasshausen, sp. nov

Fig. 4

Frutex, caules subquadrangulares, brunneoli, glabri vel parce puberuli; lamina foliorum elliptica vel anguste ovata, acuminata, basi angustata in petiolo amplectens, firma, glabra; spicae terminales, solitariae, rachidi puberula; bracteae imbricatae, viridae, anguste ovatae, glanduloso-pilosae; bracteolae minutae, lineares, glabrae; calyx campanulatus, segmenta anguste lanceolata, minute puberula; corolla rosea, glabra vel parce puberula, glanduloso-punctata, tubo leviter curvato, labio superiore erecto, conduplicato, bilobato, labio inferiore trilobato, lobis patulis, obtusis, ciliatis, lobis lateralibus ellipticis vel oblongis, lobo medio elliptico.

Shrub, 3 m tall; stem subquadrangular, brownish, glabrous or sparingly puberulous; leaf blades petiolate; elliptic to narrowly ovate, 15–22 cm long, 5–7.5 cm wide, acuminate at apex, narrowed from below middle to rounded, clasping base 5 mm wide, entire, undulate, moderately firm, glabrous, cystoliths conspicuous; petioles 2.5–6.5 cm long, glabrous or sparingly and inconspicuously puberulous; inflorescence consisting of solitary, terminal spike 15–25 cm long, rachis puberulous; bracts imbricate, green, narrowly ovate, 2.2–2.5 cm long, 8–9 mm wide, acuminate and mucronulate at apex, gradually narrowed and attenuate at base, glandular-pilose and ciliate, eglandular hairs intermixed with glandular ones; bractlets minute, linear, 2 mm long, 0.4 mm wide, glabrous, ciliate; calyx campanulate, 9 mm long, segments narrowly lanceolate, 8 mm long, 1 mm wide near base, sparingly and inconspicuously puberulous and ciliate; corolla pink to orange-red, 6–6.5 cm long, glabrous or sparingly and inconspicuously puberulous, glandular punctate, tube slightly curved, 4 mm wide at base, narrowed to 2 mm at 7 mm above base, thence gradually enlarged to 9 mm at throat, upper lip erect, conduplicate, ovate, 2.5 cm long, 1.2 cm wide near base, gradually narrowed to 2.5 mm at tip, 2-lobed, lobes orbicular, 1 mm long and wide, obtuse, lower lip deeply 3-lobed, lobes spreading, obtuse and ciliate, lateral pair elliptic to oblong, 16 mm long, 6 mm wide, middle lobe elliptic, 18 mm long, 6 mm wide; stamens attached near base of corolla tube, filaments 5 cm long, sparingly puberulous, anthers 6 mm long, deeply sagittate, basal lobes muticous; staminodes rudimentary, puberulous; ovary glabrous; capsule wanting.

*Type.*—PERU: Cuzco: Prov. Paucartambo, between Pilcopata and Carbón, 720 m, *Vargas C. 23159* (holotype US).

*Paratype.*—PERU: Cuzco: Prov. Paucartambo, Atalaya, near junction of Río Carbón with Río Alto Madre de Dios, *Foster 2398* (F, US).

Hillside and riverbank, as well as margin of rainforest.

*Discussion.*—*Pachystachys rosea* is perhaps nearest in relationship to the rather widespread *P. spicata,* but differs markedly in that the latter species has triangular calyx segments about 3 mm long, a scarlet corolla which may become orange-red with age, and lower corolla lip lobes which are all linear and 3–4 mm wide. In contrast, *P. rosea* has lanceolate calyx segments 8 mm long, a corolla that is pink to possibly orange-red with age, and lower corolla lip lobes of which the lateral pair is elliptic to oblong and the middle lobe elliptic (all are 6 mm wide).

### *Pachystachys killipii* Wasshausen, sp. nov.
Figs. 6, 10

Frutex; caules teres, brunneoli, glabri; lamina foliorum elliptica vel ovata, acuminata, basi cuneata, modice firma, glabra; spicae terminales, solitariae, rachidi dense pilosa; bracteae laxe imbricatae, late ellipticae, acuminatae et mucronulatae, dense glanduloso-pilosae; bracteolae lineares, pilosae; calyx campanulatus, segmenta lanceolata, glabra, ciliolata; corolla subrosea rubra, tubo leviter curvato, praecipue prope basin hirsuto, labio superiore erecto, oblongo usque anguste lanceolato, minute bilobato, labio inferiore trilobato, lobis patulis, lobis lateralibus oblongis vel anguste ovatis, lobo medio ovato, conduplicato et obtuso.

Erect shrub 1 m tall; stem terete, brownish, glabrous; leaf blades elliptic to ovate, 10.5–18 cm long and 3.5–6 cm wide, acuminate at apex, narrowed and cuneate at base, moderately firm, entire or undulate, glabrous, cystoliths numerous both above and below; petioles 0.6–2.5 cm long, glabrous; inflorescence consisting of terminal, solitary spike 15 cm long, rachis densely pilose; bracts rather loosely imbricate, green, broadly elliptic, 1.7 cm long, 6–7.5 mm broad, acuminate and mucronulate at apex, gradually narrowed at base and attenuate, rather densely glandular-pilose, glands purplish; bractlets linear, 11 mm long, 1.25 mm wide, pilose, bearing few glandular trichomes near apex; calyx campanulate, 12 mm long, segments lanceolate, 10 mm long and 1 mm wide near base, acuminate, bearing small mucro at apex, glabrous and ciliate; corolla pinkish-red, 6.5–7 cm long, tube slightly curved, 4.5 mm wide at base, narrowed to 1.5 mm at 10 mm above base, thence gradually enlarged to 1 cm at throat, hirsute, especially near base, upper lip erect, oblong to narrowly lanceolate, 2.2 cm long, 7 mm wide near base, gradually narrowed to 1 mm at tip, minutely 2-lobed, lobes obtuse, lower lip 3-lobed, lobes spreading, lateral pair oblong to narrowly ovate, 17 mm long, 5 mm wide, rounded at tip, middle lobe ovate, 12 mm long and 5.5 mm wide, conduplicate and obtuse; stamens attached near base of corolla tube, filaments 5 cm long, glabrous, anthers 6 mm long, deeply sagittate, basal lobes muticous; pollen grains 46 μm long, 45 μm wide, tricolporate, each mesocolpium with two colpoid streaks, membrane densely granular, sexine suprareticulate, reticulation heterobrochate (Fig. 10); staminodes none; ovary glabrous; capsule wanting.

*Type.*—PERU: Junín: Puerto Bermudez, 355 m, *Killip & Smith 26621* (holotype US; isotype NY).

Occasional along clay river bank.

*Discussion.*—*Pachystachys killipii* is characterized by a combination of a pinkish-red corolla 6.5–7 cm long, rather small, loosely imbricate, glandular-pilose bracts 1.7 cm long, 6–7.5 mm broad, and a relatively large, campanulate calyx with the segments 12 mm long and bearing a small mucro at the tip. It is a pleasure to name this species for Ellsworth "Buddy" Killip, who through his extensive field work, has added so much to our knowledge of South American floras.

*Pachystachys ossolae* Wasshausen, sp. nov.
Figs. 9, 10

Suffrutex, scandens; caules subquadrangulares, brunneoli, glabri; lamina foliorum elliptica vel ovata, brevi-acuminata, basi angustata in petiolo amplectens, modice firma, glabra; spicae terminales, solitariae, rachidi puberula; bracteae imbricatae, viridae apice purpureae, oblanceolatae, mucronulatae, parce puberulae; bracteolae lanceolatae; calyx campanulatus, segmenta lanceolata, puberula, ciliolata; corolla coccinea, puberula et glanduloso-punctata, tubo leviter curvato, labio superiore erecto, ovato, bilobato, lobis obtusis, labio inferiore profunde trilobato, lobis patulis, paribus lateralibus oblongis vel anguste ovatis, obtusis, lobo medio anguste ovato, conduplicato et obtuso.

Climbing, suffrutescent shrub, 0.7–4 m tall; stem subquadrangular, brownish, glabrous; leaf blades petiolate, elliptic to ovate, 17–30 cm long and 7–12 cm wide, short-acuminate at apex, narrowed from below middle to a rounded, clasping base 10 mm wide in larger leaves, entire or undulate, moderately firm, glabrous, cystoliths inconspicuous; petioles 3–8 cm long, glabrous; inflorescence consisting of solitary, terminal spike 12–20 cm long, rachis puberulous; bracts imbricate, green with purple at tips, oblanceolate, 2–2.8 cm long, 0.6–1 cm broad, acute and mucronulate at apex, gradually narrowed and attenuate at base, sparingly puberulous and ciliate, cystoliths prominent without; bractlets lanceolate, 6 mm long, 1 mm wide, puberulous and cil-

Fig. 9. A–D, *Pachystachys ossolae* (*Wasshausen & Encarnación 729*). A, Habit; B, Bract, bractlets and calyx; C, Corolla and exserted stamens; D, Corolla expanded, showing attachment of filaments.

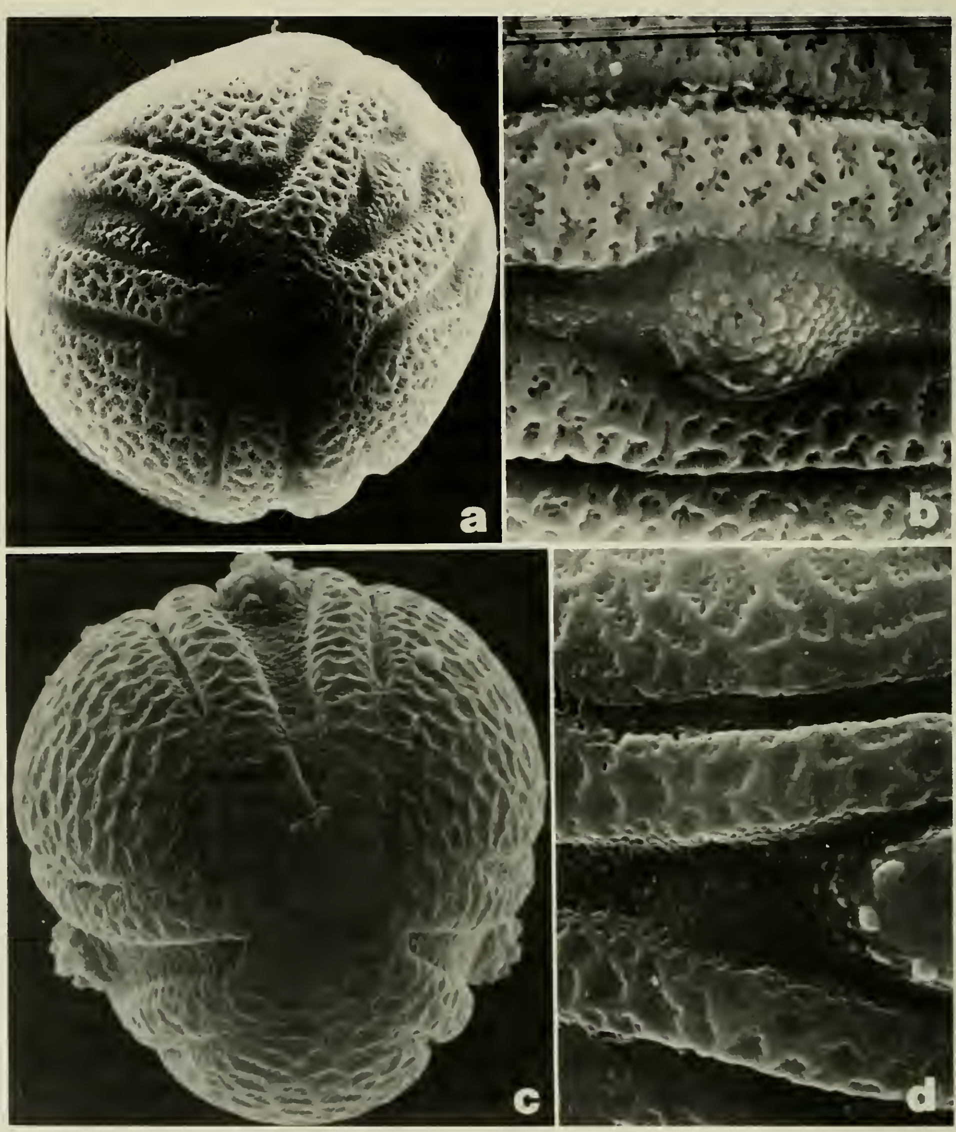

Fig. 10. SEM photomicrograph of *Pachystachys* pollen. A–B, *Pachystachys killipii* (*Killip & Smith 26621*); C–D, *Pachystachys ossolae* (*Wasshausen & Encarnación 741*). A, Polar orientation, ×1000; B, Portion of surface, including pore at ×3000; C, Polar orientation, ×1700; D, Portion of surface, including colpus and pseudocolpi at ×3000.

iate; calyx campanulate, 7 mm long, segments lanceolate, 5 mm long and 1.5 mm wide near base, puberulous and ciliate; corolla crimson, 7 cm long, puberulous and glandular punctate, tube slightly curved, 4 mm wide at base, narrowed to 2.5 mm at 8 mm above base, thence gradually enlarged to 1 cm at throat, upper lip erect, ovate, 2.2 cm long, 9 mm wide near base, gradually narrowed to 2.7 mm at tip, 2-lobed, lobes obtuse, 1.5 mm long, 1.2 mm wide, lower lip deeply 3-lobed, lobes spreading, lateral pair oblong to narrowly ovate, 2 cm long, 5 mm wide, obtuse, middle lobe narrowly ovate, 18 mm long and 4.5 mm wide, conduplicate and obtuse; stamens attached near base of corolla tube, filaments 5.5 cm long, puberulous, anthers yellow, 5.5 mm long, deeply sagittate, basal lobes muticous; pollen grains prolate, 53 μm long, 35 μm wide, tricolporate, each colpus flanked by two pseudocolpi, tectum almost complete, psilate-punctate (Fig. 10); staminodes none; ovary glabrous; capsule wanting.

*Type.*—PERU: Cuzco: Prov. de Quispicanchis, 3 km E of Quincemil, 960 m, *Wasshausen & Encarnación 729* (holotype US; isotypes USM, US-3).

*Additional specimens.*—PERU: Cuzco: 25 km SW of Quincemil, 1340 m, *Wasshausen & Encarnación 741* (US); 5 km E of Quincemil, 960 m, *Wasshausen & Encarnación 833* (US). Madre de Dios: 17 km N of Pilcopata, near Río Carbón, 480 m, *Gentry, Dillon, Aronson & Berry 23588* (MO). Parque Nacional del Manu, Río Manu, Cocha Cashu Station, 350 m *Terborgh & Foster 6499* (F). Puno: Prov. de Carabaya, San Gaban, *Lechler 2501* (K); vicinity of San Gabán, 900 m, *Wasshausen & Salas 1246* (US, USM); below San Gabán on Río San Gabán, 500–1000 m, *Dillon, Aronson, Herra & Berry 1215* (MO); San Gabán to Ollachea, 1000–2000 m, *Dillon, Aronson, Herra & Berry 1249* (MO); Ollachea-San Gabán road, Arica, *Boeke & Boeke 3141* (NY).

Occasional, along edge of lowland rainforest.

*Discussion.*—*Pachystachys ossolae* is nearest in relationship to the widespread species *P. spicata,* but differs markedly in that the latter species has a glabrous to sparingly hirtellous corolla 5.5–7 cm long, green, ovate-lanceolate, acuminate bracts, and narrowly triangular calyx segments about 3 mm long. In contrast, *P. ossolae* has a puberulous and glandular punctate corolla 7 cm long, green with distinctly purple, oblanceolate, acute and mucronulate bracts, and lanceolate calyx segments about 5 mm long.

It is a great pleasure to name this new species for my good friend and confidant, the late Charles A. Ossola, in recognition for his outstanding dedication and devotion to the advancement of systematic biology.

*Pachystachys coccinea* (Aubl.) Nees in DC. Prodr. 11: 319. 1847.

*Justicia coccinea* Aubl. Guyan. 1: 10, pl. 3. 1775. *Jacobinia coccinea* (Aubl.) Hiern in Warm. Symb. 23: 690. 1877.

Shrub 1–2 m tall; branches puberulous when young, soon glabrous, constricted and easily broken just above nodes, bark thin and usually striate; leaves petiolate, blades elliptic to oblong-obovate, 18–25 cm long and 6–9 cm wide, acuminate (often abruptly so) at apex, when not elliptic, narrowed from above middle to acute or obtuse base, entire or undulate, glabrous except costa and lateral veins, these puberulous but soon glabrescent, cystoliths 0.25 mm long; petioles 2–6 cm long, glabrous; inflorescence consisting of terminal spike 9–22 cm long bearing conspicuous bracts and flowers, peduncles 1–3 cm long; bracts green, ovate to lanceolate, 1.5–2.5 cm long and 4–9 mm wide, lower bracts decussate, upper ones ternate and quaternate, narrower, all acute or subacuminate, apiculate, abruptly narrowed to short-winged base, more or less puberulent, usually glandular, margins and costa short-pubescent; bractlets linear-lanceolate, 5 mm long, 0.5 mm wide, puberulous; calyx campanulate, 5.5–6 mm long, slightly irregular, tube 1 mm long, segments lanceolate, equal, 5 mm long, 0.5 mm wide, sparingly and inconspicuously puberulent; corolla bright red, 5–7 cm long, rather sparingly pubescent with minute spreading hairs (hirtellous), 4 mm wide at base, narrowed to 3 mm above base, 7–10 mm wide at throat, upper lip erect, 2–2.5 cm long, emarginate, lobes 1 mm long and 0.5 mm wide, lower lip oblong, obtuse, 1.7–2 cm long, 4–5 mm wide; filaments 5.5 cm long, mature white-pubescent, densely so below, sparing-

Fig. 11. Isotype of *Pachystachys nutans* Nees (*Ehrenbers 1060,* BM).

ly so above; staminodes when present minute, vestigial; ovary and style glabrous.

*Material.*—FRENCH GUIANA: Massif des Emerillons, centre N Sources de l'Approuague, ca. 250 m, *Cremers 6707* (CAY, US); Cayenne, *Aublet s.n.* (BM, holotype of *Justicia coccinea* Aubl.); *Rothery 489* (K); Rorota, île de Cayenne, *Prévost 1259* (CAY, US); vicinity of Cayenne, Montagne de Mahury, *Sagot s.n.* (K); 50–150 m, *Maas, Mennega & Koek-Noorman 2215* (NY, US); Matabon, *Broadway 509* (NY, US); Mt. Bruyere, 4°5'N, 51°43'W, *Irwin, Egler & Pires 47334* (NY, US); Village Kaw, *Black & D'Aage 54-17539* (IAN, US). Without exact locality: Jul 1824, *Poiteau s.n.* (K, photo F, US); 1842, *Melinon 263* (GZU, P, US); 1850, *Leprieur s.n.* (P, US); *Perrottet 204* (GZU). BRAZIL: Territorio Amapa: Río Oiapoque, Mt. Tipac, 3°36'N, 51°19'W, 0–100 m, *Irwin 48661* (NY, US); Porto Grande, Região do Vila Nova, *Rosa 1051* (MG, NY, US). Pará: Belém, *Pires 14.871* (IAN, US).

Common in shade of forest clearings and margins at elevations between 50 and 250 meters.

*Discussion.*—*Pachystachys coccinea* is a very showy and beautiful species, with its large, conspicuously bracted terminal spike and bright red corollas. The species is nearest in relationship to *P. spicata.* The major difference between the two species is discussed under the latter species.

### Excluded Species

*Pachystachys nutans* Nees in DC., Prodr. 11: 320. 1847, ≡ *Jacobinia nutans* (Nees) Hemsley, Biol. Centr. Amer., Bot. 2: 521. 1882. This species, based on *Ehrenberg 1060* (holotype B, destroyed; isotype BM, sterile; fragment GZU), is known only from the type locality, Mexico, Barranca de Río de Tolimea, near Ajuntas in Caracol (Fig. 11).

The description by Nees states that the plant is suffrutescent, pubescent; stem slender, very much branched; leaf blades ovate, 2.4–2.8 cm long, attenuate and obtuse at apex, short-acute at base, costa hirtellous; petioles 6–8 mm long; inflorescence terminal, sessile, short, dense, nodding, branched spike; bracts pale green, ovate, cuspidate-mucronulate at apex, membranous, ciliate; bractlets linear-subulate; calyx rather short; corolla short, apparently purple.

The ultimate disposition of this taxon must await the recollecting of additional material.

### Acknowledgments

My sincerest thanks to Cathy Pasquale for the excellent line drawings and to Dr. Stephen F. Smith and the staff of the SEM laboratory for their high-quality pollen photomicrographs.

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# INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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3 October 1985

The Commission hereby gives six months notice of the possible use of it plenary powers in the following cases, published in the *Bulletin of Zoological Nomenclature,* volume 42, part 3 on 30 September 1985, and would welcome comments and advice on them from interested zoologists.

Correspondence should be addressed to the Executive Secretary at the above address, if possible within six months of the date of publication of this notice.

*Case No.*

2464 *Berytus* Fabricius, 1803 (Insecta, Heteroptera, Berytidae): proposed designations of a type species.

2490 *Thylacites* Germar, 1817; *Brachyderes* Schönherr, 1823; *Cycloderes* Sahlberg, 1823; and *Cycloderes* Schönherr, 1823 (Insecta, Coleoptera): proposal to maintain current usage.

2467 *Neodorippe* Serène & Romimohtarto, 1969 (Crustacea, Decapoda): proposed designation of type species.

2363 *Sagartia luciae* Verrill, 1898 (Coelenterata, Actiniaria): proposed conservation.

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3 October 1985

The following Opinions have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature,* volume 42, part 3 on 30 September 1985:

| *Opinion No.* | |
|---|---|
| 1328 (p. 222) | *Belemnites mucronatus* Schlotheim, 1813 (Coleoidea): conserved and neotype designated. |
| 1329 (p. 226) | *Galago crassicaudatus* E. Geoffroy, 1812 (Primates, Galigidae): neotype designated. |
| 1330 (p. 228) | *Prodorylaimus* Andrassy, 1959 (Nematoda): type species designated. |
| 1331 (p. 230) | SPHAERIIDAE Jeffreys, 1862 (1820) (Mollusca, Bivalvia) and MICROSPORIDAE Reichardt, 1976 (Insecta, Coleoptera): placed on the Official List. |
| 1332 (p. 233) | *Calamoecia australica* Sars, 1908 and *Calamoecia australis* (Searle 1911) (Crustacea, Copepoda): proposals to remove the confusion rejected. |
| 1333 (p. 236) | *Ipnops murrayi* Günther, 1878 (Ostiechthyes): conserved. |
| 1334 (p. 238) | *Harminius* Fairmaire, 1851 (Coleoptera): type species designated. |
| 1335 (p. 241) | *Nepa cinerea* Linnaeus, 1758 (Insecta, Heteroptera): conserved. |
| 1336 (p. 244) | Five specific names proposed for *Heterodera* A. Schmidt, 1871 (Aschelminthes, Nematode) by B. A. Cooper, 1955 ruled to be available. |
| 1337 (p. 249) | *Selkirkia columbia* Conway Morris, 1977 designated as type species of *Selkirkia* Walcott, 1911 (Priapulida). |
| 1338 (p. 251) | *Thrips rufus* Haliday, 1836 (Insecta, Thysanoptera): conserved for the type species of *Aptinothrips* Haliday, 1836. |
| 1339 (p. 255) | *Papilio fatima* Fabricius, 1793 (Insecta, Lepidoptera): ruled to be exempt from the application of the Principle of Homonymy. |
| 1340 (p. 258) | *Attus otiosus* Hentz, 1846 (Arachnida, Araneae): conserved. |
| 1341 (p. 261) | *Simulium amazonicum* Goeldi, 1905 (Insecta, Diptera): neotype designated. |
| 1342 (p. 264) | *Damalis planiceps* Fabricius, 1805 designated as type species of *Damalis* Fabricius, 1805 (Insecta, Diptera). |
| 1343 (p. 266) | *Kinosternon alamosae* Berry & Legler, 1980 and *Kinosternon oaxacae* Berry & Iverson, 1980 (Reptilia, Testudines): conserved. |
| 1344 (p. 269) | *Mayorella* Schaeffer, 1926 given nomenclatural precedence over *Dactylamoeba* Korotneff, 1880 (Rhizopoda, Amoebida). |

1345 (p. 271) *Laomedea flexuosa* Alder, 1857, *Sertularia volubilis* Linnaeus, 1758 and *Campanularia johnstoni* Alder, 1856 designated as type species of *Laomedea* Lamouroux, 1812, *Campanularia* Lamarck, 1816 and *Clytia* Lamouroux, 1812 (Coelenterata, Hydroida) respectively.

1346 (p. 274) *Cythereis distinguenda* Neviana, 1928, *Cythere crispata* Brady, 1868 and *Cythere pavonia* Brady, 1866 (Crustacea, Ostracoda): type material conserved.

1347 (p. 277) *Anthalia schoenherri* Zetterstedt, 1838 designated as type species of *Anthalia* Zetterstedt, 1838 (Insecta, Diptera).

1348 (p. 279) *Bos gaurus* H. Smith, 1827 (Mammalia, Artiodactyla): conserved.

1349 (p. 281) *Antilope depressicornis* H. Smith, 1827 and *Anoa quarlesi* Ouwens, 1910 (Mammalia, Artiodactyla): conserved.

1350 (p. 283) *Conus antiquus* Lamarck, 1810 (Mollusca, Gastropoda): neotype suppressed.

1351 (p. 285) *Galeopsomyia* Girault, 1916 (Insecta, Hymenoptera): conserved.

1352 (p. 287) *Eurhinus* Schönherr, 1825 (Insecta, Coleoptera): ruled as a justified emendation of *Eurhin* Illiger, 1807.

1353 (p. 291) *Myzus festucae* Theobald, 1917 (Insecta, Hemiptera): conserved.

The Commission regrets that it cannot supply separates of Opinions.

P. K. TUBBS
Executive Secretary

## INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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11 December 1985

The Commission hereby gives six months notice of the possible use of its plenary powers in the following cases, published in the *Bulletin of Zoological Nomenclature,* volume 42, part 4 on 6 December 1985, and would welcome comments and advice on them from interested zoologists.

Correspondence should be addressed to the Executive Secretary at the above address, if possible within six months of the date of publication of this notice.

*Case No*

2434 *Semionotus* Agassiz, 1832 (Osteichthyes): proposed designation of *Semionotus bergeri* Agassiz, 1833 as type species.

2470 *Cephalopholis argus* Schneider, 1801 and *Cephalopholis sexmaculata* (Rüppell 1830) (Osteichthyes, Serranidae): proposed conservation by suppression of *Bodianus guttatus* Bloch, 1790, *Anthius argus* Bloch, 1792 and *Serranus zanana* Valenciennes, 1828.

2337 *Cheirurus* Beyrich, 1845 (Trilobita): proposed designation of *Cheirurus insignis* Beyrich, 1845 as a type species.

2503 *Eugynothrips* Priesner, 1926 (Insecta, Thysanoptera): proposed designation of *Cryptothrips conocephali* Karny, 1913 as type species.

2496 HETEROGYNIDAE Rambur, 1866 (Insecta, Lepidoptera) and HETEROGYNINAE Nagy, 1969 (Insecta, Hymenoptera): proposals to remove the homonymy.

2307 THAIDIDAE Jousseaume, 1888 (Mollusca, Gastropoda) and THAIDIDAE Lehtinen, 1967 (Arachnida, Araneae): proposals to remove the homonymy.

2345 *Drasterius bimaculatus* (Rossi, 1790) (Insecta, Coleoptera, Elateridae): proposed suppression of *Elater bimaculata* Fourcroy, 1785.

2453 *Microchrysa* Loew, 1855 (Insecta, Diptera): proposed conservation by the suppression of *Chrysomyia* Macquart, 1834.

2454 *Musca trilineta* Linnaeus, 1767 (Insecta, Diptera): proposed conservation by the suppression of *Musca graeca* Pontoppidan, 1763.

2024 The family names for the storm petrels and the dippers.

P. K. TUBBS
Executive Secretary

## INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
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11 December 1985

The following Opinions have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature,* volume 42, part 4 on 6 December 1985.

*Opinion No*

1354 (p. 330) *Agrotis redimicula* Morrison, 1874 (Lepidoptera): conserved from 1874.

1355 (p. 332) *Lingula anatina* Lamarck, 1801 is the type species of *Lingula* Bruguière, [1797] (Brachiopoda).

1356 (p. 335) *Dactylopusia* Norman, 1903 (Crustacea, Copepoda): type species designated.

1357 (p. 338) ANUROPODIDAE Bacescu, 1980 (Crustacea, Tanaidacea) and ANUROPODIDAE Stebbing, 1893 (Crustacea, Isopoda): a ruling to remove the homonymy.

1358 (p. 341) *Calaphis* Walsh, 1862 and *Callaphis* Walker, 1870 (Insecta, Hemiptera): a ruling to remove the confusion.

1359 (p. 344) UROPLAT—as the stem of family-group names in Reptilia, Sauria and Insecta, Coleoptera: a ruling to remove the homonymy.

1360 (p. 347) *Oeciacus vicarius* Horváth, 1912 (Insecta, Hemiptera): conserved.

1361 (p. 349) *Larentia capitata* Herrich-Schäffer, 1839, given nomenclatural precedence over *Phalaena posticata* Fabricius, 1794 (Insecta, Lepidoptera).

1362 (p. 351) *Phalaena coracina* Esper, 1805, given nomenclatural precedence over *Phalaena hirtata* Fabricius, 1794 (Insecta, Lepidoptera).

1363 (p. 353) *Ancistroceroides* Saussure, 1855 (Insecta, Hymenoptera): type species designated.

1364 (p. 355) *Kassina* Girard, 1853 (Amphibia, Anura): conserved.

1365 (p. 357) *Allygus* Fieber, 1872 (Insecta, Homoptera): type species designated.

1366 (p. 359) *Mactra sachalinensis* Schrenk, 1862 (Mollusca, Bivalvia): conserved.

1367 (p. 361) *Alpheus lottini* Guérin, 1829 (Crustacea, Decapoda): conserved.

1368 (p. 365) The generic names *Pan* and *Panthera* (Mammalia, Carnivora): available as from Oken, 1816.

The commission regrets that it cannot supply separates of Opinions.

P. K. TUBBS
Executive Secretary

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# *NEASTACILLA FALCLANDICA* (OHLIN), TYPE SPECIES OF THE GENUS, AND *N. TATTERSALLI,* NEW SPECIES (CRUSTACEA: ISOPODA: ARCTURIDAE)

Helen M. Lew Ton and Gary C. B. Poore

*Abstract.*—*Neastacilla falclandica* (Ohlin) is redescribed and figured from topotypic material. It is shown to be different from material from New Zealand which Tattersall (1921) assigned to *N. falclandica* and on which he based the new genus *Neastacilla.* Tattersall's specimen and more recent material are described as a new species, *N. tattersalli.*

Tattersall (1921) erected the genus *Neastacilla* and recorded the type species, *Astacilla falclandica* Ohlin, from New Zealand. Comparison of Tattersall's specimen with topotypes from the Falkland Islands has revealed that Tattersall misidentified his specimen. As there is no modern description of *Neastacilla falclandica* a redescription was felt to be desirable and the New Zealand species should be described. It was not possible to locate the holotype of *Astacilla falclandica* in Hamburg, Berlin, or Stockholm, and it is presumed lost.

We are appealing to the International Commission for Zoological Nomenclature to rule that *Astacilla falclandica* Ohlin be type species of the genus *Neastacilla* to preserve current usage.

This contribution forms part of a larger work on Australian species of *Neastacilla* in which the genus is rediagnosed and contrasted with *Astacilla* Cordiner. The format of the descriptions of the two species described here follows that of the larger work in preparation. Mouthparts of *N. falclandica* are figured but these contribute little to generic distinctions.

## *Neastacilla falclandica* (Ohlin)
Figs. 1, 2

*Astacilla falclandica* Ohlin, 1907:266, pl. 20.—Schultz, 1981:91.
*Astacilla falclandicus.*—Stebbing, 1914:353.
*Neastacilla falclandica.*—Nordenstam, 1933:119–122, fig. 28.—Kussakin, 1967: 357.—Sivertsen and Holthuis, 1980:67, fig. 18c.

*Material examined.*—Swedish Museum for Natural History, Stockholm, Isopoda 7305, female (6.2 mm), Falkland Islands, Port Louis, Swedish South Polar Expedition 1901–3, Station 43. USNM 222665, juvenile (3.1 mm), Falkland Islands, off Lighthouse, 22 Apr 1927. USNM 222666, juvenile (3.0 mm), Falkland Islands, Port Stanley, 14 Apr 1927, No. 107.

*Description.*—Female: Anterolateral lobe of head rounded, rostral point absent. Eyes subtriangular, slightly prominent in dorsal view. Fusion of head and first pereonite indicated by obsolete groove, incomplete dorsally and not extending to lateral margin; lateral margin not incised; combined length of head and pereonite 1 1.7 times combined length of pereonites 2 and 3. Lateral margin of pereonite 1 not expanded ventrally. Pereonites 2 and 3 subequal, smooth; lateral margins rounded, visible in dorsal view. Pereonite 4 one-third total body length, slightly wider than preceding pereonites; anterolateral margins produced, rounded; dorsolateral margin produced ventrally. Pereonites 5–7 smooth, shorter posteriorly. Pleon smooth, 1.5 times combined lengths of pe-

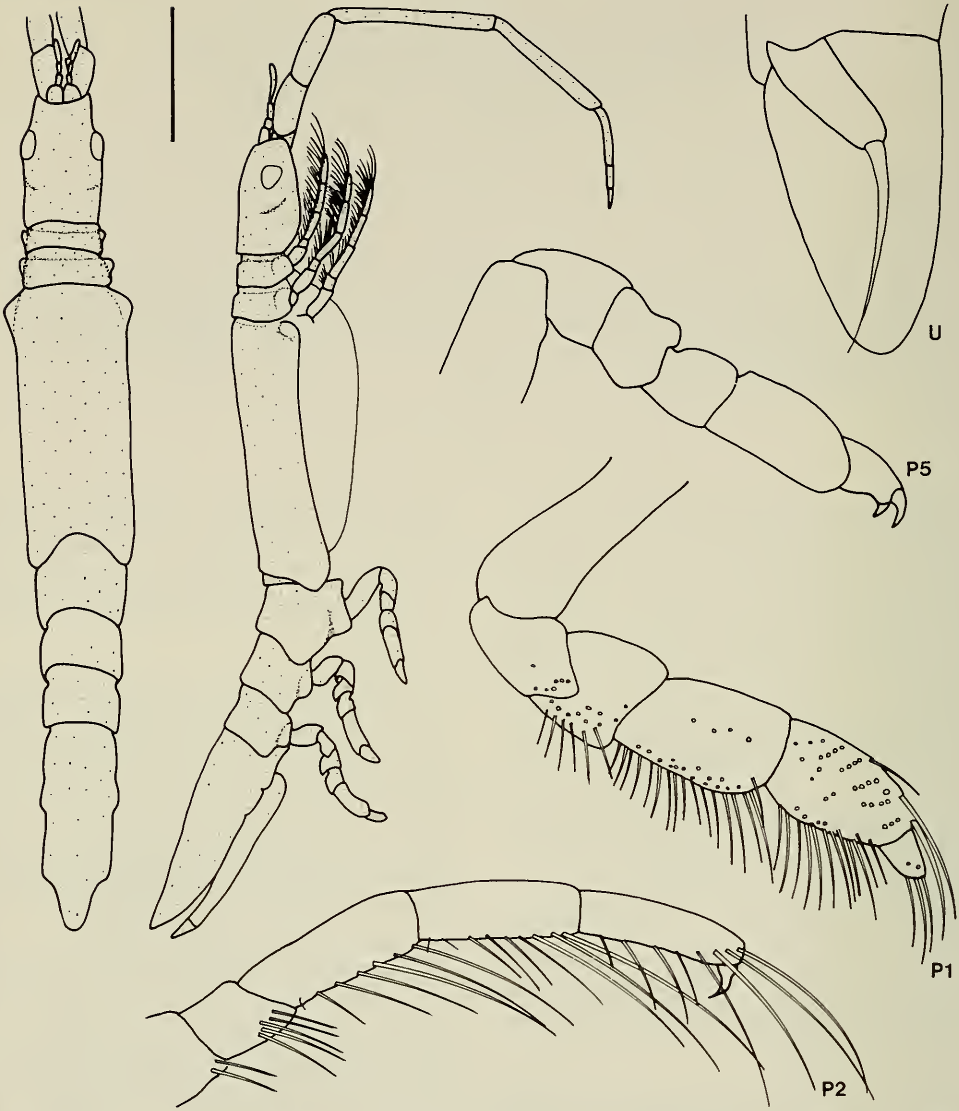

Fig. 1. *Neastacilla falclandica,* female, 6.2 mm (NHRM Isopoda 7305): P1, P2, P5, Pereopods 1, 2 and 5; U, Uropod. Scale = 1 mm.

reonites 5–7; profile a smooth slope. Two pleonal somites indicated by lateral indentations; in dorsal view, second pleonal somite protrudes laterally. Pleotelson with poorly developed posterolateral expansions, apex rounded but with steeply sloping sides.

Antenna 1 reaching one-third along article 3 of antenna 2. Antenna 2 almost two-thirds body length, not excessively slender or stout; flagellum of 3 articles. Ratio of articles 3–5 1.0:2.1:1.1. Pereopod 1 dactyl with terminal setae, claw absent. Pereopods 2–4 of moderate build, densely setose; small claw-like dactyl present. Pereopod 5 with slight ventral expansion, barely more than pereopods 6 and 7; lacking marked ventral expansion. Pereopods 5–7 smooth, dactyl

Fig. 2. *Neastacilla falclandica,* juvenile, 3.1 mm (USNM 222665): MD, Mandibles (left and right); MX1, MX2, Maxillae 1 and 2; MP, Maxilliped.

with 2 well-developed claws, larger claw half length of dactyl. Uropod outer ramus, length 1.7 times base width, apex rounded; inner ramus, distal margin with single stout seta reaching beyond distal margin of outer ramus.

*Distribution.*—Falkland Islands.

*Remarks.*—Mouthparts of this species are figured because it is the nominal type species of the genus.

### *Neastacilla tattersalli,* new species
Fig. 3

*Neastacilla falclandica.*—Tattersall, 1921: 244, pl. 10, fig. 1.—Hurley, 1961:264.

*Material examined.*—Holotype, British Museum (Natural History) 1921:11:29:316, female (8.9 mm), New Zealand, North Cape (34°25′S, 173°02′E), British Antarctic ("Terra Nova") Expedition station 96, 129 m. Paratypes, Zoological Museum, Copenhagen, female (7.8 mm), juvenile (3.2 mm), New Zealand, Hauraki Gulk, Kawau Island (36°25′S, 174°51′E), 10 fathoms, coll. Dr. Th. Mortensen, 29 Dec 1914.

*Description.*—Female: Anterolateral lobe of head angular, with small spine-like projection on ventral margin, rostral point small. Eyes large, ovoid, slightly prominent in dorsal view. Fusion of head and first pereonite indicated by poorly defined groove; lateral margin incised; combined length 1.7 times combined length of pereonites 2 and 3. Pereonite 1 smooth, lateral margin not expanded ventrally. Pereonites 2 and 3 subequal, smooth; lateral margins visible in dorsal view. Pereonite 4 less than one-third total body length, smooth; not markedly wider than preceding pereonites. Antero-

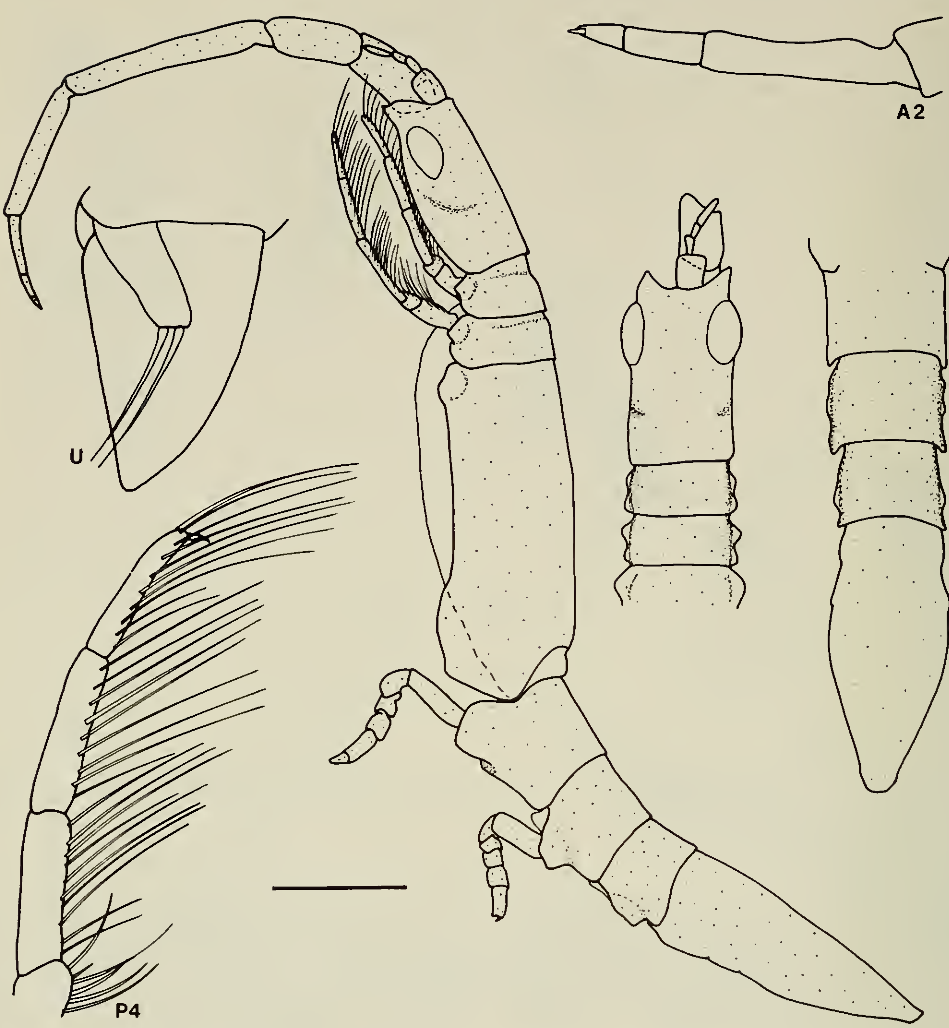

Fig. 3. *Neastacilla tattersalli,* holotype: A2, Antenna 2 flagellum; P4, Pereopod 4; U, Uropod. Scale = 1 mm.

lateral margins produced, rounded. Dorsolateral margin angular, produced ventrally in posterior one-third of pereonite. Pereonites 5–7 smooth, progressively shorter posteriorly. Pleon longer than pereonites 5–7 combined, smooth, profile a smooth slope; 2 pleonal somites indicated by obsolete lateral grooves. Pleotelson tapering to truncate apex, posterolateral expansions absent.

Antenna 1 reaching distal margin of article 2 of antenna 2. Antenna 2 little over half body length, not excessively slender or stout; flagellum of 3 articles. Ratio of articles 3–5 1.0:2.0:1.5. Pereopod 1 dactyl with terminal setae, claw absent. Pereopods 2–4 of moderate build, densely setose; dactyl present. Oostegites on pereopods 1–4. Pereopod 5 coxa with slight ventral expansion, barely more than pereopods 6 and 7. Pereopods 5–7 smooth, dactyl with 2 well-developed claws, larger claw as long as dactyl. Uropod outer ramus length approximately 1.5 times base width, apex angular; inner ramus less than half length of outer ramus, distal margin with 2 subequal setae; setae reach distal margin of outer ramus.

*Distribution.*—Northern North Island of New Zealand.

*Remarks.*—The holotype specimen is in poor condition with mouthparts and several limbs, including pereopod 1, missing. Examination of the paratypes which bear pereopod 1 confirm the species' generic placement. Although only three specimens were examined some variation was observed. The distinct spine on the anterolateral lobe of the head of the holotype is absent from the other specimens.

This is one of few species of *Neastacilla* in which the females lack spines and tubercles. It most closely resembles *Neastacilla falclandica.* The most obvious differences separating the two are the size and shape of the eye, the number of setae on the inner ramus of the uropods, and the shape of the pleotelson.

## Acknowledgments

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PROC. BIOL. SOC. WASH.
99(2), 1986, pp. 196–197

# *ALPHEOPSIS CORTESIANA*, A NEW SNAPPING SHRIMP FROM THE GULF OF CALIFORNIA

Mary K. Wicksten and Michel E. Hendrickx

*Abstract.*—A new species of subtidal snapping shrimp has been dredged off Sinaloa, Mexico. The species, most closely resembling *Alpheopsis harperi* of the Gulf of Mexico, has a large chela with an arched dactyl. There are no grooves on the large chela. A key to the eastern Pacific species of *Alpheopsis* is provided.

Species of *Alpheopsis,* like other members of the family Alpheidae, commonly are called snapping shrimps. In the eastern Pacific, species of *Alpheopsis* often are infaunal inhabitants of offshore bottoms. Most records come from material taken in box cores, grabs, and dredges.

During benthic studies by the R.V. *El Puma* in the Gulf of California, a new species of snapping shrimp was discovered, and is described herein. The drawings are by Debbie Meier, Texas A&M University.

## *Alpheopsis cortesiana,* new species
Fig. 1

*Description.*—Rostrum short, acute, carinate, exceeding ocular spines, falling far short of distal end of first article of antennular peduncle. Orbital teeth acute. Eyes covered in dorsal view, covered or partly exposed in lateral view. Pterygostomial angle of carapace rounded.

Antennular peduncle long, second article longest. Stylocerite long and acute, reaching beyond end of first antennular article. Scaphocerite reaching as far as or falling slightly short of distal end of antennular peduncle, its lateral spine overreaching blade. Carpocerite longer than scaphocerite and antennular peduncle. Basicerite with small lateral tooth.

Large cheliped with chela having palm 1.5× as long as broad. Margins of chela without grooves or notches. Fixed finger with 7 large teeth and 5–7 denticles distal thereto. Dactyl with 5–6 weak teeth. Dactyl lamellate, upper margin strongly convex. Carpus short, cup-shaped. Merus slender, 3× as long as broad, with 2–3 spines on superior margin. Ischium short. Small chela missing in both specimens.

Second leg with ratio of carpal articles 10:4:4:4:4.

Third leg slender. Dactyl sickle-shaped, 7× as long as wide. Propodus 2× length of dactyl, slender, without spines but bearing long setae. Carpus 0.8× length of propodus, merus 1.5× length of carpus. Ischium 0.5× merus, without spines. Fourth and fifth legs similar to third.

Telson more than 2× long as wide, wider at proximal end than at distal; with 2 pair dorsolateral spines and pair of spines on distal margin. (Constriction at end of anterior third, as shown in illustration, probably due to damage to specimen.) Uropods longer than telson.

*Holotype.*—Female, total length 19.7 mm. Off Río Fuerte, Sinaloa, Mexico (25°48′N, 109°34′W), 90 m, mud, 12 May 1982, Van Veen grab, R.V. *El Puma,* CORTES cruise 1, Allan Hancock Foundation (University of Southern California) type number 82-2.

*Paratype.*—Female, total length 9.0 mm. Off Mazatlán, Sinaloa, 20 m, compact mud, 13 March 1981, in oyster dredge, R.V. *El Puma,* Estación Mazatlán catalog number EMU-2096.

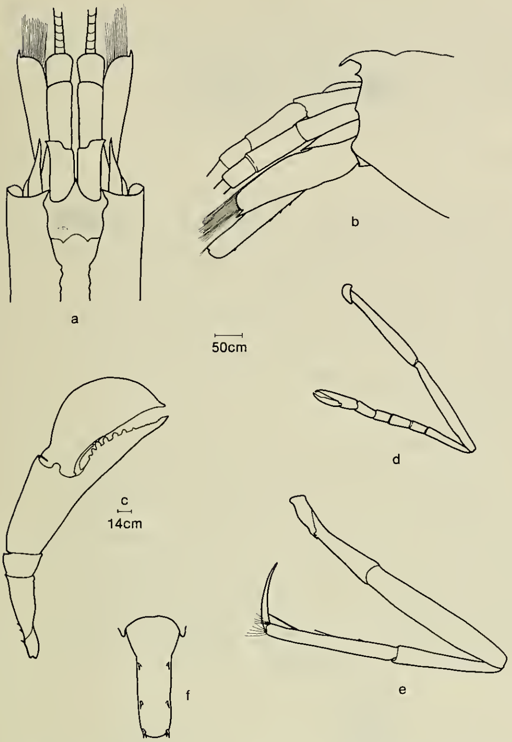

Fig. 1. *Alpheopsis cortesiana,* holotype female. a, Frontal region in dorsal view; b, Frontal region in side view; c, Major cheliped; d, Second pereopod; e, Third pereopod; f, Telson.

*Etymology.*—The specific epithet refers to the Sea of Cortés, from which the species was collected.

*Discussion.*—*Alpheopsis cortesiana* most closely resembles *A. harperi* Wicksten, 1984, from the Gulf of Mexico. Both are offshore infaunal species with large chelae lacking grooves but having dactyls with convex margins. *Alpheopsis harperi,* however, lacks teeth on the fingers of the chela. It has spinules on the propodus of the third leg. The second article of the carpus of the second leg is longer than in *A. cortesiana,* and the dactyl of the third leg is shorter.

There are no published reports of other species of *Alpheopsis* in the Gulf of California or off the coast of Sinaloa. However, a single ovigerous female of a different species, resembling *A. aequalis* Coutière, was collected at Isla Candelero, Sonora (6 July 1983, 10 m, commensal with zooanthid, Alex Kerstitch, collector, Allan Hancock Foundation collections). This specimen agrees with the description of *A. aequalis* given by Banner and Banner (1973:342) except that the blade of the scaphocerite tapers to a point instead of having a broadly rounded margin. More specimens are needed before the species can be formally described.

## Key to the Species of *Alpheopsis* in the Eastern Pacific

1. Anterior region of carapace with rostrum and orbital teeth ........ 2
– Anterior region of carapace with rostrum only, no orbital teeth .... 3
2. Large chela with longitudinal groove. (Southern-central California, U.S.A.) .................... ..*Alpheopsis equidactylus* (Lockington)
– Large chela without longitudinal groove. (Off Sinaloa, Mexico) .... ....*Alpheopsis cortesiana,* new species
3. Large chela with notch on dorsal surface. (Chile-Peru) ............ .........*Alpheopsis chilensis* Coutière
– Large chela without notch on dorsal surface. (Off Sonora, Mexico) .... ....*Alpheopsis* cf. *A. aequalis* Coutière

## Literature Cited

Banner, D. M., and A. H. Banner. 1973. The alpheid shrimp of Australia. Part I: The lower genera.—Records of the Australian Museum 28(15):291–382.

Wicksten, M. K. 1984. *Alpheopsis harperi* (Decapoda: Alpheidae): A new species of snapping shrimp from Texas.—Northeast Gulf Science 7(1):97–100.

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# FRESHWATER SHRIMPS FROM VENEZUELA I: SEVEN NEW SPECIES OF PALAEMONINAE (CRUSTACEA: DECAPODA: PALAEMONIDAE)

Guido Pereira S.

*Abstract.*—Seven new species of palaemonid shrimps are described: *Macrobrachium reyesi, Macrobrachium pectinatum, Macrobrachium atabapense, Macrobrachium rodriguezi, Macrobrachium pumilum, Macrobrachium dierythrum,* and *Palaemonetes* (*Palaemonetes*) *mercedae.* All the specimens were collected in Venezuela. Details of living color patterns, fecundity, and variation are provided. The new species are compared with previously described, and morphologically related, South American species.

*Resumen.*—Se describen siete especies de camarones palaemónidos nuevos para la ciencia: *Macrobrachium reyesi, Macrobrachium pectinatum, Macrobrachium atabapense, Macrobrachium rodriguezi, Macrobrachium pumilum, Macrobrachium dierythrum,* and *Palaemonetes* (*Palaemonetes*) *mercedae.* Todos los especímenes fueron colectados en Venezuela. Se dan detalles del patrón de coloración en vivo, de la fecundidad, y de la variación morfológica. Se hacen comparaciones con especies previamente descritas y en especial con las especies suramericanas consideradas más relacionadas morfológicamente.

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The decapod fauna of part of South America is relatively well known (Hulbert et al. 1981). The revision of Holthuis (1952) remains the most comprehensive taxonomic work treating the palaemonid shrimps. However, some geographical areas have not been extensively studied because of the inaccessibility of many parts of the continent, and the few available collections. Some of the poorer known regions are the Orinoco and Amazon basins, where recently several new species of palaemonids were found (Kensley and Walker 1982, Rodriguez 1982, Pereira 1985). While making a survey of the freshwater shrimps of Venezuela the author found seven undescribed species of palaemonid shrimps, six belonging to the genus *Macrobrachium* and one to the genus *Palaemonetes.* The purpose of the present paper is to present descriptions of these species. The following abbreviations are used: cl., for carapace length; tl., for total length; MBUCV, Museum of Biology Universidad Central de Venezuela; and USNM, National Museum of Natural History, Smithsonian Institution, U.S.A.

### *Macrobrachium* Bate, 1868
### *Macrobrachium reyesi,* new species
Figs. 1, 6C

*Holotype.*—Male MBUCV (XI-1707), 44 mm tl.; 10.3 mm cl. Paratypes 18 males MBUCV (XI-1706), 3 males and 3 females (USNM 228619). Collected 16 Jan 1982 by Guido Pereira and Matias Reyes.

*Type locality.*—Quebrada (stream) Corral de Piedra. El Limón, Maracay, Edo. Aragua, Venezuela, 10°15′N, 67°35′W.

*Etymology.*—The species is dedicated to Matias Reyes who first collected specimens of this species in 1974, kindly gave me the sample, and helped me in the field.

*Additional material.*—8 specimens, MBUCV (XI-1216), Bocono River, between Barrancas and Portuguesa, Edo. Trujillo, Venezuela. 9°5′N, 70°10′W, Nov 1974;

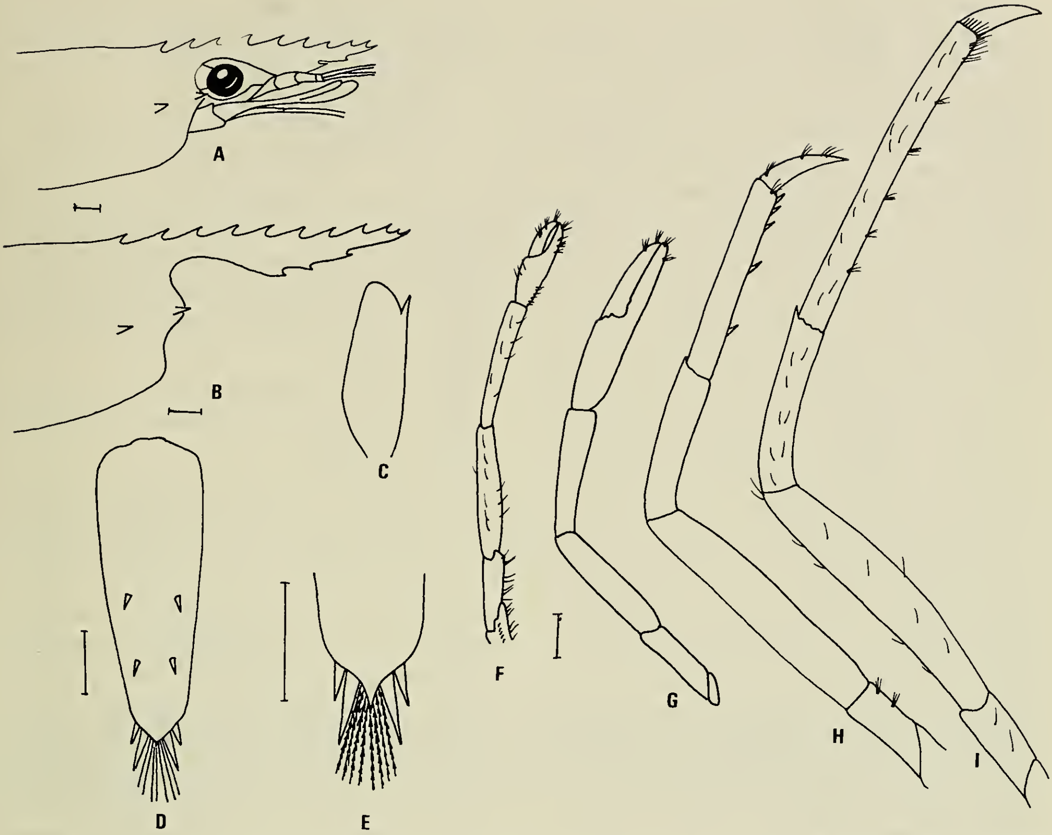

Fig. 1. *Macrobrachium reyesi,* new species. A, Cephalic part of cephalothorax; B, Same in detail; C, Scaphocerite; D, Telson; E, Posterior part of telson; F, First pereiopod; G, Second pereiopod; H, Third pereiopod; I, Fifth pereiopod. All from paratypic male. Scale = 1 mm.

coll. F. Mago.—5 specimens, MBUCV (XI-1331), pond in the road between Guanare and Guanarito, Edo. Portuguesa, Venezuela, 8°50'N, 69°10'W, May 1981; coll. D. Taphorn and J. Reid.—2 specimens, MBUCV (XI-1615), Stream Grande, Cojedes River system, Edo. Yaracuy, Venezuela, 10°5'N, 68°45'W, May 1978; coll. F. Mago.—3 specimens, MBUCV (XI-1630), Stream Corral de Piedra, El Limón, Maracay, Edo. Aragua, Venezuela, 10°15'N, 67°35'W, 1974; coll. M. Reyes.—4 specimens, MBUCV (XI-1781), Stream Grande, Cojedes River system, Edo. Portuguesa, Venezuela, 9°50'W, 68°45'W, 1978; coll. F. Mago.—25 specimens, MBUCV (XI-1708), Stream Corral de Piedra, El Limon, Maracay, Edo. Aragua, Venezuela, 10°15'N, 67°35'W, Jan 1982; coll. G. Pereira and M. Reyes.

*Description of holotype.*—Rostrum straight with tip slightly pointing upward, apex reaching slightly beyond distal end of scaphocerite; upper border bearing 9 (6 to 9 paratypes) regularly distributed teeth; 2 of which behind posterior margin of orbit; small subapical tooth frequently present; lower margin with 3 (3 to 4 paratypes) teeth. Carapace smooth. Scaphocerite 2.7 times longer than wide. Abdomen smooth, posteroventral angle of fifth pleuron acute. Sixth abdominal segment 1.3 times length of fifth, 0.4 times that of telson. Telson with 2 pairs of dorsal spines, situated at ½ and ¾ of length from base; posterior margin, tapering abruptly to median apex, bearing 2 pairs of lateral spines, inner of which overreaching median apex, and 8 plumose setae between inner spines. First pereiopods smooth and slender, with tip of dactyl overreaching scaphocerite; palm cylindrical in cross section, thickest at midlength, and 0.9 times as long as dactyl; carpus 3.2 times length of palm, subequal to merus. Second pair of pereiopods slender, smooth, equal in size, and overreaching distal border of scaphocerite by ½ length of palm; fingers smooth, closing over entire length; proximal tooth on opposable margin of each; palm cylindrical in cross section, 2.4 times longer than wide, 0.75 times length of dactyl; carpus 1.3 (1.2–1.5 paratypes) times length of palm, subequal to merus; ischium smooth. Third pair of pereiopods reaching distal border of scaphocerite; propodus with longitudinal row of 5 spines on inner margin, 2.2 times length of dactyl, 1.3 times that of carpus. Fifth pair of pereiopods reaching distal border of scaphocerite; propodus, with longitudinal row of 4 (3–5 paratypes) spines on inner margin, 4.0 times length of dactyl, 2.0 times that of carpus.

*Size.*—Largest male measures 38.6 mm tl. and 10.3 mm cl. Largest female 35 mm tl. and 9.0 mm cl.

*Fecundity.*—One ovigerous female, 32.0 mm tl. and 8.5 mm cl. with 22 oval eggs, 2.2–1.5 mm diameter.

*Larval development.*—Abbreviated (Pereira, in prep).

*Color.*—Translucent in life.

*Remarks.*—This species is similar to *M. jelskii* (Miers) from which it can be distinguished by the shape of rostrum: it is relatively shorter, and straight in *M. reyesi,* the apex overreaching the scaphocerite, while *M. jelskii* has the rostrum slightly arcuate over the eye, overreaching the scaphocerite by about ⅙ of its length; a diagnostic feature of this species is the short length of the second pair of legs overreaching the scaphocerite by half the length of the palm, while in other American species, at least by the entire palm.

### *Macrobrachium pectinatum,* new species
Figs. 2, 3, 6B

*Holotype.*—Male MBUCV (XI-1759) 46.8 mm tl. and 9.3 mm cl. Paratypes, 2 males and 2 females MBUCV (XI-1760), 1 male and 2 females (USNM 228620) collected 17 April 1982 by Guido Pereira and Ramiro Ruyero.

*Type locality.*—Atabapo River, Sta. Cruz, Territorio Federal Amazonas, Venezuela 3°20′N, 67°29′W.

*Etymology.*—The specific name is derived from the Latin word *pecten,* a comb, to note the pectinate appearance of the cutting edges of fingers.

*Description of holotype.*—Rostrum straight with anterior ⅓ curved upwards, and distal ¼ overreaching distal border of scaphocerite; upper border bearing 8 teeth, 6 of them regularly distributed along posterior half, 2 basal ones located behind posterior margin of orbit; anterior half unarmed except for 2 small subapical teeth; lower margin with 7 (6–8 paratypes) teeth. Carapace smooth. Scaphocerite 2.3 times longer than wide. Abdomen smooth, posteroventral angle of fifth pleuron acute. Sixth abdominal segment 1.4 times length of fifth, 0.8 times length of telson. Telson with 2 pairs of dorsal spines, situated near ½ and ¾ its length from base; posterior margin tapering abruptly to median apex, bearing 2 pairs of lateral spines, inner of which overreaching median apex, and 8 plumose setae between inner spines. First pereiopods smooth and slender, reaching distal ⅓ of scaphocerite; palm cylindrical, thickest at midlength, 0.8 times length of dactyl; carpus 4.1 times length of palm, 1.2 times length of merus, 3.5 times length of dactyl; fingers gaping when closed; cutting edge bearing single series of strong hairs, giving pectinate appearance. Second pair of pereiopods smooth and subequal in size, overreaching

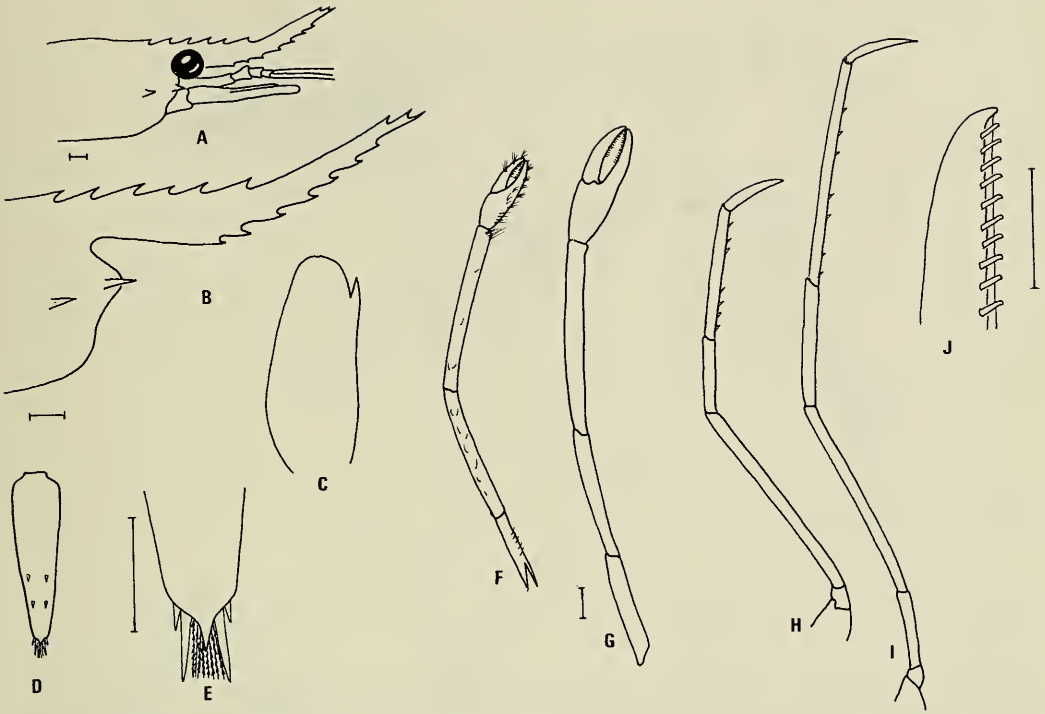

Fig. 2. *Macrobrachium pectinatum,* new species. A, Cephalic part of cephalothorax; B, Same in detail; C, Scaphocerite; D, Telson; E, Posterior part of telson; F, First pereiopod; G, Second pereiopod; H, Third pereiopod; I, Fifth pereiopod; J, Detail of dactyl of second pereiopod. All from paratypic male. Scale = 1 mm.

distal border of scaphocerite by entire palm; fingers gaping when closed, with cutting edges bearing single row of strong hairs giving pectinate appearance; palm cylindrical in cross section, 1.6 times longer than wide, same length as dactyl; carpus 3.0 times length of palm, 1.6 times length of merus, 2.8 times length of dactyl. Third pair of pereiopods overreaching distal border of scaphocerite by ⅓ of propodus; propodus with row of 8 (7–9 paratypes) spines longitudinally on inner margin, 2.1 times length of dactyl, 1.8 times length of carpus. Fifth pair of pereiopods overreaching distal border of scaphocerite by entire propodus; propodus, with longitudinal row of 8 (7–9 paratypes) spines on inner margin, 3.0 times length of dactyl, 1.8 times length of carpus.

*Size.*—Largest male 33.9 mm tl. and 9.3 mm cl. Largest female 44.0 mm tl. and 10.7 mm cl.

*Fecundity.*—One ovigerous female, 42.0 mm tl. and 9.9 mm cl. with 24 oval eggs, 2.3–1.5 mm diameter.

*Color.*—Body ground color pink, with some darker zones on base of rostrum, on posterolateral and posterodorsal surfaces of cephalothorax. Abdomen striped with very dark, almost black, bands at junction of segments. Telson with narrow longitudinal dorsal band; uropods with darker zone proximally.

*Remarks.*—This species is similar to *M. jelskii* (Miers) and *M. reyesi,* from which it can be distinguished by the gaping fingers of the chela, and the rostral shape, which is distally curved upwards in *M. pectinatum,* while straight in *M. reyesi*; the proximal half of the rostrum is curved over the eyes in *M. jelskii* while straight in *M. pectinatum*; finally there is one tooth behind the margin of the orbit in *M. jelskii,* while *M. pectin-*

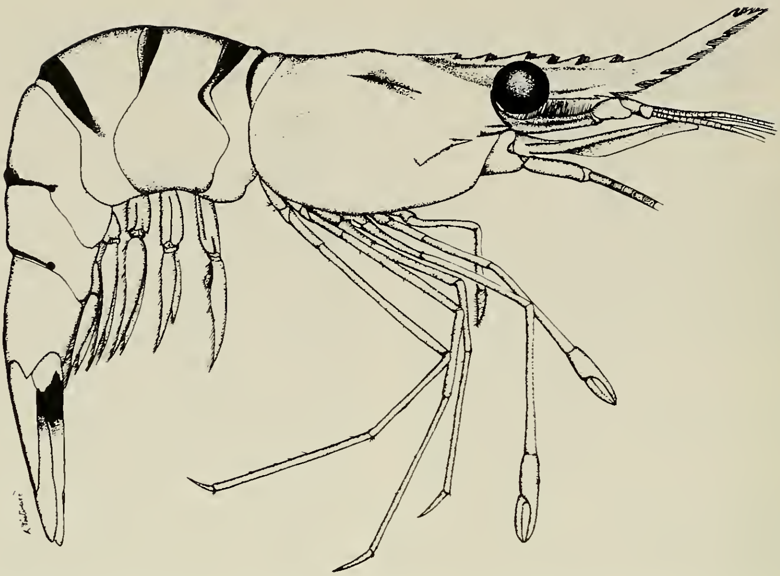

Fig. 3. *Macrobrachium pectinatum,* new species. Color pattern, lateral view of paratypic male.

*atum* usually has two teeth behind the margin of the orbit. Diagnostic features of this species are, additional to the gaping fingers, the walking legs being unusually long, and overreaching the distal border of the scaphocerite by the propodus.

### *Macrobrachium atabapense,* new species
Figs. 4, 5, 6A

*Holotype.*—Male MBUCV (XI-1781) 36.6 mm tl. and 11.0 mm cl. Paratypes: 6 males MBUCV (XI-1761), 4 males (USNM 228618) collected 17 April 1982 by Guido Pereira and Ramiro Ruyero at type locality. 2 males MBUCV (XI-1715), collected 16 Jan 1979 by Kate Clark, Temi River at Yavita, 31 Km NE of Maroa, Territorio Federal Amazonas, Venezuela 3°0′N, 67°0′W.

*Type locality.*—Atabapo River, Sta. Cruz, Territorio Federal Amazonas, Venezuela 3°20′N, 67°29′W.

*Etymology.*—The specific name *atabapense* is derived from the name of the Atabapo River.

*Description of holotype.*—Rostrum straight, with apex reaching slightly beyond distal border of scaphocerite; upper border bearing 9 (9–11 paratypes) regularly distributed teeth, 2 of which behind posterior margin of orbit; lower margin with 3 (2–3 paratypes) teeth. Carapace smooth. Scaphocerite 3 times longer than wide. Abdomen smooth, posteroventral angle of fifth pleuron acute. Sixth abdominal segment 1.4 times length of fifth, 0.75 times length of telson. Telson with 2 pairs of dorsal spines, situated near ½ and ¾ its length from base, posterior margin tapering abruptly to median apex, bearing 2 pairs of lateral spines, inner of which overreaching median apex, and 9 (9–10 paratypes) plumose setae, between inner spines. First pereiopods smooth and slender, overreaching scaphocerite by distal part of merus; palm cylindrical in cross section, thickest at midlength, 1.7 times length of dactyl; carpus 3.4 times length of palm, 1.4 times length of merus. Second pair of pereiopods spiny, subequal in shape, about same length, but one more massive; overreaching distal border of scaphocerite by distal end of merus; fingers short and strong, gaping when closed; both fingers with conspicuous teeth; dactyl with 2 teeth, larger

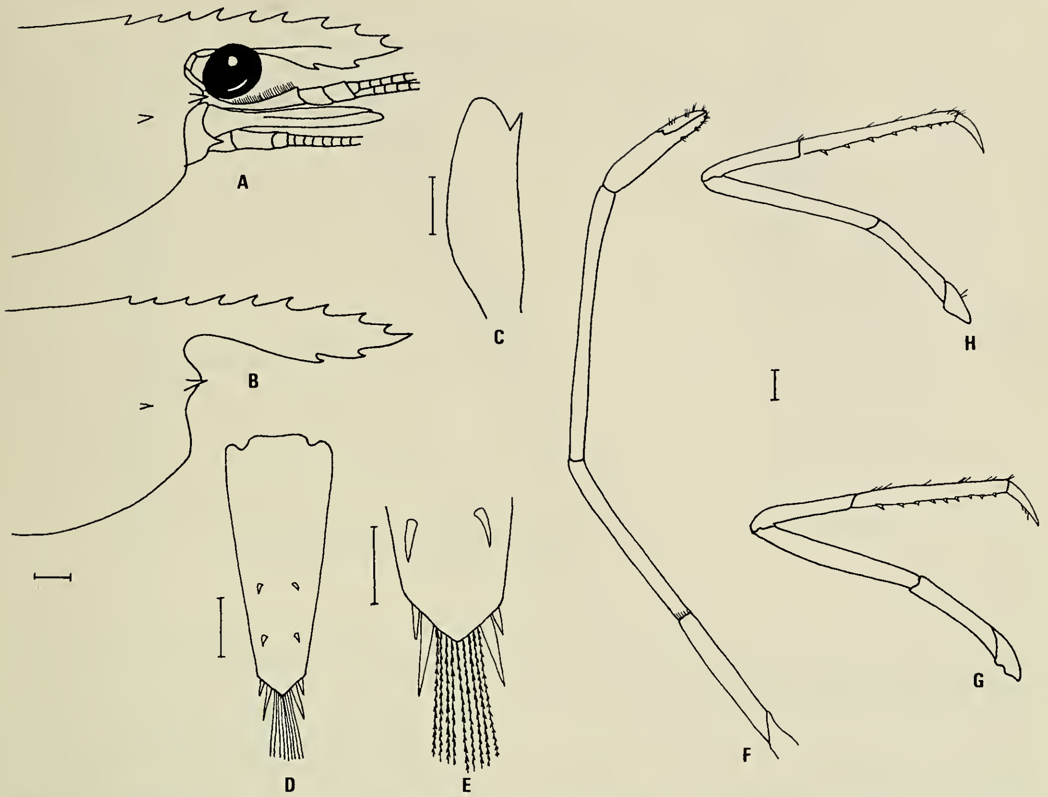

Fig. 4. *Macrobrachium atabapense,* new species. A, Cephalic part of cephalothorax; B, Same in detail; C, Scaphocerite; D, Telson; E, Posterior part of telson; F, First pereiopod; G, Third pereiopod; H, Fifth pereiopod. All from paratypic male. Scale = 1 mm.

situated at distal end of proximal third and smaller just proximal to it, remainder of cutting edge smooth. Fixed finger with strong tooth at end of proximal ¼ and series of 3 (2–4 paratypes) smaller teeth more proximal; no tubercles present on fingers; palm cylindrical in cross section, 3.0 times longer than wide, widest distally, with numerous longitudinal rows of short spines, those on lower surfaces larger than elsewhere, 1.9 times length of dactyl; carpus 0.9 times length of palm, 1.8 times length of merus; spines scarce distally on ventral margin, rest of merus and ischium smooth. Third pair of pereiopods overreaching distal border of scaphocerite by ⅕ of propodus; propodus with longitudinal row of 8 (8–9 paratypes) spines on inner margin, 3.0 times length of dactyl, 1.5 times length of carpus. Fifth pair of pereiopods reaching distal border of scaphocerite; propodus, with longitudinal row of 9 (8–10 paratypes) spines on inner margins; 3.8 times length of dactyl, 1.8 times length of carpus.

*Size.*—Largest male 31.4 mm tl. and 12.0 mm cl. Largest female 26.0 mm tl. and 8.0 mm cl. Ovigerous females not available.

*Color.*—Ground color violaceous with salmon pink longitudinal median stripe, extending from rostrum to 6th abdominal segment.

*Remarks.*—This species is similar to *M. quelchi* (De Man). The main differences are: the second leg is relatively shorter in *M. atabapense,* overreaching scaphocerite by distal end of carpus, while by ⅖ of the car-

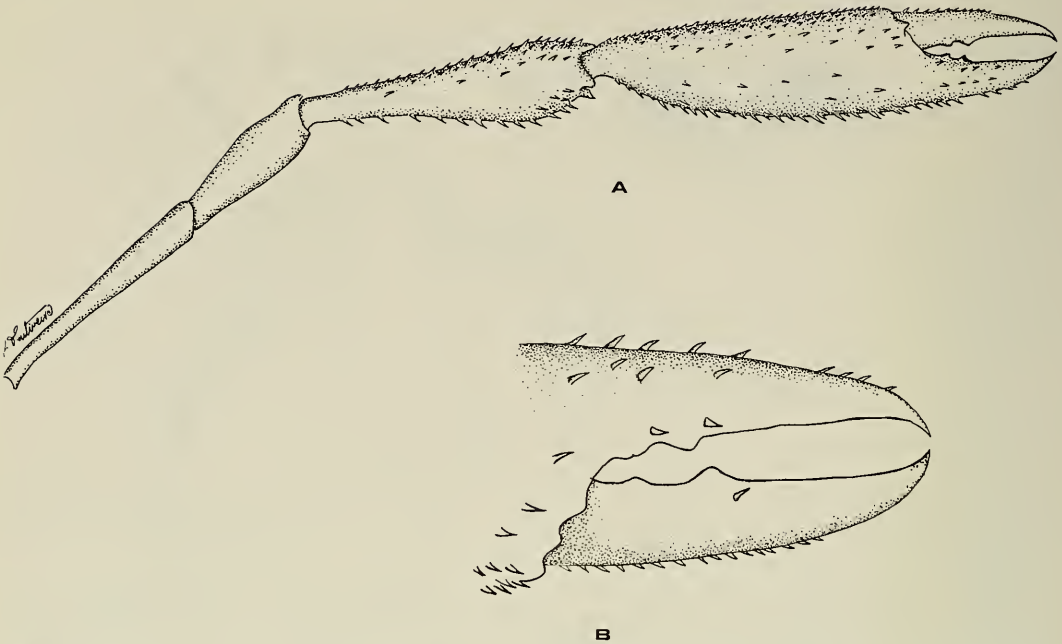

Fig. 5. *Macrobrachium atabapense,* new species. A, Second pereiopod; B, Distal part of chela of second pereiopod. From a paratypic male.

pus in *M. quelchi.* Also, the ratio carpus : palm is 0.9, and carpus : merus 1.8 in *M. atabapense,* while 0.75, and 1.2 respectively in *M. quelchi*; the second legs in *M. atabapense* have more numerous and more prominent spines than has *M. quelchi.* Finally, they have very different color patterns (Holthuis 1952, Pereira 1985).

### *Macrobrachium dierythrum,* new species

Figs. 7, 8, 12

*Holotype.*—Male USNM 228323, 18.6 mm tl. and 4.2 mm cl. Paratypes: 3 males, 17 females USNM 228324, collected 15 Jan 1984, by Guido Pereira and Ernesto Panier.

*Type locality.*—Aguaro River, Paso Garzerito, Edo. Guarico, Venezuela, 8°10′N, 66°25′W.

*Etymology.*—The specific name is derived from the Greek word *dierythros* meaning variegated with red, to call attention to the red color of shrimp.

*Additional material.*—2 males, and 470 females MBUCV (XI-2207); locality, date, and collectors same as above.

*Description of holotype.*—Rostrum straight, with tip reaching distal border of scaphocerite; upper border bearing 9 (8–10 paratypes) regularly distributed teeth, 2 of which behind posterior margin of orbit, third just over or anterior to it; lower margin with 4 (3–5 paratypes) teeth. Carapace smooth. Scaphocerite 3.1 times longer than wide. Abdomen smooth, posteroventral angle of fifth pleuron acute. Sixth abdominal segment 1.5 times length of fifth, 0.6 that of telson. Telson with 2 pairs of dorsal spines, situated at ½ and ¼ its length from base; posterior margin acute, tapering abruptly to median apex, bearing 2 pairs of lateral spines, inner of which overreaching median apex, and 4 plumose setae between inner spines. First pereiopods slender, overreaching distal border of scaphocerite by dactyl; palm cylindrical in cross section, 1.5 times

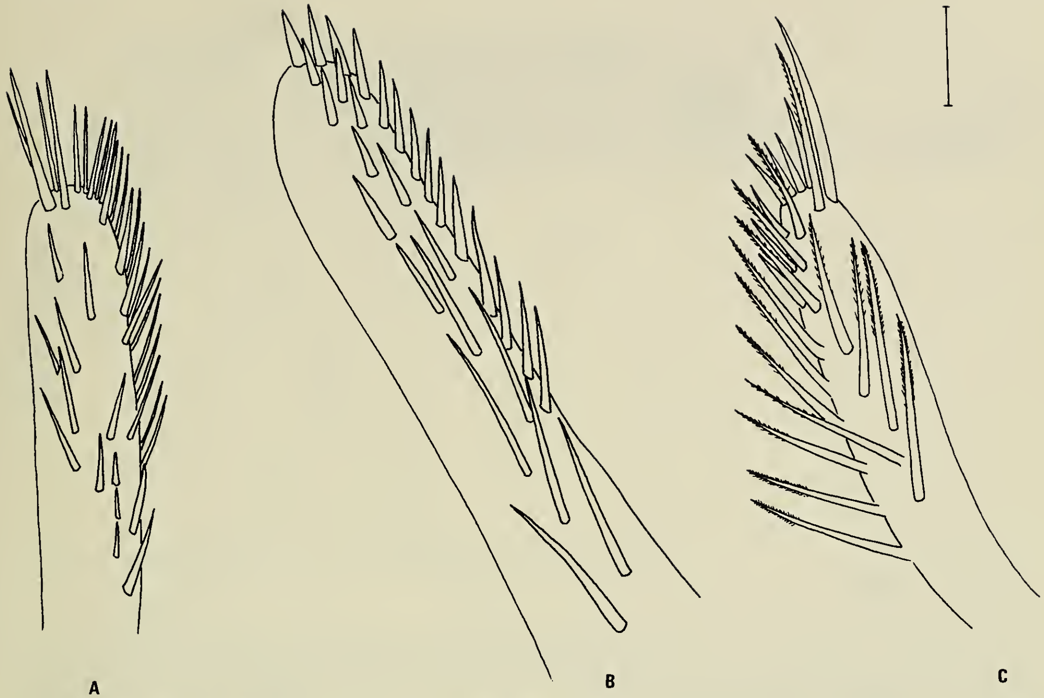

Fig. 6. Appendices masculinae. A, *M. atabapense*, new species; B, *M. pectinatum*, new species; C, *M. reyesi*, new species. From paratypes. Scale = 100 M.

length of dactyl; carpus 2.2 times length of palm, 1.1 that of merus. Second pair of pereiopods similar in shape and size, overreaching distal border of scaphocerite by ⅔ of carpus; fingers straight, both with conspicuous teeth; dactyl with 2 teeth at ⅕ and ⅖ its length from base, fixed finger with 2 teeth just proximal to each tooth on dactyl; fingers without tubercles; palm cylindrical in cross section, 3.1 times longer than wide, with several longitudinal rows of spines, 1.5 times length of dactyl; carpus 0.8 times length of palm, 0.9 times length of merus, spinulation pattern as on palm; merus with three rows of ventral spines; ischium smooth, except for scattered ventral spines. Third pair of pereiopods not reaching distal border of scaphocerite; propodus with longitudinal row of 7 spines on inner margin, 2.2 times length of dactyl, 1.9 times length of carpus. Fifth pair of pereiopods not reaching distal border of scaphocerite; propodus with longitudinal row of 7 spines on inner margin; 2.4 times length of dactyl, 2.2 times length of carpus.

*Size.*—Largest male 18.4 mm tl. and 4.2 mm cl. Largest female 26.0 mm tl. and 6.4 mm cl.

*Fecundity.*—No ovigerous female available.

*Color.*—Background color red, with numerous irregular pink spots over body. Antennal and antennular flagella deep blue. Second leg overall red, some clear pink areas, fingers white. Pereiopods 3–5 pink, with 7 transverse red stripes, 1 basally on ischium, 2 on merus, one basally and other at midlength, 2 on carpus, one basally and other at midlength, 2 or 1 on propodus, on second and third ¼ length from base.

*Remarks.*—Except for the report of Rodriguez (1982), there are no records of *Mac-*

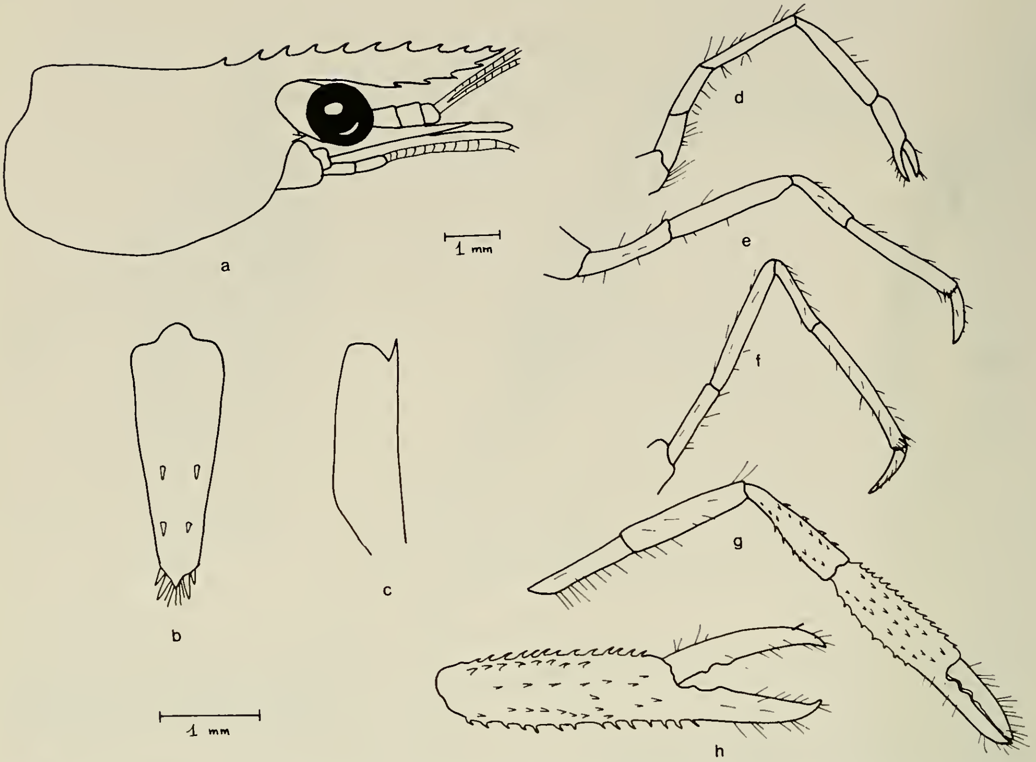

Fig. 7. *M. dierythrum,* new species. A, Cephalic part of cephalothorax; B, Telson; C, Scaphocerite; D, First pereiopod; E, Third pereiopod; F, Fifth pereiopod; G, Second pereiopod; H, Second pereiopod detail. All from paratypic male.

*robrachium* of such small size in America, probably because rivers in the Guayanas region have not been sampled adequately. Comparisons are made in Table 1.

## *Macrobrachium rodriguezi,* new species
Figs. 10, 12

*Holotype.*—Male USNM 228321, 16.2 mm tl. and 3.4 mm cl. Paratypes: 25 males USNM 228322, collected 13 Jan 1984 by Guido Pereira and Ernesto Panier.

*Type locality.*—Caris River, El Tigre, Edo. Anzoategui, Venezuela, 8°45′N, 64°50′W.

*Etymology.*—The species is named in honor of Dr. Gilberto Rodriguez, pioneer of carcinological studies in Venezuela.

*Additional material.*—10 males, 18 females MBUCV (XI-2200), locality, date, and collectors same as above.

*Description of holotype.*—Rostrum arched, with apex reaching third antennular segment; upper border bearing 8 (8–9 paratypes) regularly distributed teeth, one of which situated behind margin of orbit, second just over or behind it; lower margin with 3 teeth. Carapace smooth. Scaphocerite 2.5 times longer than wide. Abdomen smooth, posteroventral angle of fifth pleuron acute. Sixth abdominal segment 1.4 times length of fifth, 0.8 times length of telson. Telson with 2 pairs of dorsal spines, situated at ⅓ and ⅔ of its length from base; posterior margin tapering abruptly to median apex, bearing 2 pairs of lateral spines, inner of which overreaching median apex, with 7 (6–9 paratypes) plumose setae between inner spines. First pereiopods slender, overreaching distal border of scapho-

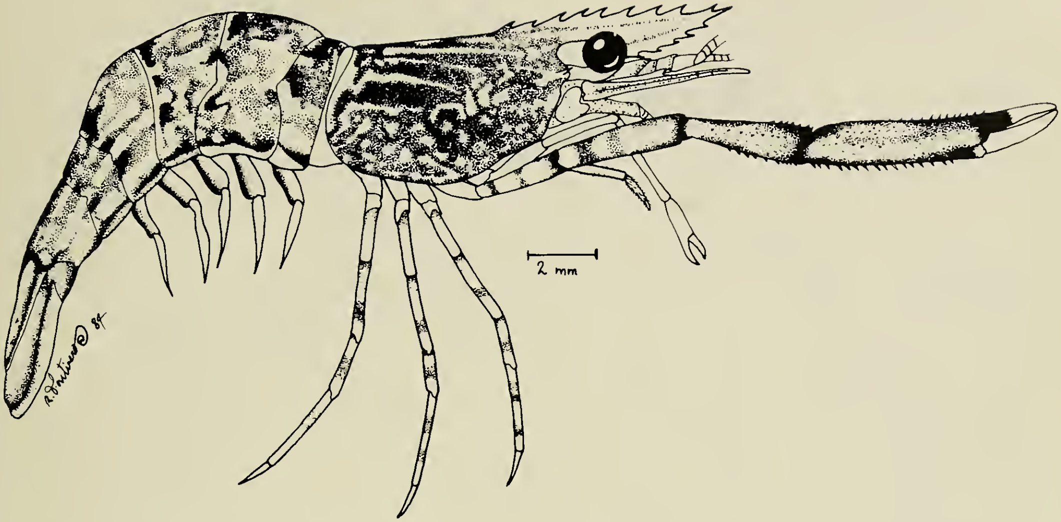

Fig. 8. *M. dierythrum* color pattern, lateral view of paratypic male.

cerite by dactyl; palm cylindrical in cross section, 1.6 times length of dactyl; carpus 1.7 times length of palm, same length as merus. Second pair of pereiopods smooth, equal in shape and length, overreaching anterior border of scaphocerite by palm; fingers straight, without conspicuous teeth; palm cylindrical in cross section, 2.9 times longer than wide, 1.4 times length of dactyl; carpus 0.8 times length of palm, and 0.8 times length of merus. Third pair of pereiopods reaching distal border of scaphocerite; propodus with longitudinal row of 7 spines on inner margin; 2.0 times length of dactyl, 1.7 times length of carpus. Fifth pair of pereiopods overreaching distal border of scaphocerite by ½ of dactyl; propodus with longitudinal row of 7 spines on inner margin, 3.2 times length of dactyl, 2.2 times length of carpus.

*Size.*—Largest male 16.2 mm tl. and 3.4 mm cl. Largest female 12.4 mm tl. and 3.0 mm cl.

*Fecundity.*—Ovigerous females with 10–22 large and oval eggs, average largest diameter 1.3 mm.

*Color.*—Background color either brown or blue, with longitudinal middorsal cream stripe, from tip of rostrum to sixth abdominal segment.

*Remarks.*—Comparisons are made in Table 1.

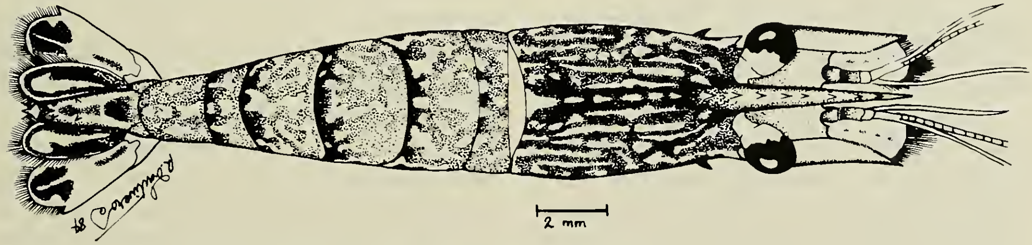

Fig. 9. *M. dierythrum* color pattern, dorsal view of paratypic male.

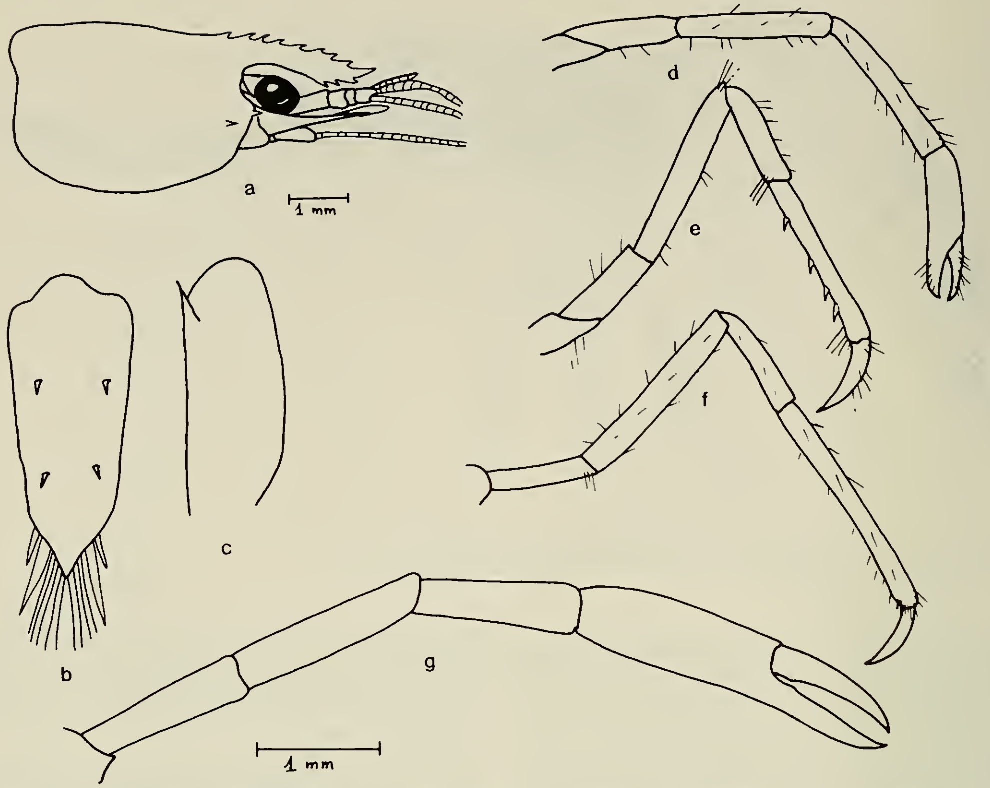

Fig. 10. *M. rodriguezi,* new species. A, Cephalic part of cephalothorax; B, Telson; C, Scaphocerite; D, First pereiopod; E, Third pereiopod; F, Fifth pereiopod; G, Second pereiopod. All from paratypic male.

### *Macrobrachium pumilum,* new species
Figs. 11, 12

*Holotype.*—Male USNM 228319, 10.5 mm tl. and 3.2 mm cl. Paratypes: 10 males, 16 females USNM 228320, collected 15 Jan 1984 by Guido Pereira and Ernesto Panier.

*Type locality.*—Aguaro River, Cachimbo pass, Edo. Guarico, Venezuela, 8°10′N, 66°35′W.

*Etymology.*—The specific name is derived from the Latin word *pumilus,* meaning little, referring to the small size of the shrimp.

*Additional material.*—2 males, 250 females MBUCV (XI-2204), locality, date, and collectors same as above.

*Description of holotype.*—Rostrum strongly arched over eyes with apex reaching distal border of scaphocerite; upper border bearing 8 (7–9 paratypes) regularly distributed teeth, 2 of which situated behind posterior margin of orbit; lower margin with 1 (1–2 paratypes) tooth. Carapace smooth. Scaphocerite 3.1 times longer than wide. Abdomen smooth, posteroventral angle of fifth pleuron acute. Sixth abdominal segment 1.8 times length of fifth, 0.8 times length of telson. Telson with 2 pairs of dorsal spines, situated near ⅓ and ⅙ its length from base; posterior margin tapering abruptly to median apex, bearing 2 pairs of lateral spines, inner of which overreaching median apex, and 6 (6–8 paratypes) plumose setae, between inner spines. First pereiopods slender, overreaching distal border of scaphocerite by dactyl; palm cylindrical, 0.8 times length of dactyl; carpus 2.2 times length of palm, 0.9 times length of merus.

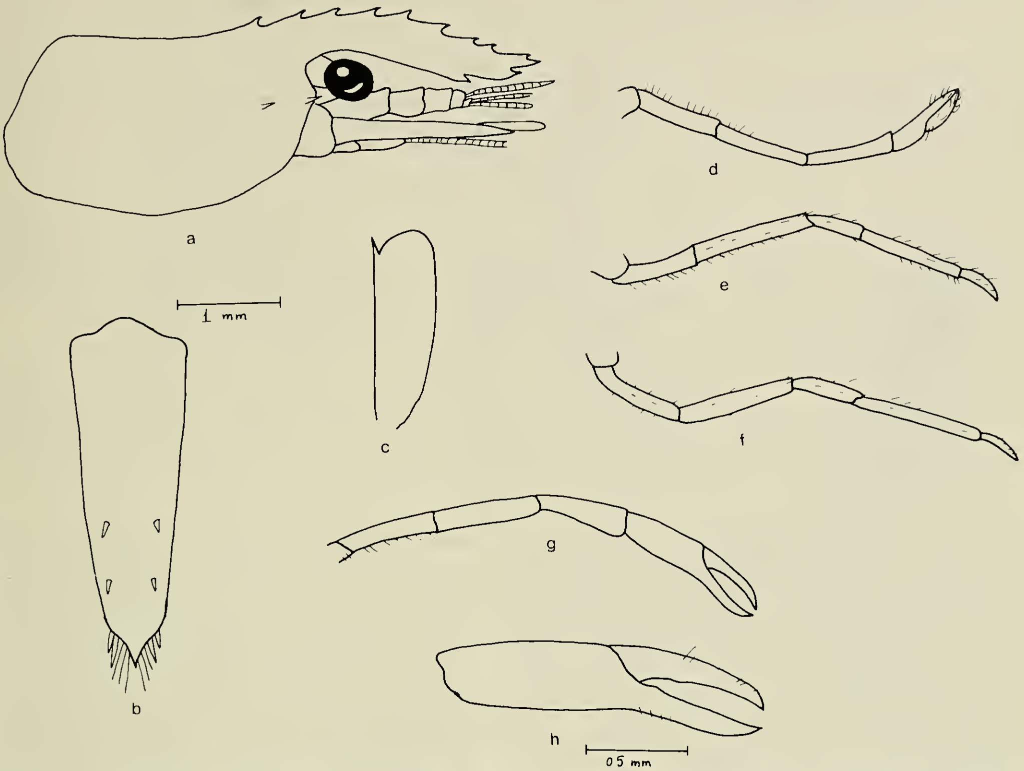

Fig. 11. *M. pumilum,* new species. A, Cephalic part of cephalothorax; B, Telson; C, Scaphocerite; D, First pereiopod; E, Third pereiopod; F, Fifth pereiopod; G, Second pereiopod; H, Detail of second pereiopod.

Second pair of pereiopods smooth, subequal in size, overreaching anterior border of scaphocerite by length of palm; fingers straight, without conspicuous teeth; palm cylindrical in cross section, 2.6 times longer than wide, 1.1 times length of dactyl; carpus 1.1 times length of palm, 0.8 length of merus. Third pair of pereiopods reaching ½ length of scaphocerite with dactyl; propodus with longitudinal row of 6 spines on inner margin, 1.9 times length of dactyl, 1.6 times length of carpus. Fifth pair of pereiopods reaching basal ¼ of scaphocerite; propodus with longitudinal row of 6 spines on inner margin, 2.6 times length of dactyl, 2.0 times length of carpus.

*Size.*—The largest male 10.5 mm tl. and 3.2 mm cl. Largest female 24.0 mm tl. and 5.2 mm cl.

*Fecundity.*—One ovigerous female, 16.4 mm tl. and 4.7 mm cl. with 12 oval eggs, 1.6 mm largest diameter.

*Color.*—Overall body lemon yellow in color.

*Remarks.*—The last three species are of very small size as compared to other South American species in the genus. Table 1 gives a summary of their most distinguishing features.

### *Palaemonetes* Heller, 1869
### *Palaemonetes* (*Palaemonetes*) *mercedae*, new species
Fig. 13

*Holotype.*—Male MBUCV (XI-1782) 3.2 mm cl. Paratypes 1 male and 1 female MBUCV (XI-1782 B), collected 18 April 1982 by Guido Pereira and Ramiro Ruyero.

*Type locality.*—Atabapo River at Cha-

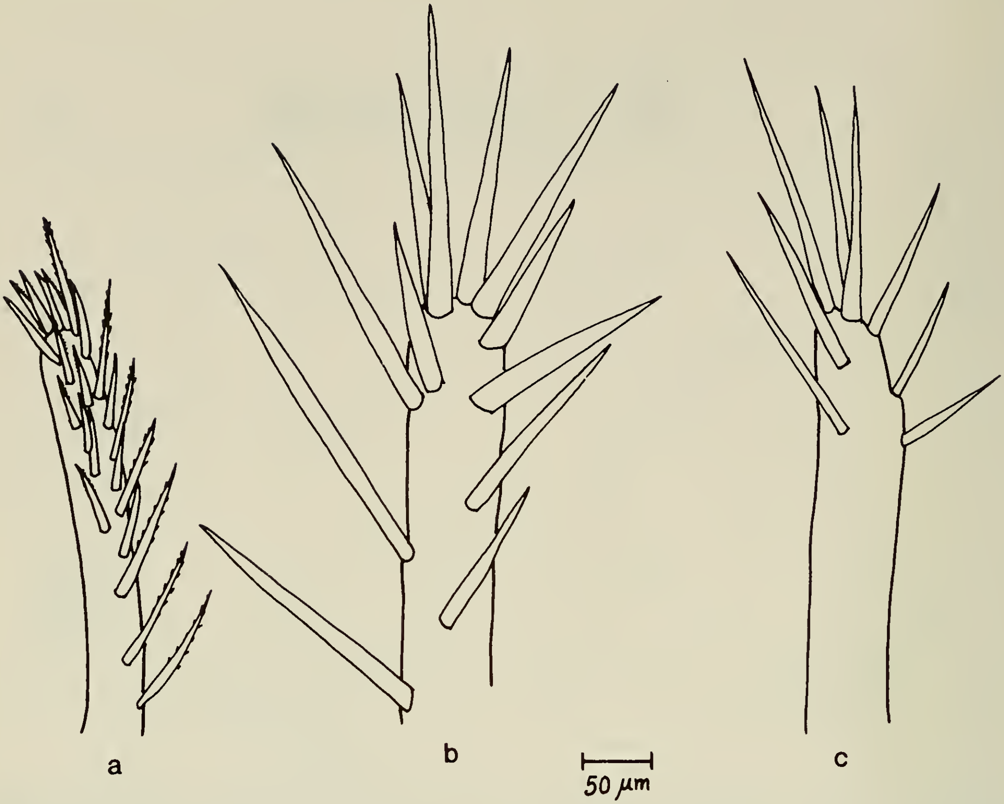

Fig. 12. Appendices masculinae. A, *M. rodriguezi,* new species; B, *M. pumilum,* new species; C, *M. dierythrum,* new species. All from paratypic males.

muchina, Territorio Federal Amazonas, Venezuela, 3°20′N, 67°29′W.

*Etymology.*—The species is dedicated to my wife Mercedes.

*Additional material.*—3 males, 17 females, USNM 228318, Departamento Ature, Puerto Ayacucho, Territorio Federal Amazonas, Venezuela, 5°35′N, 67°30′W, Dec 1984; coll. R. Vari.—4 males, 8 females USNM 228317, Departamento Río Negro, between San Carlos and Solano, Territorio Federal Amazonas, Venezuela, 1°56′N, 67°2′W, Dec 1984; coll. J. Fernandez, and O. Castillo.

*Description of holotype.*—Rostrum slender and straight, reaching distal end of scaphocerite; upper margin bearing 7 (6–7 paratypes) regularly distributed teeth, one of which placed behind orbit, and smaller than rest; lower margin with 2 teeth. Carapace smooth. Branchiostegal spine subequal in length to antennal spine, not reaching anterior border of carapace; branchiostegal groove distinct, extending from midway between branchiostegal and antennal spines. Abdomen smooth, pleura of fifth segment antero- and posteroventrally rounded. Sixth segment 1.6 times as long as fifth, 0.7 length of telson. Telson bearing 2 pairs of dorsolateral spines, at midlength and ⅔ its length from base; posterior margin rounded, ending in median point and bearing 2 pair of spines, neither overreaching tip of telson; with 12 (10–14 paratypes) plumose setae between inner spines. Eyes normal and well pigmented. Antennule with stylocerite sharp, reaching midlength of proximal segment of antennular peduncle;

Table 1.—Distinguishing features between *M. dierythrum, M. rodriguezi* and *M. pumilum*; number of post-orbital teeth in parentheses; see additional color pattern in the descriptions.

| Character | *M. dierythrum* | *M. rodriguezi* | *M. pumilum* |
|---|---|---|---|
| Rostrum | Straight, overreaching scaphocerite by apex | Arched over the eye, reaching distal antennular peduncle | Arched over the eye, overreaching scaphocerite by apex |
| Rostral formula | $\frac{8\text{–}9, (2)}{3\text{–}5}$ | $\frac{8\text{–}9, (1\text{–}2)}{3\text{–}5}$ | $\frac{7\text{–}9, (2)}{1\text{–}2}$ |
| Second leg | Spiny, overreaching scaphocerite by ⅔ carpus. Palm 3.1 longer than wide, 1.5 length of dactyl | Smooth, overreaching scaphocerite by palm. Palm 2.9 longer than wide, 1.4 length of dactyl | Smooth, overreaching scaphocerite by palm. Palm 2.6 longer than wide, 1.1 length of dactyl |
| Appendix masculina | With 7 spines on distal ⅓ | With 21 spines over its entire length | With 12 spines on distal ½ |

outer margin of basal segment straight with strong anterolateral spines almost reaching midlength of second segment; second segment about as broad as, but distinctly shorter than, third. Lateral antennal flagella with rami fused for 2 articles, free part of shorter ramus consisting of 7 articles. Scaphocerite 2.8 times as long as broad, with mesial margin convex, lateral margin straight, latter ending in distal spine overreached by lamella. Mouthparts typical of genus. First pereiopods reaching scaphocerite; palm cylindrical in cross section, widest at midlength; fingers slightly longer than palm; carpus 2.9 times as long as dactyl and merus slightly shorter than carpus. Second pereiopods relatively strong, overreaching scaphocerite by length of chela, fixed finger and dactyl each with 1 tooth on proximal third of cutting edge, and 1 less prominent posteriorly, rest of margin entire, palm cylindrical in cross section, 3.6 times longer than wide, 1.7 times as long as dactyl, 0.8 times length of carpus, slightly shorter than merus and same length as ischium. Third pereiopod overreaching scaphocerite by tip of dactyl; propodus 2.5 times as long as dactyl, 2 times length of carpus, same length of merus, 2 times length of ischium. Fifth pereiopods overreaching scaphocerite by length of dactyl; propodus 3.4 times as long as dactyl, 2 times length of carpus, 1.2 times length of merus, and 2.5 times length of ischium. Pleopods and uropods of usual shape, lateral ramus of uropods with movable spine between fixed distolateral tooth and margin of blade. Appendix masculina with 8 spines on distal ½; 4 apical spines aligned in transverse row, and 4 subapical spines in a single longitudinal row (see Flemming 1969 for terminology).

*Size.*—Male holotype tl. 13 mm; cl. 3.2 mm. Female tl. 15 mm; cl. 4.5 mm.

*Fecundity.*—Ovigerous females with 15–18 bright red spherical eggs, 1.0 mm in diameter.

*Color.*—Translucent in life.

*Remarks.*—This new species is similar to *P. ivonicus* Holthuis. I have compared my specimens with the holotype and paratypic females of the latter at the USNM. The main differences are: the chela of second leg in *P. mercedae* is relatively more robust, the ratio of dactyl : palm being 1:1.6 in *P. mercedae* and 1:1 in *P. ivonicus.* Another distinguishing feature is the shape of posterior margin of telson, which is rounded, with the median apex not overreached by the inner spines in the new species, while in *P. ivonicus* it is truncate and the apex is clearly overreached by the inner spines. There are 8–10 plumose setae on posterior margin of telson in the

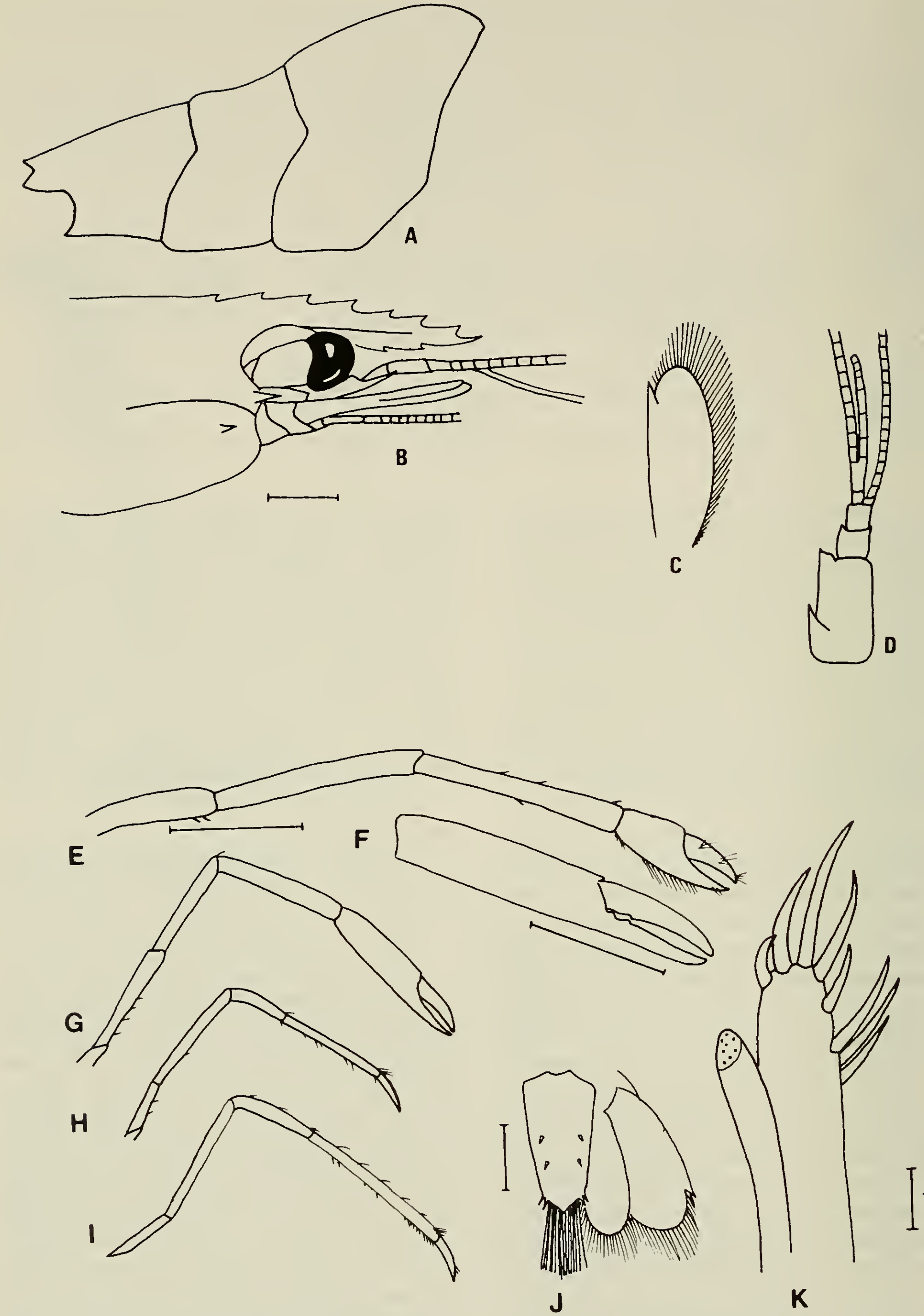

Fig. 13. *Palaemonetes* (*Palaemonetes*) *mercedae,* new species. A, 3–5 abdominal segments; B, Cephalic part of cephalothorax; C, Scaphocerite; D, Antennule; E, First pereiopod; F, Chela of second pereiopod; G, Second pereiopod; H, Third pereiopod; I, Fifth pereiopod; J, Telson and uropods; K, Appendices interna and masculina. All from a paratypic male. Scale = 1 mm.

new species, while there are only two in *P. ivonicus.* The most striking characteristic of this species is the short carpus of the second legs, which is shorter than or equal to that of chela. This character sharply separates the species from the previously known freshwater South American *Palaemonetes.* Strenth (1976) used the morphology of the upper antennular flagellum to separate marine and freshwater species occurring in North America. In this species the distal free portion of the shorter ramus in the lateral antennular flagellum is longer than the fused part, being similar in this feature to the group of South American freshwater species of *Palaemonetes* (*P. argentinus* Nobili, 1901; *P. carteri* Gordon, 1935; *P. ivonicus* Holthuis, 1950).

## Acknowledgments

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# A NEW *COLOSTETHUS* (ANURA: DENDROBATIDAE) FROM ECUADOR

Darrel R. Frost

*Abstract.*—A new species of dendrobatid frog from southeastern Ecuador, *Colostethus nexipus,* is described. This species is distinguished from other members of *Colostethus* by the combination of extensive toe webbing and the presence of distinct dorsolateral and oblique lateral light stripes.

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An undescribed member of the dendrobatid genus *Colostethus* has come to my attention through the generosity of Alice G. C. Grandison of the British Museum (Natural History). The specimens described are from a collection made by the British Los Tayos Archaeological Expedition and presented to the British Museum. Assignment of this species to *Colostethus* is a matter of convenience because dendrobatids that lack the apomorphies of *Atopophrynus, Dendrobates,* or *Phyllobates* are currently referred to the basal grade-genus *Colostethus* (see Lynch 1982, Lynch and Ruíz-Carranza 1982).

### *Colostethus nexipus,* new species
Figs. 1, 2

*Holotype.*—BMNH 1983.1061, adult male obtained at Los Tayos, Morona-Santiago Province, Ecuador, 78°12′W, 3°10′S, 9 Jul 1976 by Philip Ashmole and J. K. Campbell.

*Paratypes.*—All from the vicinity of the type locality: BMNH 1983.923 (small male), in a shallow cave adjacent to the Río Coangos (a tributary of the Río Santiago), 1 Aug 1976 by Philip Ashmole; BMNH 1983.1060 (small male), same data as holotype; KU 194164 (small male) and BMNH 1983.924 (newly transformed) from bottom (50 m) of main cave shaft, on walls, 9 Jul 1976 by Philip Ashmole and J. K. Campbell.

*Diagnosis.*—A dendrobatid frog not exhibiting bright coloration, loss of ears, or fusion of first and second toes; distinguished from all other members of *Colostethus* by the combination of extensive toe webbing and the presence of distinct dorsolateral and oblique lateral light stripes. *Colostethus nexipus* cannot be confused with any other known species.

*Description.*—Head as wide as body, slightly wider than long; snout truncate and rounded in lateral view; nostrils small, slightly protuberant and directed anterolaterally; canthus rostralis rounded but discernible; loreal region concave; lips not flared; snout short; interorbital region flat, slightly narrower than width of upper eyelid; no tubercles on head; weak supratympanic fold; tympanum evident; postrictal tubercles not evident; choanae concealed by palatal shelf of maxillary arch when viewed from directly below; vomerine odontophores absent; numerous teeth on premaxillae and maxillae; tongue longer than wide, posterior notch very broad and shallow; posterior $\frac{3}{5}$ not adherent to floor of mouth; vocal slits present; skin of dorsum finely shagreened, not easily abraded; folds on dorsum absent; skin of venter finely shagreened; vent opening at upper level of thighs; no enlarged warts in vicinity of vent; ulnar fold and tubercles absent; palmar tubercle round, about 4 times larger than thenar tubercle; supernumerary palmar tubercles absent; subarticular tubercles indistinct, round, flat; lateral fringe on fingers present as weak ridge; third finger not swol-

Fig. 1. Paratype of *Colostethus nexipus,* BMNH 1983.923. Snout–vent length equals 21.3 mm.

len; tips of fingers expanded to form pads, approximately 1.5 times width of digit; pair of scutes atop tips of fingers and toes, not differing in coloration from digits; second finger shorter than first (anomalously so on right hand; in paratypes second longer than first); condition of thumbs of breeding males unknown; tubercles absent from knee, heel, or tarsus; tarsal fold weak; inner metatarsal tubercle nearly twice as long as wide, flat, at least twice as large as flat, round outer metatarsal tubercle; supernumerary plantar tubercles absent; subarticular tubercles round to ovoid, flat; toe tips expanded to form pads; toes with prominent lateral fringes confluent with toe webbing; toe webbing formula (after Savage and Heyer 1967) I 0–1 II 0–1.7 III 1–2 IV 2–1 V; webbing incised; when hind legs flexed and held at right angles to sagittal plane, heels touch.

*Coloration in preservative.*—(Holotype is formalin-darkened so coloration has been determined, in part, from paratypes.) Dorsum dark brown with broad dorsolateral stripe extending from eye to vent (stripe broken posteriorly); flanks dark brown with broken, white, oblique lateral stripe extending from point above insertion of forelimb to groin; hind limbs pale brown with dark cross-bars; forelimbs tan with irregular dark blotches; venter pale brown with dark stippling, becoming darker in the gular region, not forming collar or discernible spots.

*Measurements of holotype in mm.*—Snout–vent length 23.9; tibia 11.9; head width 8.2; head length 7.8; distance from

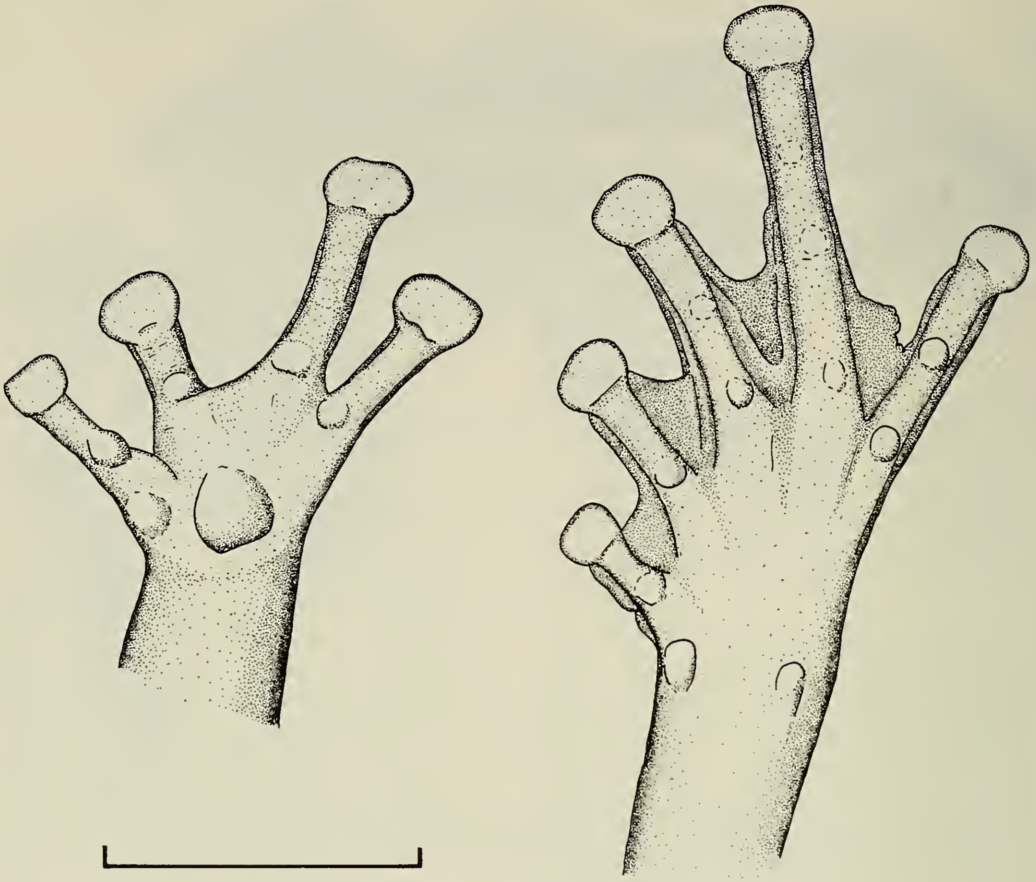

Fig. 2. Palmar views of left hand and left foot of holotype. Bar equals 5 mm.

tip of snout to angle of jaw 8.2; upper eyelid width 2.6; interorbital distance 2.4; eye length 3.5; eye to nostril distance 2.0.

*Etymology.*—The epithet, *nexipus,* is a Latin noun in apposition, derived from the Greek *nexipous,* meaning web-foot.

*Discussion.*—The type locality is in rain forest. The types were collected in the vicinity of a 50 m deep limestone cave shaft that intermittently receives from the Río Coangos a waterfall that carries with it tree trunks and other debris. Although two of the paratypes were collected from within this cave, it is doubtful that *Colostethus nexipus* is normally cave-dwelling. Noncavernicolous species also found in the cave were the gymnophthalmine teiid lizards *Alopoglossus buckleyi* and *Euspondylus guentheri. Colostethus nexipus* is a denizen of stream banks and adjacent wet forest, like many of its congeners. The phylogenetic relationships of *C. nexipus* are unclear because it lacks any of the striking apomorphies (e.g., swollen third finger in males, dark collar, or chest spots) that characterize putative monophyletic groups within *Colostethus.*

## Acknowledgments

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# SYSTEMATICS OF THE GORGETED WOODSTARS (AVES: TROCHILIDAE: *ACESTRURA*)

Gary R. Graves

*Abstract.*—*Acestrura heliodor* (sensu Peters 1945) forms a superspecies composed of two allospecies: *A. astreans* Bangs of the Sierra Nevada de Santa Marta; and *A. heliodor* (Bourcier) of the Andes of Venezuela, Colombia, and northeastern Ecuador. *Acestrura h. meridae* Zimmer and Phelps is synonymized with *A. h. heliodor. Acestrura h. cleavesi* Moore of northeastern Ecuador is a valid subspecies. Wing and tail lengths are positively correlated with latitude in the *heliodor* superspecies. Gorget color in males is subject to postmortem change.

The diminutive woodstars of the genus *Acestrura* of the Andean region in western South America are poorly known, underrepresented in museum collections, and are frequently misidentified. *Acestrura berlepschi, A. bombus,* and *A. mulsant* are currently considered to be monotypic. A fourth species, *A. heliodor,* exhibits considerable geographic variation that is recognized at the subspecific level (Peters 1945, Zimmer 1953): *A. astreans* of the Sierra Nevada de Santa Marta, Colombia; *A. h. heliodor* of the Eastern, Central and Western Cordilleras of the Colombian Andes; *A. h. meridae* of the Venezuelan Andes; and *A. h. cleavesi* of northeastern Ecuador.

The purpose of this paper is to re-evaluate the taxonomy of woodstars in the *A. heliodor* complex, incorporating data from previously unreported series of specimens collected from 1946–1952 in Colombia by M. A. Carriker, Jr. and deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Differences among populations in plumage color in both sexes and tail configuration in males suggest that the *Acestrura heliodor* (Fig. 1) is actually composed of two allospecies: *A. astreans* (Santa Marta Woodstar) of the Sierra Nevada de Santa Marta, and *A. heliodor* (Gorgeted Woodstar) (*A. h. heliodor* and *A. h. cleavesi*) of the main Andes.

## *Acestrura heliodor heliodor* (Bourcier)

*Ornismya heliodor* Bourcier, 1840:275. "Bogota."

*Acestrura heliodor meridae* Zimmer and Phelps, 1950:1. Paramo Conejos (4000 m), Mérida, Venezuela.

*Characters.*—Male: Upperparts and flanks are green and the gorget purple. The formula of rectrix length in closed tail is: 3 > 4 > 5 > 2 > 1 (retrices numbered from the inside outward). The width of rectrix 4 is greater than ½ the width of rectrix 3 and nearly intermediate in width between rectrices 3 and 5 (Fig. 2). Females: The chin, throat, breast, and flanks are rich buffy cinnamon. In adult females, the tail is rufous with a broad black band across the center. A trace of green occurs just proximal to the band on the central rectrices. The lower rump and upper tail coverts are rufous; a few feathers have a green central spot.

*Distribution.*—Scattered localities in the Andes of Venezuela, and the Eastern, Central, and Western Cordilleras of the Colombian Andes (Fig. 1). The reported occurrence of *A. heliodor* at Cana, Cerro Pirre, Panama (Wetmore 1968, Ridgely 1976) is based on a misidentified specimen of *Calliphlox mitchelli* (Robbins et al. 1985).

*Specimens examined.*—VENEZUELA: Pinos (USNM 1 ♂); "Merida" (USNM 1 ♂,

Fig. 1. Distribution of the *Acestrura heliodor* superspecies based on specimens examined in this study. Some symbols represent two closely spaced localities. Squares = *Acestrura astreans*; circles = *A. h. heliodor*; diamonds = *A. h. cleavesi.* Hatching indicates areas above 1000 feet elevation.

Fig. 2. Tail patterns of *Acestrura h. heliodor, A. h. cleavesi* and *A. astreans.* Males on the left, females on the right. Color of rectrices: stippling = green; unmarked = rufous or rich buff; shaded = black. 1.8× natural size.

2 ♀♀; AMNH 19 ♂♂, 9 ♀♀).—Conejos (USNM 1 ♀; AMNH 1 ♂ type "*meridae,*" 1 ♀).—Tambor (USNM 1 ♂, 4 ♀♀; AMNH 9 ♂♂, 2 ♀♀).—Escorial (AMNH 4 ♂♂).—Tierra (USNM 1 ♂). COLOMBIA: (unspecified localities) "Bogotá" (USNM 4 ♂♂, 2 ♀♀; AMNH 24 ♂♂ including type of *A. h. heliodor,* 9 ♀♀).—"Lower Magdalena" (USNM 1 ♂, 1 ♀).—"Colombia" (MLOC 3 ♂♂; USNM 4 ♂♂, 2 ♀♀; AMNH 2 ♂♂).—"Santiago" near Pasto? (FMNH 1 ♀).—"New Grenada" (USNM 1 ♂, 1 ♀; AMNH 2 ♂♂, 2 ♀♀). Norte de Santander: Buenos Aires (USNM 7 ♂♂, 3 ♀♀).—Ocaña (USNM 1 ♂).—Ramírez (CM 3 ♂♂, 1 ♀; ANSP 1 ♀).—Cachirí (CM 1 ♀).—Las Ventanas (CM 2 ♀♀). Caldas: Laguneta (ANSP 1 ♂, 3 ♀♀). Huila: San Agustín (USNM 4 ♂♂, 2 ♀♀; AMNH 1 ♂; ANSP 3 ♂♂, 2 ♀♀).—Belén (USNM 1 ♂). Cauca: El Tambo (FMNH 1 ♂; WFVZ 1 ♂).—Tijeras (FMNH 1 ♂).—Moscopán (USNM 1 ♀).

### *Acestrura heliodor cleavesi* (Moore)

*Chaetocercus cleavesi* Moore, 1934:1. Cuyuja, Ecuador.

*Characters.*—Male: The formula for the length of rectrices in *A. h. cleavesi* is: 3 > 4 > 2 > 5 > 1, instead of: 3 > 4 > 5 > 2 > 1, as in *A. h. heliodor* and *A. astreans.* Rectrices 4 and 5 are similar in width, and much narrower than rectrix 3. Female: Similar to *A. h. heliodor* but more richly colored on chin and throat and with rump more extensively rufous.

*Distribution.*—Known only from the Amazonian slope of the Andes in northeastern Ecuador.

*Specimens examined.*—ECUADOR: Baeza (MLOC 3 ♂♂, 6 ♀♀; USNM 1 ♂, 1 ♀; AMNH 1 ♂).—Cuyuja (MLOC 1 ♂, 1 ♀).—Pallatanga (MLOC 1 ♀).—Río Hollín (MLOC 1 ♀).—Río Oyacachi Abajo (AMNH 1 ♂, 3 ♀♀).—Río Tigre (MLOC 1 ♂, 3 ♀♀).—Tumbaco (MLOC 1 ♀).

### *Acestrura astreans* Bangs

*Acestrura astreans* Bangs, 1899:76. San Sebastian (6600 feet), Sierra Nevada de Santa Marta, Colombia.

*Characters.*—Male: In adults, the back, rump, upper tail coverts, and flanks are metallic bluish-green, instead of green as in *A. h. heliodor* and *A. h. cleavesi.* The gorget is red or reddish-purple, depending on the angle of reflection, not purple as in *A. h. heliodor.* The formula of rectrix length is the same as in *heliodor.* Rectrices 4 and 5 are very narrow, less than ½ the width of rectrix 3. Female: Adult females differ from those of *A. heliodor* in having the upper tail coverts green instead of rufous. The central rectrices of *A. astreans* are green, instead of rufous with a black band like the other rectrices, as in *A. heliodor* (Fig. 2). The venter of *A. astreans* is lighter, not as richly colored as in *A. heliodor.*

*Distribution.*—Restricted to the Sierra Nevada de Santa Marta. Specimens have been taken on the western, eastern, and southern slopes at elevations between 2700 and 6600 feet (ca. 825–2010 m).

*Specimens examined.*—Sierra Nevada de Santa Marta: San Sebastian (USNM 2 ♀♀).—Chinchicuá (USNM 4 ♀♀).—Vista Nieve (USNM 1 ♂, 2 ♀♀).—Cincinati (ANSP 1 ♂, 1 ♀).—El Mamon (AMNH 1 ♂).—No further locality data (USNM 2 ♂♂; AMNH 1 unsexed).

## Variation in Male Gorget Color

Gorget color in the *Acestrura heliodor* superspecies exhibits significant geographic variation. In contemporaneously collected specimens from the main Andes, gorget color varies clinally from pinkish-purple in northeastern Ecuador to purple in the Eastern Cordillera of Colombia and the Venezuelan Andes; specimens from the Western and Central Cordilleras are intermediate. The Santa Marta population is characterized by a dark red gorget.

Zimmer and Phelps (1950) separated the Venezuelan (*A. h. meridae*) populations from those of Colombia on the basis of "a darker, more purplish, less reddish throat" in males. Unfortunately, assessment of this character is hampered by previously unrecognized postmortem change in gorget color. They compared their Venezuelan series, collected mostly between 1903 and 1921, with a large series of pre-1900 "Bogotá" specimens, most of which were probably obtained from the Eastern Cordillera. These have consistently pinker, less purplish gorgets than more recently collected specimens from the Eastern Cordillera. For example, specimens from Buenos Aires, Norte de Santander, taken in 1946, have slightly more purplish, less pinkish gorgets than specimens collected in 1916 at Ramirez, Norte de Santander. In turn, the "1916" specimens have gorgets that are more purplish, less pinkish, than those of pre-1900 "Bogota" specimens. Specimens collected at approximately the same time in the Eastern Cordillera and the Venezuelan Andes are indistinguishable in gorget coloration. *Acestrura h. meridae* Zimmer and Phelps, 1950, should thus be considered a synonym of *A. h. heliodor* Boucier, 1840. In another apparent example of postmortem change from shorter to longer wave lengths, the gorgets of specimens (USNM 333521; MLOC 7015, 7016, 7023, 10367, 10377) included in the type series of *A. h. cleavesi*) are presently matched closely by Rose Color (capitalized names from Ridgway 1912), instead of Rhodamine Purple (Moore 1934).

The magnitude of postmortem change observed in specimens collected from a single locality equals that of the contemporaneous geographic variation found among the Colombian populations of *A. h. heliodor.* The gorgets of birds from the Central (Belén, Tijeras, Laguneta) and Western Cordilleras (El Tambo) are pinker, less purplish than those of contemporaneously collected (1942–1957) specimens from the Eastern Cordillera, but match those of older specimens from the same region.

These observations suggest that there are some discrete differences among *heliodor* populations. The lack of contemporaneously collected series from key populations, however, prevents the subspecific partition of *A. heliodor* on the basis of gorget color alone.

## Size and Shape Variation

Wing length is positively correlated with latitude in males (Fig. 3; $n = 31$, $r^2 = 0.586$, $P < 0.0001$) and females ($n = 39$, $r^2 =$

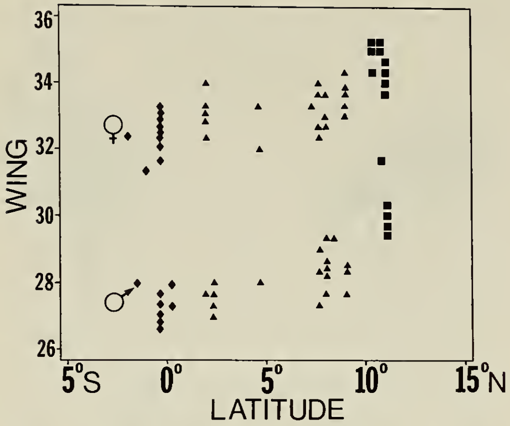

Fig. 3. Relationship of wing length with latitude in the *Acestrura heliodor* superspecies. Squares = *A. astreans*; triangles = *A. h. heliodor*; diamonds = *A. h. cleavesi.*

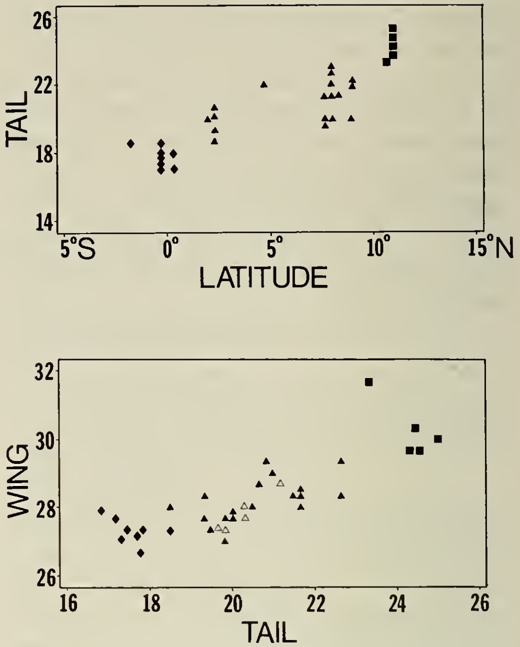

Fig. 4. Relationships of tail length with latitude and wing length in males of the *Acestrura heliodor* superspecies. Squares = *A. astreans*; solid triangles = *A. h. heliodor*; empty triangles = pre-1900 "Bogota" specimen identified as *A. h. heliodor* on basis of plumage but lacking definite locality data; diamonds = *A. h. cleavesi.*

0.522, $P < 0.0001$). Tail length in males, an important taxonomic character (Moore 1934), is also positively correlated with latitude (Fig. 4; $r^2 = 0.761$, $P < 0.0001$) and wing length ($r^2 = 0.658$, $P < 0.0001$). These correlations conform to Bergmann's Rule (cf. Handford 1983, Remsen 1984) and suggest that tail length is more closely linked with allometry and aerodynamic function, than to sexual display. Culmen length is uncorrelated with either latitude or wing length ($P > 0.05$) in either sex. Tail and wing length in males of *A. astreans* and *A. heliodor* do not overlap. I performed a Principal Components Analysis of culmen, wing, and tail lengths of males. Not surprisingly, all three taxa (*A. astreans, A. h. heliodor, A. h. cleavesi*) had nonoverlapping distributions along the axis of the first principal component (which explained 60.8% of the variance).

These taxa are also readily identified by the proportional width of the outermost rectrices (numbers 3–5) in males. The proportional width of rectrices is not clinal. Populations of *A. h. heliodor* from the Western, Central, and Eastern Cordilleras of Colombia and the Venezuelan Andes are not distinguishable from one another on the basis of tail shape, but are easily distinguished from *A. h. cleavesi* and *A. astreans.* As expected, "Bogotá" specimens have wing/tail ratios similar to specimens from known localities in the Eastern Cordillera (Fig. 4).

## Taxonomic Conclusions

*Acestrura astreans* differs from *A. heliodor* in several important characteristics that are not the terminal states of observed clinal variation, and that support the recognition of *A. astreans* as a full species. The most important of these are: (1) the distinctive shape of the rectrices in the males; (2) the coloration of body plumage in both sexes; (3) pattern and color of the central rectrices of females; (4) the gorget color in males. Because of their allopatric distributions, the existence of reproductive isolating mechanisms between *astreans* and *heliodor* can only be surmised. However, the morphological differences between these taxa are of the same scale as those observed among the other species of *Acestrura* and *Chaetocercus jourdanii.* The high degree of endemism in the Santa Martas has long been recognized (Chapman 1917, Todd and Carriker 1922). At least 12 other avian taxa endemic to the Santa Marta massif, with affinities in the northern Andes, are recognized as specifically distinct from their most closely related congeners (*Pyrrhura viridicata, Campylopterus phainopeplus, Coeligena phalerata, Ramphomicron dorsale, Synallaxis fuscorufa, Cranioleuca hellmayri, Grallaria bangsi, Myiotheretes pernix, Myioborus flavivertex, Basileuterus basilicus, Anisognathus melanogenys, Atlapetes melanocephalus*).

The systematic status of *Acestrura h. cleavesi* is uncertain. Except for rectrix shape in males, plumage differences between *A. h. cleavesi* and *A. h. heliodor* appear to be primarily quantitative and clinal. The report of *A. h. heliodor* in Ecuador (Moore 1934) is based on three specimens with definite locality data: Two adult females (MLOC 3083, Pallatanga, 1°59′S; MLOC 3084, Tumbaco, 0°13′S); and an immature male (MLOC 3086, Pallatanga). Both localities are on the Pacific slope of the Andes. Because the plumage of the immature male of *A. h. cleavesi* is unknown, the male specimen cannot be identified to subspecies. The females resemble the more heavily pigmented individuals of the nominate race from Colombia but also match the palest examples of *A. h. cleavesi* from Baeza, near the type locality. Adult male specimens will be needed to determine the racial affinity of the Pacific slope population in Ecuador. On geographical grounds alone, I tentatively consider these specimens as *A. h. cleavesi.*

A female (FMNH 45429, received from the "Museum Boucard") was collected by Delattre before 1850 at "Santiago, Colombia." If correctly located (de Schauensee 1949, Paynter and Traylor 1981), Santiago (1°08′N) is ESE of Pasto, midway between populations of *A. h. cleavesi* at Cuyuja (0°24′N) on the Amazonian slope of the Ecuadorian Andes and those of *A. h. heliodor* at San Agustín (1°53′N) in the Upper Magdalena Valley. Apparently, no specimens of *Acestrura heliodor* have been collected between Cuyuja and San Agustín during the past century. The Santiago specimen is indistinguishable from typical females of *A. h. heliodor,* and differs from all specimens of *A. h. cleavesi* in the intensity and distribution of rufous and cinnamon buff on the underparts and rump.

Appropriate habitat is available in the distributional hiatus, and the two taxa almost certainly intergrade or come into contact somewhere between Santiago and Cuyuja. I recommend that *cleavesi* should best be regarded as a subspecies, rather than a full species, until specimens from the appropriate regions are obtained.

## Acknowledgments

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# *TONOCOTE,* A NEW GENUS AND SPECIES OF ZOBRACHOIDAE FROM ARGENTINA (CRUSTACEA: MARINE AMPHIPODA)

Janice Clark and J. L. Barnard

*Abstract.*—A new genus and new species of marine zobrachoid amphipod, *Tonocote magellani,* is described from the Magellan Strait. It is a fossorial amphipod digging in shallow sands like a sand-crab. It differs from *Prantinus,* an Australian genus, in the broad article 4 of antenna 2, the much reduced epimeron 2 and the absence of posterior spines on article 5 of pereopods 3–4. Like *Prantinus* it differs from other zobrachoids in the urothoe-like antenna 1 with article 3 elongate.

The new genus *Tonocote* and its new species *T. magellani* are described from Argentina. Owing to the presence of small epimeron 2 the inclusion of *Tonocote* in the Zobrachoidae requires emendation of the diagnosis in that family.

Within the Zobrachoidae *Tonocote* resembles *Prantinus,* from Australia, in the urothoe-like antenna 1 with article 3 elongate. These two genera therefore comprise a subgroup differing from the other two genera of the family having a normal haustoriid antenna 1 with article 3 short. Owing to the early stages of investigation into these antipodeal groups, there may be future cause to divide these groups at subfamily level or higher.

References used in the identification process are: Barnard and Drummond (1978, 1982), Barnard and Clark (1982a, b, 1984). Methods of morphological description follow Barnard and Drummond (1978).

## Master Legend

Uppercase 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 below:

A, antenna; B, body; C, coxa; D, dactyl; E, eye (? or brain), subdivisions marked as E1, E2, E3, E4 (latter = ganglion); G, gnathopod; H, head; I, inner plate or ramus; J, pleopodal coupling hooks; L, labium; M, mandible; N, epimera; O, outer plate or ramus; P, pereopod; R, uropod; S, maxilliped; T, telson; U, labrum; W, pleon; X, maxilla; Y, pleopod; Z, gill; d, dorsal; r, right; s, setae removed; t, left.

## Zobrachoidae Barnard and Drummond, 1982

*Diagnosis* (emendations in italics).—Rostrum well developed (for haustoriids), 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, these articles 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) bulbar-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, weakly 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 discrete 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 oblique facial row of setae but poorly developed. Maxillipeds with unexpanded bases, normally enlarged plates, outer spinose; palp 4-articulate, article 2 expanded, article 4 clavate, 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, wrists 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 5–6 weakly expanded; no pereopod with underslung articulation.

Pleopod 2 usually inferior in size, number of articles, or setation; peduncles of pleopods 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*); palp article 3 outer setae 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 (*Tonocote*).

*Type genus.*—*Zobracho* J. L. Barnard, 1961.

*Composition.*—*Bumeralius, Prantinus, Tonocote.*

*Relationship.*—Until our new genus came to light zobrachoids differed from urothoids in the absence of a ventral cephalic cheek, in the full development of the haustorius antenna 2, especially in the ventral armament, and in the dominance of setation (or actual size) on epimeron 2. This epimeron in *Tonocote* is much smaller than epimeron 3 and barely has dominant setation (2 setae versus 1 on epimeron 3). Zobrachoids bear linguiform rami of uropods 1–2, in contrast to urothoids (but 1 genus of urothoid lacks rami). *Prantinus* is furnished with a urothoid antenna 1, and has epimeron 2 dominant, but antenna 2, though not fully expanded, lacks seriate ranks of spines, and bears the ventral spination diversity not typical of urothoids. There is not a great deal of difference between Urohaustoriidae and Zobrachoidae except that zobrachoids have gnathopod 1 subchelate, epimeron 1 is clearly defined, the mandibular molar is less strongly triturative, weaker and furnished more with side cusps, mandibular rakers are better developed, article 2 on the outer ramus of uropod 3 is usually better developed, coxae 1–2 are both small and contrasted with a very large coxa 3, and the rostrum is larger. However, *Prantinus* of the Zobrachoidae intergrades some of these differences. In addition our new genus *Tonocote* differs from urohaustoriids in the less expanded article 2 of the maxillipedal palp, the dactyl lacking inner setae.

### 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, posterior spines on article 5 of pereopods 3–4 absent (distals present) ........ ................ *Tonocote,* new genus
– Antenna 2 article 4 slender, epimeron 2 as large as 3, posterior spines present on article 5 of pereopods 3–4 ................ *Prantinus* Barnard and 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 and Drummond, 1982

### *Tonocote,* new genus

*Diagnosis.*—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 haustorius form, article 4 expanded, article 5 small, articles 4–5 with facial armaments, 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. Mandibular lobes of lower lip well developed. Inner plate of maxilla 1 of medium size, sparsely setose, outer plate with 8 spines, palp short. Inner plate of maxilla 2 with weakly submarginal row of setae. Inner plate of maxilliped ordinary; outer plate with spines; palp article 2 expanded, article 3 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, wrists elongate, hand somewhat smaller, mitelliform, subchelate, but palm more transverse on gnathopod 2 than on gnathopod 1. Dactyls of pereopods 3–7 distinguishable, those of pereopods 3–5 large, those of pereopods 6–7 very small; dactyl of pereopod 5 bladelike, lacking spines. Article 2 of pereopods 5–7 expanded less strongly on pereopod 6 than on 5 and 7; pereopod 5 of haustorius form; distal articles of pereopods 6–7 not underslung, 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 styliform, each outer ramus bearing 2 apical plumose setae, each inner ramus bearing 1 apical plumose seta; peduncles weakly setose. Uropod 3 outer ramus biarticulate and dominant, inner ramus with one basomedial seta. Telson short, broader than long.

*Description.*—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.

No right lacinia mobilis; 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 (right side missing 2).

Coxae 1–3 poorly setose, coxae 4 moderately setose. Gills forming stepped intergrades with gill 2 dominant. Gnathopod 2 lacking surficial buttons.

Pereopods 3–4 lacking extensive secondary facial rows of spines and ventral spines on article 5.

Uropods with sparse dorsal setae, medial margins of peduncles sparsely setose.

*Type species.*—*Tonocote magellani,* new species.

*Etymology.*—Named for a group of Indians in South America; masculine.

*Composition.*—Unique.

### *Tonocote magellani,* new species
Figs. 1–6

*Diagnosis.*—With the characters of the genus.

*Description of male.*—Holotype male "a," 2.87 mm; head about 90 percent as long as wide, rostrum about 31 percent as long as remainder of head, eyes represented by granular tissue patches, no distinct ommatidia, ocular ganglia visible. Facial formula of setae on article 1 of antenna 1, ventral = 4 penicillate, dorsal = 2 setae + 1 medium, 1 tiny penicillate, (noting that dorsal–ventral aspect reversed from normal, non-urothoid kind of antenna 1); article 2 with partial circle of 8 long plumose setae; primary flagellum with 4 articles, aesthetasc formula = 1-1-1-0; accessory flagellum of 4 articles. Article 3 of antenna 2 with 2 medium setae; facial formula of spines on article 4 = 2-2-1-2; article 5 = 1 seta dorsally and 2 setae, 1 tiny penicillate; flagellum of 4 articles.

Upper lip with granulations. Right and left mandibular incisors with 3 and 5 teeth; 6 right rakers (no lacinia mobiles), 5 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 slightly longer than article 2, latter with 1 inner seta, spine formula on right and left article 3 = 4-1-2. Inner plate of maxilla 1 bearing 2 apical setae and pair of mediofacial setae; outer plate with 8 spines; palp with 3 apical setae.

Inner plate of maxilliped with 3 stout spines, 2 medial and 2–4 apical setae; medial margin of outer plate with ragged mixture of spines and scattered small setae; apex with 1 seta; article 2 of palp with row of 5 mediofacial setae; article 3 with one subfacial seta and large serrate spine at base of dactyl.

Coxa 1 subrectangular, convex anteriorly, bearing 1 seta on ventral margin and posteroventral long plume and setule; coxa 2 similar in shape to coxa 1 but anterior convexity greater, with 2 long plumes and 2 setules; coxa 3 similar to coxa 2 but more elongate, with 3 plumose posteroventral setae and 1 seta more anterior; coxa 4 adze-shaped with 7 long plumose setae along ventral and posterior margins, 1 short anteroventral seta.

Setal and spine formulas on pereopod 3 = 2,2, 2-0, 2+1+1; on pereopod 4 = 2,2, 2-0, 2+1+1; margins of articles 5–6 not serrate. Article 2 of pereopods 5–7 armed sparsely with long setae posteriorly; dactyl of pereopod 5 with small anterior tooth.

Peduncular spine formulas of pleopods 1–3 = 2 and 0,2 and 0,2 and 0; segmental formulas = 8-5, 7-4, 8-6; basal setal formulas = 7-0-1-1, 4-1-1-1, 6-1-1-2, one peduncular seta each on pleopods 1 and 3 (2 naked).

Epimeron 1 rounded quadrate, with 1 tiny setule posteroventrally; epimeron 2 extended posteroventrally, posterior margin "crimped," 1 marginal posteroventral seta

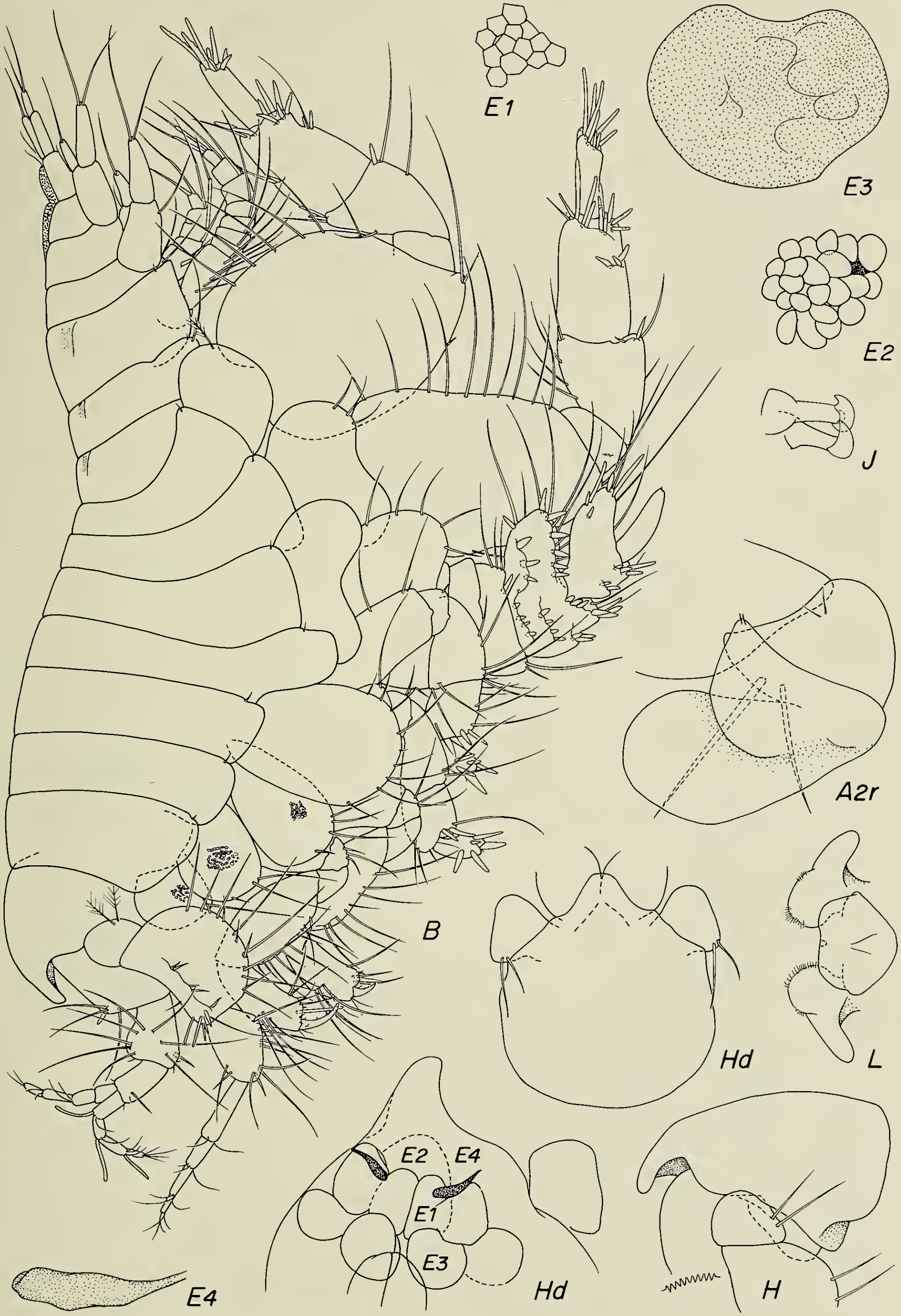

Fig. 1. *Tonocote magellani,* holotype male "a" 2.87 mm.

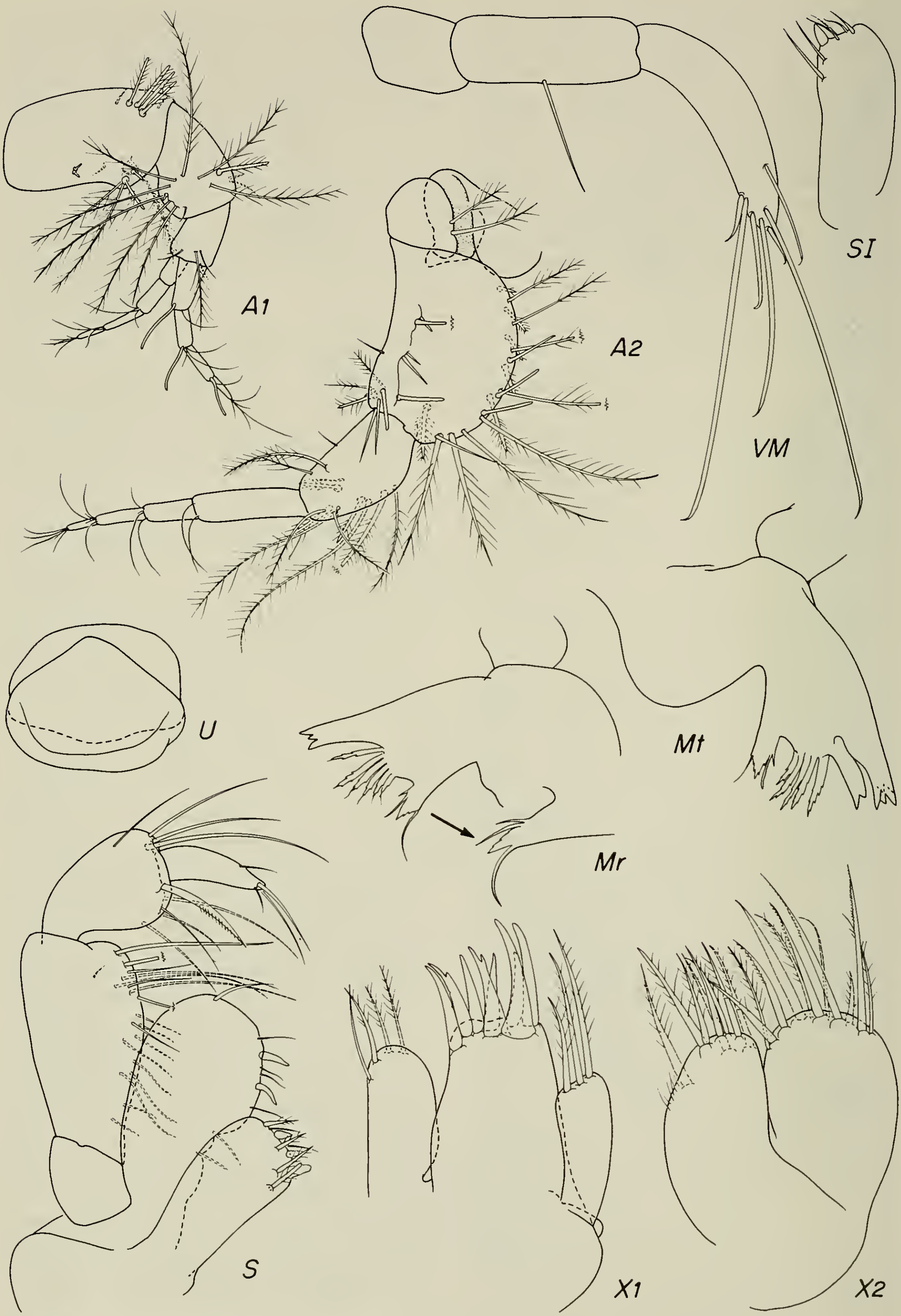

Fig. 2. *Tonocote magellani*, holotype male "a" 2.87 mm.

Fig. 3. *Tonocote magellani*, holotype male "a" 2.87 mm.

and 1 tiny facial seta near corner; epimeron 3 subsharply produced posteroventrally with 1 setule on posterior margin.

Apicomedial corners of peduncles on uropods 1–3 with 1 plumose seta; apicolateral corner on peduncle of uropod 1 with 1 plumose seta; uropod 3 peduncle medial margin with 1 small seta; inner rami of uropods 1–2 extending 50 percent along outer; setae of rami on uropods 1–3 = 1 plumose seta on medial margin of inner ramus, each outer ramus with 2 apical setae.

Telson about 1.5 times as wide as long, weakly alate laterally, cleft about 75 percent of its length, each apex with one long plume, each side with 2 small penicillate setules.

Glands discernible in coxae 1–3, peduncles of uropods 1–3, and telson.

Male "b," 2.78 mm: right mandible with 5 rakers, left with 4; epimeron 2 with an additional long facial seta at posteroventral corner; uropod 2 peduncle with 1 lateral seta; segmental formulas of pleopods 1–3 = 7-4, 7-4, 7-5, basal setal formulas = 8-1-2-1, 5-1-1-1, 3-1-9-1.

*Relationship.*—*Tonocote* resembles *Prantinus* in the following: shapes and setosity of coxae 1–4; similar molars; maxilliped inner plate shape and spination, outer plate shape, dactyl and palp 3 shape; and pleopods.

*Tonocote* differs from *Prantinus* in having: less reduced coxa 5; stouter antenna 1; larger article 4 of antenna 2; maxilla 1 inner plate more slender, outer plate with 8 spines (versus 11); maxilla 2 inner plate with many fewer medial setae; maxilliped outer plate spines fewer; gnathopods 1–2 lacking short penicillate spines on article 6, with posterior brushes on articles 2 and 3, more poorly developed on right; pereopods 3–4 lacking posterior spines on article 5, with sparser anterior setation on articles 4–5; pereopods 6–7 article 5 poorly spinose laterally; uropods 1–2 inner ramus short, peduncle poorly setose, outer ramus with 2 apical setae (versus 1); uropod 3 poorly setose; telson broader; epimeron 2 poorly developed in size and setation.

*Tonocote* differs from *Bumeralius* in the following: urothoid form of antenna 1; no bifid setae on antenna 2 article 4; weak to absent right lacinia mobilis; non-triturative molar with marginal cusps; maxilla 1 outer plate with eight spines (versus 11), inner plate lacking basomedial setae; maxilla 2 inner plate with only one seta in facial row (versus many); maxilliped inner plate truncated, with thick blunt spines, few setae, outer plate poorly armed medially, armaments stout, dactyl with apical setae only; coxae 1–7 sparsely setose, coxa 2 lacking large posteroventral lobe, coxa 7 lacking angles (versus angular); pereopods 6–7 poorly spinose on faces of articles 5 and 6, pereopods 3–4 lacking marginal posterior spines on article 5, pereopod 3 article 5 poorly setose anteriorly; gnathopods 1–2 poorly setose, palm well serrate, dactyl heavily armed; inner rami of pleopods slightly shorter than in *Bumeralius*; uropods 1–2 outer rami lacking basomedial setae, peduncles very poorly setose, uropod 2 outer ramus lacking lateral setae, uropod 3 and telson poorly setose in adult; mandibular palp not as clavate and spinose.

*Tonocote* differs from other zobrachoids in having epimeron 3 dominant in size (versus epimeron 2) although the original difference cited by Barnard and Drummond (1983) refers only to dominance in setation. *Tonocote* barely dominates in setation as epimeron 2 has only one to two long and one short setae compared to one short seta on epimeron 3. Other items of "variables" show *Tonocote* to be aberrant in the absence of right lacinia mobilis and lacking posterior spines on article 4 of pereopods 3–4 (but apical [?] spines remain). There is not a great deal of difference between Zobrachoidae and Urohaustoriidae except the latter have gnathopod 1 simple, loss of integrity in epimeron 1, large differential in size of epimeron 2 (tiny) and epimeron 3 (large and extended posteroventrally), small number of setae on palp article 1 of maxilla 1, reduction in extension and presence of cusps of mandibular molar and usually a reduc-

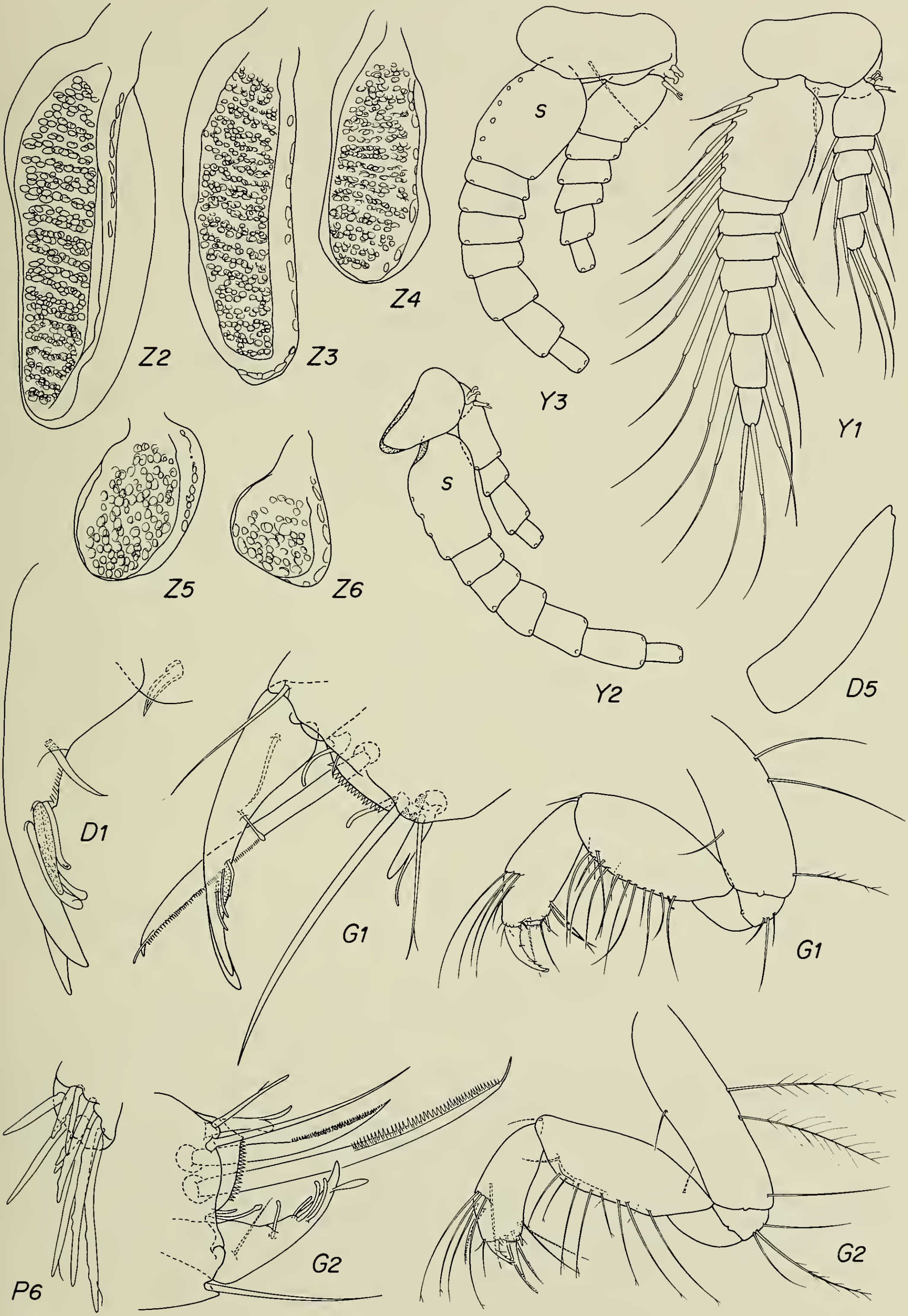

Fig. 4. *Tonocote magellani,* holotype male "a" 2.87 mm.

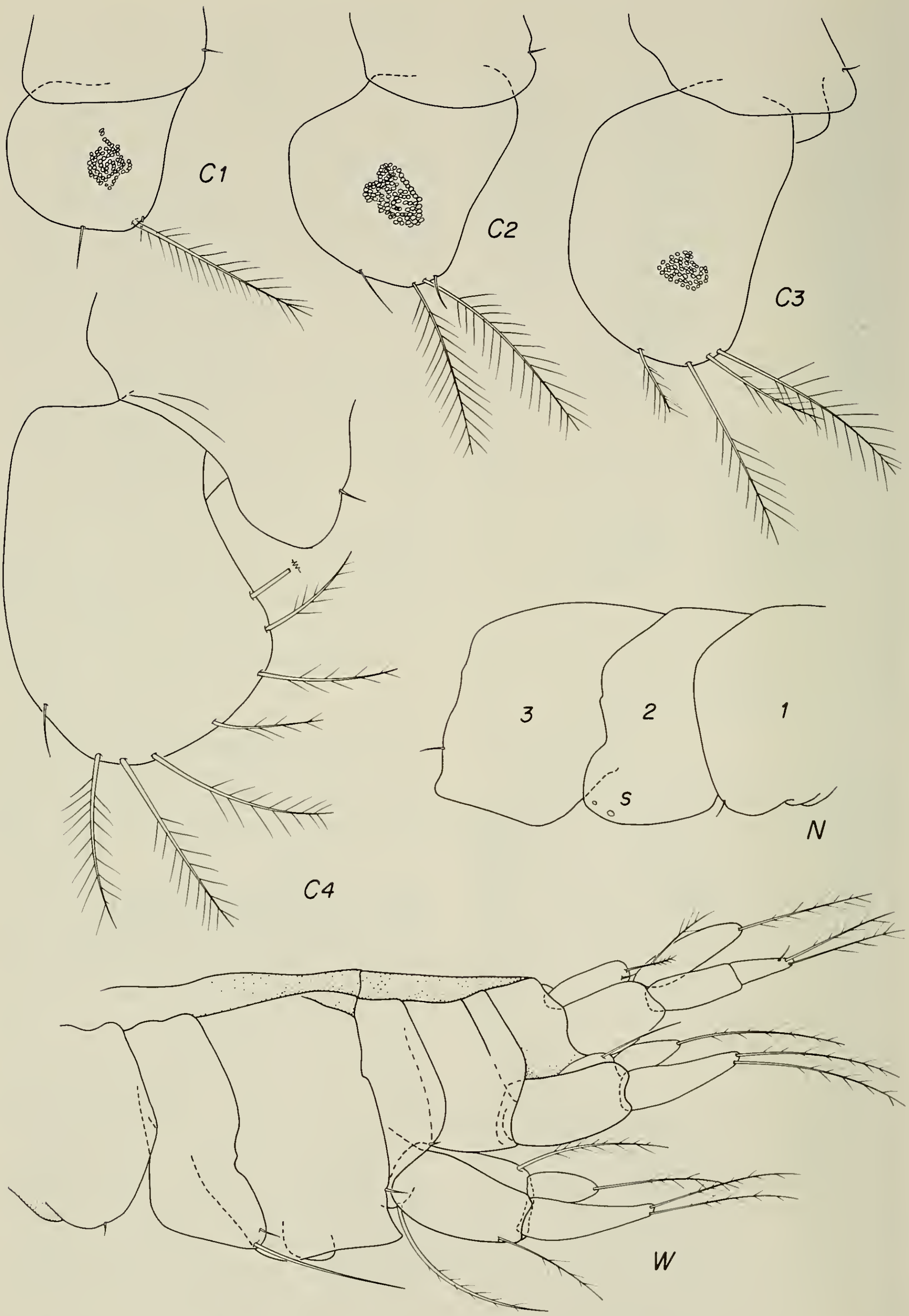

Fig. 5. *Tonocote magellani,* holotype male "a" 2.87 mm.

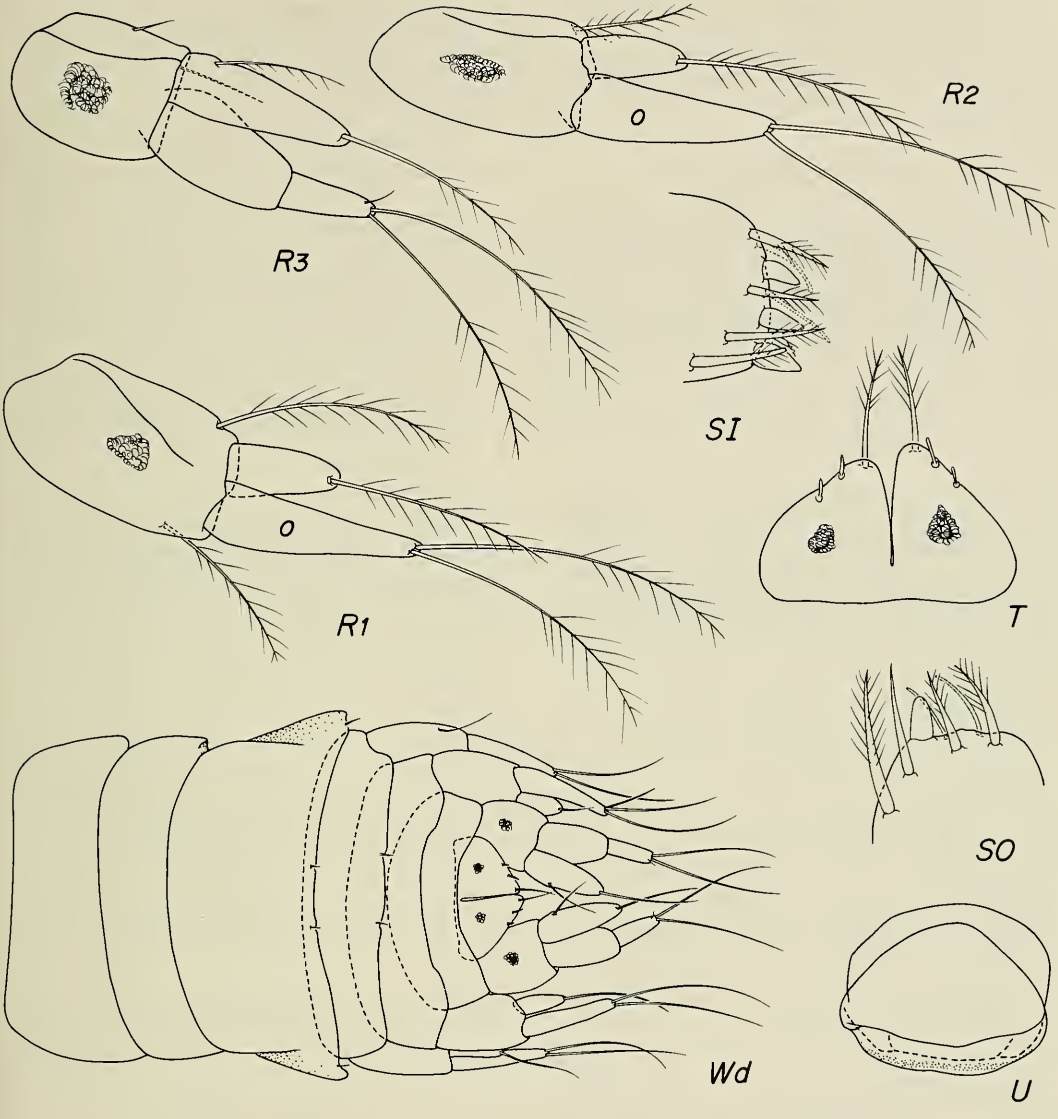

Fig. 6. *Tonocote magellani,* holotype male "a" 2.87 mm.

tion in article 2 of uropod 3 outer ramus and weaker rostrum. *Prantinus* of Zobrachoidae intergrades in the condition of epimeron 1 and the outer ramus of uropod 3. *Tonocote* has antenna 2 article 4 expanded; pereopods 3–4 lacking posterior spines (only terminal spines on article 5); and epimeron 2 much smaller than epimeron 3.

*Illustrations.*—Palp of mandible probably more clavate than shown owing to preservational defects.

*Holotype.*—USNM No. 195148, male "a," 2.87 mm (illustrated).

*Type locality.*—Eastern Straits of Magellan, 52°29.9′S, 69°05.9′W, 11–12 m, 9 Apr 1976, coll. Dr. Victor A. Gallardo.

*Voucher material.*—Type locality: male "b," 2.78 mm.

*Etymology.*—Named for the type locality.

*Distribution.*—Straits of Magellan, 11–12 m.

## Acknowledgments

We thank Dr. Victor A. Gallardo of Universidad de Concepción, Chile, for making this material available; Linda B. Lutz of Mobile, Alabama for inking our drawings; and Patricia B. Crowe for laboratory assistance.

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# *PARALEBBEUS ZOTHECULATUS,* N. GEN., N. SP., A NEW HIPPOLYTID SHRIMP FROM THE AUSTRALIAN NORTHWEST SHELF

A. J. Bruce and F. A. Chace, Jr.

*Abstract.*—A new species of hippolytid shrimp found in association with hexactinellid sponges on the Australian Northwest Shelf at depths of 450–500 m is described, and a new genus designated for its accommodation. *Paralebbeus zotheculatus,* n. gen., n. sp., represents the first record of an association between a caridean shrimp and a hexactinellid sponge. *Paralebbeus* is most closely related to *Lebbeus* White, 1847, and is distinguished by the reduced, unarmed rostrum, and absence of lateral spines on the meri of the ambulatory pereiopods.

A survey of the Australian Northwest Shelf area, off Port Hedland, Western Australia, carried out by the F.R.V. *Soela* of the Fisheries Laboratory, Commonwealth Scientific and Industrial Research Organizations, has produced, from this little-studied region, numerous examples of crustacean taxa that are new to science or new to the Australian fauna. Among the caridean material collected were several examples of a commensal hippolytid shrimp. This could be referred to none of the described genera, and a new genus is proposed for its accommodation.

CL. refers to the postorbital carapace length. NTM refers to the Northern Territory Museum, Darwin, Australia.

## *Paralebbeus,* new genus

*Diagnosis.*—Carapace smooth; rostrum feebly developed, acute, edentate; supraorbital, antennal, and pterygostomial spines present, branchiostegal and hepatic spines absent. Abdomen smooth, segments dorsally rounded, sixth with posteroventral angle without moveable plate; first 3 pleura rounded, fourth convexly produced, fifth acutely produced; telson with 4–6 pairs of dorsal spines, about 6 pairs of posterior spines. Eyes pigmented. Antennule without statocyst, stylocerite large, peduncle without mobile distal plate; upper flagellum uniramous. Mandible with 2-segmented palp, molar and incisor processes present. First and second maxillipeds with exopods; epipod of second maxilliped with podobranch; third maxilliped without exopod, with epipod. All pereiopods without arthrobranchs; first and second pereiopods chelate, first pair with robust, similar, subequal chelae, second with chela small, carpus 7-segmented; ambulatory legs with dactyl biunguiculate, merus unarmed, first 3 pereiopods with epipod, all 5 pairs with mastigobranchs. Uropods normal.

*Type species.*—*Paralebbeus zotheculatus,* n. sp.

*Etymology.*—From *para* (Greek) beside, and *Lebbeus,* a hippolytid generic name cited by White, 1847, from a manuscript by Leach. The etymology of the name *Lebbeus* is unknown. The gender is masculine.

*Systematic position.*—*Paralebbeus* is most closely related to the genus *Lebbeus* White, 1847, and shares with it the following major characteristics:

1. Supraorbital and antennal spines present on carapace, branchiostegal spines absent; pterygostomial spines generally present, minute.

Fig. 1. *Paralebbeus zotheculatus* in host sponge.

2. Abdominal segments smooth, dorsally rounded.
3. Posteroventral angle of sixth abdominal segment without moveable plate.
4. Mandible with incisor process and 2-segmented palp.
5. Third maxilliped without exopod, with epipod.
6. Arthrobranchs absent.

One of the features that distinguish *Paralebbeus* from *Lebbeus* is the markedly reduced and toothless rostrum in *Paralebbeus*; most species of *Lebbeus* show a well developed, strongly toothed rostrum, often continuous posteriorly with a very marked, strongly dentate postrostral carina. Also, *Paralebbeus* generally has only a minute pterygostomial spine, which is well developed in all species of *Lebbeus*. *Lebbeus* has the meri of the ambulatory pereiopods strongly armed with spines laterally, which are completely absent in *Paralebbeus*. The commensal association of *Paralebbeus* with hexactinellid sponges is probably also a characteristic feature; some species of *Lebbeus* are known to be commensals but they are apparently associated with coelenterates, particularly actiniarians.

### *Paralebbeus zotheculatus*, n. sp.
Figs. 1–6

*Material examined.*—(i) 1 ♀, F.R.V. *Soela*, cruise 0184, sta NSW/57, 17°30.1'S, 118°28.9'E, 505–506 m, 3 Feb 1984, coll. A. J. Bruce. Holotype, NTM Cr. 00574A (ii) 1 ovig. ♀, collected with above. Paratype, NTM Cr. 00574B. (iii) 1 ♀, F.R.V. *Soela* cruise 0184, sta NWS/68, 16°14.0'S, 120°20.4'E, 456–452 m, 5 Feb 1984, coll. A. J. Bruce, NTM Cr. 00577 (iv) 1 ♀(?), F.R.V. *Soela* cruise 0784, sta NWS/66, 16°45.3'S, 119°46.4'E, 502–504 m, 5 Feb 1984, coll. A. J. Bruce, NTM Cr. 00575. All specimens collected by prawn trawl.

*Description.*—Adult female paratype. Body of stout, subcylindrical form, generally glabrous (Fig. 2).

Carapace with stout, acute, straight, lat-

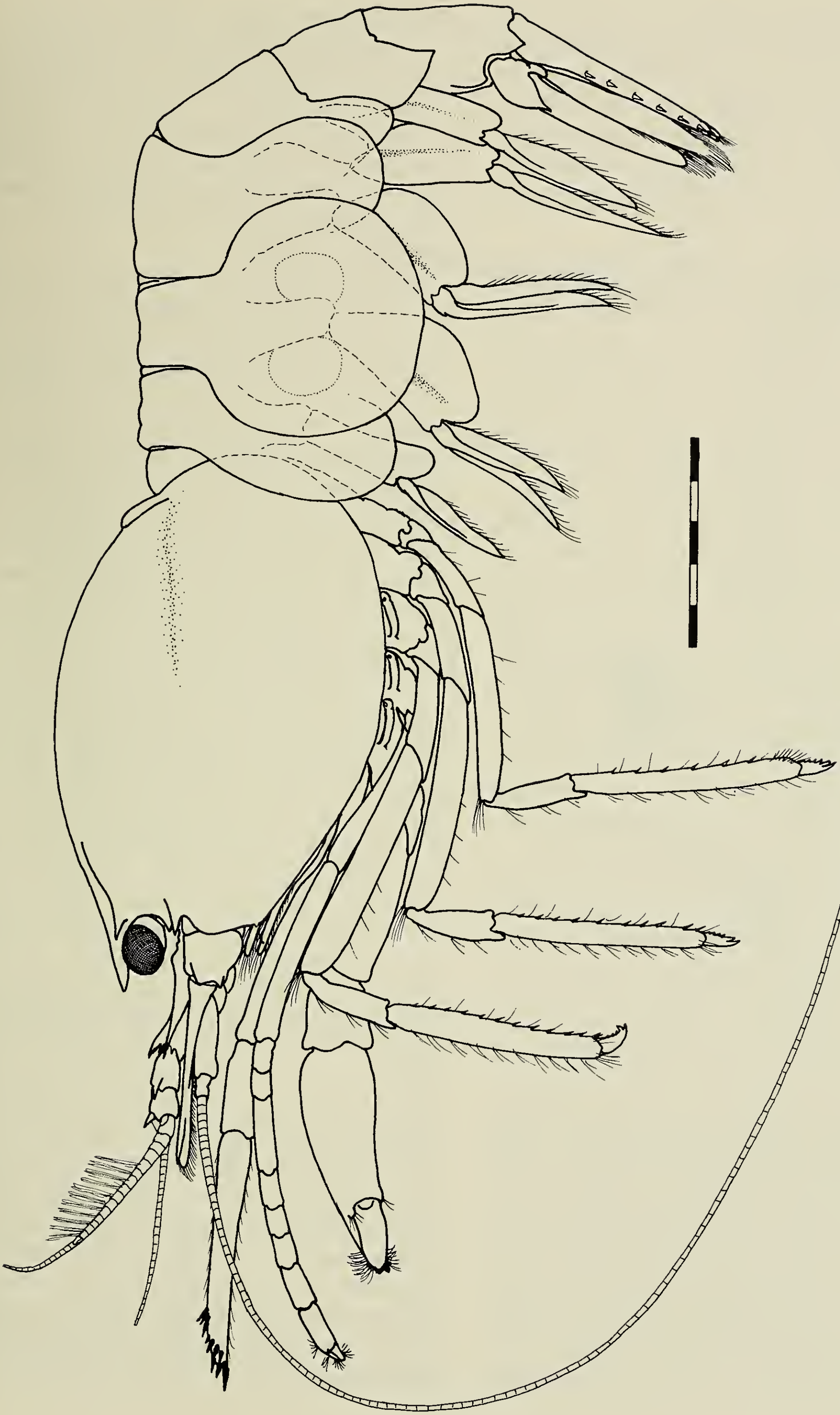

Fig. 2. *Paralebbeus zotheculatus*, ovigerous female paratype (NTM Cr. 000574B).

erally compressed, toothless rostrum reaching slightly beyond eyes; smooth, with acute supraorbital and antennal spines, inferior orbital angle produced, subacute, anterolateral angle rounded, not produced, with minute pterygostomial spine present on right, absent on left side of carapace (Fig. 3A).

Abdomen with segments dorsally rounded, not carinate or produced; pleura of first 3 segments broadly rounded, fourth convexly produced, fifth acutely produced. Sixth segment about 1.5 times length of fifth, 1.5 times longer than deep, posterolateral angle acutely produced, posteroventral angle bluntly produced. Telson (Fig. 3F) about 1.7 times length of sixth abdominal segment, about 2.7 times longer than anterior width, sides subparallel anteriorly, convergent posteriorly to broadly rounded posterior margin, equal to about 0.5 of anterior width; with 5–6 lateral dorsal spines and 13 posterior spines, sublateral spines longest, about 1.7 times length of lateral spines and 1.3 times length of submedian spines (Fig. 6L).

Eyes prominent, cornea hemispherical, well pigmented, without accessory pigment spot; stalk slightly flattened, central length subequal to corneal diameter (Fig. 3D).

Antennular peduncle (Fig. 3B) with large, broad acute stylocerite reaching to base of intermediate segment, proximal segment about 2.2 times longer than central width, medial border setose, distolateral angle tridentate, with small distal ventromedial tooth; statocyst obsolete; intermediate segment 1.5 times longer than distal width, tapered proximally, with acute distolateral tooth; distal segment shorter than width, half length of intermediate segment, with upper and lower distolateral teeth. Upper flagellum uniramous, short, proximal 18 segments stout with about 10 groups of esthetascs, 8 distal segments slender; lower flagellum short and slender, with 28 segments.

Antenna (Fig. 3C) with basicerite bearing small distolateral tooth, carpocerite about 3.0 times longer than wide, exceeding middle of scaphocerite, flagellum slender, about 3.5 times postorbital carapace length; scaphocerite extending well beyond antennular peduncle, lamella about 2.7 times longer than broad, distal margin bluntly angular, exceeding tip of distolateral tooth, lateral margin straight.

Mandible (Fig. 4A) with corpus stout, with feebly setose 2-segmented palp laterally; left molar process (Fig. 6A, B) robust, obliquely truncate distally, well developed marginal setose fringe dorsally and row of small teeth ventrally; incisor process (Fig. 6C) feeble, with 4 small, irregular acute teeth distally. Maxillula (Fig. 4B) with well developed, feebly bilobed palp (Fig. 6D), upper lobe with 2 slender simple setae, lower lobe with 1 stouter setulose seta; upper lacinia broad, with about 14 short stout simple spines distally, upper and lower borders sparsely setose; lower lacinia slender, setose, with few slender spines distally (Fig. 6E). Maxilla (Fig. 4C) with well developed, distally narrowed palp, lateral border with short plumose setae, 3 longer simple setae distally; basal endite large, deeply bilobed, medially setose on both lobes, coxal endite small, simple, with sparser, longer setae medially, scaphognathite about 3.5 times longer than central width, posterior lobe short and rounded, anterior lobe distally narrowed. First maxilliped (Fig. 4D) with 2-segmented palp, distal segment 2.0 times longer than wide and 2.0 times length of proximal, both sparsely setose medially; basal endite short and broad, medially setose, coxal endite feebly convex medially, sparsely setose; exopod with flagellum normally developed, numerous plumose setae distally and small caridean lobe proximally; epipod large, feebly bilobed, with triangular lobes. Second maxilliped endopod (Fig. 4E) with distal segment narrow, 3.0 times longer than wide, with numerous long finely setulose setae medially, propodal segment distomedially

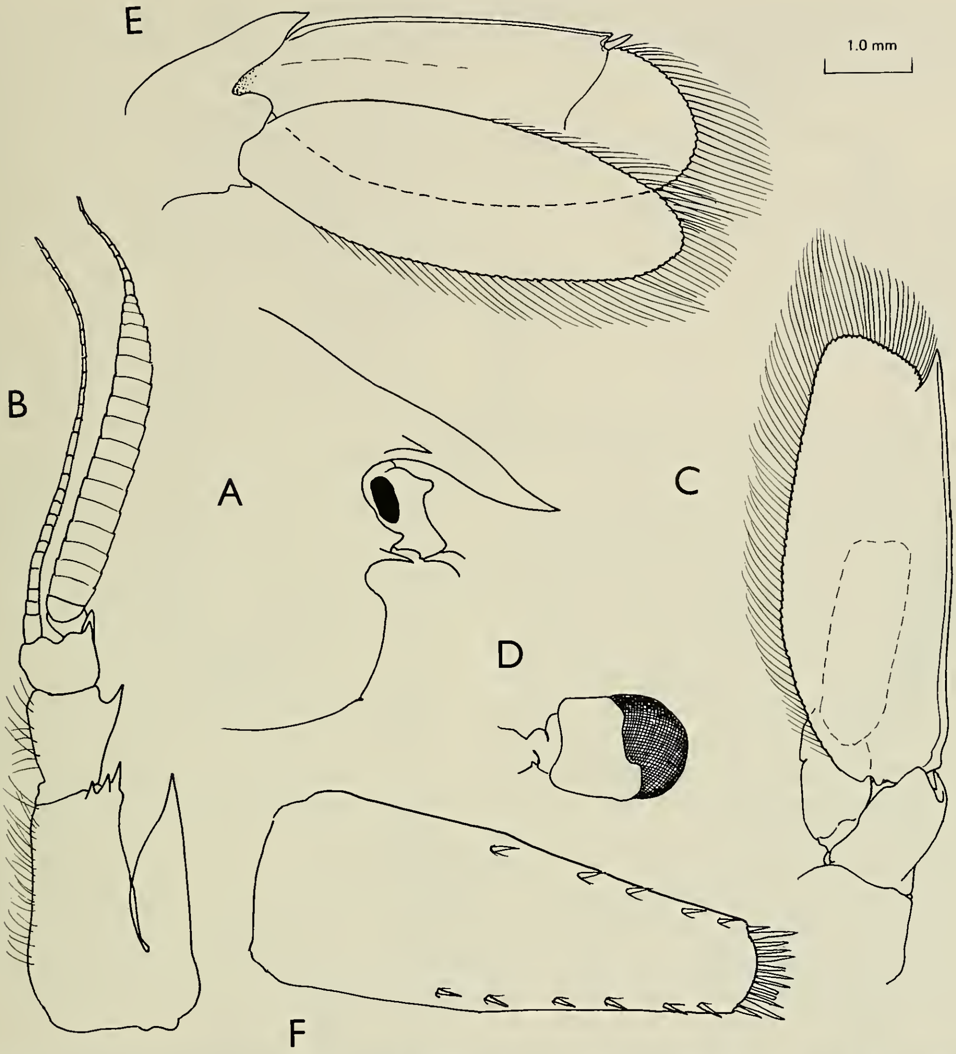

Fig. 3. *Paralebbeus zotheculatus*: A, Anterior carapace and rostrum, lateral aspect; B, Antennule; C, Antenna; D, Eye; E, Uropod; F, Telson. A, D, Female holotype; B, C, E, F, Female paratype.

angulate with medial margin setose; carpus and merus normal; ischiomerus medially excavate; coxa not medially produced, nonsetose; with large oval epipod bearing small podobranch with 5 pairs of lamellae proximally; exopod damaged on left, normal on right. Third maxilliped (Fig. 4F) elongate and slender, exceeding antennular peduncle by length of distal segment, reaching anteriorly about as far as extremity of second pereiopod; terminal segment about 8.0 times longer than proximal width, subcylindrical and tapering distally, laterally setose, with numerous short robust cornified spines (Fig. 6F); penultimate segment short, twice as long as wide and 0.3 times length of antepenultimate segment, medially setose; ischiomerus and basis completely fused, combined segment about 5.0 times longer than wide, slightly narrowed proximally; coxa not medially produced, without oval lateral plate, small hooked epipod present.

Branchiae as follows:

| | Maxillipeds | | | Pereiopods | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 1 | 2 | 3 | 4 | 5 |
| Pleurobranchs | – | – | – | + | + | + | + | + |
| Arthrobranchs | – | – | – | – | – | – | – | – |
| Podobranchs | – | + | – | – | – | – | – | – |
| Mastigobranchs | – | – | – | + | + | + | + | + |
| Epipods | + | + | + | + | + | + | – | – |
| Exopods | + | + | – | – | – | – | – | – |

Thoracic sternites narrow and armed with slender acute submedian spines on sixth to eighth thoracic segments.

First pereiopods (Fig. 5A) robust, short, subequal and similar, exceeding carpocerite by chela and carpus. Chela (Fig. 5B) robust with palm subcylindrical, smooth, about 2.4 times longer than wide, slightly tapered distally, with grooming setae proximally, dactyl (Fig. 6G) strongly curved, acute, 3.2 times longer than deep, about 0.5 of palm length, with 2 strongly cornified teeth distally, medial and lateral cutting edge entire; fixed finger (Fig. 6H) similar, with 1 cornified distal tooth; carpus short and stout, about as wide as long, subcylindrical, distal end feebly excavate, unarmed but provided with grooming setae; merus about 2.4 times length of carpus and 2.8 times longer than central width, subcylindrical and unarmed, obliquely articulated with ischium; ischium about 2.0 times longer than wide and twice length of basis, with short longitudinal row of 5 spines proximally; coxa robust, without processes but with hooked epipod.

Second pereiopods (Fig. 5C) slender, subequal and similar, reaching to tip of third maxilliped. Chela (Fig. 5E) small with palm subcylindrical, about 2.2 times longer than deep, dactyl 0.65 of palm length, acute, feebly curved, with unarmed cutting edge, 2 strongly compressed cornified teeth distally, fixed finger similar, with single distal tooth only; carpus (Fig. 5D) slender, 3.5 times length of chela, 7-segmented, with segments in following ratios from proximal end 2.0: 1.0:3.3:1.8:1.0:1.0:2.0, merus undivided, about 0.6 of carpus length, 7.0 times longer than wide, uniform and unarmed; ischium subequal to merus, about 7.6 times longer than deep, ventral border sparsely setose, with 3 conspicuous spines proximally; basis short, without special features; coxa robust, with hooked epipod and small setose process ventrally.

Ambulatory pereiopods moderately slender. Third pereiopod (Fig. 5F) extending to about 0.6 of terminal segment of third maxilliped and exceeding carpocerite by propod and dactyl; dactyl (Fig. 6I) with corpus compressed, about 1.8 times longer than deep, about 0.15 of propod length, unguis distinct from corpus, about 3.0 times longer than wide, ventral border of corpus with 6 spines, distal spine shorter but more robust than unguis, other spines decreasing in size proximally; propod (Fig. 5G) about 6.5 times length of dactyl, 8.0 times longer than wide, with 2 rows of about 12 spines ventrally and tufts of setae dorsally; carpus barely 0.5 of propod length, about 6.3 times longer than wide, unarmed; merus about 1.2 times propod length, 6.3 times longer than deep, unsegmented, without lateral spines or distoventral tooth; ischium about 0.45 of merus length; basis and coxa without special features, latter with hooked epipod (Fig. 6J). Fourth pereiopod similar to third. Fifth pereiopod (Fig. 5H) similar, more slender than third, dactyl (Fig. 6K) with 7 ventral spines, propod 1.1 times length of third and 10.5 times longer than deep, with fewer ventral spines, transverse rows of short, serrate setae distolaterally.

Pleopods (Fig. 5I, J) normally developed, biramous, with protopodite broadly expanded laterally on second to fourth abdominal segments, endopods of second to fifth segments with appendix interna.

Uropods (Fig. 3E) with protopodite acutely angulate posterolaterally; exopod 2.5 times longer than broad, lateral margin feebly convex, with small acute distal tooth

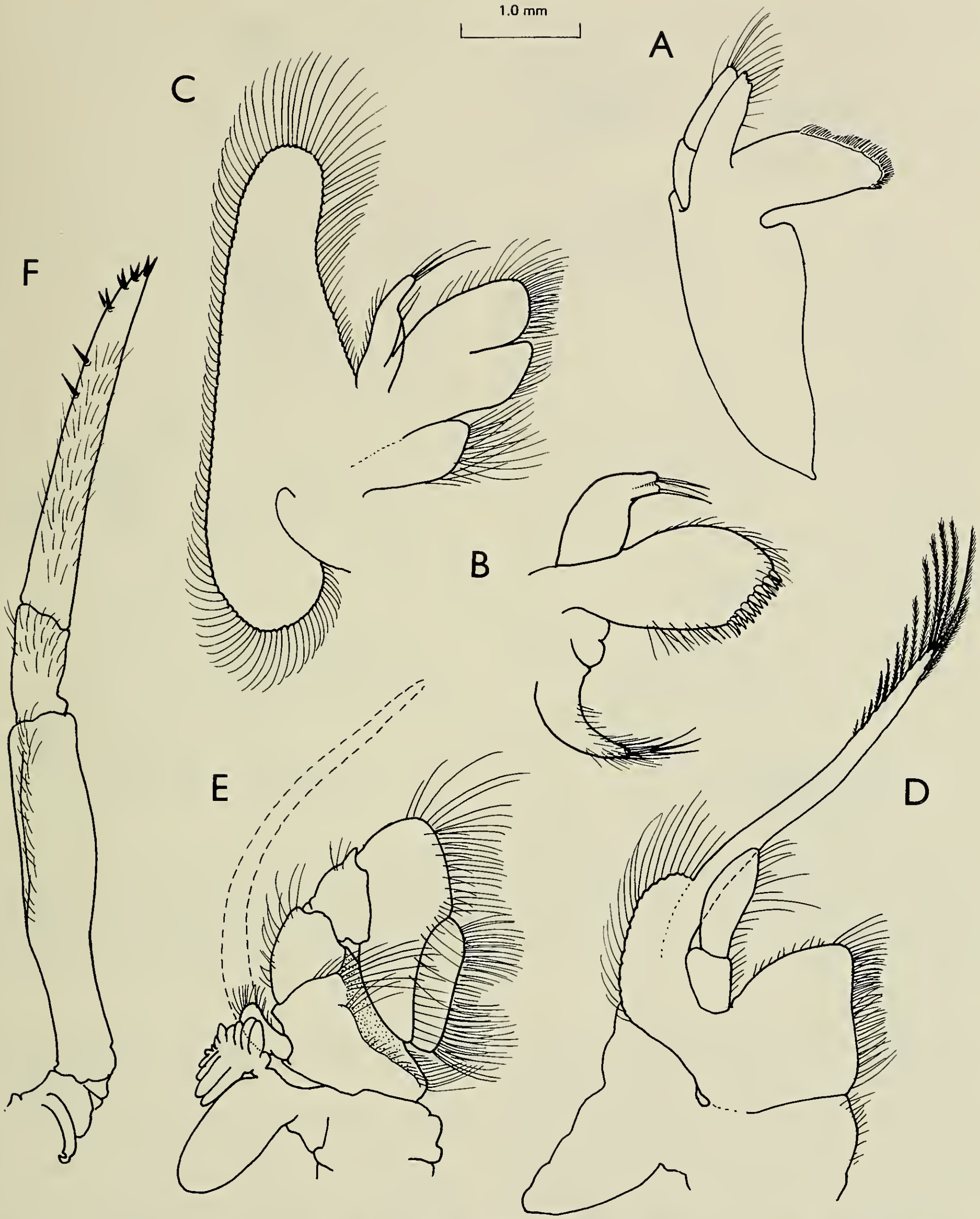

Fig. 4. *Paralebbeus zotheculatus,* ovigerous female paratype: A, Left mandible; B, Maxillula; C, Maxilla; D, First maxilliped; E, Second maxilliped; F, Third maxilliped.

accompanied medially by larger mobile spine; endopod subequal to exopod, about 3.1 times longer than broad.

Ova few and large, length about 1.5 mm.

*Adult female holotype.*—Generally very similar to described paratype, smaller and less robust. Rostrum slightly longer relatively and more acute, distally slightly up-

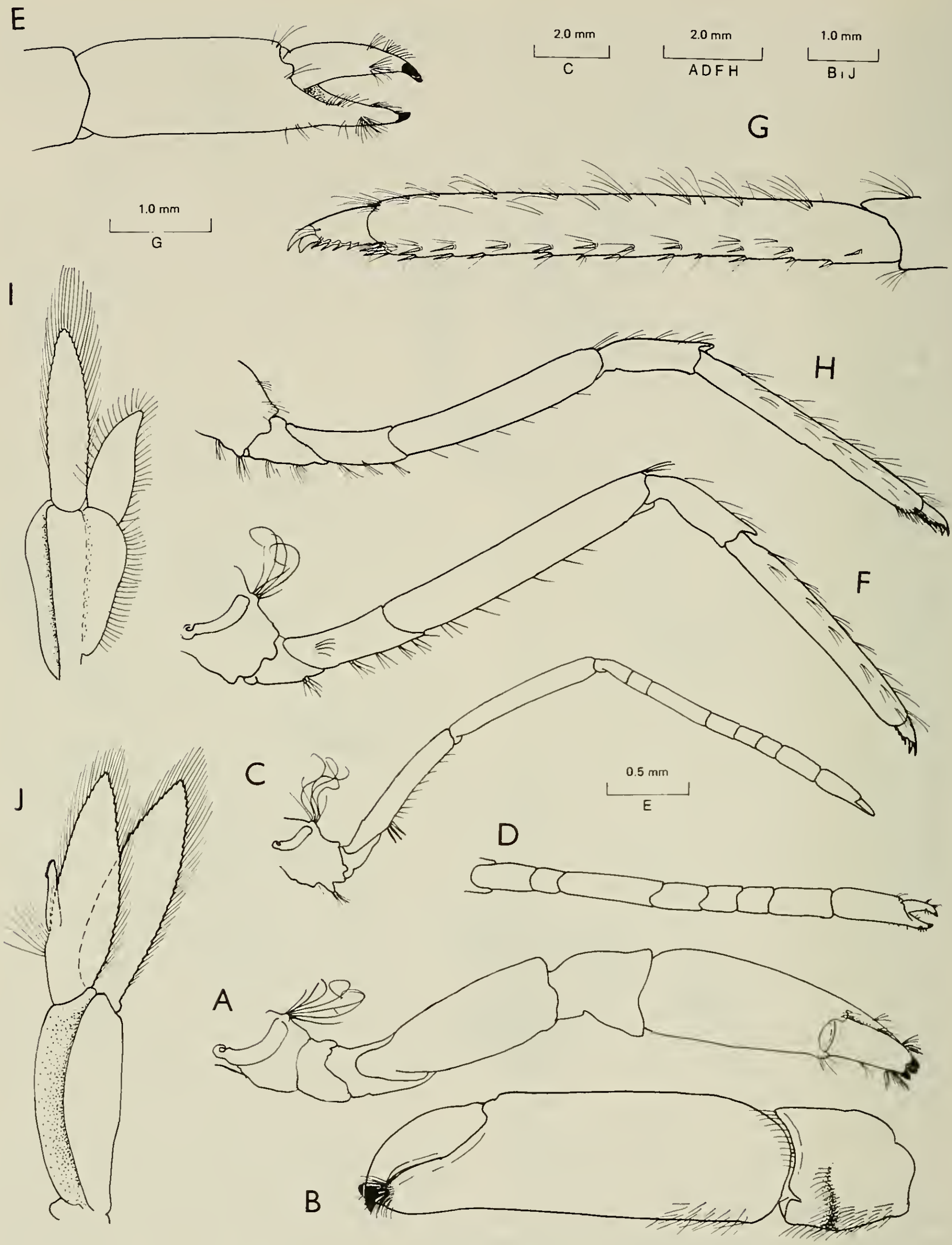

Fig. 5. *Paralebbeus zotheculatus*: A, First pereiopod; B, Same, chela; C, Second pereiopod; D, Same, carpus and chela; E, Same, chela; F, Third pereiopod; G, Same, propod and dactyl; H, Fifth pereiopod; I, First pleopod; J, Second pereiopod. A–H, Female paratype; I, J, Female holotype.

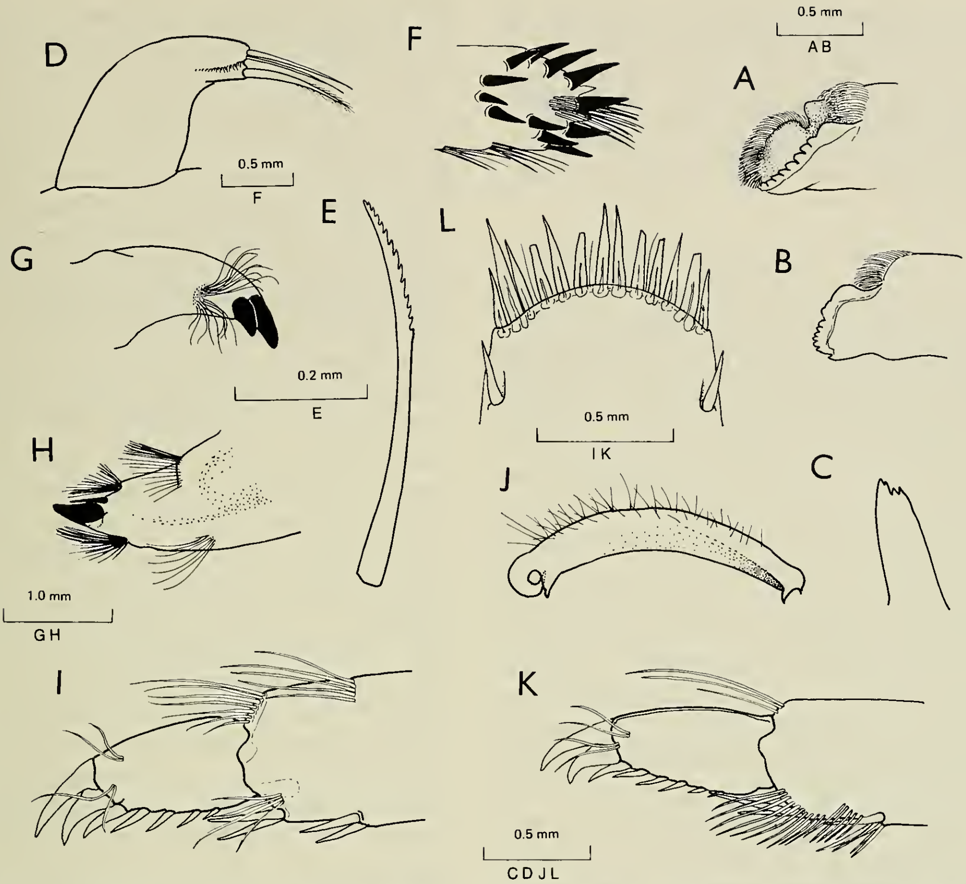

Fig. 6. *Paralebbeus zotheculatus,* female paratype: A, Molar process of mandible, anterior aspect; B, Same, posterior aspect; C, Incisor process of mandible; D, Palp of maxillula; E, Lower lacinia of maxillula, distal spine; F, Third maxilliped, distal end of terminal segment; G, First pereiopod, dactyl; H, Same, fixed finger; I, Third pereiopod, dactyl and distal end of propod; J, Same, epipod; K, Fifth pereiopod, dactyl and distal end of propod; L, Telson, posterior margin.

turned. Small pterygostomial spine present on each side of carapace.

*Additional paratypes.*—In close agreement with holotype. Specimen from NWS/68 lacking first and fifth pereiopods and one of fourth pereiopods. Pterygostomial spines absent from both sides. Telson with 4 dorsal spines on one side, 5 on other. Specimen from NWS/66 complete and also with 4 dorsal spines on one side of telson and 5 on other. Pterygostomial spines present on both sides of carapace.

*Coloration.*—Body mainly transparent, abdomen whitish speckled with small red chromatophores increasing in density posteriorly, caudal fan reddish; antennae whitish; third maxilliped deep red; fingers of first pereiopod reddish, third to fifth pereiopods red, especially distally. Cornea black. Intrathoracic organs orange. Ova turquoise.

*Host.*—All specimens collected from small chambers in hexactinellid sponges, probably of the genus *Euplectella.*

*Habitat.*—Bottom temperatures 7.88°–8.70°C.

*Parasites.*—One specimen with pair of

bopyrid isopods in right branchial chamber. These have been identified as *Bopyroides lamellatus* (Krøyer), a species not previously recorded from Southern Hemisphere.

*Etymology.*—The specific epithet is derived from "zothecula" (Latin), a small chamber.

## Discussion

The specimens of *Paralebbeus zotheculatus* described above were all obtained from inside trawl-caught hexactinellid sponges, in small closed chambers only found on breaking up the sponges, leaving their association with the sponge beyond any doubt (Fig. 1). Most of the sponges collected were damaged and incomplete, which probably accounts for only single specimens of shrimps being found; it seems probable that they were originally in heterosexual pairs.

The discovery of *Paralebbeus zotheculatus* is of particular interest as it represents the first established example of an association between a caridean shrimp and a hexactinellid sponge. This niche has been largely taken over by stenopodid shrimps, such as *Spongicola, Spongiocaris,* and *Spongicoloides* (Saint Laurent and Cleva 1981).

The genus *Lebbeus* White contains about 25 species (Wicksten and Méndez 1982, Butler 1980) which occur predominantly in northern seas, although one species, *L. indicus,* has been described from Indonesian waters (Holthuis 1947). Most of these have been trawl-caught specimens and no details of their associations, if any, have been preserved. One of the boreal species found in shallow waters has been observed to live in association with sea anemones (Butler 1980, *L. grandimanus* [Brazhnikov] on *Cribrinopsis* and *Tealia* spp.) but none have been reported in association with hexactinellid or any other sponges. The only hippolytid shrimp so far recorded as an associate of Porifera is *Gelastocaris paronae* Nobili, which lives on the external surface of shallow-water Indo-West Pacific sponges.

Three specimens of a hippolytid shrimp that probably belongs to this genus and possibly to the same species were collected during the *Albatross* Philippine Expedition, 1907–1910, but, as each specimen differs in some respects from the above description, they are not considered to be part of the type series of *Paralebbeus zotheculatus.* A female (CL 9.7 mm) from Verde Island Passage, Philippines, agrees most closely with the Australian series but it has a more slender rostrum, the anterior margin of the carapace not deeply recessed below the antennal spine, the scaphocerite with the lateral margin slightly concave rather than faintly convex at midlength, and the chela of the first pereiopod with the distal corneous teeth on the dactyl subequal rather than staggered. A male (CL 6.9 mm) from west of Halmahera, Indonesia, has a small supraorbital spine on the left side and none on the right, no pterygostomial denticle on either side, the telson with only two and three left and right lateral dorsal spines, and the corneous subdistal spines on the third maxilliped more numerous and extending somewhat farther proximally on the terminal segment. A female (CL 11.7 mm) from southern Celebes, Indonesia, resembles the male in the spination on the third maxilliped but it has no supraorbital spine on either side, a vestige of a pterygostomian denticle on the left side of the carapace but none on the right, the telson with two lateral dorsal spines on the left side and one on the right, and the right scaphocerite shorter than the left. These specimens will be discussed in greater detail in the report now in preparation by the junior author on the alpheoid families of the *Albatross* Philippine Expedition.

## Acknowledgments

We are most grateful to Dr. T. Davis and Dr. T. Ward of the Fisheries Laboratory, C.S.I.R.O., Cronulla, for the opportunities and facilities provided aboard the F.R.V.

*Soela,* and to Dr. J. C. Markham, for the bopyrid identification.

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# *RHOMBOPSAMMIA*, A NEW GENUS OF THE FAMILY MICRABACIIDAE (COELENTERATA: SCLERACTINIA)

Joan Murrell Owens

*Abstract.—Rhombopsammia*, a new genus of deep-water micrabaciid corals, and two new species, *R. squiresi* and *R. niphada*, are described and figured. *Rhombopsammia* bears a marked superficial resemblance to *Letepsammia*, but examination of the corallum structure, microstructure, and microarchitecture of the new genus through thin-section and light microscope study reveals that it differs from *Letepsammia* in having essentially imperforate septa, prominent vepreculae which alternate in position on either side of the septum, ridge-like tracings of trabeculae on septal flanks and dentate columella. Its known geographic distribution (China and Philippine seas) is more restricted than that of *Letepsammia*, but its bathymetric range (68–930 m) is only slightly less. Allusions by Squires (1967 and ca. 1967) to an undescribed species of micrabaciid coral from the Pliocene of Italy suggest that this species may belong to the new genus. If true, *Rhombopsammia* will conform with the evolutionary trend of the family towards increasing depth of occurrence with progressive geologic age.

The Micrabaciidae is a small family of solitary, ahermatypic corals known from the shallow waters of Cretaceous continental shelves and inland seas to the deep waters of today's Indo-Pacific. When Vaughan (1905) defined the family, he included in it *Micrabacia* Milne-Edwards and Haime, *Diafungia* Duncan, *Microsmilia* Koby, *Podoseris* Duncan, and *Antilloseris* Vaughan, largely on the basis of their solid septa and perforate walls. Later, Wells (1933) emended the family to emphasize the structural significance of an alternation of septa and costae. He thus excluded from it all but *Micrabacia* and *Diafungia*, and included in it *Stephanophyllia* Michelin and *Leptopenus* Moseley. In revising the Scleractinia, Vaughan and Wells (1943) determined that *Micrabacia* and *Diafungia* were synonymous, and defined the Micrabaciidae as consisting of three genera: *Micrabacia*, *Stephanophyllia*, and *Leptopenus*. Most current workers accept this definition of the family.

For many years most of the species of these genera were classified primarily on the basis of external characters observable in whole-mount study; consequently, many species were grouped together more or less according to superficial resemblances and broadly defined generic characteristics that sometimes masked structural and microstructural differences that are significant enough to warrant generic separation. This was particularly true of many of the species comprising *Stephanophyllia*. On re-examination of this genus, Yabe and Eguchi (1932) detected subtle but fundamental differences in morphology and component elements among the species which led them to erect four subgenera of *Stephanophyllia*, one of which was *Letepsammia*, a group of micrabaciid corals distinguishable by their highly perforated septa. Wells (1956) considered

*Letepsammia* to be synonymous with *Stephanophyllia,* but more recent workers, particularly Squires (1967 and ca. 1967) and Owens (1984), have deemed septal perforations to be a valid generic characteristic and have therefore referred to *Letepsammia* as a discrete genus of micrabaciid corals.

In examining the *Albatross* collection of deep-sea corals, Squires (ca. 1967) separated from those sorted by National Museum workers as *Stephanophyllia* a group which differed from that genus in having essentially imperforate septa. Although he obviously felt this group deserved further study, he left it undescribed. This group was later included in a study of the structure, microstructure, and microarchitecture of the Micrabaciidae (Owens 1984). As a result of this latter study of the family both in whole mount and in thin section, a new genus, *Rhombopsammia,* is designated in this paper.

*Rhombopsammia* consists at present of two species, *R. squiresi* and *R. niphada,* both Recent. Squires (1967 and ca. 1967) alluded to a fossil coral of the Pliocene of Italy that apparently belongs to this new taxon; however, his fossil species could not be found or verified for this study. This paper, therefore, describes only the two Recent species, but acknowledges the possible existence of a Pliocene member. In light of the evolutionary trend of the family (Steinmann 1908, Squires 1967, Owens 1984) towards increasing depth of occurrence with progressively younger geologic age, a Pliocene member of this genus with a depth range similar to the Recent species is highly probable.

Order Scleractinia Bourne, 1900
Suborder Fungiida Duncan, 1881
Superfamily Fungioidea
Vaughan and Wells, 1943
Family Micrabaciidae Vaughan, 1905
*Rhombopsammia,* new genus

*Diagnosis.*—Corallum large, loosely built, strongly convex orally and nearly flat to patellate aborally, with narrow to wide marginal shelf formed by non-elevated extensions of septa alternating with costae. Septa essentially imperforate, coarsely dentate, rising steeply proximally and distally, forming a crown above the basal wall. Tracings of trabeculae visible on septal flanks. Deltas broad, porous. Vepreculae numerous, alternating in position on either side of septa. Synapticulae scarce, mainly near base of septa. Calicular depression deep, elongate. Costae thin, finely serrate or complex with recumbent teeth, connected by closely spaced concentric rows of synapticulae. Intercostal loculi broader than costae. Wall perforate, moderately to strongly laterally flattened. Columella porous, deeply set, elongate, and dentate on exposed upper surface. Corallum completely invested in soft tissue of the polyp.

*Occurrence.*—(?)Pliocene, Italy; Recent, China and Philippine seas; 68–930 m.

*Type species.*—*Rhombopsammia squiresi,* new species.

*Etymology.*—The generic name refers to the convexo-patellate shape of *R. squiresi,* and is derived from the Greek *rhombos* = spinning top + *psammos* = sand. Gender: feminine.

*Discussion.*—Specimens of both *Rhombopsammia* and *Letepsammia* have generally been sorted by museum workers as *Stephanophyllia.* The three do bear a resemblance, though the former two are more alike than either is like the latter. The resemblances are greatly diminished, however, when specimens of *Rhombopsammia* are closely examined by use of a light microscope and thin sections, or when septal perforations are taken into account. *Rhombopsammia* differs from *Stephanophyllia* in its imperforate septa, convexo-patellate corallum, marginal shelf, spongy columella, and large, loosely built corallum; it differs from *Letepsammia* in its imperforate septa, prominent vepreculae which alternate in position on either side of the septum, ridgelike tracings of trabeculae on septal flanks, and dentate upper margin of the columella. In thin section, the trabecular structure in *Rhombopsammia* is seen to be more widely spaced than in *Stephanophyllia,* less sinuous than in *Letepsammia.*

Only two species of *Rhombopsammia* are described below. A third species, a fossil form from the Pliocene of Italy, was reported by Squires (1967 and ca. 1967), but was not described and could not be located for this study.

Steinmann (1908), Squires (1967), and Owens (1984) have noted an evolutionary trend of the Micrabaciidae towards increasing depth of occurrence with progressively younger geologic age. *Rhombopsammia,* with its bathymetric range of 68–930 m and its probable age of Pliocene to Recent, fits well into this trend. However, its virtually imperforate septa present a departure from another apparent trend of the family towards increasing septal perforations with depth (Steinmann 1908, Owens 1984). *Stephanophyllia* is moderately perforated, whereas *Letepsammia* is highly perforated. Inasmuch as *Rhombopsammia* falls between *Stephanophyllia* and *Letepsammia* in both age and depth of occurrence, one would anticipate its also falling between the two in septal perforations.

In many respects, *Rhombopsammia* appears to be a transitional genus between *Stephanophyllia* and *Letepsammia,* for its species have characters found in each genus, and though its bathymetric range is close to that of *Letepsammia,* its maximum depth of occurrence nonetheless falls more than 50 m shorter. However, the evolutionary placement of *Rhombopsammia* between two genera with well-developed septal perforations is troublesome. The question arises as to whether *Rhombopsammia* is indeed part of a linear evolutionary progression toward adaptation to life at deeper and deeper depths and, possibly, also a transitional genus between *Stephanophyllia* and *Letepsammia,* or a divergent member of the family following a different but parallel evolutionary path. More study along the lines of alternative solutions to the problem of adapting to life in deep waters is needed before that question can be satisfactorily answered.

### *Rhombopsammia squiresi,* new species

Figs. 1, 2A

*Description.*—Corallum large, loosely built, and strongly convexo-patellate, with wide marginal shelf. Calicular depression deep and long, but narrow. Wall finely perforate. Deltas broad, porous, with proximal edges of secondaries distinct. Diameter of specimens 30.3–32.6 mm; height 13.3–13.7 mm; average H:D ratio 43:100. Ninety-six septa.

Costae thin, finely granulated axially, coarsening distally; costae and synapticulae adorned with irregular, recumbent teeth, beginning about midway between axis and periphery. Intercostal loculi as broad or broader than costae axially, but obscured distally. Costae begin as 6 (first cycle) at apex of wide cone forming basal wall and bifurcate immediately (second cycle); all new costae immediately bifurcate again (third cycle); outer costae bifurcate before inner at about one-tenth and one-seventh, respectively, distance from center to periphery (fourth cycle); final bifurcations (fifth cycle) begin at one-third distance to periphery with first and fourth costae of each quartuplet in each system bifurcating first.

Septa imperforate and thin, with interspaces as wide or wider than septa. Vepreculae radially aligned and alternate in position on either side of each septum, giving septal margins a fluted appearance. Dentation slightly lobulate, becoming slightly lacerate at inner margins of all but primaries. All but highest cycle septa tall and approximately same height; inner margins of primaries more rounded than those of the deltas. Primaries inserted straight and free

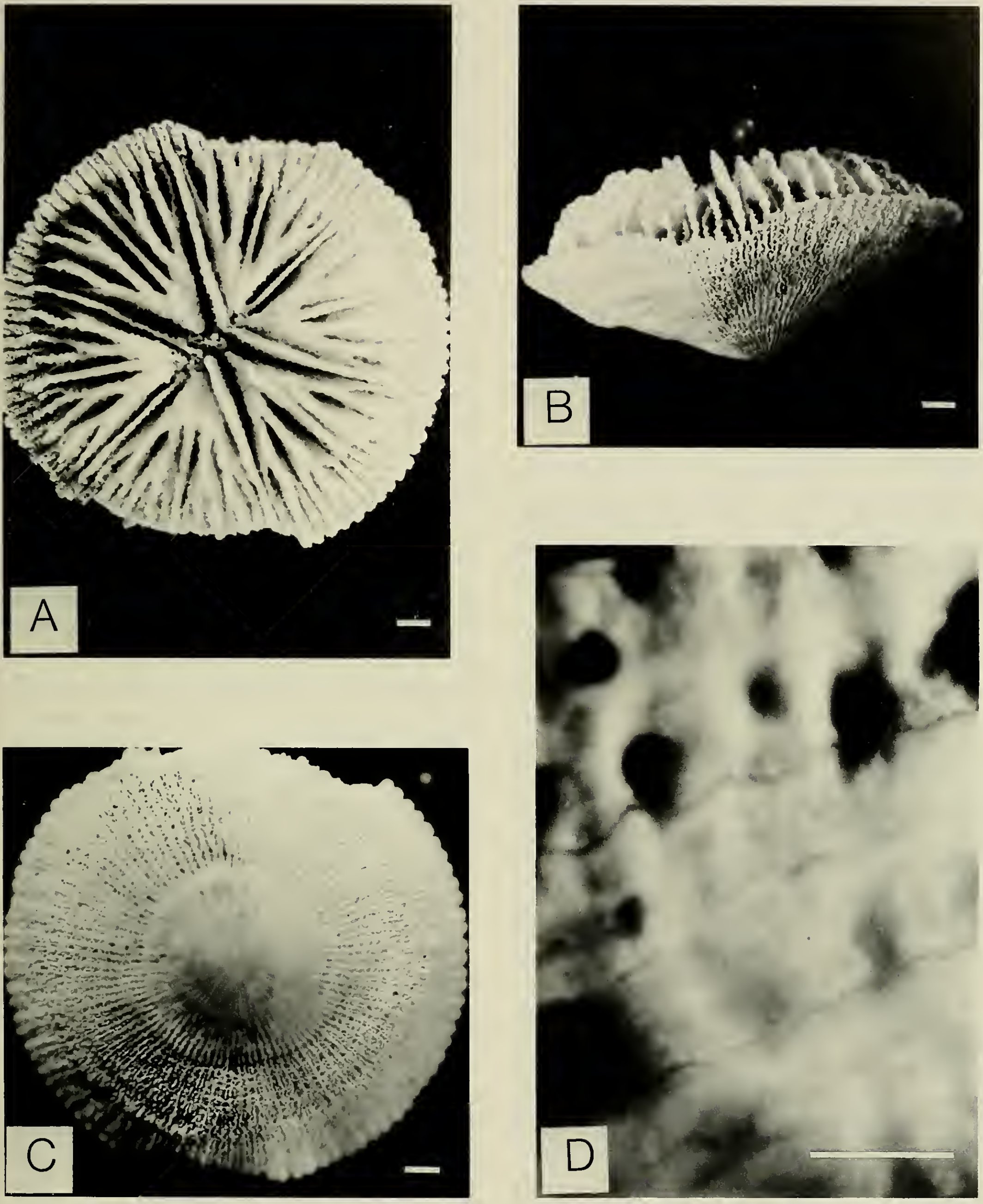

Fig. 1. *Rhombopsammia squiresi*: A, Oral view of holotype (USNM 72797), *Albatross* 5423: 9°38′30″N, 121°11′E, 930 m; B, Side view of holotype; C, Aboral view of holotype; D, Thin section of septum of a paratype (USNM 72798), under reflected light, showing thin, wavy trabeculae with growth laminae. Holes in septum were caused by mechanical grinding to make thin section. *Albatross* 5427: 9°11′30″N, 118°37′08″E, 68 m. Scale bars = 2 mm.

and extend to columella. Secondaries straight and free until joined with others in deltas. Tertiaries divide just beyond deltas, and these septa successively divide symmetrically, with final division occurring at inner edge of shelf. Slightly porous sheets mark points of division. Synapticulae scarce, mainly at base of septa, particularly distally.

Columella porous, spongy, terminating at upper surface in mass of lacerate-like teeth.

Trabeculae in slightly diffuse fan system, visible along septal flanks as faint tracings. Growth laminae prominent, expressed as undulating ridges along the sides of the septa.

*Types.*—Holotype: USNM 72797; *Albatross* Sta 5423 (9°38′30″N, 121°11′E; 930 m). Paratypes: USNM 72799, 72800, 72798; *Albatross* Sta 5513 (8°16′45″N, 124°02′48″E; 924 m), 5425 (9°37′45″N, 121°11′E; 906 m), and 5427 (9°11′30″N, 118°37′08″E; 68 m), respectively.

*Occurrence.*—Recent, China Sea, Philippine Sea; 68—930 m.

*Remarks.*—The pronounced convexo-patellate corallum, high crown of septa, wide marginal shelf, and recumbent costal and basal synapticular teeth make *R. squiresi* a very distinctive species, quite unlike any other micrabaciid coral save *R. niphada,* with which it bears a slight structural but stronger microstructural resemblance. That it is a micrabaciid coral is obvious from its alternation of septa and costae. Its pattern of septal insertions (Fig. 2A) is very similar to that seen in other micrabaciids which possess true deltas, and typically has the quinaries proximal to the primaries merging with the quaternaries closer to the center than the inner quinaries.

One or two random pores were observed in a few septa in each specimen, but as these pores lacked any regularity in frequency, position, or even cycle of septa in which they occurred, the septa are considered essentially imperforate.

In thin section, the arcuate manner in which the ends of the sclerodermites of neighboring trabeculae merge proved to contribute to the fluted appearance of the septa. The arcs described by the sclerodermites persist not only in the plane of the septum, but also swing laterally to form cusps along the flanks. This arcuate pattern between trabeculae is found also in *R. niphada* but to a lesser degree, and explains why the septa in the latter species are less wavy.

*Etymology.*—The species name is in honor of Donald F. Squires, whose recognition that this group of corals differed from the other species of *Stephanophyllia* inspired this study.

### *Rhombopsammia niphada,* new species
Figs. 2B, 3

*Description.*—Corallum large, delicate, loosely built, with narrow to wide prominent shelf; strongly convex orally and slightly patellate to nearly flat basally, but with pronounced basal apex. Calicular depression deep, long, and narrow. Deltas broad, porous, slightly spinose on inner margin. Diameter of specimens 21.5–36.0 mm; height 6.7–12.0 mm; H:D ratio 31:100. 144 septa.

Costae smooth, very thin, finely serrate on outer surface. Intercostal loculi broader than costae, but interrupted by closely spaced synapticulae connecting costae to bases of septa. Basal synapticulae smooth, lacking serration. Costae begin as 6 (first cycle) at apex of protuberant basal tip and bifurcate immediately (second cycle); each costa immediately bifurcates again (third cycle); outer pairs bifurcate fractionally before inner ones at about one-tenth distance from center to periphery (fourth cycle); bifurcations of fifth cycle begin about one-sixth distance from center with outermost costae of each system dividing first, followed closely by next outer and then innermost, other inner costae do not divide in this cycle; sixth cycle, also incomplete, begins again with outermost and next outer

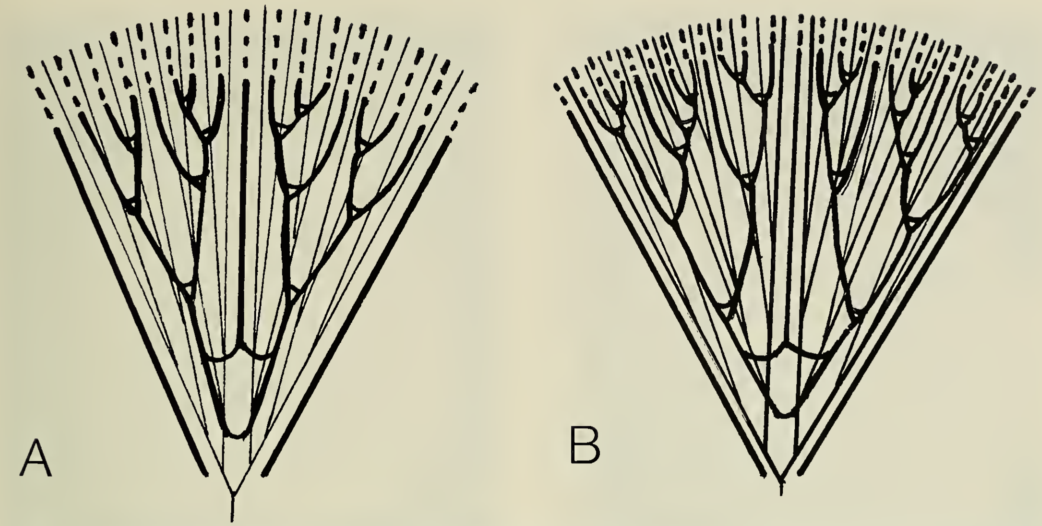

Fig. 2. Diagrammatic representations of one system: A, *Rhombopsammia squiresi*; B, *Rhombopsammia niphada*. Heavy lines represent septa; thin lines, costae; dotted lines, non-elevated extensions of septa.

dividing; followed symmetrically by 3 adjacent inner costae, those flanking each side not dividing. Final bifurcations occurring about one-third the distance to periphery.

Septa imperforate and thin, with interspaces wider than septa. Vepreculae radially aligned and alternate in position on either side of a septum, but produce only slight fluting effect. Dentation lobulate-like on upper and outer margins of septa, less so on inner margins of primaries. Synapticulae broad relative to width of septa and irregularly spaced deep in calice. Primaries straight, free, extending from shelf to columella. Secondaries straight and free to deltas. Tertiaries divide just beyond deltas, and quaternaries thus formed divide halfway between deltas and outer edge of calice, with outer quaternaries dividing slightly before inner ones. Quinaries proximal to the primaries and secondaries do not bifurcate until three-fourth distance from delta to shelf whereas of the two inner quinaries, the one closer to secondary does not bifurcate at all. At inner edge of shelf, beginning with no bifurcation of septa proximal to primaries, every other septum bifurcates for a final time, giving each system total of 24 septa. Coarsely porous sheets mark points of division.

Columella porous, spongy, elongate, but broader than in *R. squiresi*; ornamented at center with cluster of small, slightly spinose teeth.

Trabeculae, often ramified near distal margins, in moderately well-spaced fan system, and clearly visible as tracings along septal flanks. Ends of sclerodermites either joining together in arcuate pattern between trabeculae or diverging normally from axis to form vepreculae.

*Types.*—Holotype: USNM 72802; *Albatross* Sta 4911 (31°38′30″N, 129°19′E; 716 m). Paratypes: USNM 72801, 72804, 72803, 72805; *Albatross* Sta 4911 (same as holotype), 5283 (13°48′30″N, 120°28′40″E; 512 m), 5348 (10°57′45″N, 118°38′15″E; 686 m), and ND (no data), respectively.

*Occurrence.*—Recent, China Sea and Philippine Sea; 512–716 m.

*Remarks.*—*Rhombopsammia niphada* bears a close resemblance to species of *Letepsammia,* in that it shares with them a delicate, lacy corallum with a generally narrow marginal shelf, narrow columella, and highly perforated wall. However, close ex-

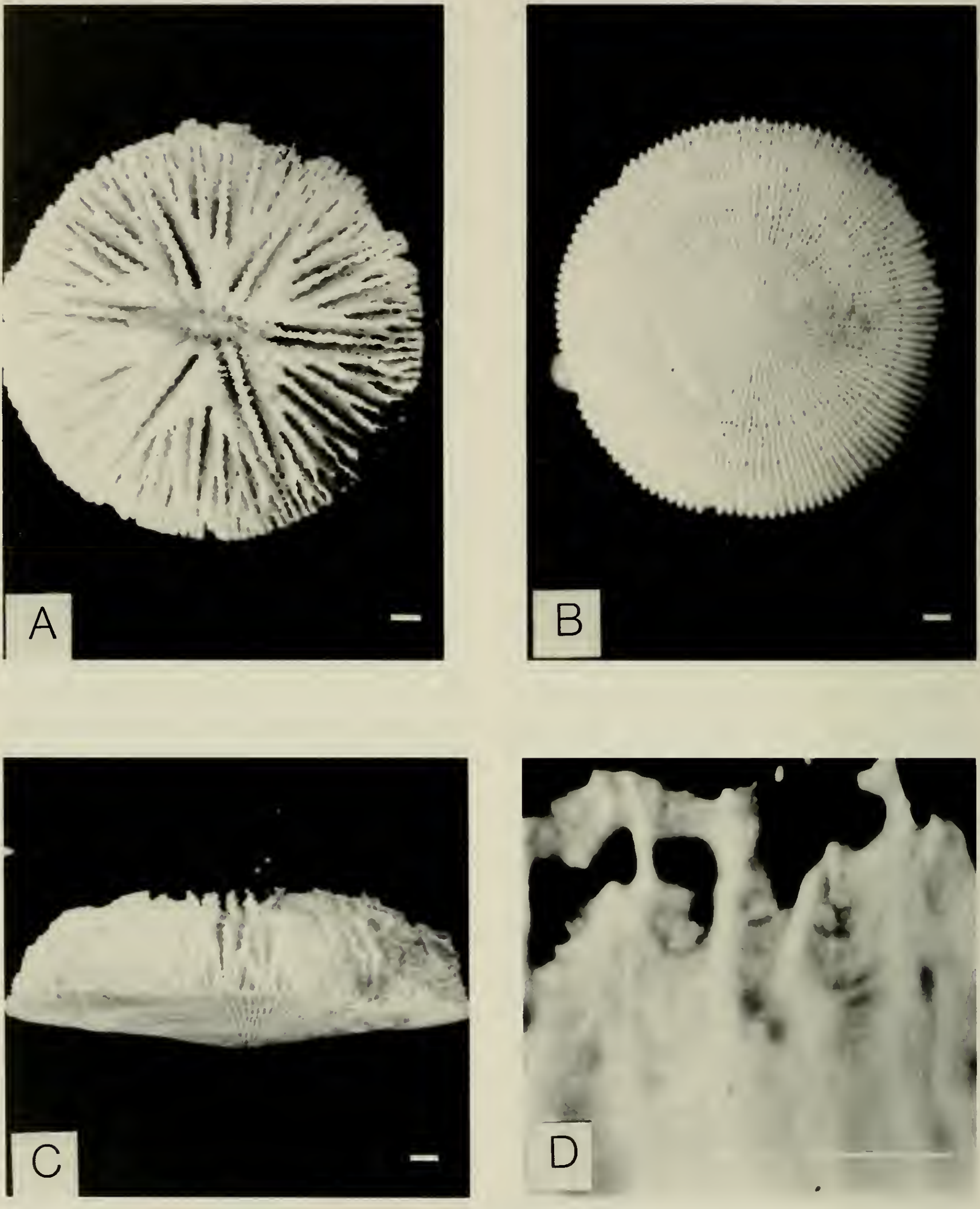

Fig. 3. *Rhombopsammia niphada*: A, Oral view of holotype (USNM 72802), *Albatross* 4911: 31°38′30″N, 129°19′E, 716 m; B, Aboral view of holotype; C, Side view of holotype; D, Thin section of septum of a paratype (USNM 72804), under reflected light, showing thin, wavy trabeculae with ends of sclerodermites merging in an arcuate pattern in the interarea. Note ramified trabecula at distal margin of septum in upper left. *Albatross* 5283: 13°48′30″N, 120°28′40″E, 512 m. Scale bars = 2 mm.

amination of the structure, microstructure, and microarchitecture of *R. niphada* distinctly separates it from *Letepsammia* and reveals its closer relationship with *R. squiresi.*

Both *R. niphada* and *R. squiresi* have essentially imperforate septa, numerous well-developed vepreculae, and strong fan-like trabeculae that impart ridge-like tracings on the sides of the septa and project along the outer margins as lobulate-like teeth. Also, in both the vepreculae alternate in position on either flank, giving the septa a fluted appearance. Both have a very protuberant basal apex, and their costal-intercostal spacings are similar.

As in all micrabaciid corals, *R. niphada* has an alternation of septa and costae. Its pattern of septal insertions (Fig. 3) is similar to that of other micrabaciids with true deltas, and is virtually identical with that seen in *R. squiresi* for an equal number of cycles and septa.

*Rhombopsammia niphada* differs most conspicuously from *R. squiresi* in its total number of septa (144) and its very slightly patellate to nearly flat base. It also lacks the recumbent basal teeth found in *R. squiresi.* Although the marginal shelf in *R. niphada* varies from narrow to wide, the shelf, even when as wide as in *R. squiresi,* is not as prominent due to the less steeply sloping distal edges of the septa.

*Etymology.*—The species name is derived from the Greek *niphados* = snowflake, and refers to the intricate design of the oral surface of the corallum. Gender: feminine.

*Discussion.—Rhombopsammia niphada* is distinguished by its 144 septa, which poses the most perplexing problem in its generic identity with *R. squiresi,* which has 96. In all other micrabaciid corals studied or described in the literature, the number of septa, except in an occasional deviant individual, has been so consistent within a genus as to suggest that it is a valid generic characteristic. But in *Rhombopsammia* a sufficient number of specimens in each species was examined to indicate that the difference in number of septa between the two species is not due to random deviation. *Within* each species the number of septa is consistent. The structural and microstructural similarities between *R. niphada* and *R. squiresi* argue convincingly for their generic identity in spite of the difference in septal number. Perhaps too much emphasis should not be placed on that character as a generic characteristic.

Interestingly, 144 septa are also found in the lectotype of *Letepsammia formosissima,* though all other specimens of that species studied had 120. Even if the lectotype of *L. formosissima* should prove to be a deviant individual, the occurrence of this unusual number of septa in both it and all specimens of *R. niphada* may be more than coincidental. When the similarities of *R. niphada* with *R. squiresi* and with species of *Letepsammia* are thoroughly considered, the strong suggestion arises that *R. niphada* may be an intermediate between *Rhombopsammia* and *Letepsammia.*

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# DISCOVERY OF A NEW LIVING *CERITHIOCLAVA* SPECIES IN THE CARIBBEAN (MOLLUSCA: PROSOBRANCHIA: CERITHIIDAE)

Richard S. Houbrick

*Abstract.*—*Cerithioclava garciai* occurs on the shallow-water banks of the Caribbean off Honduras and is the only living member of the Pliocene Caloosahatchian genus *Cerithioclava* Olsson and Harbison, 1953. The group was previously thought to be extinct and is here accorded full generic status. The species is the largest of all Caribbean cerithiids and closely resembles members of the Indo-Pacific genera *Rhinoclavis* and *Pseudovertagus.*

Specimens of a very large, distinctive cerithiid have recently been collected by fishermen in the western Caribbean on the shallow-water, continental shelf off Honduras. These shells, sent to me for identification by Dr. E. Garcia, proved to represent an undescribed species in the genus *Cerithioclava* Olsson and Harbison, 1953, a taxon previously thought to be extinct and limited to the Tertiary Caloosahatchian Province of Florida. The genus *Cerithioclava* includes two described and one undescribed fossil species.

Although only three specimens of the new species were available for study, the discovery of a living *Cerithioclava* was deemed sufficient justification for immediate description. A description of the new species and a discussion of the genus *Cerithioclava* follows.

## Genus *Cerithioclava*
## Olsson and Harbison, 1953

Type species, by original designation: *Cerithium caloosaensis* Dall, 1892.

*Remarks.*—This taxon was regarded as a subgenus of *Cerithium* Bruguière by Olsson and Harbison (1953) although they noted a close affinity to *Rhinoclavis* Swainson and indicated that it might be considered a division of that genus rather than of *Cerithium.* In a previous monograph (Houbrick 1978:119), I considered *Cerithioclava* to be a subgenus of *Pseudovertagus* Vignal but pointed out that *Cerithioclava* lacks the distinctive cancellate sculpture of the early whorls so distinctive of *Pseudovertagus* species and, in addition, does not have the central columellar fold characteristic of members of the genus *Rhinoclavis. Cerithioclava* species differ considerably from Caribbean *Cerithium* species by being much larger and in having a long narrow anal canal that is an adpressed extension of the outer lip. In retrospect, I think *Cerithioclava,* comprising four species, differs sufficiently from other cerithiid genera to be given full generic status. It represents an independent cerithiid radiation, having its roots in the Caloosahatchian Province (Petuch 1981) of the northwestern Caribbean and Florida, and has as its sole survivor the new species described herein. There are two described fossil species: *Cerithioclava caloosaensis* (Dall, 1887) and *C. dalli* (Olsson and Petit, 1964). Another fossil species from the Burmont Formation of the Miami area, is undescribed.

## *Cerithioclava garciai,* new species
Fig. 1, Table 1

*Description.*—Shell large, up to 86.5 mm in length, robust, turreted, comprising 15–

18 slightly convex whorls sculptured with 0–9 axial plications per whorl and with numerous fine spiral and sinuous axial striae. Axial plicae strongly developed on earlier whorls, weaker on last 3. Each whorl having broad subsutural constriction that divides axial plicae into 2 rows, producing an upper subsutural spiral cord with smooth nodular elements, lower remainder of whorl having axial plicae and giving shell an overall wrinkled appearance. Axial plicae absent on body whorl and sometimes very weak on last 3–4 whorls. Fine axial and spiral striae coarser at base of each whorl and on entire body whorl, producing a microscopic beaded texture. Large, prominent varix opposite outer lip of body whorl. Suture impressed, slightly wavy. Aperture (excluding long extension of anal canal) round-ovate, nearly one-fourth shell length. Anterior siphonal canal long, reflected upwards toward the left. Columella concave, smooth, thick and with strong lip. Outer lip smooth, thick, and greatly extended and adpressed to body whorl, where it joins upper columellar lip to form long anal canal, latter almost closed. Tip of anal canal slightly detached from body whorl. Distal end of anal canal lying adjacent to suture of body whorl. Protoconch unknown. Shell color white to light brown, with light tan spiral threads and spiral band of darker brown subsutural nodules. Aperture white. Operculum and radula unknown.

*Type locality.*—Off Great Corn Island, Nicaragua; 24 meters.

*Holotype* (Fig. 1, A).—USNM 849023; length 77.4 mm, width 24 mm.

*Paratypes* (Fig. 1, B–C).—Two specimens, USNM 849024; lengths 84.7 mm and 66 mm.

*Etymology.*—Named for Dr. Emilio Garcia of Lafayette, Louisiana, who sent the specimens to me.

*Remarks.*—This large, distinctive species is unlike any other cerithiid in the Caribbean or Florida. At first glance it resembles the large *Rhinoclavis* and *Pseudovertagus* species found in the Indo-Pacific, but although it shares with them a long reflected anterior canal, it is very different in other characters. Aside from size, the chief distinguishing character of *Clavocerithium garciai* is the long extension of the outer lip, adpressed onto the body whorl and forming a long, narrow anal canal. The three specimens upon which this description is based were obviously collected alive as may be seen from shell condition and traces of the animal's mantle, dried in the aperture of the shells. Unfortunately, there were no remains of the radula or operculum. Although only three specimens are available for comparison, the range of sculptural variation is considerable, one specimen lacking or having weaker axial plications on the last four whorls. Shell color is likewise variable, one specimen being highly pigmented, the others being whiter and having only weak color patterns.

*Clavocerithium garciai* does not resemble either of the two described fossil species from Florida, but an undescribed fossil species from the Miami area, shown to me by Dr. E. Petuch, is undoubtedly closely related, ancestral, or even conspecific. However, *Cerithioclava garciai* does not appear to be a secondarily derived species, sensu Petuch (1981:1125), since it shows only slight divergence from the Florida fossil species.

The Honduran shelf region is poorly known, but recently many unusual species have been collected there by shrimp and lobster boats based at Roatan Island, Honduras. Large carnivorous prosobranchs, such as volutes, miters, and fasciolariids have turned up in this locality and several new species have been described. Petuch (1981:1110–1111) noted that this region contained many extant elements of the "Neogene Caloosahatchian Molluscan Province," and that a number of relict genera and species complexes have undergone secondary speciation. The discovery of a living *Cerithioclava* species in this locality supports Petuch's (1981:1125, 1982:292) sug-

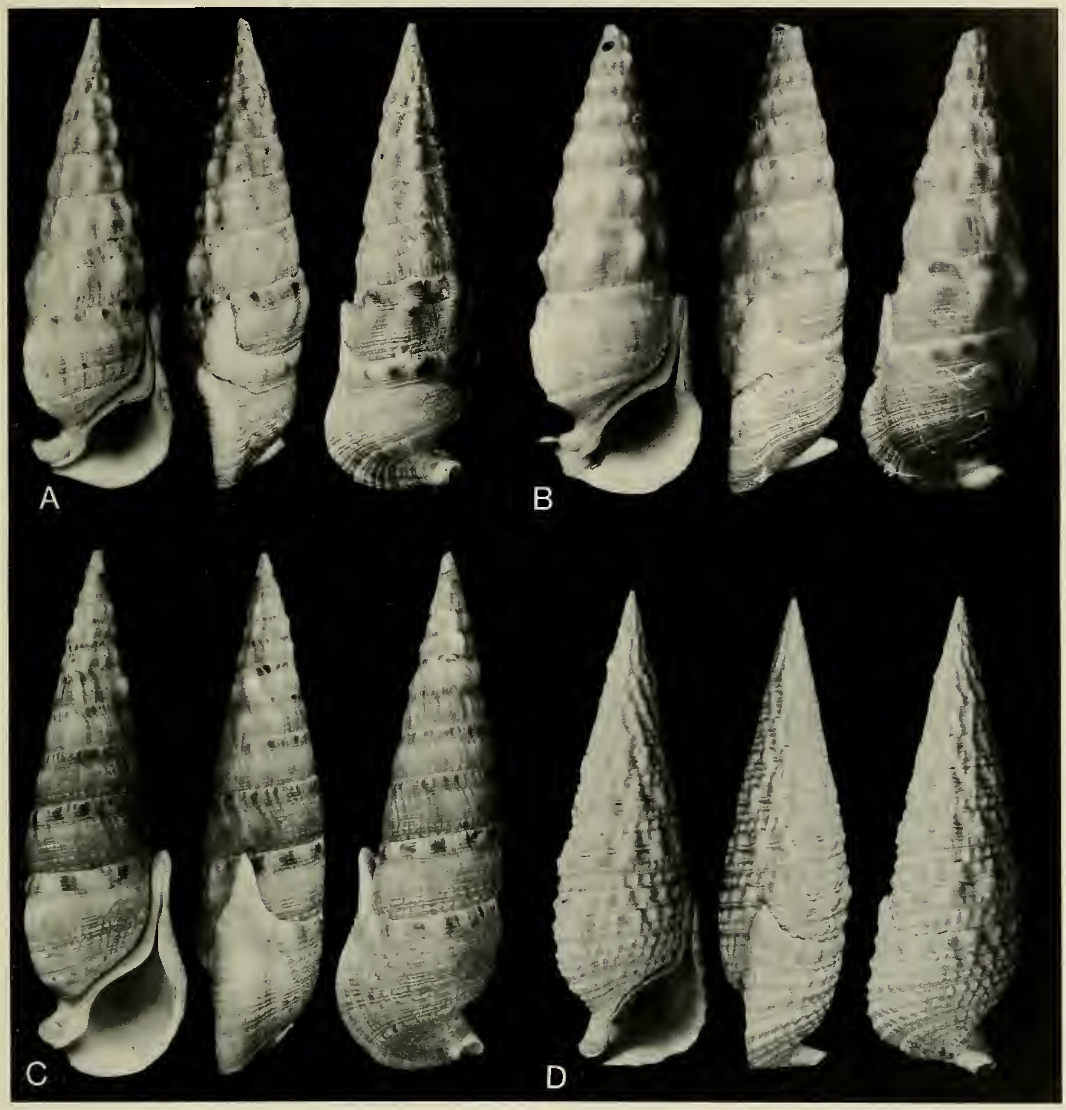

Fig. 1. A–C, *Cerithioclava garciai,* 24 meters off Great Corn Is., Nicaragua: A, Holotype (USNM 849023, length 77.4 mm); B, Large, darkly pigmented specimen with weak axial sculpture, paratype (USNM 849024, length 66 mm); C, Paratype (USNM 849024, length 84.7 mm); D, *Cerithioclava caloosaensis* (Dall, 1887), type species of the genus, from the Caloosahatchee of Florida, Tertiary (USNM 22383, length 60.3 mm).

gestion that the region is a Caloosahatchian relict pocket. A map showing the extent of this relicit pocket region was presented by Petuch (1981:1122, fig. 21).

Due to the limited collecting data, not much may be said about the ecology of this species. Live-collected specimens show calcareous and fine algal growth and other fouling organisms on the entire dorsal surface of the shell while the ventral portion is smooth and clean, indicating that this species is a partial burrower on sandy or rubble bottoms. The long anterior and anal siphons allow the animal to maintain a clear flow of water through the mantle while the shell is partially buried. Breakage scars and the bro-

Table 1.—Shell measurements of *Cerithioclava garciai*. (Total length and number of whorls estimated in shells with damaged tips. All measurements in mm.)

| Statistic (n = 3) | $\bar{x}$ | SD | Var. | Range |
|---|---|---|---|---|
| Length | 79.33 | 7.01 | 32.7 | 72.5–86.5 |
| Width | 24.33 | 1.53 | 1.56 | 23–26 |
| Length body whorl | 31.93 | 2.18 | 3.18 | 30–34.3 |
| Aperture length | 20.30 | 2.87 | 5.49 | 18.4–23.6 |
| Aperture width | 13.70 | 1.30 | 1.13 | 12.9–15.2 |
| No. axial plicae | 6.33 | 4.62 | 14.22 | 0–9 |
| No. whorls | 16.33 | 1.53 | 1.55 | 15–18 |

ken shell tips show previous unsuccessful crab attacks on all three specimens.

It is remarkable that a species as large and distinctive as *Cerithioclava garciai* has remained unknown for so long in the Caribbean. One would expect that a large cerithiid, in a family characterized by herbivorous species that usually occur in abundance, would be common in its habitat and taken more frequently than the rarer carnivorous volutes. I suspect that this species is common, but as cerithiids are not regarded as collector's items they are probably thrown back by fishermen. This may explain why only a few specimens exist, to date. It is possible that other Caloosahatchian cerithiid taxa, such as *Ochetoclava* Woodring, previously regarded as extinct in the Western Atlantic (Houbrick 1978:89), may be found here, as well as other unusual molluscan elements that are of little interest to shell collectors. The region needs a thorough scientific survey.

## Acknowledgments

I thank Dr. Emilio Garcia for first calling my attention to this unusual species and for sending me the specimens described herein. Dr. David Reid, Smithsonian Postdoctoral Fellow, critically read the original draft of the manuscript and offered helpful suggestions. Photography was done by Mr. Victor Krantz, Smithsonian Photographic Services, National Museum of Natural History.

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# NOTES ON THE SPECIES OF *ALLOSQUILLA* AND *PLATYSQUILLOIDES* (CRUSTACEA: STOMATOPODA)

Carlo Froglia and Raymond B. Manning

*Abstract.*—A second specimen of an *Allosquilla* from the Adriatic Sea is reported, and *A. adriatica* Stevcic, 1979, is shown to be a synonym of *A. africana* (Manning, 1970). *Allosquilla* is compared with the related *Platysquilla, Mexisquilla,* and *Platysquilloides,* and the second species of *Allosquilla, A. lillyae* Manning, 1977, is transferred to *Platysquilloides.*

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The genus *Allosquilla* was erected by Manning (1977:64) for two species from off West Africa, *A. africana* (Manning, 1970) and *A. lillyae* Manning, 1977. *Allosquilla africana* was known from the unique holotype, a female 39 mm long, taken at a depth of 174–148 m off the Niger delta, and *A. lillyae* was known from fragments of two specimens taken in depths of 260–225 and 345 m in the Azores. Two years later a third species, *A. adriatica* Stevcic (1979:642), based on our then unpublished account (Manning and Froglia 1979:178), was described from a female, 67 mm long, taken in the Adriatic Sea in 130–150 m.

Manning (1977:65) pointed out that the species then assigned to *Allosquilla* differed from other genera of lysiosquilloids in lacking the mandibular palp, having four rather than five epipods, and in the number of papillae on the antennal protopod. *Allosquilla africana* was characterized as having two papillae on the antennal protopod, one small one mesially and one larger one ventrally, and *A. lillyae* was characterized as having one mesial and two ventral papillae. *Allosquilla adriatica* also was characterized as agreeing with *A. lillyae* and differing from *A. africana* in having one mesial and two ventral papillae (Manning and Froglia 1979: 179).

Subsequently, Holthuis (1984:132) reported two specimens of *A. lillyae* from the Azores in 52 m; one of these, a female, 42 mm long, was the first intact specimen of the species to be studied.

The discovery and description by Holthuis of a complete specimen of *A. lillyae* and the capture of a second specimen of a species of *Allosquilla* in the central Adriatic Sea by one of us (C.F.) prompted us to reexamine the species of *Allosquilla,* for the second specimen differed from the holotype of *A. adriatica* in several features that initially suggested it might belong to a different species.

## The Status of *Allosquilla adriatica*

The second specimen of *A. adriatica* from the Adriatic (Fig. 1), an adult female 70 mm long with ripe ovaries, was taken at a depth of 216–222 m during trawling investigations in the western Pomo Pit (net shot 42°50′N, 14°33′E, hauled 42°48′N, 14°47′E), a few miles south of the type locality, on 7 March 1981. It is preserved in the reference collection of the Istituto di Ricerche sulla Pesca Marittima in Ancona. We are able to add some color notes made in the field from the living specimen, and some data on morphology to the original description.

In life, the background color is olive brown, with the deep pink ovaries clearly visible through the background color. The rostral plate, ocular peduncles, and antennal peduncles are light brown, and the cornea is green. The raptorial claw is covered with

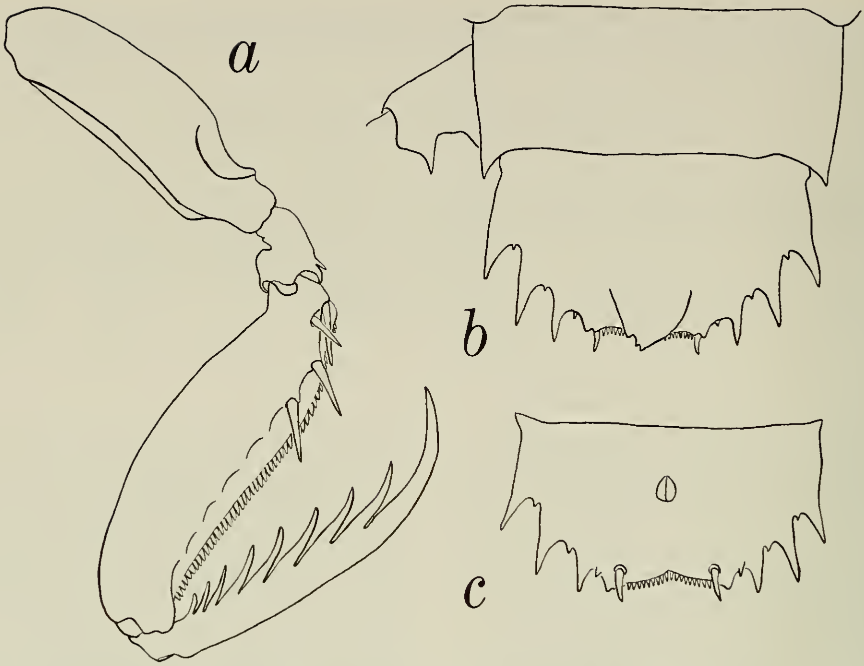

Fig. 1. *Allosquilla africana,* ♀, TL 70 mm: a, Claw; b, Sixth abdominal somite and telson; c, Telson, ventral view.

pink chromatophores, with a band of orange chromatophores proximally and brown chromatophores distally on the merus, and an orange spot on the propodus at the articulation with the dactylus. The thoracopods, pleopods, and uropods are clear. The edge of the telson is marked by a brownish white line.

Other measurements of this specimen, in mm, are as follows: carapace length 11.7; rostral plate length 3.3, width 3.2; cornea width 3.2; antennal scale length 3.9; telson length 6.1, width 10.4. There are only nine teeth on the dactylus of the claw (Fig. 1a); there are ten teeth on the claw of the holotype. There are five movable teeth on the uropod, the proximalmost very small, triangular, the remainder larger, spatulate; the holotype had three or four movable teeth on the uropod. The rounded lobe on the inner distal margin of the uropodal endopod is ornamented with 10–11 setae.

The main morphological difference between this specimen and the holotype of *A. adriatica* is in the posterior armament of the telson. The second marginal projection denticle is enlarged, so that the telson has three rather than two pairs of major, fixed marginal teeth lateral to the movable submedians, each separated by an intervening denticle. Also, the median dorsal projection on the telson (Fig. 1b) is asymmetrical; it probably has been damaged.

This specimen, like the holotype of *A. adriatica* (Fig. 2a, b), has one mesial and two ventral papillae on the antennal protopod (Fig. 2c, d). Reexamination of the holotype of *A. africana* reveals that it, too, has the same number of papillae (Fig. 2e, f). That was one of the more important characters used by Manning and Froglia (1979: 180–181) to distinguish these two species.

Manning and Froglia also used the following characters to separate the two species:

1. The submedian denticles are in two convex rows in *A. africana,* one transverse

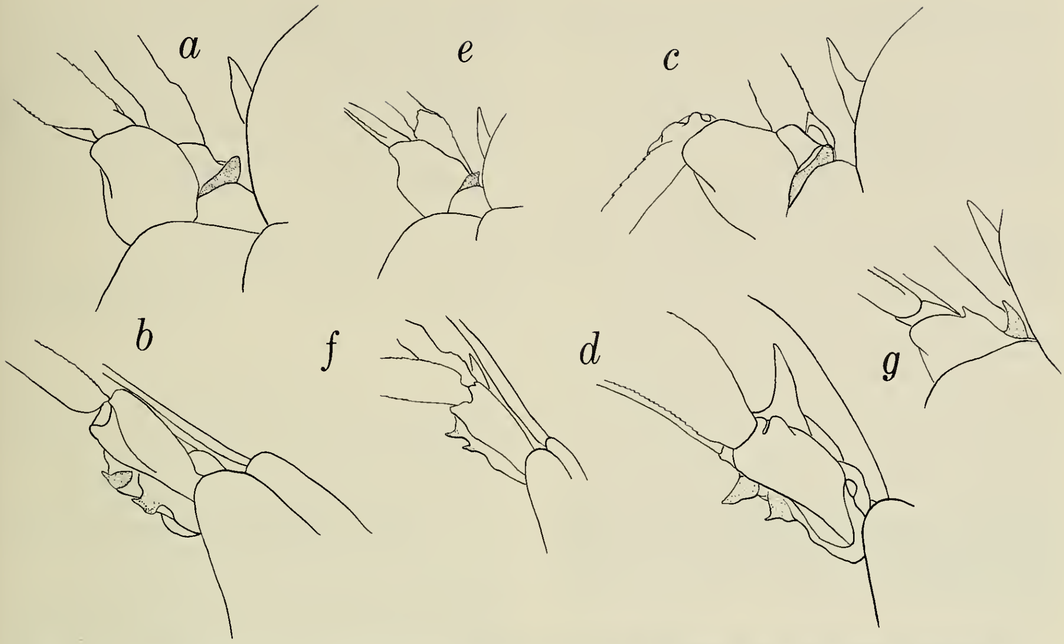

Fig. 2. Antennal protopod in dorsal (a, c, e, g) and lateral (b, d, f) views to show antennal papillae in: a, b, *Alllosquilla adriatica,* ♀ holotype, TL 67 mm; c, d, *A. africana,* Pomo Pit, ♀, TL 70 mm; e, f, *A. africana,* ♀ holotype, TL 39 mm; g, *Platysquilloides enodis,* ♀ holotype, TL 57.5 mm (note dorsal spine on antennal protopod).

row in *A. adriatica.* In the second Adriatic specimen, these denticles are arranged in two convex rows (Fig. 1c), as in the holotype of *A. africana.*

2. Both species were interpreted as having four intermediate marginal denticles on each side of the midline of the telson, with the first and third bluntly triangular and larger than the spiniform second and fourth denticles in *A. adriatica* and the first and third blunter but not much larger in *A. africana.* The second Adriatic specimen indicates that the telson has four distinct marginal teeth separated by intervening denticles, with the mesial one or two intermediate teeth smaller than the lateral two; the smallest of these marginal teeth is a low lobe flanking the movable submedian tooth. In this feature the holotypes of both *A. africana* and *A. adriatica* differ from the second Adriatic specimen.

3. The anterior prominences of the telson are less prominent in *A. adriatica* than in *A. africana.* This may be a function of size, for the holotype of the latter species is much smaller than either of the two Adriatic specimens.

4. Differences were noted in the armature of the basal segments of the walking legs in the two species. A reexamination of this feature in the types of the two species reveals that it is the same in all three specimens.

We conclude that *A. adriatica* is a synonym of *A. africana,* and that the holotype of *A. africana* is much younger than either of the two specimens collected in the Adriatic.

*Allosquilla* can be characterized as having 1 mesial and 2 ventral papillae on the antennal protopod and 4 pairs of fixed marginal teeth on the telson, the inner one or two of which can be much smaller than the lateral two; the marginal teeth are separated by smaller intervening denticles. In addition, *Allosquilla* lacks a distinct dorsal spine on the antennal protopod (Fig. 2a–f) and has

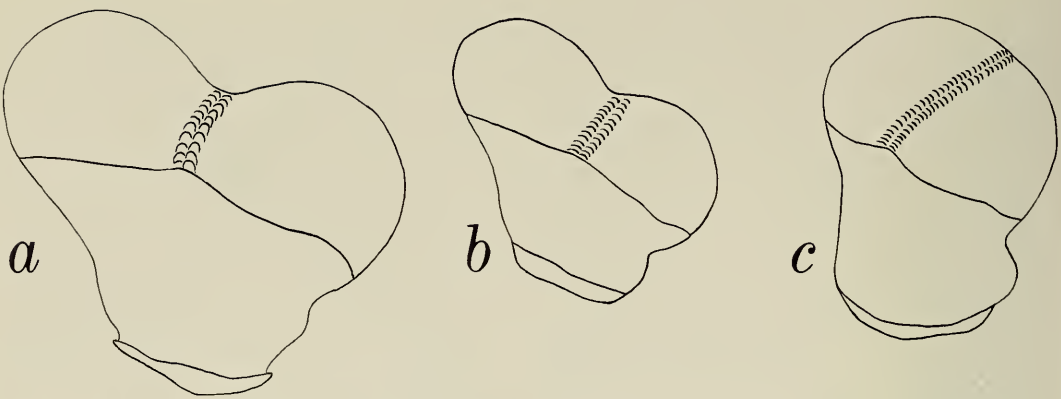

Fig. 3. Eyes of: a, *Allosquilla adriatica,* ♀ holotype, TL 67 mm; b, *A. africana,* ♀ holotype, TL 39 mm; c, *Platysquilla enodis,* ♀ holotype, TL 57.5 mm.

the cornea distinctly bilobed (Fig. 3a, b). In other features *Allosquilla* closely resembles *Platysquilloides.*

### The Status of *Allosquilla lillyae*

The account of a complete specimen of *A. lillyae* by Holthuis (1984:132) shows that it shares several features with *Platysquilloides enodis* (see Manning and Camp 1981: 593, fig. 2), as follows: the cornea is expanded laterally (Fig. 3c) but not distinctly bilobed as in *A. africana* (Fig. 3a, b); the rostral plate is subrectangular rather than distinctly cordiform; there is a distinct dorsal spine on the antennal protopod (Fig. 2g); the marginal armature of the telson comprises, on each side of the midline, four fixed teeth separated by intervening denticles; and the inner two pairs of teeth are small and distinctly spatulate, whereas the outer two pairs are produced into large, slender, sharp teeth.

In these features, *A. lillyae* closely resembles the west Atlantic *Platysquilloides enodis* (Manning, 1962) and differs from *Allosquilla africana.* We conclude that *A. lillyae* was incorrectly placed in *Allosquilla,* and we transfer it here to *Platysquilloides,* which until now was considered to be monotypic.

### Genera Related to *Allosquilla* and *Platysquilloides*

*Allosquilla* and *Platysquilloides* share many characters with two other genera of the family Nannosquillidae, *Platysquilla* Manning, 1967, and *Mexisquilla* Manning and Camp, 1981 (see Manning and Camp 1981 for accounts of these other genera). They differ from *Platysquilla* in having only one mesial papilla on the antennal protopod, a much broader cornea, only four rather than five epipods, and a much smaller median projection on the telson; they also differ in lacking a pair of spines ventrally on the sixth abdominal somite. The eyes of *Platysquilla* resemble those of *Mexisquilla* and *Platysquilloides* in being somewhat broadened, not distinctly bilobed as in *Allosquilla. Allosquilla* and *Platysquilloides* differ from *Mexisquilla* Manning and Camp, 1981, in several features, including the anteriorly spined rostral plate, having four rather than three epipods, and in overall size; species of *Mexisquilla* are not known to exceed 20 mm in length, whereas species of *Allosquilla* are as large as 70 mm and species of *Platysquilloides* as large as 67 mm are known (Howells, Karp, and Langton 1980).

*Platysquilla* differs from all of these genera in having four papillae on the antennal protopod and slender, non-spatulate movable spines on the outer margin of the uropodal exopod, and *Platysquilloides* differs from all of these genera in having a distinct dorsal spine on the antennal protopod.

## Acknowledgments

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# A SMALL TRAP FOR COLLECTING CRUSTACEANS IN SHALLOW WATER

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*Abstract.*—Results from using a small, inexpensive trap, made from plastic water-sampling bottles, to collect crustaceans in shallow water, are reported. The traps can be used to collect both decapods and microcrustaceans.

In 1982, M. Türkay published a summary of results on the use of a small trap for collecting shrimps. In the Aegean Sea, the trap, developed by H. Thiel, University of Hamburg, and Türkay, yielded representatives of eight species of caridean shrimps, of which one, *Lysmata seticaudata* (Risso), was collected only with the trap.

Türkay's paper was originally presented at the COLLOQUIUM CRUSTACEA DECAPODA MEDITERRANEA II, held in Ancona, Italy, in 1979, and I had an opportunity to hear the original presentation. While listening to Türkay's talk I realized that he had come up with an excellent supplement to any field kit: a small, inexpensive, portable trap for decapods.

## The Trap

The Thiel-Türkay traps (Fig. 1) can be made from a 1-liter narrow-mouthed polyethylene bottle, with both the top and bottom cut off. The top is inverted and fastened into the end of the bottle to form a funnel-shaped opening. Completed traps measured 12.5 cm long, 9 cm in diameter, with an opening of 2.5 cm. The bottom is replaced by any mesh desired, held in place with a hose clamp. A weight may be attached at the mouth end to hold the trap on the bottom. The narrow mouth allows only small animals to enter the trap, which can be baited and emptied by removing the hose clamp. As many traps as desired can be run in a string.

## Results

My first opportunity to use the trap came while I was on Carrie Bow Cay, Belize, in 1982. Three traps, baited with leg segments of spiny lobsters, were set in about four feet of water in coral and shell rubble off the dock on the western side of the island. Over a 24-hour period, no decapods were taken in the traps, and after about 36 hours still no decapods were taken. The traps were then essentially abandoned, forgotten for another two days.

When the traps were finally raised, they were allowed to drain upon the dock, where a variety of small crustaceans appeared in the drain water. Included were more than 50 specimens of a red nebaliacean; one cyclopoid, one calanoid, and eight harpacticoid copepods; three gammaridean amphipods; two cirolanid isopods; eight myodocopid and three podocopid ostracodes; and one small spider crab. This catch demonstrated that the traps could be used to collect crustaceans other than decapods.

In October 1982, these traps were used in several of the marine caves in Bermuda (see Sket and Iliffe 1980), where Thomas M. Iliffe, C. W. Hart, Jr., and I were studying the cave shrimps (Hart and Manning 1981). These little traps, usually baited with fish, yielded up to four specimens of the Cuban cave shrimp, *Barbouria cubensis* (Von Martens), when left overnight. In addition, in Wonderland Cave, formerly open as a commercial cave for tourists, a trap set and left

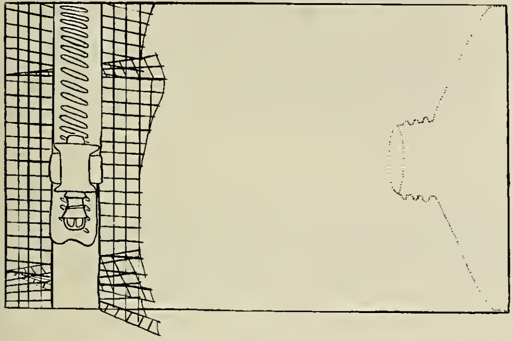

Fig. 1. Diagrammatic cross-section of the Thiel-Türkay bottle trap.

for a week yielded a specimen of *Barbouria* as well as an undescribed ostracode related to the Thaumatocyprididae.

In October 1983 the traps were again used on Bermuda in several different caves in the Walsingham system. Traps left in the water for 24 to 48 hours yielded a fish, *Bathygobius,* several crabs of the genus *Panopeus,* at that time not known to occur in the cave systems, and up to 10 specimens of *Barbouria.* These traps all had been baited with pieces of fresh fish.

Three traps baited with crushed specimens of *Panopeus* were left in an open pool in an area near the caves for five days, and two baited with fish heads were left in a small sink hole in the Walsingham cave system for four days. Both yielded the same kind of organisms. Those in the open pool yielded eight specimens of the calanoid copepod, *Exumella,* and four harpacticoid copepods. Those in the sink hole yielded 23 specimens of *Exumella* and five harpacticoids.

In September 1984 these traps, baited with fish, were left overnight in mangrove roots on the east side of Little Jim Island, in the Indian River just north of the Fort Pierce Inlet, St. Lucie County, Florida (=RBM field station 84-10, 20 Sep 1984). There several specimens of *Periclimenes americanus* (Kingsley) and *Leander tenuicornis* Say were taken. *Periclimenes americanus* was one of the most abundant decapods taken in grass beds in the Indian River in an earlier study (Gore, Gallaher, Scotto, and Wilson 1981), but *L. tenuicornis* apparently was not found in the grass beds in that survey.

## Remarks

The Thiel-Türkay trap is an effective piece of gear for collecting a wide variety of crustaceans in the field. With a fine mesh cover over the opening at the bottom of the bottle, small crustaceans are collected readily. The traps should be left in the water for relatively long periods of time, even for several days, when used to collect smaller crustaceans. When larger crustaceans are sought, the traps can be left out for much shorter periods, even overnight. Some experimental work on effectiveness of different types of baits in different habitats for varying periods of time would be most interesting.

## Acknowledgments

The samples of microcrustaceans from Carrie Bow were sorted and identified to group by Anne C. Cohen; Douglas C. Barr sorted and identified the copepods from Bermuda. Thomas M. Iliffe spent many hours introducing C. W. Hart, Jr. and me to the caves in Bermuda. Elizabeth Allen, Lilly King Manning, William D. Lee, and Marilyn Schotte provided assistance in the field and in the laboratory. This paper is contribution no. 1052 from the Bermuda Biological Station and contribution 152 from the Smithsonian Marine Station at Fort Pierce.

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# *TRIDENTELLA RECAVA,* A NEW ISOPOD FROM TILEFISH BURROWS IN THE NEW YORK BIGHT (FLABELLIFERA: TRIDENTELLIDAE)

Thomas E. Bowman

*Abstract.*—*Tridentella recava,* n. sp., described from tilefish burrows at depths of 180–304 m on the New York Bight, is characterized by its large size (up to 25.8 mm), its excavated telsonic apex, and the spines on the margins of the uropods. It lives in secondary burrows within the tilefish burrows.

The tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, a large fish reaching 60 pounds is the object of a major fishery along the east coast of the United States and the Gulf of Mexico. It occurs on the outer continental shelf at depths between about 100 m to more than 300 m, and is restricted to a rather narrow band of bottom water that remains between 9–14°C year round. It constructs burrows whose function appears to be to provide refuge from predators. Several species of crustaceans and fishes are associated with the tilefish burrows (Able et al. 1982, Grimes et al., in press). The isopod described below is a previously undescribed associate in tilefish burrows.

### Family Tridentellidae Bruce, 1984
### Genus *Tridentella* Richardson, 1905
### *Tridentella recava,* new species
Figs. 1–3

*Material.*—All collected with the R/V *Johnson Sea Link II.*—Dive 901, sample 3, 40°00.91′N, 70°05.79′W, 242–304 m, 29 Jul 1984: juv. ♂ 9.9 mm; juv. ♀ 10.1 mm, USNM 227074.—Dive 906, sample 10, 40°01.05′N, 70°20.98′W, 196–230 m, 31 Jul 1984: 2 ♀ without oostegites, 20.0 and 24.6 mm, USNM 227073.—Dive 909, sample 6, 40°02.96′N, 70°20.84′W, 180–195 m, 2 Aug 1984: 2 ♀ without oostegites, 24.1 and 25.0 mm; ♂ 20.5 mm; ♂ in 2 fragments; 4 mancas, 5.9, 6.0, 6.3, and 6.3 mm, USNM 227072.—Dive 909, sample 8, 40°02.69′N, 70°21.35′W, 180–195 m, 2 Aug 1985: ♀ without oostegites, 25.2 mm; juv. ♀ 10.2 mm; juv. ♀, damaged; ♂ without head, USNM 227071; ♀ with empty marsupium, 25.8 mm (holotype, USNM 227070). All specimens listed, except the holotype, are paratypes.

*Description.*—Length up to about 26 mm, about 2.4 × as long as wide. Head with small pointed rostrum meeting frontal lamina and slightly separating bases of antenna 1. Eyes large, with well developed facets. Pereonite 1 with complete transverse furrow; pereonites 2–3 with lateral furrows. Coxae 2–3 rounded posteriorly, not produced posteriorly; coxae 4–7 progressively more pointed and produced posteriorly, coxa 7 reaching pleonite 3. Pleonites 1–3 progressively wider and more produced posteriorly; pleonite 4 about as wide as pleonite 3, produced posterolaterally to midlength of peduncle of uropod. Pleonite 5 covered laterally by pleonite 4. Pleotelson nearly 1.5 × as wide as long, subtriangular; lateral margins slightly convex, armed with short setae; apex with U-shaped excavation, base of excavation crenulate, with short setae between the crenulations. Antenna 1 peduncle segment 3 about 1.7 × length of segments 1 and 2 combined; flagellum about 21-merous, segments distal to segment 4 each bearing 2–3 esthetes. Antenna 2 reaching pereonite 3 or 4; peduncle segment 5 about ⅓ longer

Fig. 1. Clay from margin of tilefish burrow, collected from submersible by grab sampler on manipulator arm and broken to show *Tridentella recava* in its burrow.

than segment 4; flagellum with about 34 segments.

Frontal lamina pentagonal, moderately elongate. Clypeus narrow, extending laterally well beyond labrum; latter with convex free margin. Mandible with narrow 2-pronged incisor; molar triangular, fleshy, with hirsute margin; segment 2 of palp with several rows of long setae on distal ⅖; segment 3 with closely spaced row of shorter setae and a few longer apical setae. Maxilla 1 exopod with 5 long terminal spines and 5 short subterminal spines; endopod less than half length of exopod, with 2 short subterminal setae. Maxilla 2 apex with about 5 scalelike spines with 3 or 4 teeth; proximal to these a patch of smaller bicuspid spinules. Maxilliped with narrow endite bearing a few terminal setae, reaching distal margin of palp segment 3.

Pereopods 1–3 similar, prehensile; pereopod 1 somewhat stouter than pereopods 2–3. Carpus with strong spine on posterodistal corner; posterior margin of merus with row of shorter spines. Pereopods 4–7 slender; distal corners of segments, except basis, with groups of long spines.

Pleopod 1 exopod with proximal spine on lateral margin. Pleopods 1–5 with 8, 7, 7, 6, 0 retinacula. Exopods of pleopods 3–5 divided by transverse suture. Appendix masculina of pleopod 2 widening distally into lanceolate tip reaching slightly beyond distal margin of endopod.

Uropods reaching beyond telson, endopod slightly longer than exopod, both rami rather narrow, pointed, margins armed with a few spines and close-set rows of setae.

*Etymology.*—From the Latin "recavus," hollowed or arched inward, referring to the apex of the telson.

*Comparisons.*—*Tridentella recava* is easily distinguished from the 10 known species of the genus (listed in Delaney and Brusca 1985) by its smooth pleotelson with an excavated apex. Seven of the 10 species have highly ornamented pleotelsons, and the three species with smooth telsons have smoothly rounded entire pleotelsons. Marginal spines on the uropods are found in *T. laevicephalax* Menzies (see Carvacho 1977), *T. quinicornis* Delaney and Brusca, 1985, and *T. recava,* but not in other species of *Tridentella.*

*Tridentella recava* is by far the largest known species, with a length of up to 25.8 mm. The other species range in length from 9 mm (*T. virginiana* [Richardson, 1905]; *T. japonica* Thielemann, 1910) to 20 mm in *T. ornamenta* (Menzies and George, 1972).

*Remarks.*—Thanks to the insight of Bruce (1984), *Tridentella* has been retrieved from the family Corallanidae, in which it had remained since 1905, and deservedly given its own family. Bruce's discussion of the features of the new family is clear and concise, except for the molar of the mandible. He describes the molar as "present," but in table 1 he states "molar vestigial." Elsewhere he says that the mandible is "essentially similar" to that of the Aegidae. The mandible of the Aegidae lacks a molar. Ac-

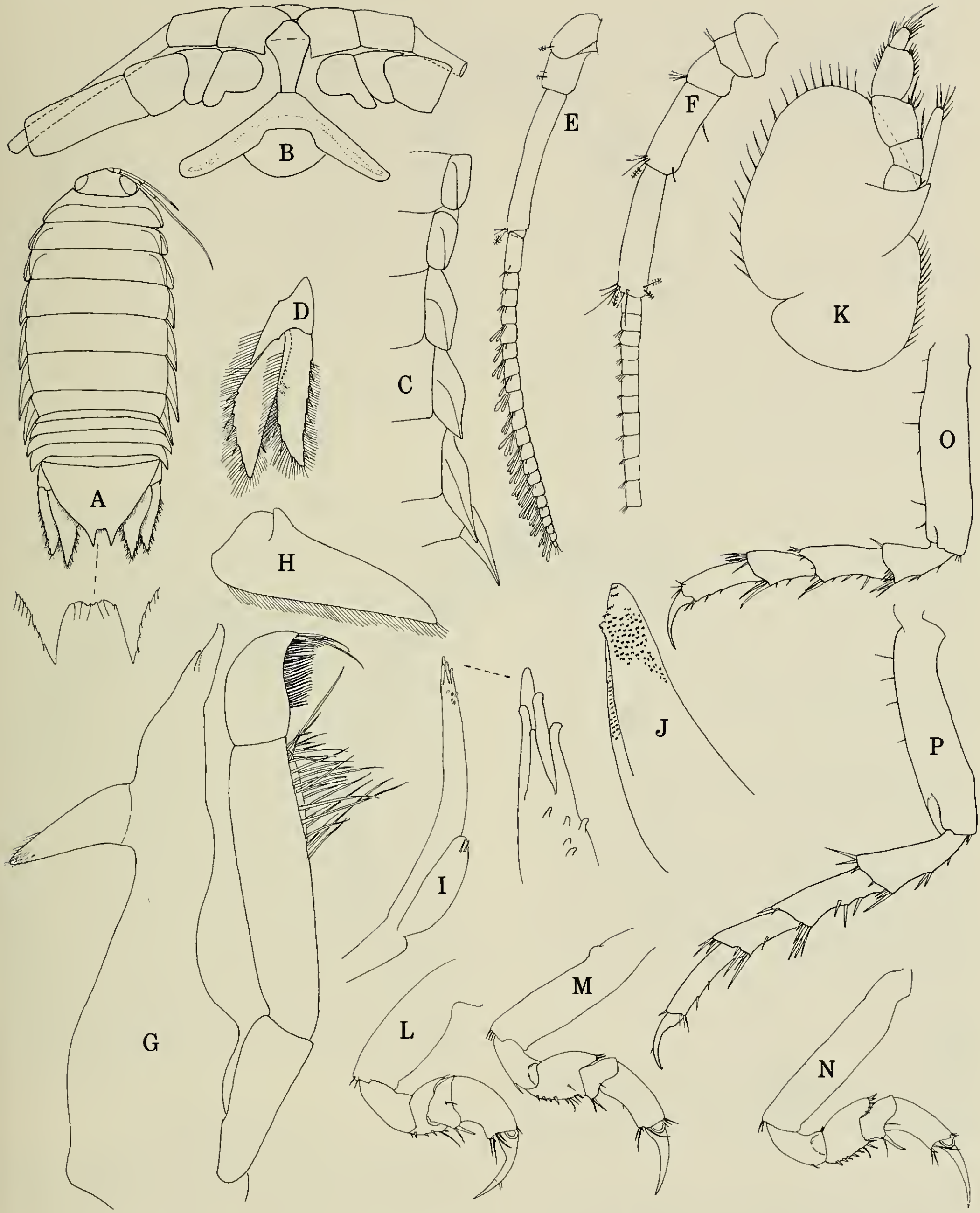

Fig. 2. *Tridentella recava,* 25 mm ♀, dive 909, sample 6: A, Habitus, dorsal; B, Head, ventral; C, Coxae 2–7, lateral; D, Uropod, ventral; E, Antenna 1; F, Antenna 2, proximal segments; G, Right mandible; H, Molar of right mandible; I, Maxilla 1; J, Maxilla 2; K, Maxilliped; L–P, Pereopods 1–5.

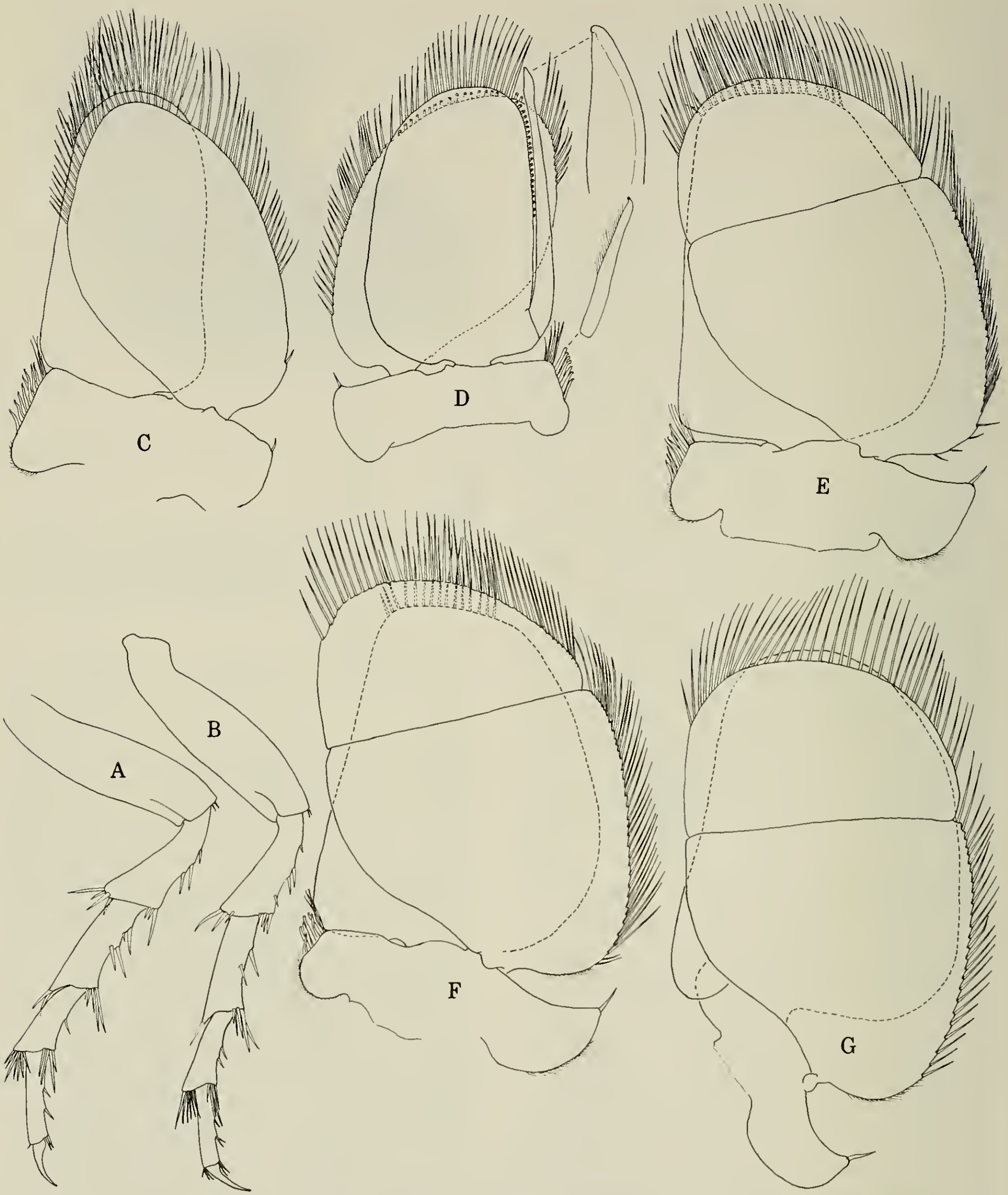

Fig. 3. *Tridentella recava,* A–C, E–G, 25 mm ♀, dive 9, sample 6; D, 20.5 mm ♂, dive 9, sample 6; A, Pereopod 6; B, Pereopod 7; C–G, Pleopods 1–5.

tually, as pointed out by Delaney and Brusca (1985), the molar in the Tridentellidae is essentially like that of the Cirolanidae, in which it is conical, fleshy, spinose on one margin, and sometimes setose. It cannot cut or grind, and presumably its function is to push food into the mouth. Its structure is clearly specialized, i.e. apomorphic, a fact overlooked by systematists who state that the Cirolanidae have generalized mouthparts.

*Habitat.—Tridentella recava* was found

in secondary burrows within the tilefish burrows. Clumps of clay collected showed isopod burrows of two kinds: larger burrows about 5.0 mm in diameter with a distinct whorled pattern of narrow marks resulting from excavation; smaller burrows about 2.0 mm in diameter without distinct excavation marks on the walls. These burrows are occupied by large and small specimens of *T. recava,* respectively. A third kind of burrow, 8–10 mm in diameter with excavation marks larger in scale and more widely spaced, may be produced by a goneplacid crab that is associated with tilefish burrows.

## Acknowledgments

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# SEXUAL DIMORPHISM AND A SEX-LIMITED POLYMORPHISM IN THE COPEPOD *PAROITHONA PACIFICA* NISHIDA, 1985 (CYCLOPOIDA: OITHONIDAE) FROM THE RED SEA

Frank D. Ferrari and Ruth Böttger

*Abstract.*—*Paroithona pacifica* Nishida, 1985, from the Red Sea is the first species of the genus known to exhibit polymorphism. Among females the number of external spines on swimming legs 3 and 4 exopods is variable; a pair of legs on one animal also may express variation in external spine number. Males do not exhibit similar variation within or among animals. Sexual dimorphism in the genus *Paroithona* is manifested in 18 differences in number, shape, and position of various exoskeletal elements. Differences in the number of segments and/or setae on swimming legs 2–4 are unique to this group relative to three other oithonid lineages.

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Farran (1908) established the genus *Paroithona* from an unspecified number of female specimens of *Paroithona parvula* found in two samples (SR 193—54°50′N, 10°30′W; SR 197—54°57′N, 10°51′W) collected below 1000 m off the northwest coast of Ireland with an open, conical net (mesh size about 20 microns). Farran's initial description noted that *Paroithona* differed from *Oithona* in having three well-developed lobes on the first maxilla (Mx1), swimming legs with 3-segmented exopods but 2-segmented endopods, and leg 5 with only one seta.

In describing four females of another species, *P. pulla,* taken in shallow, nearshore waters around Christmas Island in the Indian Ocean, Farran (1913) mentioned 2-segmented endopods on the swimming legs and the form (unspecified) of the mandibular palp as differentiating *Paroithona* from *Oithona. Paroithona pulla* differed from *P. parvula* by the reduced number of exopodal segments (2) on swimming leg 1 and the reduced number of outer spines on the exopods of swimming legs 3 and 4. Later, Sars (1918) redescribed females of *P. parvula* from the west coast of Norway, and emphasized the 2-segmented endopods of the swimming legs and the simple structure of the mandibular palp. Kiefer (1929) formalized these differences for *Paroithona*—reduced number of endopodal segments of swimming legs 1–4 and the single spine on the tip of mandible basipod 2—in his widely accepted definitions of the oithonid genera.

Greze (1963), Shmeleva (1964), and Razouls (1968) recently reported *P. parvula* from the Ionian Sea, Adriatic Sea, and Gulf of Lyon respectively in the Mediterranean Sea, and Nishida et al. (1977) collected *P. pulla* from Tokyo Bay, Sagami Bay, and the adjacent Kuroshio, in the northwest Pacific Ocean. Two new species, *P. flemingeri* from the North Atlantic Ocean off Venezuela and *P. pacifica* from the Pacific Ocean were described respectively by Ferrari and Bowman (1980) and by Nishida (1985). Descriptions of *P. pulla* females are still incomplete and one of us (FDF) recently determined that *P. flemingeri* has a one-segmented exopod with four setae on maxilla 1 and a swimming leg 1 exopod with five inner margin setae, not four as in the description of Ferrari and Bowman (1980). The genus *Paroithona* was not mentioned in Halim's (1969) review of

Red Sea copepods. However Delalo (1966) reported *P. pulla* from the northern part of the Red Sea in the winter of 1961/1962.

In describing *P. parvula,* Farran (1908: 90) noted that the numbers of setae observed "must be regarded as somewhat doubtful" due to the "minute size and extreme transparency" of the animals. In the intervening years, observations on oithonid copepods of the genus *Paroithona* have been hampered not only by small size of the animals but also by relatively small numbers of animals collected from one or a few localities. Morphological observations of preserved animals often are difficult because their exoskeleton does not stain easily.

In this paper we report 48 females and 11 males of *P. pacifica* from the Red Sea and expand the description to include a female sex-limited polymorphism in external exopodal spines. We also compile differences between female and male skeletal morphology, and compare this degree of sexual dimorphism to three other oithonid lineages.

## Material and Methods

Zooplankton samples were collected aboard the R/V *Valdivia* between 9 October and 9 November 1980 in the northern and central Red Sea, and in February 1981 in the central Red Sea. Stations are located over the Kebrit Deep and Atlantis II Deep, or a northern reference station located north of Kebrit Deep and sampled only in October 1980 (Table 1). Consecutive depth strata (usually 50 m intervals between 0–450 m) were sampled with vertical tows using a multiple opening-closing net (Weikert and John 1981) with 0.1 mm mesh size and an opening area of 0.25 $m^2$. Plankton samples were fixed in 4% formaldehyde-seawater solution buffered with hexamethylenetetramine. Specimens were sorted and preserved in 5% propylene glycol, 0.5% propylene phenoxetol and 94.5% filtered seawater (Steedman 1976).

Specimens of *Paroithona pacifica* were separated from samples during a comprehensive study of metazoan composition, abundance, and vertical distribution, whose results are presented by Böttger (1985). After examination of *Paroithona pacifica* specimens from the central Red Sea (Atlantis II Deep) in October, single samples from each region and season were checked for geographical and seasonal distribution of the species.

Specimens were cleared for morphological examination in lactic acid. After initial observations, including measurements of body length, each was stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water. After staining, specimens were transferred to lactic acid for dissection and final observations.

The following morphological abbreviations are used in the descriptive text and illustration legends:

*Body Segments*

Pr—prosome
Cph—cephalosome
Pg—pediger
Ur—urosome
CR—caudal ramus

*Appendages*

AI—antenna 1
AII—antenna 2
Mn—mandible
MxI—maxilla 1
MxII—maxilla 2
Mxp—maxilliped
P—swimming leg

*Appendage Elements*

Bspd—basipodal segment
Re—exopodal segment
Ri—endopodal segment
Li—inner lobe
Le—outer lobe
( )—adjacent segments fused
) (—adjacent segments incompletely fused

*Appendage Armament*

Se—external spine or seta
Si—internal spine or seta
St—terminal spine on P

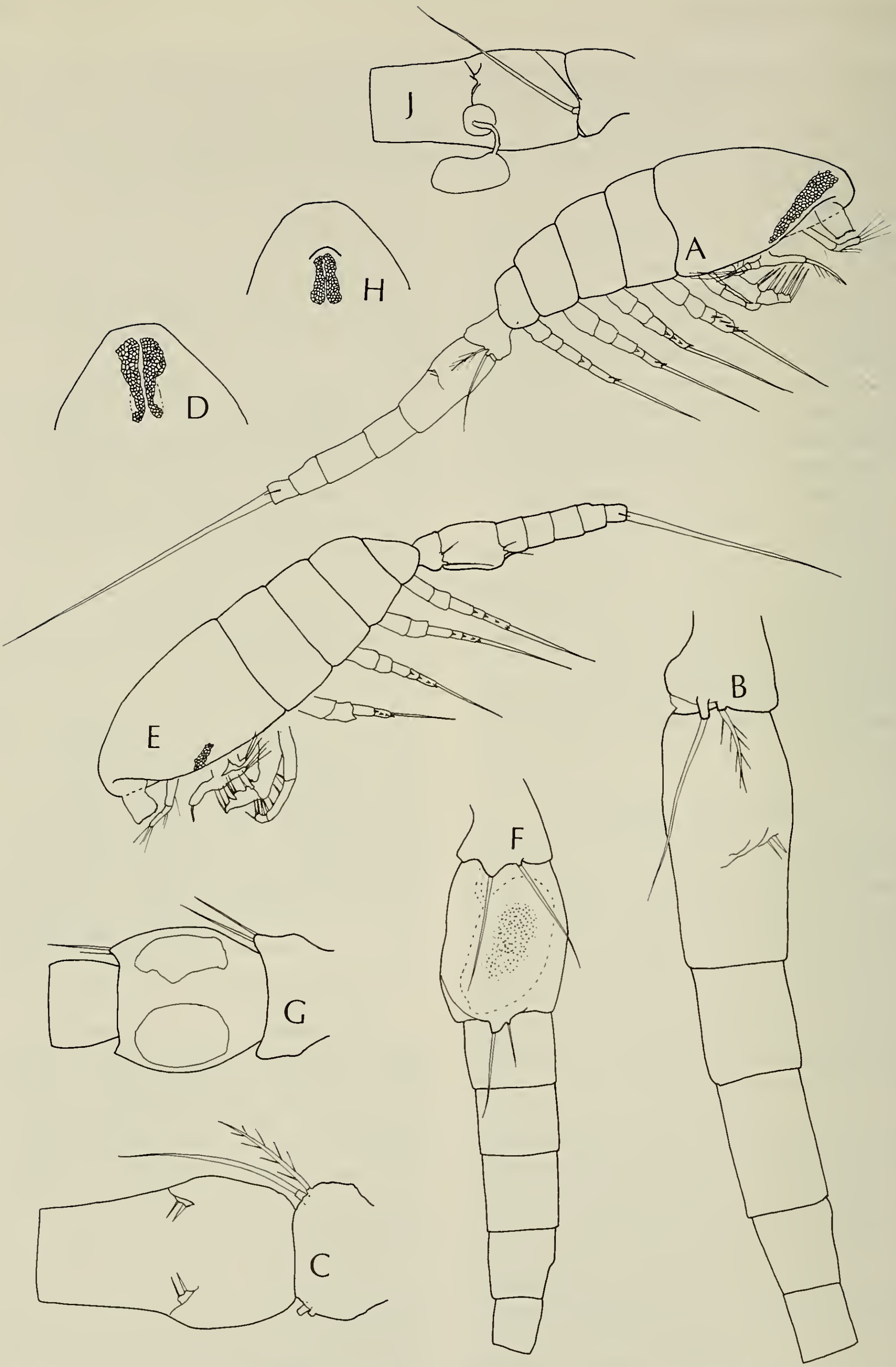

Fig. 1. *Paroithona pacifica* female: A, Lateral; B, Ur, lateral; C, Ur1–2, dorsal; D, Head, dorsal; male: E, Lateral; F, Ur, lateral; G, Ur1–3, dorsal; H, Head dorsal; female: J, Genital segment with spermatophore, lateral.

Table 1.—Occurrence of *Paroithona pacifica* in the Red Sea in autumn and winter 1980/1981.

| Station | Region | Position | Date | Depth (m) | Specimens |
|---|---|---|---|---|---|
| Va 29-03 | Northern Reference Station | 34°56.69′E,<br>26°45.36′N | 9 Oct 80 | 50–100 | 12 females<br>5 males |
| Va 29-23 | Kebrit Deep | 36°16.63′E,<br>24°43.32′N | 11 Oct 80 | 50–100 | 10 females<br>2 males |
| Va 29-125 | Atlantis II Deep | 38°04.20′E,<br>21°23.28′N | 27 Oct 80 | 60–80 | 16 females<br>4 males |
| Va 29-676 | Atlantis II Deep | 38°04.66′E,<br>21°22.56′N | 23 Feb 81 | 50–100 | 10 females |

## Results

### *Paroithona pacifica* Nishida, 1985
Figs. 1–6

*Paroithona pacifica* Nishida, 1985:109, figs. 64, 65.

*Description.*—Female: length 0.43–0.47 mm (33 specimens); Pr/Ur-1.3. Rostrum absent (Fig. 1A); forehead rounded dorsally; internally with paired clusters of polygonal cells (Fig. 1D). CR length 1.7 × width, armed (Fig. 2B) with 1 lateral seta, ventral surface hairs, 1 dorsal and 4 terminal setae; 2 setae, apparently dorsal and 2nd terminal, elongate (but see description of male). A1 (Fig. 2A) apparently 9 free segments, armature undetermined. A2 (Fig. 6A) 2 segments, 2nd with incomplete suture; respectively with 2 lateral and 5 lateral + 7 terminal setae. Mn gnathobase simple; Baspd2 (Fig. 5A) with 1 large terminal spine and 2 subterminal setae; Re 4 segments, 4–5 fused, with 5 setae, 2 terminal; Ri a non-articulated segment with 4 setae, 1 larger with setules. Mx1 (Fig. 5B) Li1 with 4 thick + 3 thin spines; Bspd2 with 1 large terminal spine and 1 subterminal seta; Re 1 segment with 4 setae; Ri 1 unarmed segment. Mx2 segmentation unclear, 3 inner and 1 terminal lobes armed as in Fig. 6B. Mxp 4 segments armed as in Fig. 6C. P1–4 (Figs. 3A, B, 4A, B); each Bspd2 with 1 small, outer seta. Bspd1P1 with 1 inner seta; Bspd2P1 with 1 inner spine + hairs—these elements absent on P2–4. Re 2–3P1 fused; Re 2–3P2 fused on anterior surface; RiP1–4 2 segments. ReSe 1-(3), 1-)3(, 1-1-2 or 1-0-2 or 1-0-1, 1-0-2 or 1-1-1 or 1-0-1 or 0-0-1 (not all combinations illustrated); Si 1-(5), 1-)6(, 1-1-5, 0-0-5; RiSe 0-1, 0-1, 0-1, 0-1; Si 1-6, 0-3, 0-3, 1-3; all setae simple except Ri 1P4 thicker. P5 (Fig. 1B) 2 simple, unarticulated, lateral cylindrical segments, with 1 seta each, dorsal with setules. P6 (Fig. 1B, C) 2 small spines, dorsal-most thicker.

Male: Length 0.37–0.40 mm (10 specimens); Pr/Ur-1.7. Rostrum absent (Fig. 1E); forehead rounded dorsally; small clusters of polygonal cells internal to upper lip (Fig. 1H). CR length 1.7 × width, armed (Fig. 2D) with 1 lateral, 1 dorsal, and 4 terminal setae; middle 2 terminal setae elongate; ventral hairs absent. A1 (Fig. 2C) a complicated digeniculate appendage. A2 (Fig. 6D) similar to female except distinctly 3-segmented. Mn gnathobase simple; Baspd2 (Fig. 5C) with 1 small thick spine and 1 thin seta terminally; Re segments incompletely fused, with 5 setae; Ri an articulated segment with 4 setae, largest with setules. Mx1 (Fig. 5D) Li1 with 4 thick + 3 thin spines; Bspd2 1 thick spine and 1 seta terminally; Re 1 segment with 4 setae; Ri 1 unarmed segment, fused to Bspd2. Mx2 segmentation unclear, 4 inner and 1 terminal lobes, armed as in Fig. 6E. Mxp apparently with 4 segments armed as in Fig. 6F. P1–4 (Figs. 3C, D, 4C, D); each Bspd2 with 1 small outer seta. Bspd1P1 with 1 inner seta; Bspd2P1 with 1 inner spine. Re 2 and 3P1 fused; ReP2–4 3 segments; RiP1 and 4 2 segments; RiP2–3

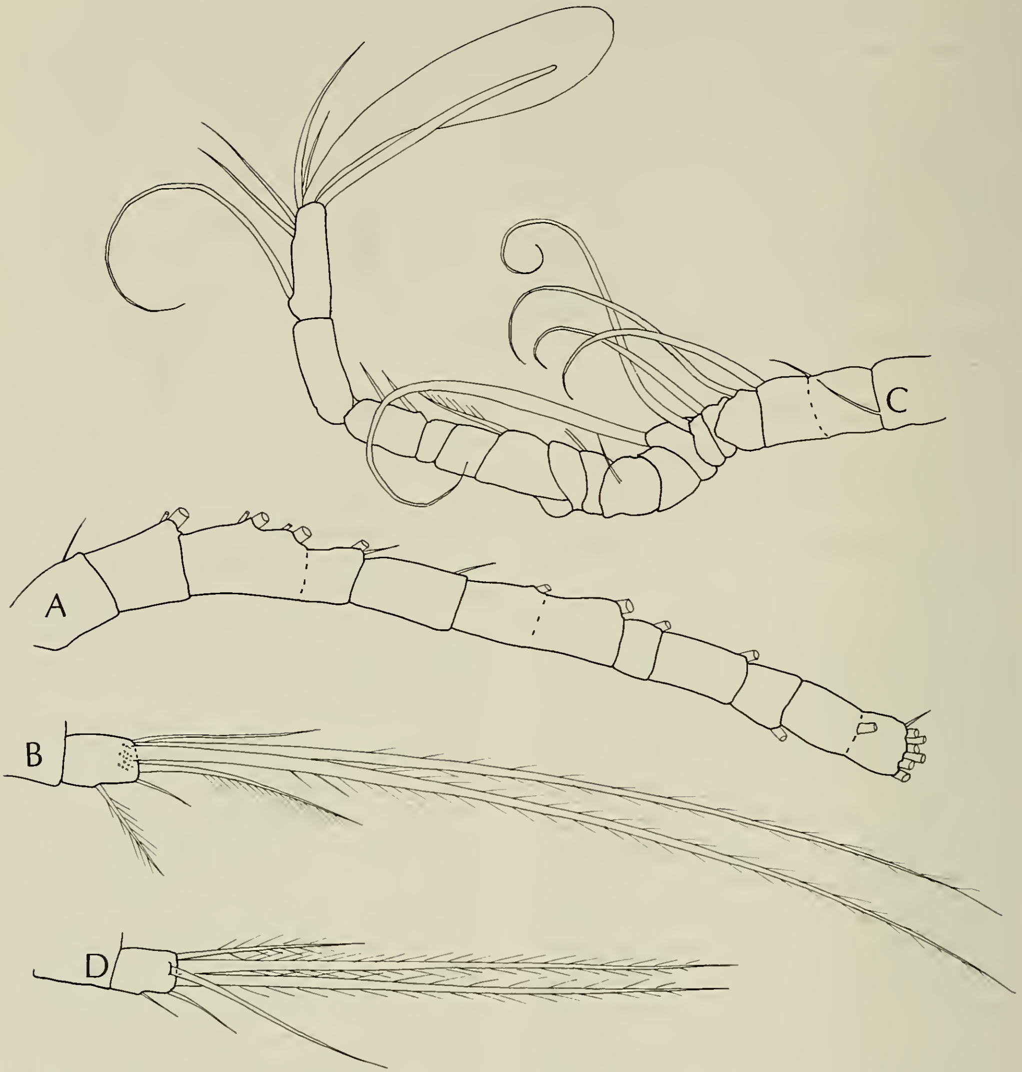

Fig. 2. *Paroithona pacifica* female: A, A1; B, CR; male: C, A1; D, CR.

3 segments. ReSe 1-(3), 1-1-2, 1-1-2, 1-1-2; Si 0-(5), 0-1-5, 0-1-5, 0-1-5; RiSe 0-1, 0-0-1, 0-0-1, 0-1; Si 1-6, 0-1-5, 1-2-5, 1-6; all setae simple except Ri 1P4 thicker. P5 (Fig. 1F) 2 unarticulated knobs, dorsal-most smaller, with 1 seta each. P6 (Fig. 1F, G) 2 unarticulated knobs, dorsal-most smaller, with 1 seta each.

*Remarks.*—Males of *P. pacifica* differ from *Paroithona pulla,* the only other *Paroithona* males described (Nishida et al. 1977) in swimming leg 2 endopod with 0-1-6 setae (1-2-6 for *P. pulla,* as illustrated) and a 2-segmented endopod (vs. 3-segmented for *P. pulla* by Nishida et al.) on swimming leg 4. Males available for this study exhibited variation in lateral curvature of the genital segment in dorsal view. This variation seems dependent on the degree of development of the spermatophores. Specimens with large, round spermatophores exhibited broadly curved, rounded genital segments; those with small, poorly-developed spermatophores had cylindrically-shaped genital segments.

## Discussion

Zooplankton samples taken over the Atlantis II Deep in late February 1981 contained only females of *P. pacifica.* Both sexes were found at two northern stations and over the Atlantis II Deep in October–November 1980; females bearing spermatophores were confined to the Northern Reference Station. Spermatophores on females (Fig. 1J) are suboval or kidney-shaped structures attached laterally by a fertilization tubule with a disc-like plug. Spermatophores occurred in pairs (three females) or multiple pairs (one female with four). Two females carried single spermatophores with remnants of a second plug; the spermatophore associated with this plug is considered to have been lost during sampling.

*Paroithona pacifica* occurred mainly at 50–100 m at all stations with an abundance of 60 adults/m$^3$ estimated from 60–80 m at Atlantis II Deep in October. The species did not show a clear relation to the thermohalocline which was situated between 40–80 m in October–November and 80–130 m in February. This subsurface distribution in the Red Sea is somewhat shallower and more compact than that reported by Nishida and Marumo (1982) for *Paroithona* spp. in the Indian Ocean and South China Sea.

Females of *Paroithona* available for this study exhibit variability in the number of external spines on swimming legs 3 and 4 exopods. Detection of such variability is complicated by the small size of these spines, especially on leg 4 where the proximal spine on exopod 3 may be found closely appressed to the exopod (Fig. 4B2). We carefully stained and examined all swimming legs of 28 females; 22 females with symmetrical exopods on legs 3 and 4 had 3 armament types:

| | | |
|---|---|---|
| leg 3 1-0-2, | leg 4 1-0-2; | 14 specimens |
| leg 3 1-0-2, | leg 4 1-0-1; | 7 specimens |
| leg 3 1-1-2, | leg 4 1-1-1; | 1 specimen |

Six females had asymmetrical armament on 1 pair of legs 3 and 4 (left/right):

leg 3 1-1-2/1-0-2, leg 4 1-0-2; 1 specimen
leg 3 1-1-2/1-0-2, leg 4 broken off; 1 specimen
leg 3 1-0-2/1-0-1, leg 4 1-0-2; 1 specimen
leg 3 1-0-2, leg 4 1-0-1/1-0-2; 2 specimens
leg 3 1-0-2, leg 4 1-0-2/1-0-1; 1 specimen

In some cases the variation may be artificial, resulting from difficulties in determining the presence of the thin subterminal 1st spine on exopod 3 of leg 4 (Figs. 4B1, 2). Presence of a thick, terminal spine on exopod 2 of leg 3 (two asymmetrical specimens) or leg 4 (one specimen) provides conclusive evidence of a sex-limited polymorphism occurring in *Paroithona pacifica.* Discovery of this sex-limited polymorphism in exopod armature has temporarily compromised use of these traditional structures in differentiating species of *Paroithona.* Whether this variation is widespread in the genus, confined to this species, or is a local phenomenon—perhaps a product of secondary contact between Atlantic and Indo-Pacific species in the vicinity of the Suez Canal—remains to be determined. Some morphs of *P. pacifica* from the Red Sea have the same spine count as Atlantic species *P. parvula* and *P. flemingeri* (Table 2). However, there is no overlap with the other Pacific species, *P. pulla.*

In *Paroithona,* a number of differences between females and males reflects the degree of sexual dimorphism. They comprise a) changes in numbers of elements, b) relative changes in shape or size of elements, c) changes in position of elements as follows: changes in number include:

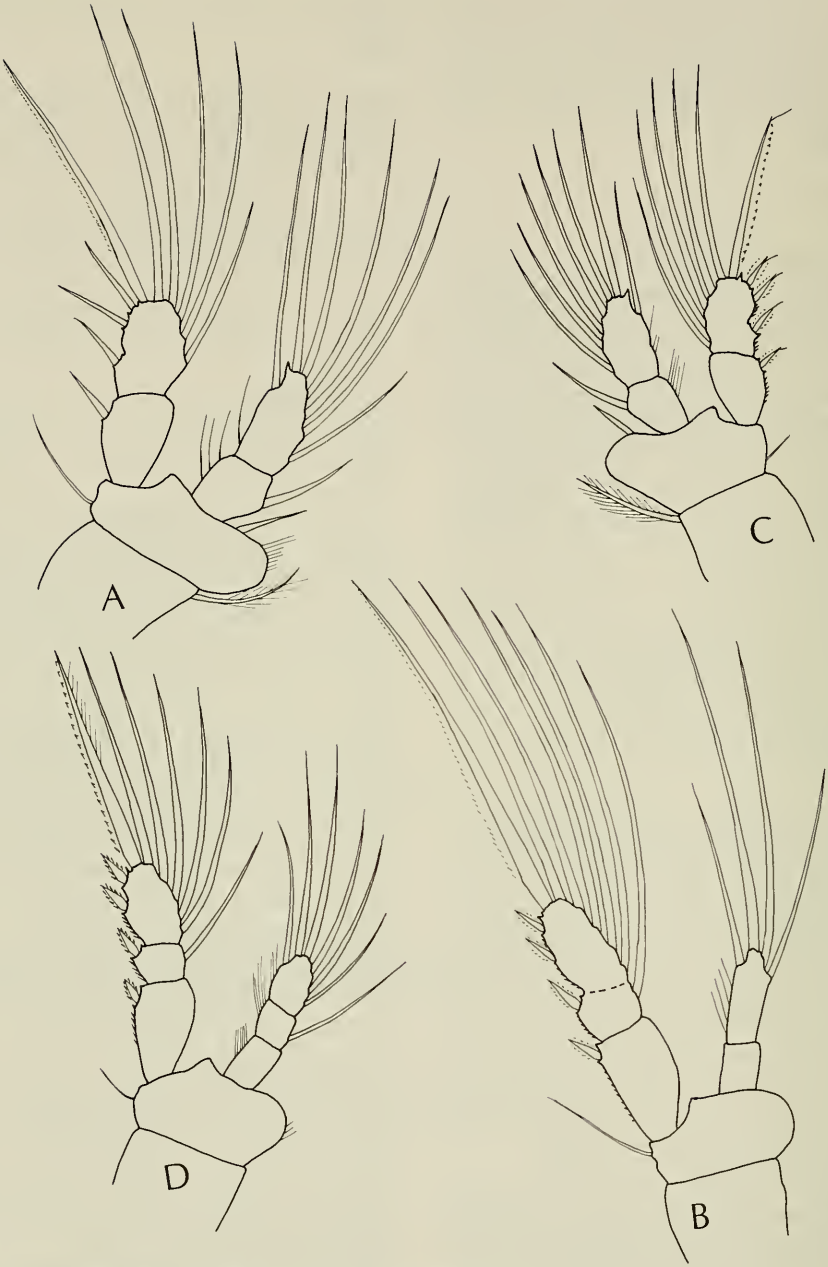

Fig. 3. *Paroithona pacifica* female: A, P1; B, P2; male: C, P1; D, P2.

1) antenna 1: male more segments and setae than female.
2) urosome: female 1 less segment than male.
3) swimming leg 2 endopod: female 1 less segment.
4) swimming leg 2 endopod: female 3 fewer setae.

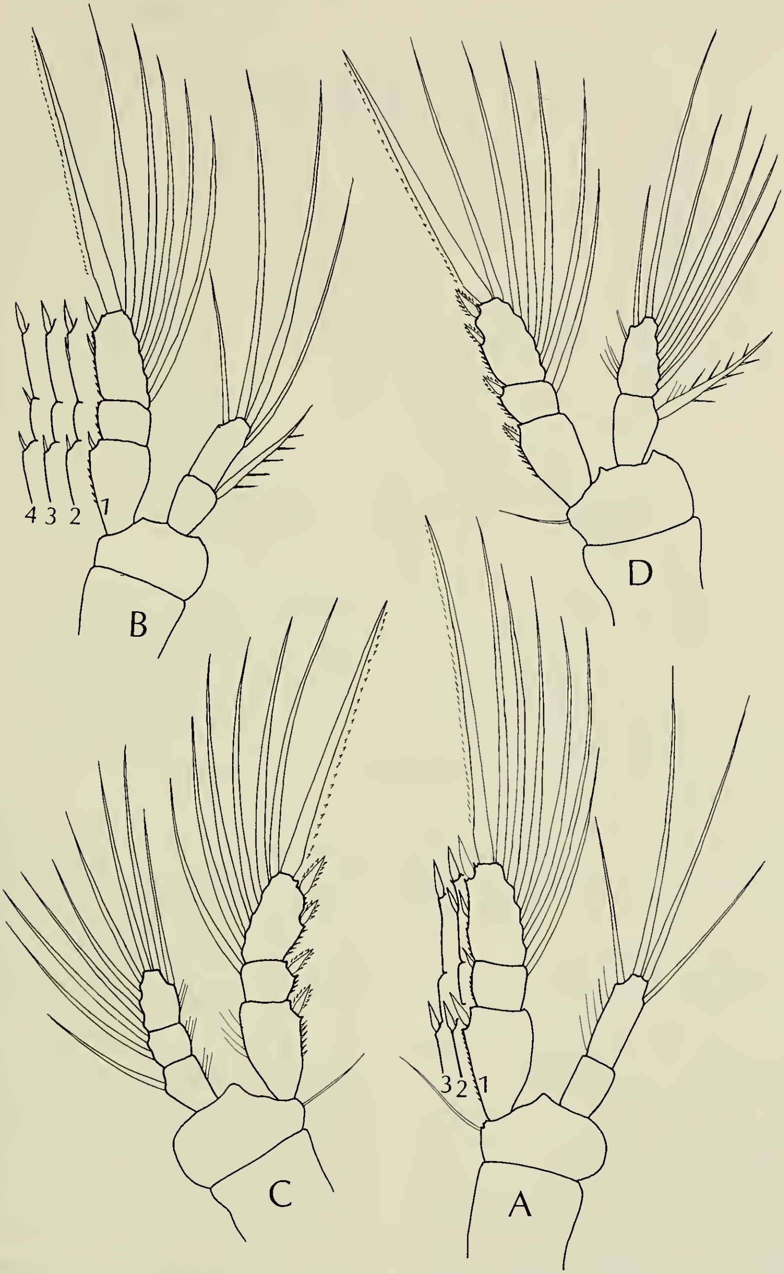

Fig. 4. *Paroithona pacifica* female: A, P3; B, P4; male: C, P3; D, P4.

5) swimming leg 3 endopod: female 1 less segment.
6) swimming leg 3 endopod: female 5 fewer setae.
7) swimming leg 4 exopod: female 1 less seta.
8) swimming leg 4 endopod: female 3 fewer setae.

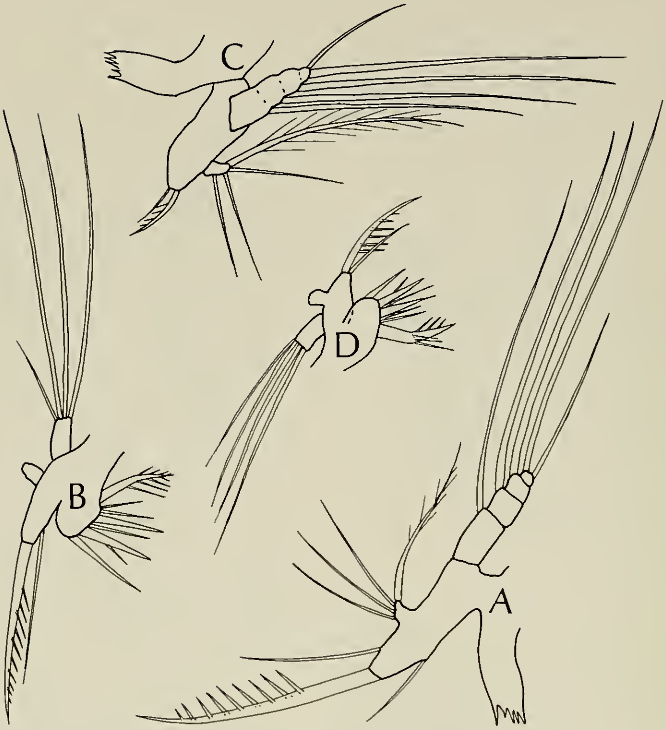

Fig. 5. *Paroithona pacifica* female: A, Mn; B, Mx1; male: C, Mn; D, Mx1.

9) swimming leg 2 exopod: segments 2 and 3 partly fused in male, completely fused in female.

Changes in shape or size include:

1) antenna 1: many segments and setae.
2) mandible exopod and basipod 2 armature: male smaller than female.
3) maxilla 1: male smaller.
4) maxilla 2: male smaller.
5) maxilliped: male smaller.
6) leg 5: male smaller.
7) leg 6 + setae: female smaller than male.
8) swimming leg 1: external spines of exopod, long and smooth in female, shorter and dentate in male.

Changes in position include:

1) leg 6: mid dorsolateral on fused urosome 2–3 in female, posterior and ventrolateral in male urosome 2.

Comparisons of degree of sexual dimorphism in *Paroithona* with other oithonid lineages is hampered by lack of descriptions of many males. At present we hypothesize four lineages: 1) "paroithona," all species of *Paroithona*; 2) "limnoithona," all species of *Limnoithona*; 3) "dioithona" all species of the subgenus *Oithona* (*Dioithona*) plus *O. bjornbergae*; 4) "oithona" all other species of subgenus *Oithona* (*Oithona*). We rely on descriptions of both sexes of *Limnoithona* in Ferrari and Orsi (1984), of *Oithona* (*Dioithona*) in Nishida (1985), of *Oithona* (*Oithona*) in Ferrari and Bowman (1980), Ferrari and Orsi (1984) and Uchima (1979) for coastal zone animals, and Nishida (1985) for several oceanic species.

In all lineages many changes including antenna 1, leg 6 and fusion of the urosome segments appear similar. Relative to "limnoithona" the following changes are unique

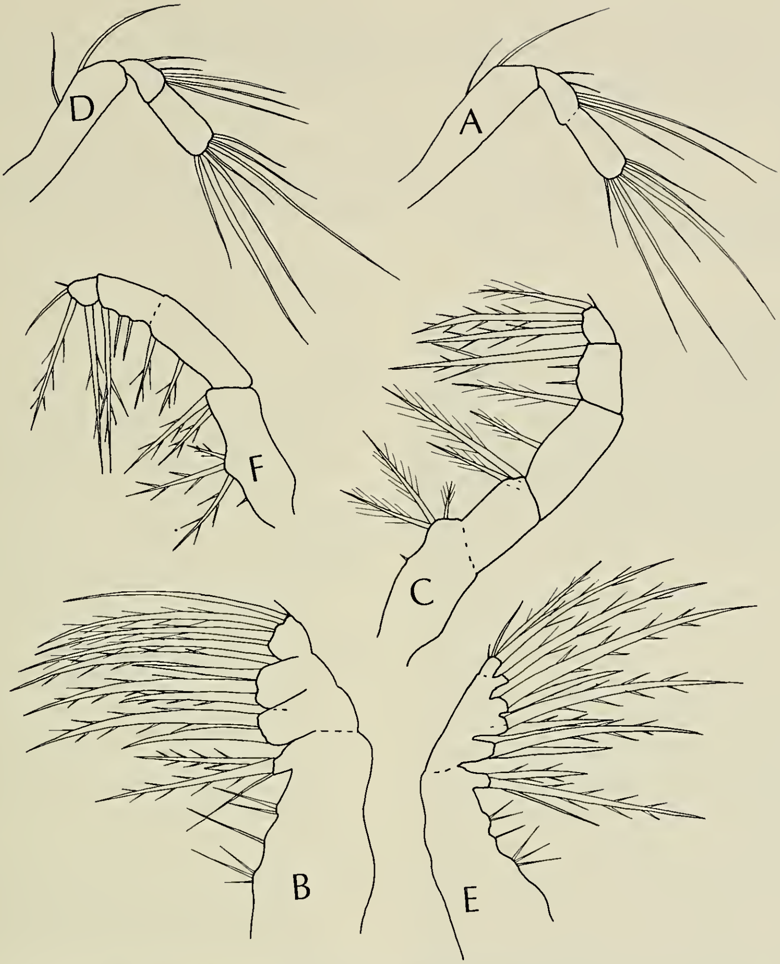

Fig. 6. *Paroithona pacifica* female: A, A2; B, Mx2; C, Mxp; male: D, A2; E, Mx2; F, Mxp.

to "paroithona"—in number of segments in swimming leg 2 exopod and swimming legs 2 and 3 endopods, in number of setae on swimming legs 2, 3, and 4 endopods and swimming leg 4 exopod, in size of male exopod and basipod armature, and in shape of external spines of swimming leg 1 exopod. A sexual dimorphism expressed in the caudal rami (segment and armature size slightly smaller in males) is unique to *Limnoithona.*

Unique differences in degree of sexual dimorphism of "dioithona" relative to "paroithona" include changes in shape of antenna 2 segment 3 (longer in males), mandibular basipod (segmented in males), shape of setae on swimming leg 4 endopod (modified in females). Unique differences in "paroithona" relative to "dioithona" include changes in shape of external spines on swimming leg 1 exopod, and changes in number of segments and setae on swimming legs 2–4 endopods, and segments or setae on swimming legs 2 and 4 exopods.

The "oithona" lineage shows a wide range in degree of sexual dimorphism among various species occupying a wide number of aquatic niches. All members of this lineage

Table 2.—Number of spines previously reported on exopodal segments of *Paroithona* swimming legs 1–4.

| Name | Leg 1 | Leg 2 | Leg 3 | Leg 4 | Source |
|---|---|---|---|---|---|
| *P. parvula* | 1-1-2 | 1-1-2 | 1-1-2 | 1-1-1 | Farran 1908, Sars 1918 |
| *P. pacifica* | 1-)3( | 1-1-2 | 1-0-2 | 1-0-2 | Nishida 1985 |
| *P. flemingeri* | 1-(3) | 1-1-2 | 1-0-2 | 1-0-1 | Ferrari and Bowman 1980 |
| *P. pulla* | 1-(3) | 1-1-2 | 1-0-1 | 0-0-1 | Farran 1913, Nishida et al. 1977 |

( )—adjacent segments fused.
) (—adjacent segments incompletely fused.

exhibit differences relative to "paroithona" in shape of antenna 2 segment 3 (longer in males), ornamentation on coupler of swimming leg 4 (present in females, absent in males), shape of setae on swimming leg 4 endopod (modified in females), changes in number of integumental organs on cephalosome (more numerous and forming an unusual pattern in males). Unique differences in degree of sexual dimorphism of "paroithona" relative to "oithona" include changes in shape of external spines on swimming leg 1 exopod, and changes in number of segments and setae on swimming legs 2–4 endopods and segments or setae on swimming legs 2 and 4 exopods. Each set of differences can be considered a character unique to one lineage and exclusive of the other three. Differences in degree of sexual dimorphism clearly separate the "paroithona" lineage from the remaining lineages in the family.

## Acknowledgments

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# MARINE TUBIFICIDAE (OLIGOCHAETA) AT HUTCHINSON ISLAND, FLORIDA

Christer Erséus

*Abstract.*—Twenty-five species of marine Tubificidae are recorded from offshore, largely coarse, shelly sediments at Hutchinson Island on Florida's lower central east coast. Nine species are described as new: *Heterodrilus hispidus, H. perkinsi* (subfamily Rhyacodrilinae), *Phallodrilus hirsutus, Bathydrilus ingens, B. formosus, B. macroprostatus, Coralliodrilus corpulentus, Olavius latus* (Phallodrilinae), and *Tubificoides annulus* (Tubificinae). Redescriptions of *Heterodrilus bulbiporus* Erséus, 1981, and *Phallodrilus acochlearis* (Erséus and Loden, 1981), n. comb., are provided. *Heterodrilus bulbiporus, H. occidentalis* Erséus, 1981, *H. pentcheffi* Erséus, 1981, and *Adelodrilus magnithecatus* Erséus, 1979, are recorded from Florida for the first time. The Hutchinson Island tubificid fauna comprises a mixture of warm-temperate (American east coast) and tropical (Caribbean) elements.

In 1943, Gates described an intertidal earthworm, *Pontodrilus gracilis* [now regarded as a synonym for *P. litoralis* (Grube, 1855), family Acanthodrilidae; Easton 1984] from the banks of a brackish river at Fort Myers, Florida. However, it was not until the middle of the 1960's that a marine fauna of aquatic oligochaetes was discovered in this part of the southeastern U.S.A. The first, very scanty, records of Tubificidae from marine waters in Florida were given by Brinkhurst (1965, 1966), while Kennedy (1966) used material from off Panama City, Florida, when describing the marine enchytraeid, *Grania americana.*

During a collecting trip to Miami in 1977, the author had the opportunity to gather a rich material of marine oligochaetes in the area just south of the city (largely Biscayne Bay). The Tubificidae dominated this material, and most of the tubificid species have now been accounted for in various taxonomic publications (Erséus 1979a, b, c, 1980a, 1981a, 1982a, b, c, 1983a, 1984b). Additional collections of Tubificidae from other parts of the state have been treated by Erséus (1981b, 1984a), Erséus and Baker (1982), Erséus and Loden (1981), and Loden (1980). The species thus recorded from Florida to date number 34 (species not asterisked in Table 1).

One enchytraeid species, *Grania monospermathecus* Erséus and Lasserre, 1976, was recently reported from the Miami area by Coates and Erséus (1985), and additional enchytraeid material will be treated elsewhere by the same authors (in preparation).

In 1981, Erséus and Loden reported on a small collection of Tubificidae (four species of the subfamily Phallodrilinae) from subtidal sites off Hutchinson Island on Florida's lower central east coast. The material was obtained in 1976–1977 during a sampling program funded by Florida Power and Light Company (FP&L). The program was a continuation of an earlier, three-year (1971–1974) environmental baseline study conducted in connection with the location of the FP&L St. Lucie Unit No. 1 nuclear power plant on Hutchinson Island. The study was designed to generate a marine ecology data base for the future assessment of possible changes in the environment of the area influenced by the heated effluent

Table 1.—Checklist of marine Tubificidae reported from Florida, with asterisks denoting new records. "Florida only" means species hitherto only reported from Florida. E. = Erséus.

| Species | Florida only | Reference |
|---|---|---|
| *Adelodrilus magnithecatus* E., 1979* | | present paper |
| *Aktedrilus floridensis* E., 1980 | x[1] | E. 1980a |
| *Bathydrilus adriaticus* (Hrabê, 1971) | | E. 1979a, 1985 |
| *B. formosus*, n. sp.* | | present paper |
| *B. ingens*, n. sp.* | | present paper |
| *B. macroprostatus*, n. sp.* | x | present paper |
| *Bermudrilus peniatus* E., 1979 | | E. 1984a |
| *Coralliodrilus corpulentus*, n. sp.* | x | present paper |
| *Heterodrilus bulbiporus* E., 1981* | | present paper |
| *H. hispidus*, n. sp.* | x | present paper |
| *H. minisetosus* E., 1981 | | E. 1981a; present paper |
| *H. occidentalis* E., 1981* | | present paper |
| *H. pentcheffi* E., 1981* | | present paper |
| *H. perkinsi*, n. sp.* | x | present paper |
| *Inanidrilus bulbosus* E., 1979 | x | E. 1979c |
| *I. ernesti* E., 1984 | x | E. 1984b; present paper |
| *I. extremus* (E., 1979) | x | E. 1979b, 1984b |
| *I. mexicanus* (E. and Baker, 1982) | x | E. and Baker 1982 |
| *I. triangulatus* E., 1984 | x | E. 1984b |
| *I. vacivus* E., 1984 | x | E. 1984b, present paper |
| *Kaketio ineri* Righi and Kanner, 1979 | | E. 1980b |
| *Limnodriloides baculatus* E., 1982 | | E. 1982c |
| *L. barnardi* Cook, 1974 | | E. 1982c |
| *L. hastatus* E., 1982 | x | E. 1982c |
| *L. monothecus* Cook, 1974 | | E. 1982c; present paper |
| *L. rubicundus* E., 1982 | | E. 1982c |
| *L. vespertinus* E., 1982 | | E. 1982c; present paper |
| *Marcusaedrilus hummelincki* Righi and Kannner, 1979 | | E. 1983a |
| *M. luteolus* E., 1983 | | E. 1983a; present paper |
| *Monopylephorus rubroniveus* Levinsen, 1884 (=*M. helobius* Loden, 1980) | | Loden 1980; Baker and Brinkhurst 1981 |
| *Olavius caudatus* (E., 1979) | x | E. 1979b, 1984b |
| *O. latus*, n. sp.* | x | present paper |
| *O. macer* E., 1984 | x | E. 1984b |
| *O. tenuissimus* (E., 1979) | | E. 1979b, 1984b |
| *O.* sp. A* | x[2] | present paper |
| *O.* sp. B* | x | present paper |
| *Parakaketio longiprostatus* E., 1982 | x | E. 1982b |
| *Phallodrilus acochlearis* (E. and Loden, 1981), n. comb. | | E. and Loden 1981; present paper |
| *P. biprostatus* (Baker and E., 1979) | | E. and Loden 1981; present paper |
| *P. hirsutus*, n. sp.* | x | present paper |
| *P. rectisetosus* E., 1979 | | E. 1979b, 1985 |
| *P. sabulosus* E., 1979 | | E. 1979b; present paper; E. and Loden 1981 |
| *Smithsonidrilus marinus marinus* Brinkhurst, 1966 | x[3] | Brinkhurst 1966; E. 1982a |
| "? *Spiridion insigne* Knöllner, 1935" (=indeterminable) | ? | Brinkhurst 1965; Brinkhurst and Baker 1979 |
| *Tectidrilus bori* (Righi and Kanner, 1979) | | E. 1982c |
| *T. squalidus* Erséus, 1982 | x | E. 1982c |
| *Thalassodrilides gurwitschi* (Hrabê, 1971) | | E. 1981c |
| *Tubificoides annulus*, n. sp.* | x | present paper |
| *T.* "*gabriellae*" (not *gabriellae* Marcus, 1950) | ? | Brinkhurst 1965; Brinkhurst and Baker 1979 |
| *T.* sp.* | ? | present paper; Brinkhurst (in preparation) |

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[1] Known also from Barbados (Erséus unpublished).

[2] A very similar form, probably the same species, known from Belize (Erséus unpublished).

[3] Subspecies *westoni* Erséus, 1982, known from New Jersey, Delaware, Maryland, Virginia, North Carolina, Bermuda, and Bahamas (Erséus 1982a).

discharge of the plant. An introduction to this extensive study was provided by Gallagher and Hollinger (1977), and several reports have been given in *Florida Marine Research Publications* (1977–1979), a series published by the Florida Department of Natural Resources Bureau of Marine Research (FDNR).

During the 1971–1974 sampling program, about 2400 specimens of marine Oligochaeta were collected at five offshore stations within a few kilometers from the FP&L plant site. Through the kind efforts of Mr. Thomas H. Perkins (FDNR), this very large collection was recently made available to the author. However, as a large majority of the specimens proved to be sexually immature and thus very difficult to identify to species in most cases, only those worms with well-developed genital organs, about 400 individuals, were more carefully scrutinized. Almost 90% of the mature oligochaetes examined are members of the Tubificidae, and they are the subject of the present account, which is devoted primarily to the taxonomy of the species. Twenty-two named and three unnamed tubificid species are recognized. Of these, nine are described as new, and four others are reported from Florida for the first time. *Heterodrilus bulbiporus* Erséus, 1981, *H. minisetosus* Erséus, 1981, *Bathydrilus ingens,* n. sp., and *B. formosus,* n. sp., are simultaneously reported from the Gulf of Mexico; *B. formosus* is reported also from Belize in Central America.

The enchytraeids in the Hutchinson Island material will be treated separately.

## Stations Sampled

The five stations off Hutchinson Island were described by Gallagher and Hollinger (1977), and their sediments more carefully examined by Gallagher (1977). A brief summary is provided here.

Sta 1. 27°22.2′N, 80°14.1′W, at seaward margin of beach terrace, 0.5 km offshore. Depth 6–9 m (mean sampling depth 7.5 m). Gray, hardpacked, fine to very fine sand. *Note:* all oligochaetes here reported from Sta 1 were from the May 1972 collection, which was taken slightly east (seaward) of the typical Sta 1, in a sediment resembling that of Sta 5 (Gallagher 1977:18).

Sta 2. 27°21.6′N, 80°13.1′W, 1.5 km ENE of Sta 1 in the offshore "trough," approximately midway between the beach terrace and offshore shoal. Depth 9–12 m (mean 11 m). Clean shell hash; very coarse to coarse sand with varying amount of granule-sized shell fraction.

Sta 3. 27°21.9′N, 80°12.4′W, Pierce Shoal, 3 km from Sta 1, in line with Sta 1 and Sta 2. Depth 5–8 m (mean 7 m). Clean, medium sands with very small amount of granule-sized shell.

Sta 4. 27°20.8′N, 80°12.9′W, 1.6 km SSE of Sta 2, 0.6 km W of southernmost tip of Pierce Shoal. Depth 9–12 m (mean 10 m). Shell hash, very similar to sediment of Sta 2, but with lesser amount of large shell.

Sta 5. 27°22.6′N, 80°14.1′W, 2.2 km NNW of Sta 2, 2.1 km E of the beach in similar depth as Sta 4 (9–12 m). Very coarse shell sands with granule-sized shell making up 28–45% of sample, and with some mud.

## Material and Methods

Five replicate Shipek grab samples (each 0.04 $m^2$) were taken at each station bimonthly between September 1971 and July 1973. Samples were preserved in 10% buffered formalin-seawater. For further information on the sampling and sorting procedures, see Gallagher and Hollinger (1977).

Sexually mature tubificids, which occurred in about one-third of the 300 samples, were sorted and separated from the juveniles by the author. A few specimens of *Heterodrilus perkinsi,* n. sp., and *Phallodrilus biprostatus* were longitudinally sectioned and stained with Azan. The remaining worms were all stained in paracarmine and mounted whole in Canada balsam.

Material from other areas included in this study comprises (1) a few worms from offshore localities in the NE Gulf of Mexico, originating from a Bureau of Land Management baseline study by personnel at

Dauphin Island Sea Lab, Alabama (courtesy Dr. M. Susan Ivester); (2) a single specimen of *Bathydrilus ingens,* n. sp., collected by Mr. Michael R. Milligan (Mote Marine Lab, Sarasota, Florida) on the west coast of Florida; (3) a number of specimens of *B. formosus,* n. sp., collected by the late Dr. H. Randall Baker (University of Victoria, B.C., Canada) in the vicinity of Carrie Bow Cay on the barrier reef of Belize in the western Caribbean Sea (courtesy Dr. Ralph O. Brinkhurst). These worms were all studied as whole mounts.

Holotypes of all the new species are deposited at the U.S. National Museum of Natural History (USNM), Washington, D.C.; paratypes (when available) and representative specimens of most of the previously known species are lodged in the Florida Department of Natural Resources Invertebrate Collection (museum prefix FSBC I; = old abbreviation for Florida State Board of Conservation), Bureau of Marine Research, St. Petersburg, Florida.

In descriptions, the following abbreviations are used: sec = sectioned; spm/spms = specimen/specimens; whm = whole-mounted. Length and width measurements refer to fixed, whole-mounted, and slightly compressed specimens. Roman numerals denote segment number.

Abbreviations used in figures are as follows: a, atrium; bs, blind sac; cs, copulatory sac; ep, epidermal pad; fp, flap-like papilla; g, glandular body of unknown function; gs, glands associated with spermathecal seta; m, muscles; mp, male pore; p, penis; pa, papilla; pp, pseudopenis; pr, prostate gland; pr 1, anterior prostate gland; pr 2, posterior prostate gland; ps, penial seta; s, spermatheca; se, seta; ss, spermathecal seta; sz, spermatozeugma; vd, vas deferens.

## Descriptions

### Subfamily Rhyacodrilinae

### *Heterodrilus* Pierantoni, 1902

### *Heterodrilus minisetosus* Erséus, 1981

*Clitellio arenicolus* (part).—Lasserre and Erséus, 1976:451–452.

*Heterodrilus minisetosus* Erséus, 1981a: 113–114, fig. 2.

*New material examined.*—FSBC I 31852–31853, 2 whm spms from Sta 4 (10 May 1972).—Author's collection: 2 whm spms from Sta 2, 14 from Sta 4; 1 whm spm from NE part of Gulf of Mexico, off Hernando Co., Florida, 28°36′N, 83°30′W, about 25 m, sediment unknown (27 Aug 1977; courtesy M. S. Ivester).

*Remarks.*—*Heterodrilus minisetosus,* which was described on the basis of extensive material from Bermuda (type locality), Bahamas, Florida (Miami area), North Carolina, and Virginia (Erséus 1981a), was named for the minute penial setae (one at each side of worm) present in most individuals. Specimens from Hutchinson Island lack penial setae (as did most worms from North Carolina and Bahamas in the original material) but otherwise fit the description completely.

*Distribution and habitat.*—Both coasts of Florida (new record from Gulf coast), North Carolina, Virginia, Bermuda, and Bahamas. Subtidal sands, 0.5–33 mm depth.

### *Heterodrilus pentcheffi* Erséus, 1981
Fig. 1

*Clitellio arenicolus* (part).—Giere, 1979: 304.

*Heterodrilus pentcheffi* Erséus, 1981a:121–123, fig. 12.—Erséus, 1984c:196.

*Heterodrilus* sp.—Erséus, 1981a:123–124, fig. 14.

*New material examined.*—FSBC I 31854, 3 whm spms from Sta 2 (9 May 1972).—Author's collection: 7 whm spms from Sta 2, 2 from Sta 3, 1 from Sta 4, and 1 from Sta 5.

*Remarks.*—*Heterodrilus pentcheffi* was originally described on the basis of material from Bermuda, New Jersey, and North Carolina in the Northwest Atlantic, and the Galapagos Islands in the East Pacific (Erséus 1981a; see also Erséus 1984c). The species is characterized by (1) trifid setae in segments II–IX (sometimes –VIII, –X, –XI, or –XII), 2 per bundle, (2) thereafter bifid se-

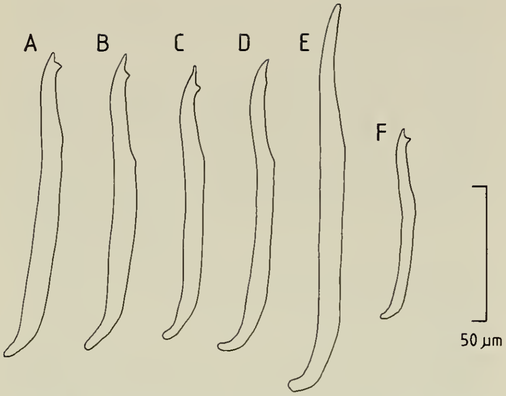

Fig. 1. *Heterodrilus pentcheffi,* postclitellar setae: A, From segment immediately posterior to clitellum; B–E, From various posterior segments; F, From posterior end of worm.

tae, 1 per bundle, with more or less developed lower tooth (cf. Fig. 1), and (3) straight, single-pointed, ectally wide, erect penial setae, 2(3) per bundle. Vasa deferentia are coiled in spirals, and atria are long and cylindrical, generally M-shaped, terminating in simple, somewhat bulbous pseudopenes.

As illustrated in Fig. 1, bifid (postclitellar) setae of the new material are highly variable. In segments immediately posterior to the clitellar region, the lower tooth of the setae is conspicuous, almost as large as the upper one (Fig. 1A), but the lower tooth generally becomes reduced on more posterior setae (Figs. 1B–D), so much so that setae may appear single-pointed, at least from certain angles (Fig. 1E). At the posterior end of the worm, setae become smaller and their bifid nature generally becomes more pronounced again (Fig. 1F).

In fact, the new material from Hutchinson Island has bifid setae very similar to those of the form described as "*Heterodrilus* sp." from Miami (Florida) by Erséus (1981a). This species was tentatively regarded as separate from *H. pentcheffi,* largely also because of its small size. As the new material contains both large (with posterior setae up to 145 µm long) and small specimens (posterior setae only about 45 µm long), it is now concluded that "*Heterodrilus* sp." is identical to *H. pentcheffi,* and that the Florida populations differ slightly from the more northern forms in terms of the appearance of the postclitellar setae.

Ranges of body length and segment number of the new material lie within those noted previously, if descriptions of *H. pentcheffi* and *H.* sp. are united (4.1–11.3 mm, 43–88 segments). In one of the new individuals, the penial setae are only about 65 µm long, which extends the length range of these setae for the species to 65–155 µm.

The small "epidermal papilla," which perhaps should be termed an "epidermal pad" and which is located mid-ventrally between the spermathecal pores in "*Heterodrilus* sp." (cf. Erséus 1981a:124), is present also in many of the original specimens of *H. pentcheffi* (Erséus, unpublished) as well as in most specimens from Hutchinson Island.

*Distribution and habitat.*—East coast of Florida (new record), North Carolina, New Jersey, Bermuda, and Galapagos Islands. Largely coarse sands, 0.5–39 m depth.

### *Heterodrilus occidentalis* Erséus, 1981
Fig. 2

*Heterodrilus occidentalis* Erséus, 1981a:121, fig. 11.—Davis, 1985:170.

*New material examined.*—FSBC I 31855–31856, 2 whm spms from Sta 2 (3 Jan and 9 May 1972, respectively).—Author's collection: 3 whm spms from Sta 2, 6 from Sta 4.

*Remarks.*—This species was originally described from shallow waters in North Carolina and off New Jersey (Erséus 1981a), and was recently reported from Georges Bank off Massachusetts by Davis (1985). It is closely related to *H. pentcheffi* (genitalia and penial setae are virtually identical in the two species), but differs from that species in the appearance of the somatic setae.

In the original material, trifid setae were found only in about the first five setigerous segments, followed by a few segments with bifid setae (cf. Erséus 1981a:figs. 11A–C); thereafter (segment X and backwards, except a few segments in posterior end), setae are sharply single-pointed (Erséus 1981a:fig. 11D). New specimens from Florida deviate slightly from this pattern. The lower tooth of the trifid setae gradually diminishes posteriorly, but this tooth can generally still be discerned in segments VIII and IX (Fig. 2A). Similarly, "single-pointed" setae, commencing in segment X, initially are actually somewhat bifid; a faint lower tooth can be seen from certain angles (Fig. 2B). Further back, however, most setae are truly single-pointed (Fig. 2C).

*Distribution and habitat.*—East coast of Florida (new record), North Carolina, New Jersey, and Massachusetts. Coarse sand and gravel, 4.5–138 m depth.

### *Heterodrilus hispidus,* new species
Fig. 3

*Holotype.*—USNM 98130, whm spm from Sta 2 (15 Sep 1971).

*Paratypes.*—FSBC I 31857, 2 whm spms from Sta 4 (14 Mar 1972).

*Other material examined.*—Author's collection: 5 whm spms from type locality (Sta 2).

*Description.*—Length (2 complete spms) 13.6–14.8 mm, 82–86 segments; third spm only 4.5 mm long, about 38 segments, but its posterior end regenerating. Width at XI, 0.29–0.41 mm. Clitellum extending over ½X–XII. Setae 2 per bundle in II–IX, 1 per "bundle" thereafter. Anterior setae (from II to IX) bifid, with teeth of approximately same length and both oriented along long axis of seta (Fig. 3A). Bifids 60–100 μm long, 2.5–5 μm thick. Posterior setae (from X to end of worm) stout, sharply single-pointed, and with curved inner end; dorsal ones (Fig. 3C) much larger (95–135 μm long, 7–9.5 μm thick) than ventral ones (Fig. 3B; 60–95 μm long, 3.5–6 μm thick). Penial setae (Figs. 3D, E, ps) 2 per bundle (bundle "doubled" at one side in one aberrant spm), slender and slightly curved, single-pointed, with inner ends generally somewhat tilted over to posterior. Penials 125–135 μm long, 4.5–5 μm thick. Male pores paired, slightly ventral to lines of ventral somatic setae, posteriorly in XI. Spermathecal pores paired, slightly ventral to lines of ventral setae, anteriorly in X.

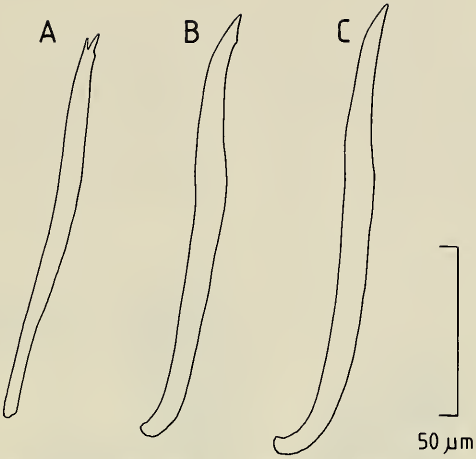

Fig. 2. *Heterodrilus occidentalis,* setae: A, From segment VIII; B, From segment XII; C, From posterior segment.

Pharyngeal glands very poorly developed (absent?). Granulated coelomocytes numerous. Male genitalia (Fig. 3E) paired. Vas deferens 9–12 μm wide, very long and tightly coiled in spiral. Atrium somewhat C-shaped, about 300 μm long, 25–35 μm wide entally, narrower ectally, with thin outer lining and densely granulated inner epithelium; lobes of prostate glands attached to ventral surface of atrium. Ectal part of atrium nongranulated, tapering, opening to exterior through simple pore (possibly a very simple pseudopenis). Spermathecae (Fig. 3E, s) variable in shape and extension, with slender ducts and large ampullae, latter with large mass of sperm in irregular lumen and with large granules of secretion in wall.

*Remarks.*—Most species of *Heterodrilus* have trifid setae in at least some anterior segments; only *H. subtilis* (Pierantoni, 1917)

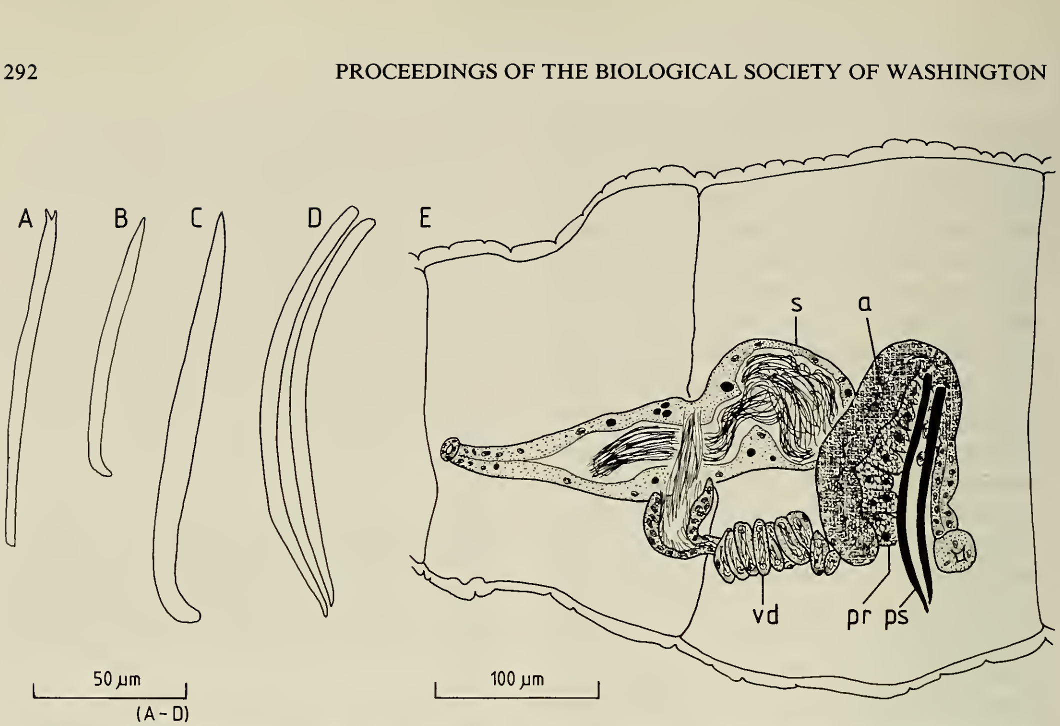

Fig. 3. *Heterodrilus hispidus,* n. sp.: A, Anterior bifid seta; B, Posterior ventral seta; C, Posterior dorsal seta; D, Penial setae; E, Lateral view of spermatheca and male genitalia in segments X–XI.

and this new species lack such setae altogether. *Heterodrilus hispidus* is distinguished from the other Mediterranean and poorly known form by the consistently single-pointed tips of its setae from segment X to the posterior end of the worm (penial setae absent in *H. subtilis*).

The great difference in size between the dorsal and ventral postclitellar setae is a striking feature of *H. hispidus*; a similar case has not been noted for any other species of the genus, and it may thus prove to be a reliable specific character.

In most species of the genus, penial setae are either erect or with inner ends obliquely pointing toward the anterior, but in *H. hispidus* and the aberrant *H. perkinsi,* n. sp., described below, inner ends of penial setae tend to be directed toward the posterior.

*Etymology.*—The specific name *hispidus* is Latin for "shaggy, rough" and alludes to the appearance of the worm with regard to the very large setae.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Shell hash, 10–12 m depth.

### *Heterodrilus bulbiporus* Erséus, 1981
Fig. 4

*Heterodrilus bulbiporus* Erséus, 1981a:123, fig. 13.

*New material examined.*—FSBC I 31858, 2 whm spms from Sta 2 (1 Mar 1972).—Author's collection: 2 whm spms from Sta 1 (but see note under "Material and methods" above), 18 from Sta 2, 3 from Sta 4, and 21 from Sta 5; 1 whm spm from NE part of the Gulf of Mexico, off Clearwater, Florida, 27°55′N, 83°28′W, 20 m, sediment unknown (26 Aug 1977; courtesy M. S. Ivester).

*Redescription* (based on the new material).—Length (5 worms measured) 6.5–11.3 mm, 48–65 segments (original material: 5–12 mm, 38–58 segments). Width at XI, 0.31–0.56 mm. Clitellum extending over ½X–XII. Setae 2 per bundle in II–IX, 1 per "bundle" thereafter. Anterior setae (in II–IX) trifid (Fig. 4A), with upper and middle teeth pointed and basally narrow, lower tooth basally much wider. Trifids 75–125 µm long, 4.5–7 µm thick (original material: 40–115

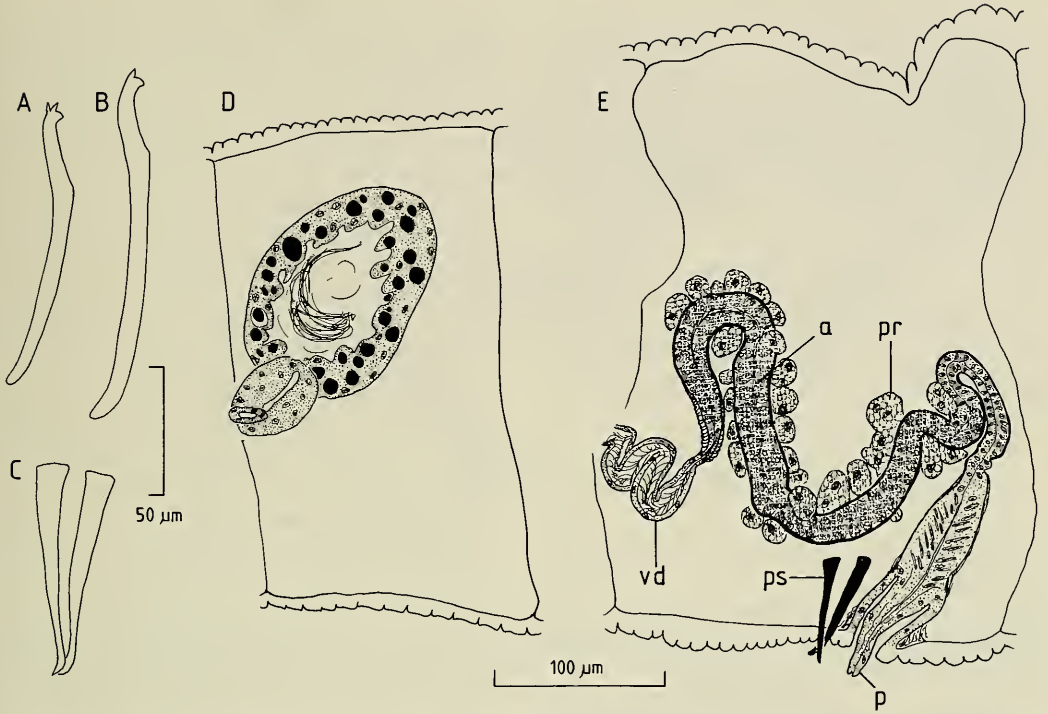

Fig. 4. *Heterodrilus bulbiporus*: A, Anterior trifid seta; B, Posterior seta; C, Penial setae; D, Spermatheca in segment X; E, Lateral view of male genitalia in segment XI.

µm, 3–5 µm). Posterior setae (from X and backwards) bifid (Fig. 4B), with upper tooth slightly thinner than lower, both teeth basally wide. Bifids 65–140 µm long, 4.5–9 µm thick (original material: 50–115 µm, 4–7 µm). Penial setae (Figs. 4C, E, ps) 2 per bundle, erect, single-pointed, 80–95 µm long (original material: 95–125 µm), about 7 µm thick at middle, 12–13 µm wide at ental end. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores paired, slightly ventral to lateral lines, anteriorly in X.

Pharyngeal glands in IV–V, but poorly developed. Granulated coelomocytes numerous. Male genitalia (Fig. 4E) paired. Vas deferens 16–21 µm wide (original material: 7–13 µm), long and coiled. Atrium cylindrical, slender, about 0.8 mm long (original material: 0.4–1.0 mm), 25–40 µm wide, with 2–4 µm thick outer muscular lining (original material: up to 5 µm thick), and granulated inner epithelium along most of its length; narrow ectal portion of atrium not granulated, but containing numerous nuclei. Atrium ectally terminating in bulbous copulatory apparatus, consisting of inner widened part (most ectal part of atrium) and outer, narrow, tapering penis, latter enclosed in copulatory sac (whole complex probably somewhat eversible; cf. Erséus 1981a:fig. 13C). Small lobes of prostate glands present along granulated part of atrium. Spermathecae (Fig. 4D) consisting of short but broad ducts and large, more or less oval ampullae, latter with thick walls containing large granules of secretion and irregular lumen containing large bundles of sperm.

*Remarks.*—*Heterodrilus bulbiporus* was originally described from Bermuda, New Jersey, and North Carolina. Some dimensional differences between the old and the new material are indicated in the redescription above. In addition, the new material deviates slightly from the original description with regard to the morphology of the male terminalia; the copulatory organ of *H. bulbiporus* was previously perceived as a pseudopenis (Erséus 1981a), but in the new material it rather appears more like a proper pendant penis and should be described as such. This penis discriminates *H. bulbiporus* from all the other species of the genus.

*Distribution and habitat.*—Both coasts of Florida (new records), North Carolina, New Jersey, and Bermuda. Subtidal sands, 6.5–130 m depth.

### *Heterodrilus perkinsi,* new species
Fig. 5

*Holotype.*—USNM 98131, whm spm from Sta 4 (4 Jan 1972).

*Paratypes.*—FSBC I 31860–31861, 1 sec (10 May 1972) and 2 whm spms (4 Jan 1972) from Sta 4 (type locality).

*Other material examined.*—Author's collection: 2 sec and 16 whm spms from Sta 2; and 1 sec and 24 whm spms from Sta 4 (type locality).

*Description.*—Length (5 complete spms measured) (5.7)8.9–11.2 mm, (42)58–72 segments; smallest spm still growing posteriorly. Width at XI 0.41–0.50 mm. Clitellum extending over ½X–XII. Somatic setae 2 per bundle in II–IX (–VIII in single spm with genitalia shifted one segment forward), 1 per "bundle" thereafter. Anterior setae (from II to IX) trifid (Fig. 5A), with upper tooth smaller than other two, middle tooth longer than upper and lower teeth. Trifids 65–110 μm long, 4–7 μm thick. Posterior setae (from X to end of worm) bifid (Fig. 5B), with lower tooth slightly larger than upper, both teeth with broad bases. Bifids 60–120 μm long, 4.5–9.5 μm thick. Penial setae (Figs. 5C, D, ps) small and straight, (1)2 per bundle, often retracted into copulatory sac and with inner ends generally directed obliquely toward posterior; ectal ends single-pointed and hooked. Penials 60–85 μm long, 4.5–5.5 μm thick. Male pores paired, located close together posteriorly in mid-ventral bursa in XI (X in aberrant spm); bursa laterally delimited by two flap-like papillae (Fig. 5D, fp). Spermathecal pores paired in line with ventral setae anteriorly in X (IX in aberrant spm).

Pharyngeal glands in IV–V(VI). Granulated coelomocytes present. Male genitalia (Fig. 5D) paired. Vas deferens remarkably short and wide, with very thin and densely ciliated wall; vas deferens about 150–175 μm long, 34–45 μm wide, abruptly narrowing at entrance into atrium. Atrium long and slender, basically cylindrical but with somewhat varying width, coiled and extending through 2–3 segments. Atrium about 1.4–3.2 mm long (exact length difficult to establish), maximally 50–70 μm wide (many parts narrower), with 9–15 μm thick outer layer of muscles, and poorly granulated inner epithelium; cilia not observed. Lobes of prostate glands scattered along most of atrium. Atrium tapering ectally, terminating in somewhat pointed, conical penis. Penis 45–80 μm long, basally 23–37 μm wide, with thin cuticular lining, located in hollow inner part of deep copulatory sac. Spermathecae (Fig. 5D, s) with elongate, thick-walled ducts, and ampullae of variable shape, latter containing at least one large bundle of sperm in postcopulatory spms; ampullae often dislocated into IX.

*Remarks.*—The most striking feature of *Heterodrilus perkinsi* is its extremely long and muscular atria, which discriminate the species from all its congeners. Noteworthy, and somewhat paradoxical, is that the vasa deferentia are among the shortest in the genus, measuring only about one-tenth or less of the atrial length.

*Etymology.*—This species is named for Mr. Thomas H. Perkins, who placed the Hutchinson Island Oligochaeta at my disposal and provided most valuable information, moral support, and assistance during the preparation of this paper.

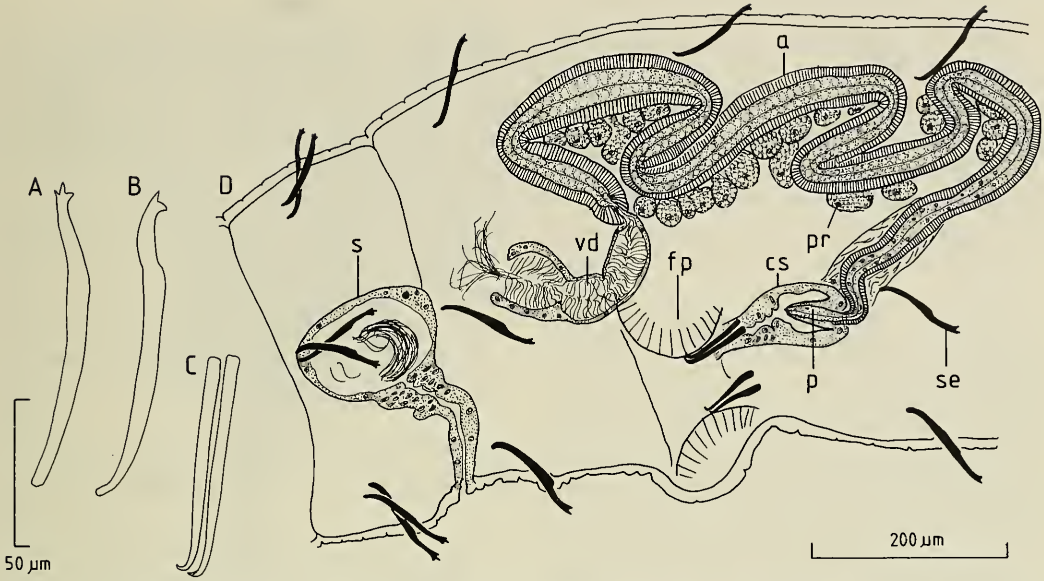

Fig. 5. *Heterodrilus perkinsi,* n. sp.: A, Anterior trifid seta; B, Posterior seta (from segment immediately posterior to clitellum); C, Penial setae; D, Somewhat lateral view of spermatheca and male genitalia in segments X–XIII (note that flap-like papillae and penial setae of both sides of worm are shown; the spermatheca and the vas deferens depicted are not from the same side as the atrium in the specimen used).

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Shell hash, 10–12 m depth.

### Subfamily Phallodrilinae

### *Phallodrilus* Pierantoni, 1902

### *Phallodrilus sabulosus* Erséus, 1979

Fig. 6

*Phallodrilus sabulosus* Erséus, 1979b:188–189, figs. 1–2.—Erséus and Loden, 1981: 820–821, fig. 1A.—Erséus, 1984d:813.

*New material examined.*—FSBC I 31862, 3 whm spms from Sta 4 (14 Mar 1972).—Author's collection: 2 whm spms from Sta 2, 9 from Sta 4, and 1 from Sta 5.

*Remarks.*—*Phallodrilus sabulosus* was first described from a coral reef off Miami (Erséus 1979b), but as the two type specimens were both precopulatory, the mature spermathecae of the species were not described until new material was recovered from off Hutchinson Island by Erséus and Loden (1981). Recently *P. sabulosus* was found off New Jersey, further north along the North American east coast (Erséus 1984d).

The new material from Hutchinson Island is highly variable in terms of overall size: length 2.8–9.0 mm, segments 22–63 (previously studied individuals 5.5–6.1 mm long, 44–61 segments).

According to the original description, bifid setae either have an upper tooth that is slightly longer than the lower one (anterior bundles) or the two teeth are equally long (posterior bundles). In the present material, however, many posteriormost setae have a lower tooth which is clearly longer than the upper one (Fig. 6A); in fact, the lower tooth appears prolonged as compared to that of anterior setae.

The most striking feature of this species is the possession of both penial and spermathecal setae. Penial setae (illustrated by Erséus 1979b:figs. 1–2) are stout, somewhat

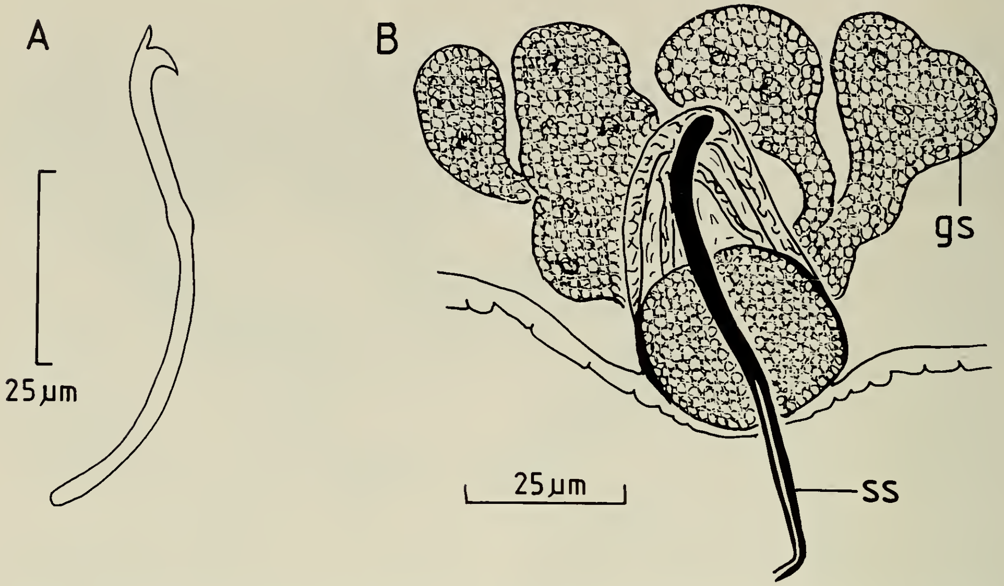

Fig. 6. *Phallodrilus sabulosus*: A, Seta from one of posteriormost segments; B, Spermathecal seta with associated glands.

spoon-shaped, always one per "bundle," and located near the atrial openings in segment X. These setae are 60–80 µm long and up to 7 µm wide in the present material.

Spermathecal setae (Fig. 6B, ss) are more slender than penial setae, ectally deeply forked (now established; cf. statement by Erséus 1979b:189), one or two per bundle and located either posterior to spermathecal pores in segment X (in 13 of the 16 present worms), or anterior to these pores, posteriorly in segment IX (in the remaining three worms). The middle part of each seta is enclosed in a glandular body, which bears a few lobes of external glands (Fig. 6B, gs), which are somewhat reminiscent of prostate glands; these external glands were not noted in the original description. Spermathecal setae are 60–100 µm long.

Male efferent ducts of the new material conform to the original account, although the length range of the atrium is now extended to 60–140 µm. Spermathecae are variable in size and shape but basically conform to the description provided by Erséus and Loden (1981:fig. 1); they are very slender, consisting of (1) a long duct, which is ectally distended and often contains sperm, and (2) an oval, thin-walled ampulla, generally with very dense mass of sperm.

*Distribution and habitat.*—East coast of the U.S.A., from Florida to New Jersey. Largely coarse sands, 3–15.5 m depth.

### *Phallodrilus biprostatus*
### (Baker and Erséus, 1979)

*Peosidrilus biprostatus* Baker and Erséus, 1979:506–508, figs. 1–2.—Erséus and Loden, 1981:819–820.

*Phallodrilus biprostatus.*—Erséus, 1984d: 819–820.—Davis, 1985:table 1.

*New material examined.*—FSBC I 31863–31864, 3 whm spms from Sta 2.—Author's collection: 1 sec and 12 whm spms from Sta 2, 2 whm spms from Sta 3, 2 sec and 19 whm spms from Sta 4, and 1 whm spm from Sta 5.

*Remarks.*—This species, which occurred at several stations in the present material, was originally described as a member of a monotypic genus *Peosidrilus* Baker and Erséus, 1979, from New Jersey and North Carolina. It was reported from Hutchinson Island by Erséus and Loden (1981), and later also from Georges Bank off Massachusetts (Erséus 1984d; Davis 1985). The species was recently transferred to *Phallodrilus* (Erséus 1984d); its voluminous penes are now regarded as an elaboration of, and thus homologous to, the smaller copulatory structures (pseudopenes and true penes) possessed by several other *Phallodrilus* forms.

One of the new specimens consists of 70 segments (previously studied worms: 44–62 segments).

*Distribution and habitat.*—East coast of U.S.A., from Florida to Massachusetts. Largely coarse sands, 5.5–73 m depth.

### *Phallodrilus acochlearis* (Erséus and Loden, 1981), new combination
Fig. 7

*Adelodrilus acochlearis* Erséus and Loden, 1981:821–823, figs. 1B–C, 2.—Erséus, 1983b:77–78.

*New material examined.*—FSBC I 31865, 2 whm spms from Sta 4 (4 Jan 1972).—Author's collection: 7 whm spms from Sta 4.

*Redescription* (modified after Erséus and Loden 1981).—Length 2.5–3.9 mm, 27–39 segments. Width at XI, 0.15–0.25 mm. Clitellum extending over ½X–XII. Somatic setae bifid, 3–5 per bundle anteriorly, (2)3–4(5) per bundle in postclitellar segments. Anterior dorsal setae and all ventral setae with upper tooth shorter and much thinner than lower. Several setae in dorsal bundles of most posterior segments modified with lower tooth extremely long, curved downwards and parallel to setal shaft (Erséus and Loden's fig. 1C). Bifids 42–62 μm long, 1.5–2.5 μm thick. Penial setae straight, 30–50 μm long, 0.5–1 μm thick at middle, each with ectal "club" bearing apical hook (Fig. 7A). Penial setae about 8–14 per bundle (exact number difficult to establish as setae situated very near each other within bundle), with ectal ends protruding into small copulatory sac (sac everted in Fig. 7B) immediately posterior to atrial opening. Male pores paired in line with ventral somatic setae posteriorly in XI. Spermathecal pores paired in lateral lines in anteriormost part of X.

Pharyngeal glands inconspicuous, but extending as far back as VII or VIII. Male genitalia (Fig. 7B) paired. Vas deferens very wide and heavily muscular, longer than atrium, often convoluted (as shown in Erséus and Loden's fig. 2); cilia observed along inner epithelium of vas deferens in well-preserved spms, but sperm not stored in lumen (cf. Remarks). Vas deferens entering atrium sub-apically together with anterior prostate gland. Atrium 58–82 μm long, 35–43 μm wide, divided into two histologically different portions; ental portion with granulated and ciliated inner epithelium, ectal portion neither granulated nor ciliated but eversible to form bulbous pseudopenis (everted in Fig. 7B; cf. also Erséus and Loden's fig. 2); muscular lining of atrium thin. Prostate glands moderately large, both subapical on atrium, with attachments more or less opposite to each other. Spermathecae (Fig. 7B, s) consisting of short ducts and slender ampullae, latter 90–180 μm long, maximally 33–44 μm wide and variable in shape, with sperm in random masses.

*Remarks.*—This species was originally described on the basis of specimens from a site very near that of the present material. One additional individual was subsequently reported from shallow inshore water of North Carolina (Erséus 1983b).

The new material has necessitated a redescription of the species, as the true appearance of its vasa deferentia was not previously recognized; the vasa deferentia are ciliated, but they do not store sperm as initially conceived, and thus the species does not qualify for inclusion in the genus *Ade-*

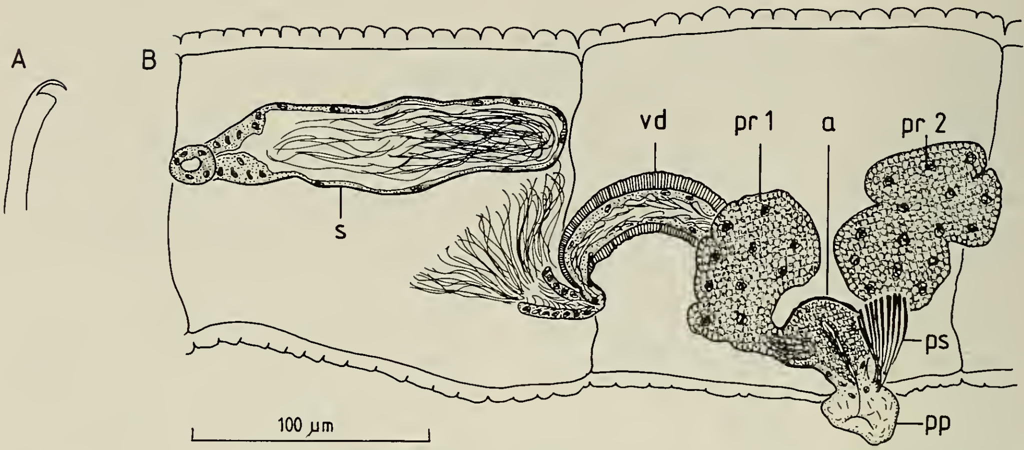

Fig. 7. *Phallodrilus acochlearis,* n. comb.: A, Tip of penial seta; B, Lateral view of spermatheca and male genitalia in segments X–XI.

*lodrilus,* where it was originally placed. Instead it should be assigned to *Phallodrilus* as defined by Erséus (1984d).

The revised description of *P. acochlearis* shows that the species is closely related to another North American east coast form, *P. boeschi* Erséus, 1984, which has posterior dorsal setae (with prolonged lower teeth; cf. Erséus 1984d:fig. 2B), penial setae, atria, and spermathecae that are very similar to those of *P. acochlearis.* However, the latter species is easily distinguished from *P. boeschi* by its conspicuously muscular vasa deferentia, its more elaborate pseudopenes and even longer lower teeth of the posterior dorsal setae (cf. Erséus and Loden 1981:fig. 1C).

*Distribution and habitat.*—East coast of Florida and North Carolina. Very coarse sands, 5.5–11 m depth.

### *Phallodrilus hirsutus,* new species
Fig. 8

*Holotype.*—USNM 98132, whm spm from Sta 2 (5 Mar 1973).

*Paratype.*—FSBC I 31866, 1 whm spm from Sta 5 (5 Jan 1973).

*Description.*—Length of holotype (paratype not complete) 16.1 mm, 86 segments. Width at XI, 0.44 mm. Clitellum extending over ½X–XII. Somatic setae 2 per bundle in II–IX(X), 1 per "bundle" thereafter. Anterior setae (Fig. 8A) bifid, with upper tooth reduced; these setae 70–140 µm long, 3.5–10 µm thick. Setae from about X and backwards straight and single-pointed (occasionally bifid, similar to anterior setae); these setae dorsally (Fig. 8A) 140–165 µm long, 12–13 µm thick, ventrally (Fig. 8C) 85–95 µm long, about 7 µm thick. Ventral setae of XI modified into penial setae (Figs. 8D, F, ps), 4–6 per bundle, more or less straight, ectally single-pointed and hooked; in holotype (Fig. 8D), tips of penial setae obliquely pointing toward posterior; in paratype (Fig. 8F), penial setae and male genitalia somewhat distorted and dislocated. Male pores paired in line with ventral setae in XI. Spermathecal pores paired in lateral lines, anteriorly in X.

Pharyngeal glands in IV–VI. Male genitalia paired. Vas deferens 16–19 µm wide, longer than atrium, entering apical end of latter. Atrium (Fig. 8F, a) somewhat spindle-shaped and curved, about 105 µm long, about 40 µm wide, with very thin outer lining, and thick, granulated outer epithelium. Prostate glands (Fig. 8F, pr 1–2) very large

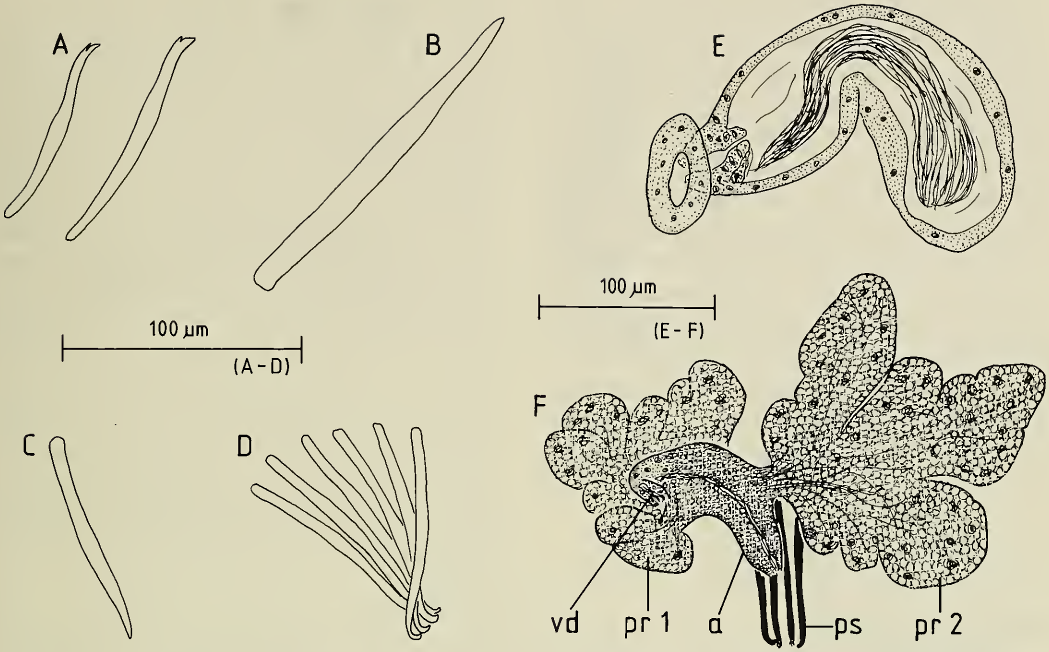

Fig. 8. *Phallodrilus hirsutus,* n. sp.: A, Anterior setae; B, Posterior dorsal seta; C, Posterior ventral seta; D, Penial setae; E, Spermatheca; F, Male genitalia.

and lobed, anterior one subapical on atrium, posterior one attaching to posterior face of atrium, at some distance from atrium opening. Copulatory sac apparently present, but details not clear in available spms. Spermathecae (Fig. 8E) elongate, consisting of indistinct ducts and long, thin-walled ampullae, latter somewhat constricted at middle, and containing large bundle of sperm.

*Remarks.*—This very large species of *Phallodrilus* is distinguished from all other members of the genus by its very large and modified setae. In particular, the postclitellar dorsal (single-pointed) setae (Fig. 8B) are very conspicuous and make the species superficially very similar to *Heterodrilus hispidus* described above, and also the NW European species *Bathydrilus rarisetis* (Erséus, 1975) (cf. Erséus 1975; 1979a:fig. 7). The latter form also inhabits very coarse sand and gravel, and it appears likely that the convergent evolution of very stiff and large setae in different groups of marine Tubificidae (including many other species of *Heterodrilus*) is explained by their functional advantage in such coarse substrates.

*Etymology.*—The specific name *hirsutus* is Latin for "shaggy, bristly, rough" and alludes to the conspicuous setation.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Coarse, clean or somewhat muddy, sands, 10–11 m depth.

### *Adelodrilus* Cook, 1969
### *Adelodrilus magnithecatus* Erséus, 1979

*Adelodrilus magnithecatus* Erséus, 1979d: 419–421, fig. 1.

*New material examined.*—FSBC I 31867, 1 whm spm from Sta 2 (3 Nov 1971).—Author's collection: 1 whm spm from Sta 2.

*Remarks.—Adelodrilus magnithecatus,*

originally described from Bermuda and inshore waters of North Carolina, is distinguished from its congeners by its large spermathecae. Its penial setae are of two types as is typical for the genus; within each bundle are one "spoon-shaped" giant seta and a number of smaller, straight setae, the latter clubbed and each with an apical hook.

The new specimens from Florida are larger (6.2–6.5 mm, 55–57 segments) than the original material (2.9–5.1 mm, 26–47 segments) but otherwise fit the description well.

*Distribution and habitat.*—East coast of Florida (new record), North Carolina, and Bermuda. Coarse sands, 4.5–17 m depth.

### *Bathydrilus* Cook, 1970

### *Bathydrilus ingens,* new species

Fig. 9B–C, E–H

*Bathydrilus* sp.—Erséus, 1979a:146.

*Holotype.*—USNM 98133, whm spm from Sta 2 (2 Nov 1972).

*Paratype.*—FSBC I 31868, 1 whm spm from type locality (2 Nov 1972).

*Other material examined.*—Author's collection: 1 whm spm from Sta 4; 1 whm spm from NE Gulf of Mexico, 1 mile off Withlacoochee River mouth, Florida, 28°58′48″N, 82°48′27″W, 3–4 m, shell hash (Nov 1984; courtesy M. R. Milligan); 2 whm spms from between Carrot Island and Middle Marsh, near Beaufort, North Carolina, 34°42′06″N, 76°37′13″W, 5 m, shells and shell gravel with some coarse sand (19 Oct 1977; cf. Erséus 1979a).

*Description.*—Length (2 complete spms) 25.6–27.0 mm, from about 127 (posterior end not fully differentiated) to 139 segments. Width at XI, 0.26–0.42 mm. Epidermal glands (Fig. 9B) as continuous dorsal band along most of body, starting few segments anterior to clitellum. Clitellum extending over ⅓X–XII. Somatic setae of 2 types. Anterior and some posterior ones bifid (Fig. 9E), with upper tooth smaller than lower; many posterior ones (particularly those in dorsal bundles; Fig. 9F), however, single-pointed and somewhat enlarged. Somatic setae 35–85 μm long, 2.5–6 μm thick at node, 2–3(4) per bundle anteriorly, 2 per bundle in postclitellar segments. Ventral setae of XI (XII in aberrant spm) modified into penial setae (Figs. 9C, H, ps), 3 per bundle; penial setae straight with somewhat curved, single-pointed tips, latter directed towards mid-ventral line, exiting at summits of 2 large papillae; tips of bundles often crossing each other (as in Fig. 9C). Penial setae 150–200 μm long (only about 80 μm long, but probably not fully grown, in spm from Gulf of Mexico), 6–9 μm thick. Male pores paired in line with ventral somatic setae in posterior part of XI (XII in aberrant spm). Spermathecal pores paired in lateral lines in anteriormost part of X (XI in aberrant spm).

Pharyngeal glands extending into VII(VIII–IX). Male genitalia (Fig. 9H) paired. Vas deferens about 7 μm wide (full length not seen in available material), entering anterior face of ectal-to-middle part of atrium together with anterior prostate gland. Atrium with ental end obliquely directed towards posterior, often extending into next segment. Atrium elongate, spindle-shaped, about 220–270 μm long (difficult to measure), 30–90 μm wide, with about 2 μm thick outer lining of muscles, and granulated and ciliated inner epithelium. Atrium opening at outer end of deep blind sac, atrial opening hidden behind lateral fold of body wall; whole complex forming elaborate pseudopenis. Posterior prostate gland large, attached to apex of atrium. Spermathecae (Fig. 9G) consisting of short, triangular ducts and large elongate, somewhat bilobed ampullae; former opening into middle of latter. Sperm as rhomboid or elongate spermatozeugmata, as bundles, or as loose masses, in ampullae of postcopulatory spms.

*Remarks.*—One specimen from Hutchinson Island has its sexual organs shifted backwards to occupy segments XI–XII instead of X–XI.

*Bathydrilus ingens* is a very large species,

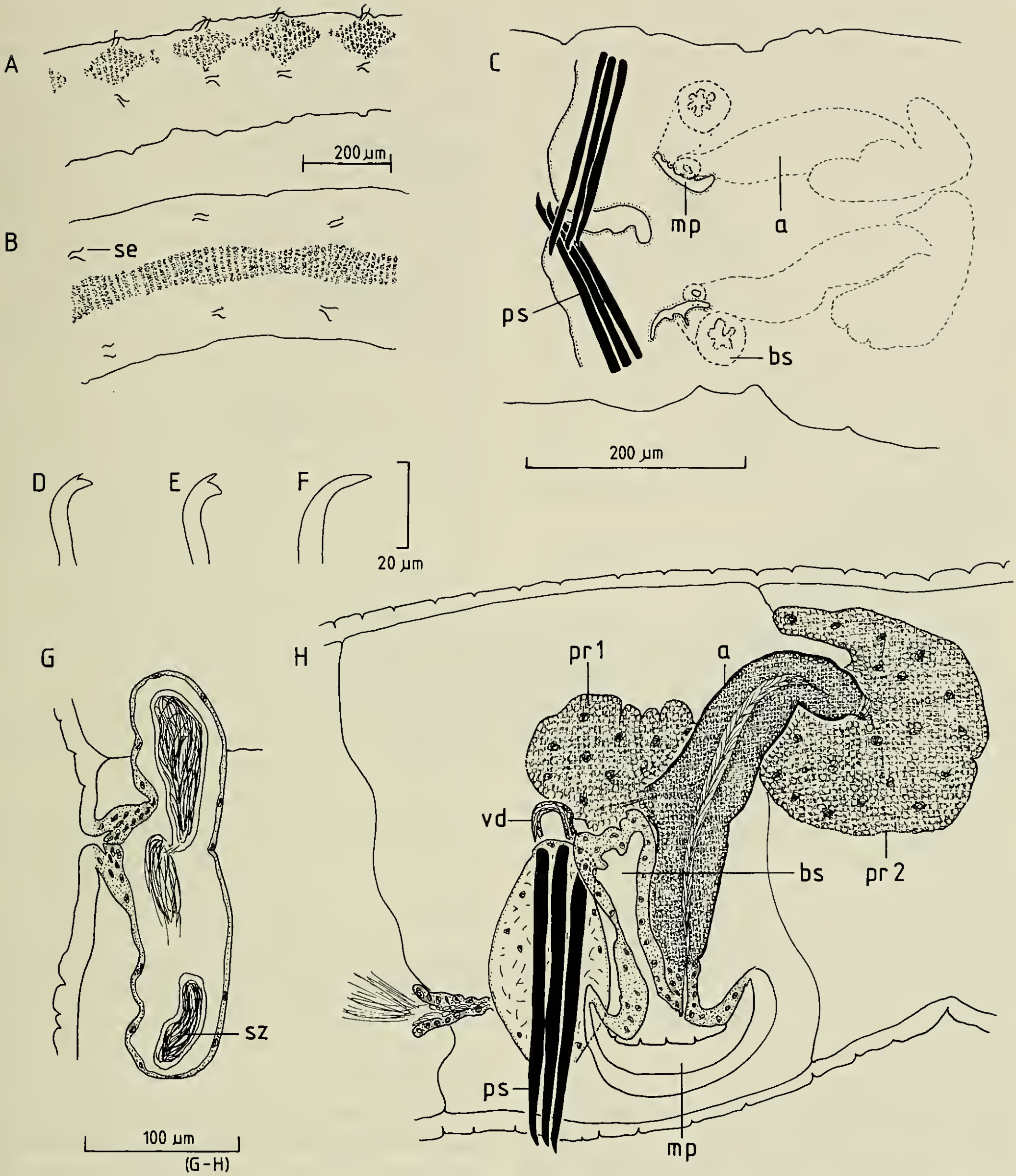

Fig. 9. *Bathydrilus longus* (A, D) and *B. ingens,* n. sp. (B, C, E–H): A and B, Patterns of dorsal epidermal glands (shown for a few successive segments in postclitellar part of body); C, Ventral view of penial setae and male pores in segment XI (*ingens*); D, Posterior dorsal seta (*longus*); E, Anterior seta (*ingens*); F, Posterior dorsal seta (*ingens*); G, Spermatheca (*ingens*); H, Lateral view of male genitalia in segment XI (*ingens*).

a feature shared with the very similar *B. longus* Erséus, 1979, reported from deeper (70–165 m) stations off New Jersey (Erséus 1979a) and Massachusetts (Davis 1985). Both species have two or three very conspicuous, straight penial setae per bundle. The new, southern form is distinguished from *B. longus* by four important characters: (1) the dorsal epidermal glands form a continuous dorsal band along body except for anteriormost segments (Fig. 9B; in *B. longus* these glands in rhomboid, segmentally arranged patches as shown in Fig. 9A); (2) the aberrant appearance (Fig. 9F) of many posterior setae (in *B. longus* posterior setae always have a small upper tooth; Fig. 9D); (3) the thin atrial musculature (only about 2 μm thick; about 5–7 μm thick in *B. longus*); and (4) the possession of a pair of deep invaginations lateral to ectal parts of atria, and at the outer ends of which atria open (such blind sacs absent in *B. longus*).

*Etymology.*—The species name *ingens* is Latin for "huge, enormous."

*Distribution and habitat.*—North Carolina and both coasts of Florida. Coarse sands, 3–11 m depth.

### *Bathydrilus formosus,* new species

Fig. 10

*Holotype.*—USNM 98134, whm spm from Carrie Bow Cay, Barrier reef of Belize, edge of *Thalassia* bed near north end of island, subtidal shallow water, mixed coral sand with some organic debris (6 Apr 1982; coll. H. R. Baker).

*Paratypes.*—USNM 98135, 1 whm spm from type locality. USNM 98136, 1 whm spm from near reef crest at Carrie Bow Cay, Belize, about 0.5 m, coral sand and *Halimedia* debris in small pocket of bedrock coral (12 Apr 1982; H. R. Baker).—FSBC I 31869, 1 whm spm from Hutchinson Island; Sta 5 (5 Jan 1973).

*Other material examined.*—Author's collection: 4 whm spms from type locality; 2 from Tobacco Reef, Barrier reef of Belize, back reef of South Water Cay (about 0.5 km N of the cay), 1 m, small patch of coral sand (9 Apr 1982; H. R. Baker).—1 from Carrie Bow Cay, Belize, *Thalassia* bed very near Research Station, barely subtidal, coral sand with some organic debris (12 Apr 1982; H. R. Baker).—1 whm spm from NE Gulf of Mexico, off Clearwater, Florida, 27°55′N, 83°28′W, 20 m, sediment unknown (26 Aug 1977; courtesy M. S. Ivester).

*Description.*—Length (only 3 complete spms) 15.9–18.0 mm, 84–108 segments. Width at XI, 0.27–0.40 mm. Epidermal glands as continuous dorsal band in many posterior segments. Clitellum extending over ⅓X–XII. Somatic setae (Fig. 10A) bifid, sigmoid, with upper tooth thinner and shorter than lower; 45–55 μm long, 3–3.5 μm thick at node, 3 per bundle in anteriormost segments, 2 per bundle from few segments anterior to clitellum and along rest of worm. Ventral setae of XI modified into penial setae (Figs. 10D, C, E, ps), 2(3) per bundle; penial setae strongly curved with tips directed towards and located near mid-ventral line, exiting at summit of oval epidermal pad mid-ventrally in middle of XI (cf. Fig. 10C, ep). Penial setae 100–155 μm long, 4.5–7 μm thick at swelling (modified node) near ectal end, with bifid tips; upper tooth shorter and much thinner than lower, but not always visible (hidden behind lower tooth; cf. 1 seta in Fig. 10D). Male pores paired in line with ventral somatic setae in posterior part of XI, on 2 bulbous protuberances (= pseudopenes; cf. below and Fig. 10C, pp). Spermathecal pores paired in lateral lines in anteriormost X.

Pharyngeal glands extending into VIII. Male genitalia (Fig. 10E) paired. Vas deferens 9–12 μm wide, longer than atrium, entering middle of anterior face of latter together with stalk of anterior prostate gland. Atrium with ental end obliquely directed towards posterior, sometimes extending into XII (indicated in Fig. 10C). Atrium elongate, pear-shaped or spindle-shaped, 150–235 μm long, 50–80 μm wide, with 1–2.5 μm thick outer lining of muscles and ciliated inner epithelium, latter densely granulated except for most ectal part. Atrium terminating ectally into bulbous and muscular pseudopenis, latter more or less protruded in all spms available. Prostate glands moderately developed, anterior one attached to middle of atrium, ectal one to apex of atrium. Spermathecae (Fig. 10B, s) consisting of short, triangular ducts and large, extremely thin-walled ampullae; latter containing roundish, rhomboid or elongate spermatozeugmata in postcopulatory spms.

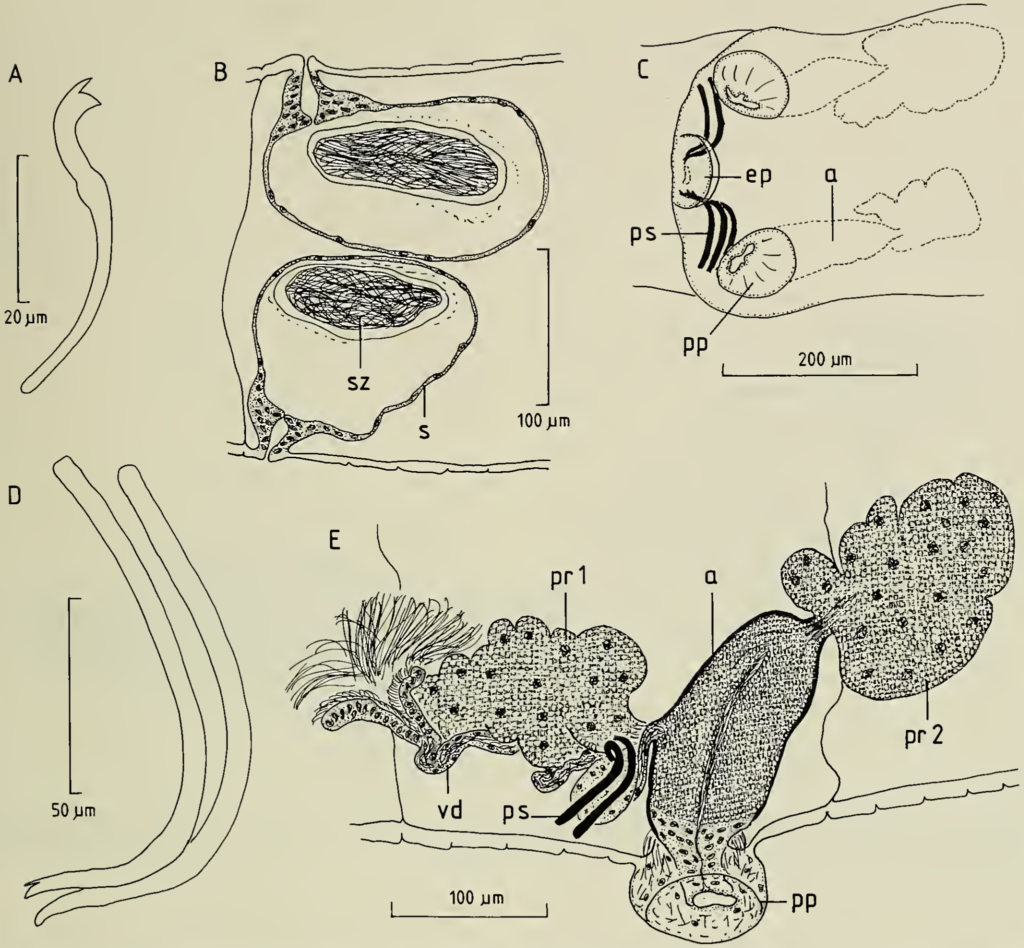

Fig. 10. *Bathydrilus formosus,* n. sp.: A, Somatic seta; B, Spermathecae in segment X; C, Ventral view of penial setae and male pores in segment XI; D, Penial setae; E, Lateral view of male genitalia in segment XI.

*Remarks.*—This species is distinguished from the closely related *B. longus* and *B. ingens,* n. sp., by its externally more conspicuous and bulbous pseudopenes and by its curved penial setae. In addition, *B. formosus* is the only species within the genus known to possess bifid penial setae; in all congeners, penial setae (when present) are described as single-pointed. [Note, however, that Baker (1983) reported that in a single specimen of the NE Pacific *B. litoreus* Baker, 1983, penial setae in one bundle were bifid.]

*Etymology.*—The species name *formosus* is Latin for "finely formed, beautiful"; here primarily referring to the penial setae, which in the author's opinion are esthetically appealing.

*Distribution and habitat.*—Belize and both coasts of Florida. Subtidal sands, 0.5–11 m depth.

### *Bathydrilus macroprostatus,* new species
Fig. 11

*Holotype.*—USNM 98137, whm spm from Sta 2 (15 Sep 1971).

*Paratype.*—FSBC I 31870, 1 whm spm from type locality (3 Jan 1972).

*Description.*—Length more than 5.7 mm, more than 25 segments (no complete spm

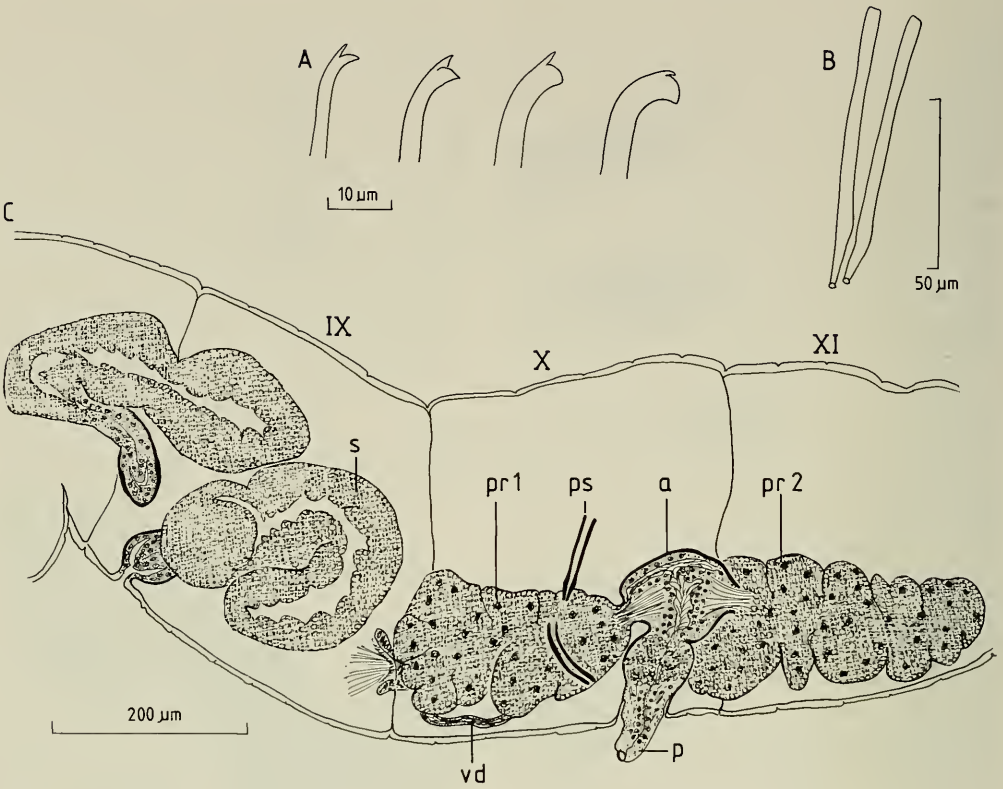

Fig. 11. *Bathydrilus macroprostatus,* n. sp.: A, Somatic setae; B, Penial setae; C, Somewhat lateral view of atrium (of one side only), penial setae and spermathecae in segments IX–XI (note that this location is an anomaly, characterizing the holotype only; see text).

available). Width at male pores, 0.37–0.47 mm. Epidermal glands not observed. Clitellum extending over ½X–XII in paratype, not developed in holotype. Somatic setae (Fig. 11A) bifid, slender in most anterior segments, only 50–55 µm long, about 2.5 µm thick at node, thereafter stouter and larger, 70–85 µm long, 4–6 µm thick at node; teeth variable, but upper tooth always smaller than lower. Bifids 2–3(4) per bundle anteriorly, 2 per bundle in postclitellar segments. Ventral setae of XI (X in holotype) modified into penial setae (Fig. 11B), 2 per bundle, with tips directed towards and located near mid-ventral line (cf. Fig. 11C). Penial setae straight to somewhat curved, 70–90 µm long, 4–5 µm thick at swelling (modified node) near ectal end, with flat, hooked tips. Spermathecal and male pores paired in line with ventral somatic setae, former in most anterior part of X (IX in holotype), latter in posterior part of XI (X in holotype).

Pharyngeal glands extending into VIII. Male genitalia (Fig. 11C) paired. Vas deferens thin, 8–9 µm wide, longer than atrium, but whole length not visible in available material. Vas deferens entering anterior face of ental part of atrium together with anterior prostate gland (indicated by ciliation inside atrium), but exact position of entrance not ascertained. Atrium erect or somewhat tilted over to posterior, totally (including penial organ) 230–245 µm long, separated into two main parts by constriction: ental part 115–140 µm wide with broad, somewhat rounded, truncate apex, ectal part 70–85 µm wide, somewhat spindle-shaped and terminating in elongate (permanently pendant?) penis protruding from male pore. Penis lacking cuticular sheath. Lumen of vas deferens continuous with ciliated narrow canal running beneath apex of ental part of atrium, perpendicular to main lumen of atrium. Inner epithelium of ental part of atrium with (paratype) or without (holotype; Fig. 11C) granulation (=different degrees of maturation), that of ectal part of atrium granulated in both spms. Muscular lining of atrium 2.5–4 μm thick. Prostate glands attached by thick stalks to anterior and posterior faces of ental part of atrium, almost opposite to each other, anterior prostate somewhat more ectal than posterior one. Microtubules of prostatic cells conspicuous at entrances into atrium. Prostate glands large and lobed, posterior gland extending into XII (XI in holotype). Spermathecae (Fig. 11C, s) not fully developed in available material (spms pre-copulatory), but nevertheless very large, consisting of short, muscular ducts and elongate, folded ampullae, latter with glandular, thick inner epithelium.

*Remarks.*—The holotype has its genitalia in segments IX–X and not in X–XI as is normal for a tubificid; this is regarded as an anomaly of this particular specimen.

The atrial morphology (bipartite, erect atrium terminating in an elongate penis) and the very large prostate glands and spermathecae distinguish *B. macroprostatus* from other species of the genus.

*Etymology.*—This species has very large prostate glands; hence the name *macroprostatus.*

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Shell hash, 10–11 m depth.

## *Coralliodrilus* Erséus, 1979

## *Coralliodrilus corpulentus,* new species

Fig. 12

*Holotype.*—USNM 98138, whm spm from Sta 4 (4 Jan 1972).

*Paratypes.*—FSBC I 31871-31872, 2 whm spms, from Sta 2 (4 Jan 1973) and 4 (5 Jan 1973), respectively.

*Description.*—Length 5.4–5.9 mm, 56–63 segments. Width at XI, 0.47–0.53 mm. Prostomium rounded triangular, not very large. Fixed spms very stout; segments short. Secondary annulation present, several annuli per segment. Clitellum over ½X–XII (in one paratype ½IX–XI). Somatic setae bifid, of general phallodriline type in most bundles, with upper tooth slightly smaller than lower and with subdental ligament (Fig. 12A). Posterior dorsal setae (Fig. 12B) modified, with minute upper tooth (sometimes not visible; absent?) and prolonged, sharply pointed lower tooth, and without or with very inconspicuous subdental ligament. Anterior setae 55–70 μm long, 1.5–3 μm thick, (2)3 per bundle. Posterior setae (from few segments posterior to clitellum and backwards) up to 80 μm long, 3–5 μm thick. Ventral setae of XI (X in one paratype) modified into penial bundles, each containing about 12 straight, ectally strongly hooked single-pointed setae (Fig. 12C), 80–95 μm long, about 2.5 μm thick (shown at one side only in Fig. 12D). Male pores paired in line with ventral setae, posteriorly in XI (X in one paratype). Spermathecal pores paired in lateral lines, in most anterior part of X (IX in one paratype).

Pharyngeal glands poorly developed in (III)IV–VI. Male genitalia (Fig. 12D) paired. Vas deferens not observed in complete length, but appearing short; ectally about 20 μm wide with strong circular muscles. Atrium spindle-shaped, somewhat sigmoid, 210–290 μm long, 55–80 μm wide at middle, with 3.5–12 μm thick outer layer of muscles, in which fibers arranged in somewhat spiral pattern; inner epithelium of atrium ciliated and for most parts granulated. Atrium tapering ectally into short, narrow duct surrounded by very strong muscles; duct terminating in simple, minute male pore (only that of 1 side shown in Fig. 12D). Spermathecae (Fig. 12D, s) consisting

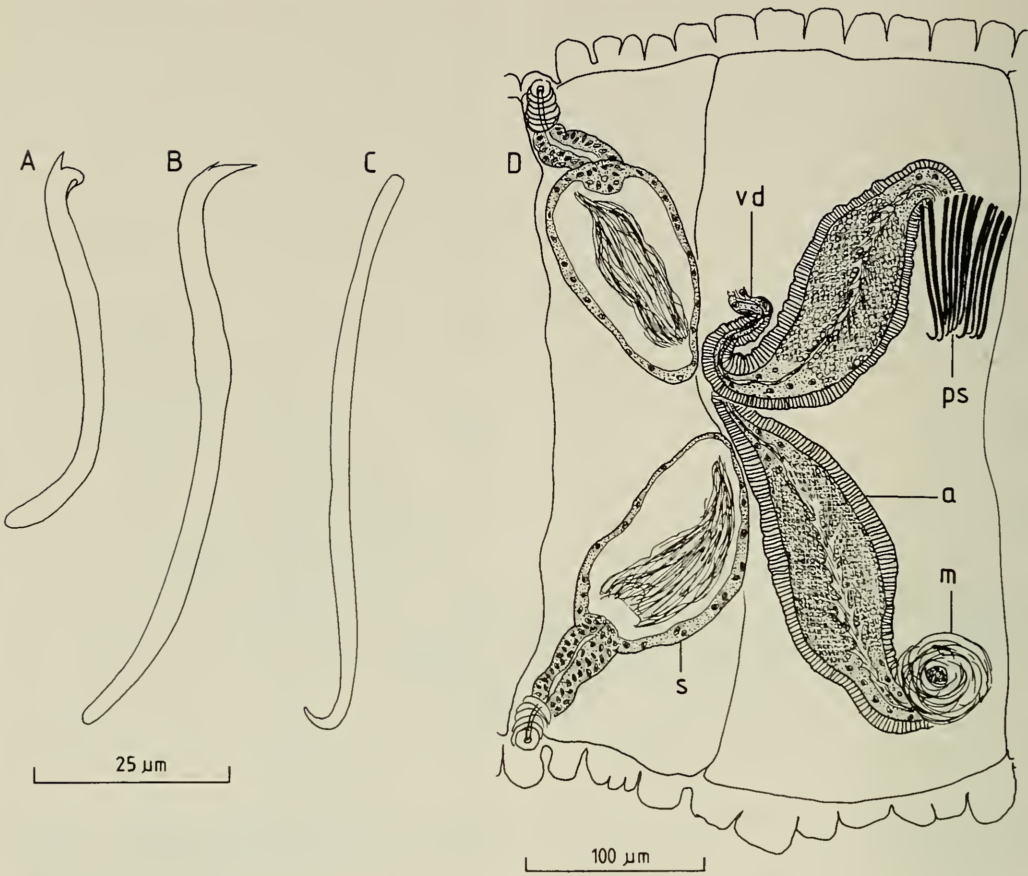

Fig. 12. *Coralliodrilus corpulentus,* n. sp.: A, Somatic seta; B, Posterior dorsal seta; C, Penial seta; D, Ventral view of spermathecae and male genitalia in segments X–XI (note that musculature is shown at one of the two male openings, penial setae at the other).

of ducts about 80 µm long, entally about 25 µm wide, ectally strongly muscular and narrower, and oval, thin-walled ampullae, 130–140 µm long, about 75 µm wide; latter containing large bundle of sperm.

*Remarks.*—In one paratype, the clitellum and the genitalia are shifted forward to occupy segments IX–X, not X–XI which is the normal position for the Tubificidae.

*Coralliodrilus corpulentus* is distinguished from all its shallow-water congeners by its very thick atrial muscles, and is unique within the genus in having modified bifid setae in the posterior dorsal bundles. The atrium of the new species is somewhat similar to that of the South Atlantic deep-sea species *C. longiductus* Erséus, 1983 (Erséus 1983c), but the latter lacks the voluminous muscular mass around the ectal part of the atrial duct which characterizes *C. corpulentus,* and has only five to seven penial setae per bundle.

It should be noted that the gutless species described as *Coralliodrilus aviscerалis* by Erséus (1981b), which also has heavily muscular atria, is now regarded as a member of the genus *Olavius* Erséus, 1984 (subgenus *Coralliodriloides* Erséus, 1984; see Erséus 1984b).

*Etymology.*—The species name *corpulentus,* which is Latin for "stout, corpulent," refers to the shape of the fixed specimens.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Shell hash, 10–11 m depth.

### *Inanidrilus* Erséus, 1979

### *Inanidrilus ernesti* Erséus, 1984

*Phallodrilus* sp.—Erséus and Loden, 1981: 821.

*Inanidrilus ernesti* Erséus, 1984b:251, fig. 14.

*New material examined.*—FSBC I 31873, 2 whm spms from Sta 2 (9 May 1973).—Author's collection: 5 whm spms from Sta 2, 5 from Sta 4.

*Remarks.*—The gutless species *Inanidrilus ernesti* was described (Erséus 1984b) on the basis of four specimens found in another collection of oligochaetes from off Hutchinson Island, provided by Applied Biology, Inc., first to M. S. Loden (Louisiana State University) (cf. Erséus and Loden 1981), subsequently to the author. The new material conforms to the original description.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Coarse sediments, 10–12 m depth.

### *Inanidrilus vacivus* Erséus, 1984

*Inanidrilus vacivus* Erséus, 1984b:249–250, fig. 12.

*Holotype.*—USNM 96540, whm spm from Sta 2 (3 Jan 1972).

*Paratype.*—FSBC I 31263, 1 whm spm from Sta 4 (6 Jul 1972).

*Remarks.*—*Inanidrilus vacivus* is described elsewhere (Erséus 1984b) on the basis of two specimens in the present material.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Shell hash, about 10 m depth.

### *Olavius* Erséus, 1984

### *Olavius latus*, new species

Fig. 13

*Holotype.*—USNM 98139, whm spm from Sta 2 (7 Sep 1972).

*Description.*—Length 9.5 mm, 80 segments. Width at XI, 0.40 mm. Body flat with elongate prostomium and with pygidium possessing long filiform caudal process (Fig. 13A). Secondary annulation indistinct (this may be a preservation artifact of the only spm at hand). Epidermal glands scattered over most of body surface (the fact that they are visible may be due to the preservation method used and should not be regarded as a specific character). Clitellum well developed over ½X–XII. Somatic setae (Fig. 13B) bifid, but variable, with upper tooth thinner and shorter than lower, and with conspicuous subdental ligament; upper tooth not always visible (oblique view?). Bifids 3–4 per bundle anteriorly, 2–3 per bundle in postclitellar segments. Penial setae (Figs. 13C, D, ps) 5–6 per bundle, more or less parallel and somewhat spread out within bundle, about 35 μm long, entally about 2 μm thick, ectally much thinner, single-pointed and curved. Male pores paired in line with ventral setae posteriorly in XI. Spermathecal pores paired between lateral lines and lines of dorsal setae, anteriorly in X.

Alimentary canal absent. Male genitalia (Fig. 13D) paired. Vas deferens longer than atrium, up to 10 μm wide, but whole length not visible in available spm. Atrium somewhat comma-shaped, 50–60 μm long, 25 μm wide, with thin outer lining and thick inner epithelium, but details of lumen not clear. Atrium tapering ectally into short duct opening at inner end of very complex, folded and deep penial sac; one "fold" of sac appearing as somewhat granulated and pendant(?) papilla. Prostate glands two per atrium, large and lobed; posterior one attached by long stalk to ectal part of atrium. Pair of glandular bodies of unknown function located anterior to male pores near body wall. Spermathecae (Fig. 13D, s) consisting of inconspicuous ducts, about 20 μm long, about 15 μm wide, and bipartite ampullae, 135–165 μm long; parts of each ampulla separated from each other by constriction, ectal part 30–35 μm wide and devoid of

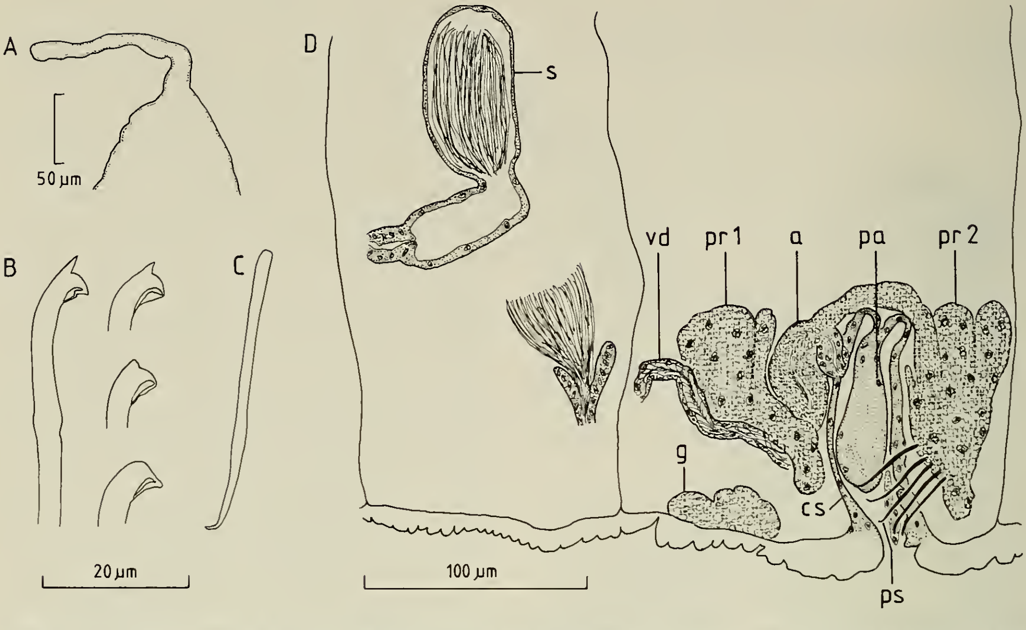

Fig. 13. *Olavius latus*, n. sp.: A, Pygidium with caudal process; B, Somatic setae; C, Penial seta; D, Lateral view of spermatheca and male genitalia in segments X–XI.

sperm, ental part 35–45 µm wide and containing broad bundle of sperm.

*Remarks.*—This species appears closely related to *O. planus* (Erséus, 1979) from Bermuda, another large species of *Olavius* characterized by a flat body shape and possession of a long caudal process (Erséus 1979b). However, the new species has a more complex penial sac than has *O. planus,* and its penial setae are single-pointed, not bifid as in the other species.

*Etymology.*—The species name *latus* is Latin for "broad, wide," and refers here to the flattened shape of the worm.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Shell hash, 11 m depth.

### *Olavius* sp. A

*Material.*—Author's collection: 1 whm spm from Sta 2.

*Remarks.*—This single specimen is very similar to *O. latus* described above, but lacks penial setae and is probably a separate species. However, it is not considered appropriate to describe it as such until additional material becomes available.

### *Olavius* sp. B

*Material.*—Author's collection: 2 whm spms from Sta 2.

*Remarks.*—This large, most probably new, gutless species is briefly characterized as follows: body wide and flat; pygidium rounded, without filiform appendage; penial setae 6–10 per bundle. Unfortunately, male genital organs are not clearly visible in the two specimens at hand.

## Subfamily Limnodriloidinae

### *Limnodriloides* Pierantoni, 1903

### *Limnodriloides vespertinus* Erséus, 1982

*Limnodriloides vespertinus* Erséus, 1982c: 215–216, fig. 2.

*New material examined.*—FSBC I 31874, 1 whm spm from Sta 4 (10 May 1972).

*Remarks.*—This species was described from near Miami, Florida, and from Andros Island, Bahamas, by Erséus (1982c). The single specimen from Hutchinson Island has poorly developed spermathecae and its posterior end is not fully grown (specimen only 3.5 mm long, consisting of about 36 segments), but otherwise it fits the original description.

*Distribution and habitat.*—East coast of Florida and Bahamas. Subtidal, generally somewhat muddy sands, down to 11 m depth.

### *Limnodriloides monothecus* Cook, 1974

*Limnodriloides monothecus* Cook, 1974: 131–132, fig. 2.—Brinkhurst and Baker, 1979:1664.—Erséus, 1982c:250–253, figs. 28–29.

*Bohadschia monotheca* Hrabě, 1975:112–114, figs. 1–3.

*New material examined.*—FSBC I 331875, 1 whm spm from Sta 2 (2 Nov 1972).—Author's collection: 2 whm spms from Sta 2.

*Remarks.*—This species is widely distributed in North America (including the Pacific coast) and the Caribbean area (cf. Erséus 1982c:fig. 14B for map), and it has been reported also from the Mediterranean Sea (as *Bohadschia monotheca* Hrabě, 1975, which is regarded as both a synonym and a homonym for *L. monothecus*). The new material largely conforms to the previous descriptions, but a slight deviation from the latter regarding some setal characteristics (cf. Erséus 1982c:table 1) should be noted. In the present specimens, preclitellar setae are up to four (occasionally five) per bundle, which is more than the two to three previously stated, and ventral setae are present in X in two of the three worms (these setae absent in both X and XI of previously studied material). In one specimen, the spermatozeugmata are short and stout as noted for material from Barbados by Erséus (1982c), but in the other two individuals they are of the "normal," very slender type.

*Distribution and habitat.*—Pacific coasts of British Columbia, California, and Mexico; Atlantic coast of Florida through New Jersey; Gulf coast of Florida; Bermuda; Barbados; Yugoslavia. Euryoecious, occurring also in brackish water; in various kinds of sand and silt, generally with rich organic material, down to 370 m depth.

Fig. 14. *Marcusaedrilus luteolus*, spermatheca.

### *Marcusaedrilus* Righi and Kanner, 1979

### *Marcusaedrilus luteolus* Erséus, 1983

Fig. 14

*Marcusaedrilus luteolus* Erséus, 1983a:27–29, fig. 3.

*New material examined.*—FSBC I 31876–31877, 2 whm spms, from Sta 2 (2 Nov 1972) and Sta 5 (10 May 1972), respectively.—Author's collection: 4 whm spms from Sta 2, 2 from Sta 4, and 45 from Sta 5.

*Remarks.*—*Marcusaedrilus luteolus* was described on the basis of material from Barbados and from near Miami, Florida (Erséus 1983a). New specimens are consistently larger (12.6–15.7 mm long, 77–88 segments) than the original material (6.1–6.9 mm, 53–68 segments), and spermathecae of all individuals from Florida (see Fig. 14) are larger than those of the original material from Barbados (Erséus 1983a:29, fig. 3D).

*Distribution and habitat.*—Barbados and east coast of Florida. Subtidal muds and sands, down to 21 m depth.

### Subfamily Tubificinae

### *Tubificoides* Lastockin, 1937

### *Tubificoides annulus,* new species

Fig. 15

*Holotype.*—USNM 98140, whm spm from Sta 4 (14 Mar 1972).

*Paratypes.*—FSBC I 31878–31879, 2 whm spms from Sta 4 (type locality; 6 Mar 1973) and Sta 5 (1 Mar 1972), respectively.

*Description.*—Length (only 1 complete spm) 7.8 mm, about 47 segments (still growing posteriorly). Width at XI, 0.20–0.22 mm. Prostomium rounded, well demarcated from peristomium, appearing somewhat retractile within latter. Body wall smooth, without adhering foreign particles, but cuticle thick and finely ridged. Clitellum poorly developed over XI–½XII. Anterior dorsal bundles with 1–2 single-pointed setae (possibly bifid with teeth very close together) and 1–2 hair setae; single-pointed setae (Fig. 15A) 35–55 μm long, hair setae 85–150 μm long. Anterior ventral bundles with 40–50 μm long bifid setae (Fig. 15B), with upper tooth thinner and slightly shorter than lower. Dorsal and ventral bundles in postclitellar segments each represented by 1 bifid seta (Fig. 15C), similar to anterior bifids but generally more curved entally. Ventral setae absent in XI. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores paired immediately anterior to ventral setae in X.

Pharyngeal glands in IV–V. Part of esophagus enlarged and somewhat glandular in IX. Male genitalia (Figs. 15D–E) paired. Vas deferens 11–18 μm wide, thin-walled and densely ciliated, at least 5 times as long as atrium, entering latter sub-apically. Atrium about 200 μm long, cylindrical and curved, entally (at caecum) about 30 μm wide, at middle about 20 μm wide. Atrium with wide, distinct outer layer of muscles, 1–2 μm thick, arranged in circles around long axis; muscles more developed in ental than in ectal part. Inner epithelium of atrium histologically bipartite; inner part (caecum and area with entrances of vas deferens and prostate gland) with glandular, discrete bodies, lumen wide and containing few cilia near entrance of vas deferens; outer part evenly granulated, lumen not observed. Prostate gland attached by short stalk to atrium, clearly more ectal than, but on opposite side to, that of entrance of vas deferens. Penial sheath short (only about 15 μm long), somewhat ring-shaped, but with inner end somewhat wider (about 20 μm) than outer. Spermathecae (Fig. 15D, s) with very slender ducts and oblong ampullae; sperm trap indistinct but appearing to be present. Spermatozeugmata slender with rounded tips, but not very long (as compared to most congeners).

*Remarks.*—The characteristic shape of penial sheaths distinguishes *T. annulus* from the other species of the genus. Sheaths are reminiscent of those of *T. brevicoleus* Baker, 1983, a littoral form from the Pacific coast of Canada, which also possesses hair setae and very long vasa deferentia. *Tubificoides brevicoleus,* however, bears hair setae in postclitellar segments as well as anteriorly (hairs restricted to anterior segments in *T. annulus*) and papillae along most of the body (naked in *T. annulus*).

*Etymology.*—The name *annulus,* which is Latin for "ring," alludes to the shape of the penial sheaths in this species.

*Distribution and habitat.*—Known only from off Hutchinson Island, east coast of Florida. Coarse, clean or somewhat muddy, sands, 10–11.5 m depth.

### *Tubificoides* sp.

*Material examined.*—Author's collection: 4 whm spms from Sta 1 (but see note under 'material and methods' above), 23 from Sta 2, 6 from Sta 4, and 23 from Sta 5.

*Remarks.*—This species, which occurred

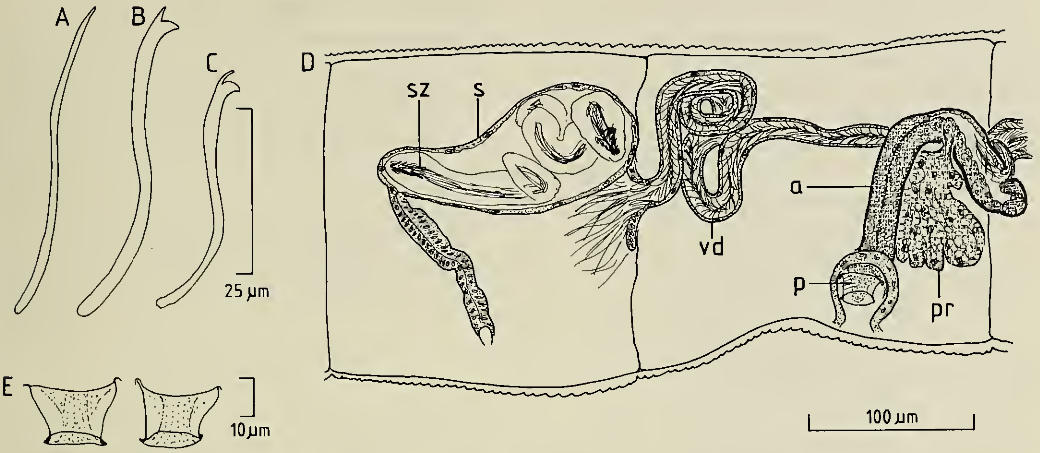

Fig. 15. *Tubificoides annulus,* n. sp.: A, Anterior, single-pointed, dorsal seta; B, Anterior ventral seta; C, Posterior seta; D, Lateral view of spermatheca and male genitalia in segments X–XI; E, Penis sheaths.

at four of the stations, belongs to a complex of species within *Tubificoides* lacking hair setae. The complex is currently under revision by Dr. R. O. Brinkhurst in Canada, and, therefore, the species will not be further treated here. It appears closely related to *T. wasselli* Brinkhurst and Baker, 1979.

## Discussion

Summarized data on the local distribution of the Hutchinson Island Oligochaeta show that all but one of the 25 species occurred at either Sta 2 or Sta 4, or, for most of the species, at both stations (Table 2). Specimens from these two stations clearly dominate the material, although the sampling effort was the same for all stations. The overwhelming similarity between Sta 2 and Sta 4, in terms of distance from shore, depth, sediment composition (very coarse, shell hash), and oligochaete fauna, appears to suggest that they can be "united" for a total characterization of the particular trough in which they are located. Thus, it can be concluded that the benthic community of the coarse, shelly bottom of this trough includes an association of at least 24 interstitial, tubificid species. This is a remarkably high figure, as it outnumbers all other similar oligochaete associations that have been more carefully examined to date; for instance, only eight coarse-sand tubificids were found in Cape Cod Bay, Massachusetts (Cook 1971), and the corresponding species were only four in some Norwegian fjords studied by Erséus (1976). In a recent paper on the Oligochaeta of Georges Bank off Massachusetts, Davis (1985) noted that when sampling in some medium-to-coarse-sand habitats, as many as 20 species could occur in the same sample, but this figure also includes some species belonging to families other than the Tubificidae. High diversity of interstitial tubificids will also be reported from medium to coarse sands off Virginia (approximately midway between Massachusetts and Florida) (Diaz et al., in press), but nowhere reaching the level recorded at Hutchinson Island.

By adding nine species new to science and a further four (named) species new to the state's fauna, the Hutchinson Island material has considerably increased our knowledge about the marine Tubificidae of Florida. The present checklist now comprises 50 species (Table 1). It should be noted that several additional records of estuarine and offshore species along the Gulf of Mexico

Table 2.—Numbers of sexually mature specimens of Tubificidae collected (1971–1973) at Stations 1–5 off Hutchinson Island. Numbers are pooled for all replicates over the whole sampling period for each station. Species are ranked after abundance.

| Rank | Species | Total n | Sta 1* | Sta 2 | Sta 3 | Sta 4 | Sta 5 |
|---|---|---|---|---|---|---|---|
| 1 | *Tubificoides* sp. | 56 | 4 | 23 | | 6 | 23 |
| 2 | *Marcusaedrilus luteolus* | 53 | | 6 | | 2 | 45 |
| 3 | *Heterodrilus perkinsi* | 47 | | 18 | | 29 | |
| 4 | *Heterodrilus bulbiporus* | 46 | 2 | 20 | | 3 | 21 |
| 5 | *Phallodrilus biprostatus* | 40 | | 16 | 2 | 21 | 1 |
| 6 | *Heterodrilus minisetosus* | 18 | | 2 | | 16 | |
| 7 | *Phallodrilus sabulosus* | 15 | | 2 | | 12 | 1 |
| 8 | *Heterodrilus pentcheffi* | 14 | | 10 | 2 | 1 | 1 |
| 9 | *Inanidrilus ernesti* | 12 | | 7 | | 5 | |
| 10 | *Heterodrilus occidentalis* | 11 | | 5 | | 6 | |
| 11 | *Phallodrilus acochlearis* | 9 | | | | 9 | |
| 12 | *Heterodrilus hispidus* | 8 | | 6 | | 2 | |
| 13 | *Bathydrilus ingens* | 3 | | 2 | | 1 | |
| 14 | *Coralliodrilus corpulentus* | 3 | | 1 | | 2 | |
| 15 | *Limnodriloides monothecus* | 3 | | 3 | | | |
| 16 | *Tubificoides annulus* | 3 | | | | 2 | 1 |
| 17 | *Adelodrilus magnithecatus* | 2 | | 2 | | | |
| 18 | *Bathydrilus macroprostatus* | 2 | | 2 | | | |
| 19 | *Inanidrilus vacivus* | 2 | | 1 | | 1 | |
| 20 | *Phallodrilus hirsutus* | 2 | | 1 | | 1 | |
| 21 | *Olavius* sp. B | 2 | | | | 2 | |
| 22 | *Bathydrilus formosus* | 1 | | | | | 1 |
| 23 | *Olavius latus* | 1 | | 1 | | | |
| 24 | *Limnodriloides vespertinus* | 1 | | 1 | | | |
| 25 | *Olavius* sp. A | 1 | | 1 | | | |

All samples: 355

* For habitat purposes, this should be regarded as Sta 5 (cf. "Material and methods" section).

coast will soon be available (M. R. Milligan, pers. comm.).

The east coast of Florida has been recognized as a transitional zoogeographic zone for shallow-water marine invertebrates (see review by Briggs 1974). The area at Hutchinson Island is characterized by an overlap of warm-temperate and tropical faunal elements (e.g., Work 1969; Camp et al. 1977); in the terminology of Valentine (1973) and Dobzhansky et al. (1977), the area is at the border between the Carolinian and Caribbean provinces. The present material and previous records of Florida east coast Tubificidae (cf. Table 1) seem to support this view, although the distribution of marine oligochaetes is still not very well known, as indicated by the fact that about 40% of the species known from Florida are known from nowhere else.

*Heterodrilus bulbiporus, H. occidentalis, H. pentcheffi, L. barnardi, L. rubicundus, O. tenuissimus, P. prostatus,* and *P. sabulosus* appear to be warm-temperate species, present as they are along a great part of the U.S. east coast, several even as far north as off Massachusetts. *Adelodrilus magnithecatus, B. ingens,* and *P. acochlearis* are possibly more restricted to the southeastern states (the first species known also from Bermuda). Caribbean forms include *B. formosus, M. luteolus, M. hummelincki, K. ineri,* and *T. bori.* None of the latter has been taken north of Florida on the U.S. east coast, but the last three are present at Bermuda, which can be regarded as a Caribbean "satellite."

Some species occurring along the Florida east coast are so widely distributed in the world that they may be regarded as circumtropical (*B. adriaticus, P. rectisetosus, L. monothecus,* and *T. gurwitschi*) or even cosmopolitan (*M. rubroniveus*; cf. Baker and Brinkhurst 1981).

The only more general discussion published on marine tubificid zoogeography and diversity is a tentative review by Baker (1984).

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# *CAECIDOTEA DAUPHINA,* A NEW SUBTERRANEAN ISOPOD FROM A BARRIER ISLAND IN THE NORTHERN GULF OF MEXICO (CRUSTACEA: ISOPODA: ASELLIDAE)

Richard F. Modlin

*Abstract.*—*Caecidotea dauphina,* a phreatobitic asellid of the Hobbsi group, is described and identified. Its type habitat is located on a sandy barrier island in the Gulf of Mexico off the coast of Alabama.

Records of subterranean isopods of Alabama are limited to four. *Caecidotea alabamensis* was reported originally from a well located in the Piedmont of east-central Alabama (Stafford 1911), while *C. bicrenata* (Steeves 1963) and *C. meisterae* (Lewis and Bowman 1981; Modlin, unpublished record) were collected in caves in the northern Appalachian region. Steeves (1964) synonymized *C. bicrenata* with *C. alabamensis,* but Lewis and Bowman (1981) reinstated its species status. The species list of Fleming (1972) includes *C. richardsonae* in addition to *C. alabamensis* from locations in Alabama. Morphologically, all four species align with Steeves' Stygius group (Steeves 1963, 1966). Herein is the description of a new species of the Hobbsi group collected on Dauphin Island, Mobile County, Alabama, a sandy barrier island in the southernmost part of the state.

## *Caecidotea dauphina,* new species
Figs. 1–4

*Material examined.*—Alabama, Mobile County, Dauphin Island, Audubon Sanctuary, 9 Aug 1984, R. F. Modlin, 1 male (7.5 mm) holotype, partly dissected on 5 slides and in alcohol (USNM 227076); 8 females (3.3–4.5 mm) and 1 juvenile (2.4 mm) paratypes, in alcohol (USNM 227077). 27 Aug 1984, R. F. Modlin, 1 female (4.2 mm), dissected on 7 slides, in author's collection (082784F22); same locality. Type-specimens are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

*Diagnosis.*—Blind, unpigmented. Antenna 1 esthete formula 0-1-0. Male pereopod 1 palm defined by robust proximal spine, small triangular mesial process, and truncate distal process. Male pleopod 1 longer than pleopod 2, protopod with 6 retinacula. Endopodial tip of male pleopod 2 with short straight cannula, triangular mesial process with tip curved medially, and truncate lateral process.

*Description.*—Lateral sides of body slightly concave, narrowest at pereonites 3 and 4. Average width of 7.5 mm male is 1.6 mm. Head about 0.6× wider than long; anterior margin concave. Telson about 0.8× longer than wide; lateral margins parallel, posterior margin with distinct caudomedial lobe.

Antenna 1 reaching to about midlength of last segment of antenna 2 peduncle. Flagellum composed of 10 segments, esthete formula 0-1-0. Single esthete located on segment 9. Antenna 2 flagellum about 2.5× length of peduncle, reaching to about 6th pereonite.

Mandible with 4-cuspate incisors and lacinia, spine-row with 8 and 10 spines respectively on right and left. Medial spine row on segment 3 of mandibular palp in-

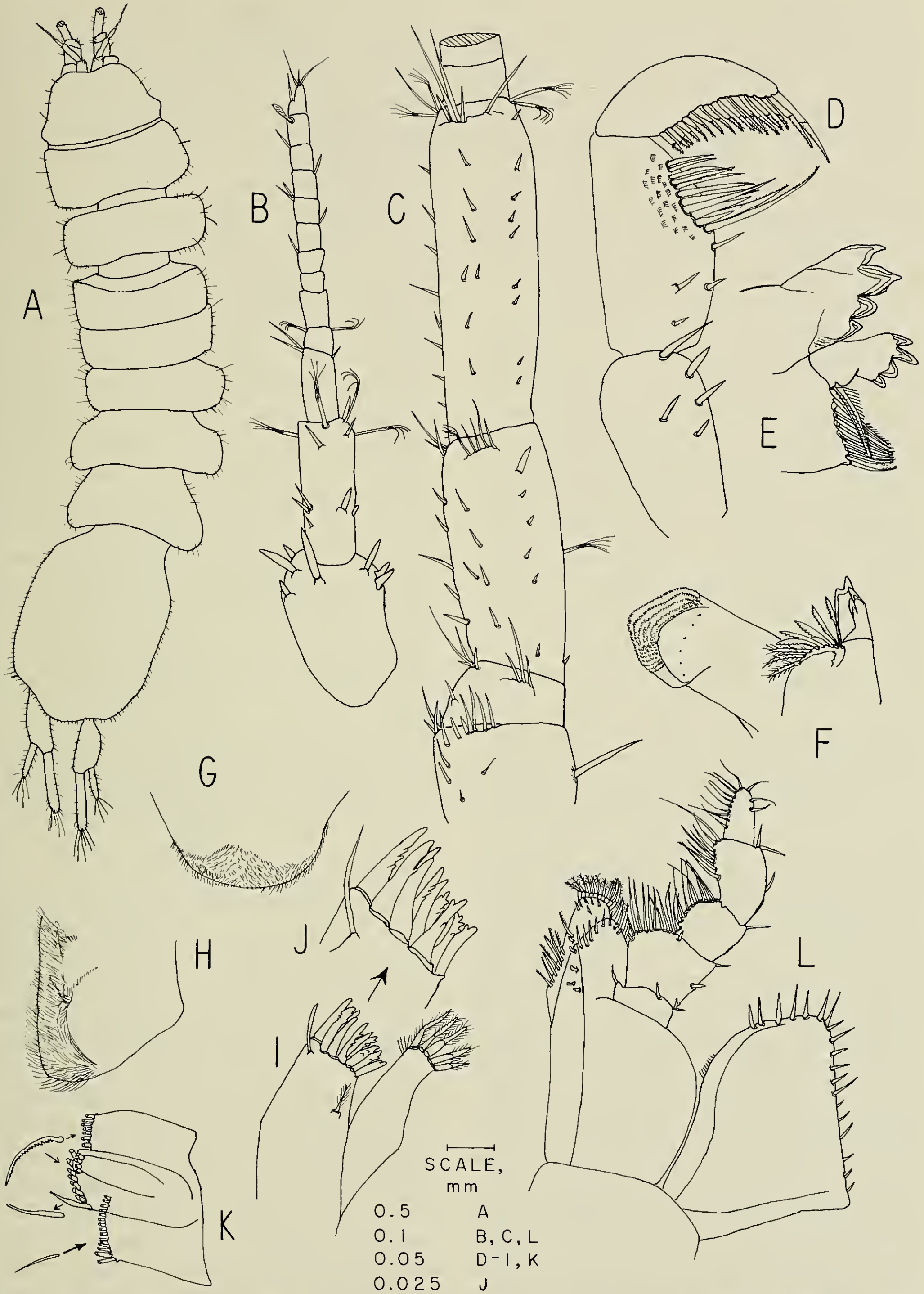

Fig. 1. *Caecidotea dauphina,* A–E, L = 7.5 mm male holotype; F–K = 4.2 mm female: A, Habitus, dorsal; B, Antenna 1; C, Antenna 2, peduncle; D, Mandibular palp; E, Left mandible; F, Right mandible; G, Labrum; H, Left labium; I, Maxilla 1; J, Maxilla 1 outer lobe; K, Maxilla 2; L, Maxilliped.

creasing slightly in length distally, 2 distalmost spines about 2.5 × longer than others; distal row of spines on segment 2 strongly increasing in length proximally, minute setae arranged in linear clumps located lateral to spine row. Maxilla 1 inner lobe with 5 apical plumose setae; outer lobe with 13 apical robust spines (not all spines shown in Fig. 1I, J) and 2 subapical setae, one simple and one plumose. Maxilliped with 5 retinacula in male and 3–4 in females.

Male pereopod 1 propodus about 0.9 × as wide as long; palm defined by robust proximal articulated spine, triangular mesial process separated from lower truncate distal process by shallow cleft, distal process about twice as wide as mesial process; carpus with 3 robust articulated spines and 3 slender simple setae on anterodistal margin. Female pereopod 1 propodus about 1.6 × as wide as long; palm defined by robust proximal articulated spine, without mesial and distal processes; carpus with 1 robust and 2 smaller articulated spines and 1 long simple seta on anterodistal margin. Sexual dimorphism in pereopods 2–7 exhibited only by fewer spines on female pereopods.

Male pleopod 1 longer than pleopod 2, protopod with 6 retinacula; endopod about 0.4 × as long as wide, medial and distal margins convex, lateral margin slightly concave in distal half, distal margin with 4 long plumose setae and 5 shorter simple setae, lateral margin with 8–10 very small simple setae in distal half and about 5 simple setae of moderate length in proximal half, about 5 small setae subterminal to distal margin.

Male pleopod 2 protopod with 3 simple setae on medial margin; exopod basal segment triangular with 3 short simple setae on lateral edge, distal segment oval, about 0.8 × as long as wide, with 14 plumose marginal setae; endopod with rounded lateral basal apophysis, distal end of lateral margin weakly striated, tip with 4 processes: 1) cannula straight, subapical, slightly directed medially, partly obscured in anterior view by mesial process, but completely visible in posterior view; 2) mesial process with apex rising above other processes, apex twisted strongly in medial direction, proximal ⅔ of medial edge with many striae, lateral edge almost straight forming medial edge of endopodial groove; 3) lateral process rectangular, height about 0.7 × distance from base of endopodial groove to tip of the mesial process, apex truncate, lateral edge dropping straight to small shelf; 4) caudal process low, rounded, traversing entire tip of endopod. Female pleopod 2 with 7 plumose marginal setae. Male pleopod 3 exopod with about 20 long plumose setae along and around distal margin, short plumose setae interspersed with simple setae along distal ⅔ of lateral margin, short simple setae line lateral margin proximal to suture, many short simple setae on anterior surface. Pleopod 4 exopod with about 5 long plumose setae near lateral edge of distal margin, many minute setae interspersed with long simple setae on proximal ⅓ of lateral margin, false suture pattern A with transverse suture terminating on lateral margin just below midlength. Pleopod 5 with 2 false sutures and 5 simple setae on lateral margin proximally. Uropods spatulate, about 0.6 × length of telson, endopods 1.7 × longer than exopods.

*Etymology.*—This species' name refers to Dauphin Island, Alabama on which the specimens were collected.

*Habitat.*—The type habitat of *C. dauphina* is located in the Audubon Sanctuary on Dauphin Island, Mobile County, Alabama (30°15′N, 88°05′W) (Fig. 5). Specimens were collected in a depression located about 1–2 m from the outfall of a tile drain pipe that crosses under a service road. This depression is on the periphery of a black gum, *Nyssa sylvatica,* swamp and it is periodically dry. The swamp is a remnant of the once expansive Alligator Swamp system that covered much of the eastern part of Dauphin Island. Consequently, the sanctuary and contiguous areas contain several artesian wells that become active during the rainy season (McNeely 1974). Specimens were collected in the company of the epigean isopod *C. obtusus* several days after a

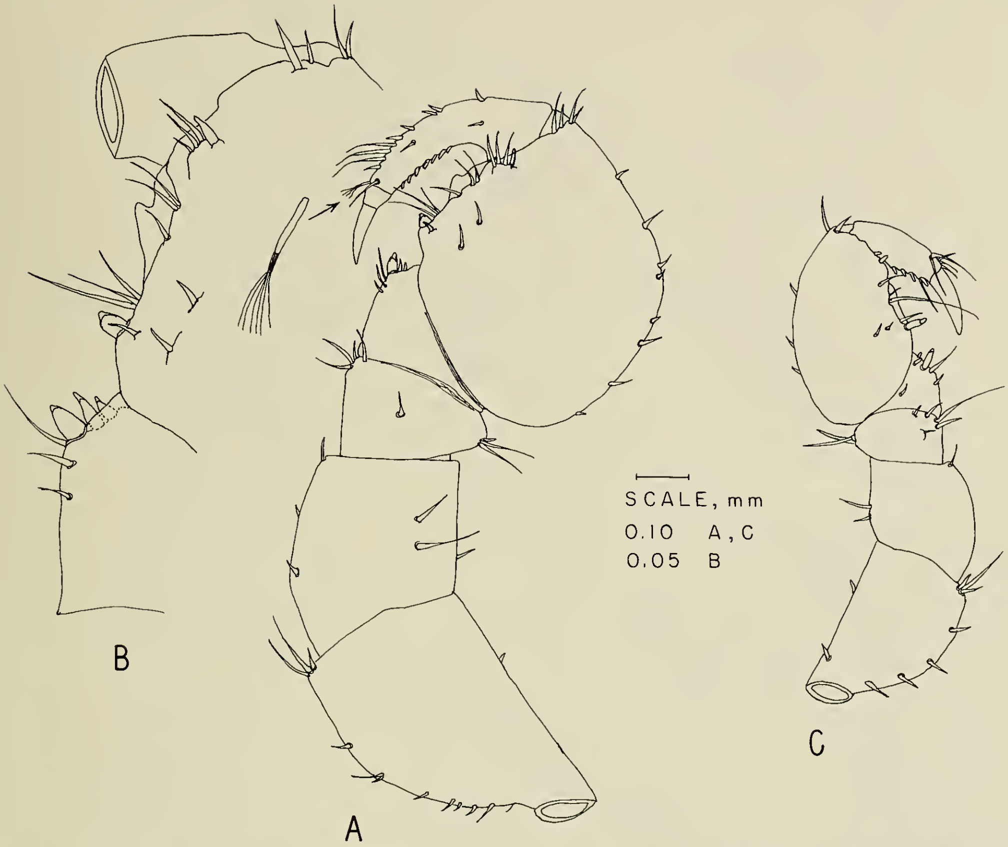

Fig. 2. *Caecidotea dauphina,* Pereopod 1: A, 7.5 mm male holotype, structure of multiflagellated spine enlarged; B, detail of palmar margin of propodus and anterior margin of carpus; C, 4.2 mm female.

major rain storm. *Caecidotea dauphina* was probably flushed from the tiles by the increased water flow.

Some physical and chemical data were collected to characterize the habitat; water temperature ranged from 25–26°C, pH 5.3–5.6 and conductivity 236–360 μMhos at 25°C.

Interestingly, the type habitat is about 500 m from the saline water of the Gulf of Mexico and on an island whose last surface land connection to the mainland occurred during the Pleistocene (Price 1954).

*Relationships.—Caecidotea dauphina* shows affinity to the Hobbsi group because it has all the morphological characteristics that define this group (Steeves 1964; Lewis 1982). An evolutionary link may exist between *C. dauphina* and *C. tridentata, C. spatulata, C. teresae,* and *C. parvus.* All these species have a mesial process on the tip end of the endopod of male pleopod 2 that curves, to varying degrees, medially. Setal structure and arrangement on the distal margin of the exopod of male pleopod 1, endopod of male pleopod 2 and margins of the female pleopod 2 suggest that *C. dauphina* has more in common with *C. teresae* than with the others. However, the geographic ranges of *C. teresae, C. tridentata* and *C. spatulata* are in close proximity and may overlap, but they are greatly separated from that of *C. dauphina.* The former three are known from the midwestern United States (Lewis and Bowman 1981; Lewis 1982), while *C. dauphina* is located in the coastal region of Alabama, slightly west of the Hobbsi geographic range originally pro-

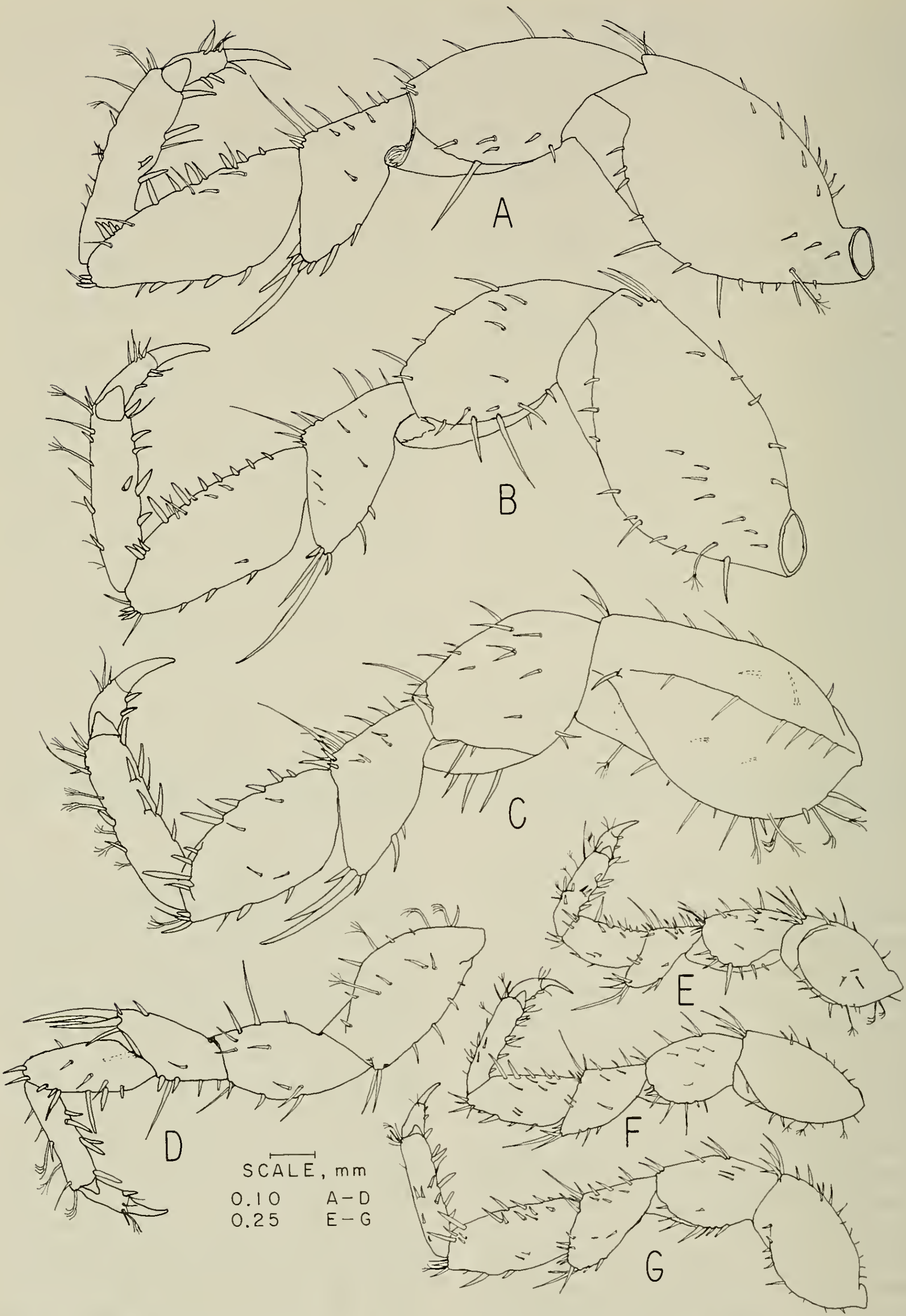

Fig. 3. *Caecidotea dauphina,* A–C, E–G = 7.5 mm male holotype; D, 4.2 mm female: A–C, Pereopods 2–4; D, Pereopod 4; E–G, Pereopods 5–7.

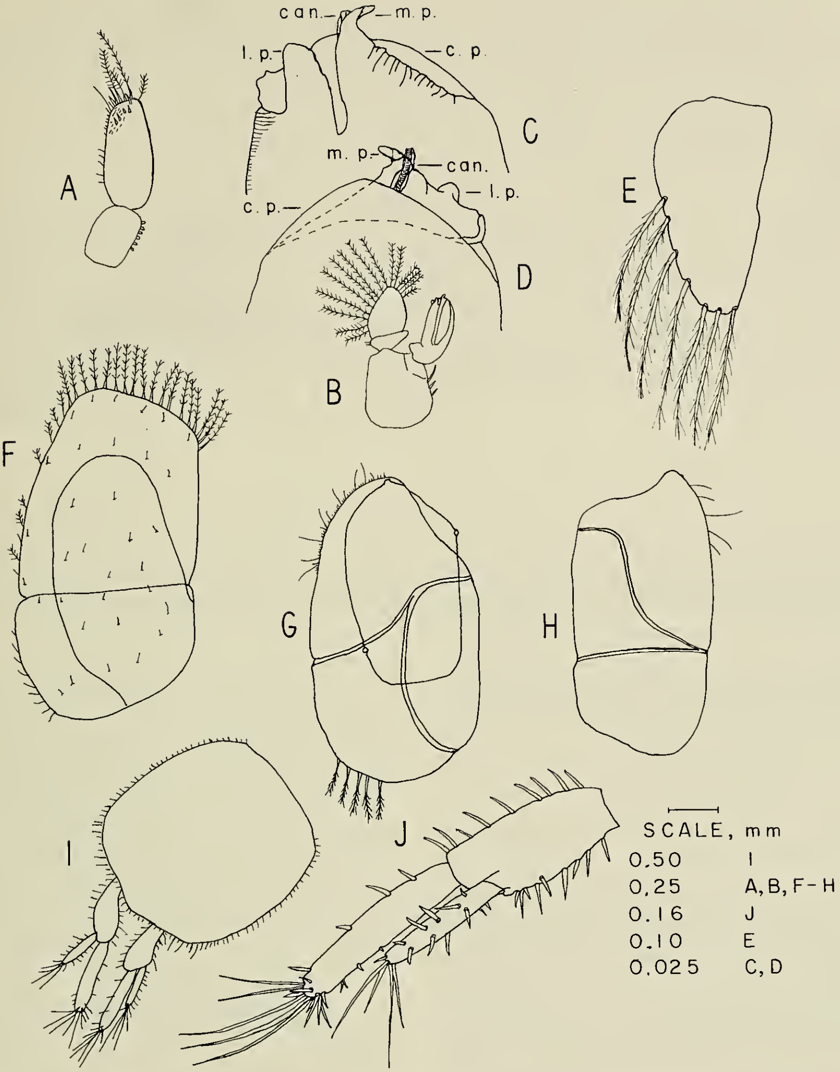

Fig. 4. *Caecidotea dauphina,* A–D, F–J = 7.5 mm male holotype; E = 4.2 mm female: A, Pleopod 1; B, Pleopod 2; C and D, Pleopod 2 endopodial tip, ventral and dorsal views, can = cannula, c.p. = caudal process, l.p. = lateral process, m.p. = mesial process; E, Pleopod 2; F, Pleopod 3; G. Pleopod 4; H, Pleopod 5; I, Telson-uropod complex; J. Uropod.

posed by Steeves (1964). The type habitat of *C. dauphina* appears contiguous with that of *C. parvus* which occurs in north central Florida (Steeves 1964). However, *C. parvus* does not belong to the Hobbsi group (Lewis 1982). Its only similarity to *C. dauphina* and the other three species above is the structure of the mesial process on the endopodial tip of the male pleopod 2. Additionally, *C. dauphina* along with *C. teresae, C. tridentata,* and *C. spatulata* are phreatobitic and occupy drain tile habitats (Lewis and Bowman 1981; Lewis 1982), while *C. parvus* is a troglobite inhabiting caves (Steeves 1964). Recently *C. parvus* was placed into the new genus *Remasellus* be-

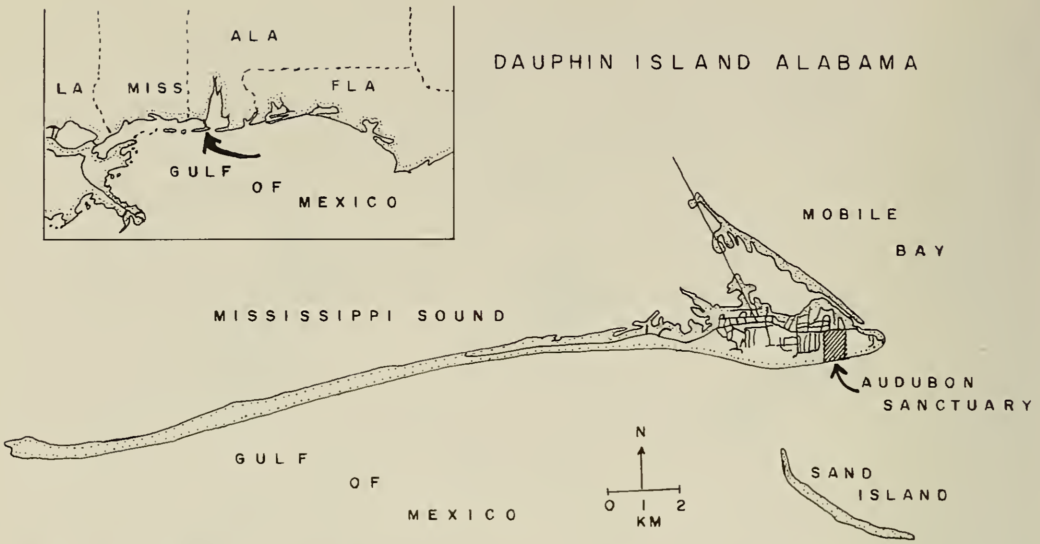

Fig. 5. Dauphin Island, Alabama, showing the Audubon Sanctuary where specimens of *Caecidotea dauphina* were collected. Inset indicates the position of Dauphin Island along the northern coast of the Gulf of Mexico.

cause it was found to be a swimming isopod (Bowman and Sket 1985).

## Acknowledgments

I wish to thank Dr. Thomas E. Bowman, USNM, for critically reviewing this manuscript and for providing helpful comments, and the Marine Environmental Sciences Consortium, Dauphin Island Sea Lab, Dauphin Island, Alabama, for providing laboratory space and other facilities during this project. This is M.E.S.C. Contribution #088.

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# SETAL MORPHOLOGY OF THE OLIGOCHAETES *TUBIFEX TUBIFEX* AND *ILYODRILUS FRANTZI* (*CAPILLATUS*) AS REVEALED BY SEM

Peter M. Chapman and Ralph O. Brinkhurst

*Abstract.*—Scanning electron microscope observations of *Tubifex tubifex* reveal details of the serrations on hairs, pectinations on dorsal setae, and more extensive pectinations on the ventral setae than previously described. Lack of serrations on *Ilyodrilus frantzi* (*capillatus*) hairs is documented as are details of dorsal setal pectinations. Three new features of this species are shown: the concave nature of the upper and lower setal teeth, pectinate ventral setae, and an apparent ability to retract setal bundles.

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Scanning Electron Microscopy (SEM) is an extremely valuable technique for establishing and documenting, at a greater level of resolution than is possible with light microscopy, the presence of fine differences in organism morphology. Previous uses of SEM with oligochaetes include documentation of external sense organs (Chapman 1979; Smith 1983) and of fine setal differences in two species of Naididae (Smith 1985). In previous studies (Chapman and Brinkhurst, in press; Brinkhurst and Chapman, in prep.), we used the SEM technique to document setal variations inducible in naidid and tubificid oligochaetes under varying environmental conditions. As a result of these previous studies, we obtained various new descriptive observations on the structure of the setae of *Tubifex tubifex* and *Ilyodrilus frantzi* (*capillatus*) which are provided herein, related to taxonomic descriptions of these species.

## Materials and Methods

*Tubifex tubifex* specimens were collected from the Fraser River, B.C.; *I. frantzi* (*capillatus*) specimens were collected from the Fraser River and from the Columbia River, Oregon. Worms were fixed in cold 3% buffered glutaraldehyde, washed in 0.1 M phosphate buffer and post-fixed in 1% buffered osmium tetroxide for ½ h at room temperature. Specimens were then washed in 0.1 M phosphate buffer and dehydrated through an ascending ethanol series before being critical-point dried with $CO_2$, mounted on aluminum stubs, and sputter coated with gold. A Cambridge S100 Stereoscan Scanning Electron Microscope was used for viewing.

## Results

Details of serrations on *T. tubifex* hairs, pectinations of dorsal setae, and pectinations of ventral setae, are provided in Fig. 1. Hairs in the same setal bundle can vary from virtually non-serrate to heavily serrate. Similarly, the degree of ventral setal pectination is highly variable, even within the same bundle and can approach the dorsal setal condition.

Details of hairs, dorsal and ventral setae of *I. frantzi* (*capillatus*) are provided in Fig. 2. Hairs are shown to be essentially non-serrate. Dorsal and ventral setae have concave outer teeth, may have varying degrees of pectination, and can apparently be retracted.

## Discussion

*Tubifex tubifex.*—*T. tubifex* are described as having serrate or non-serrate hairs

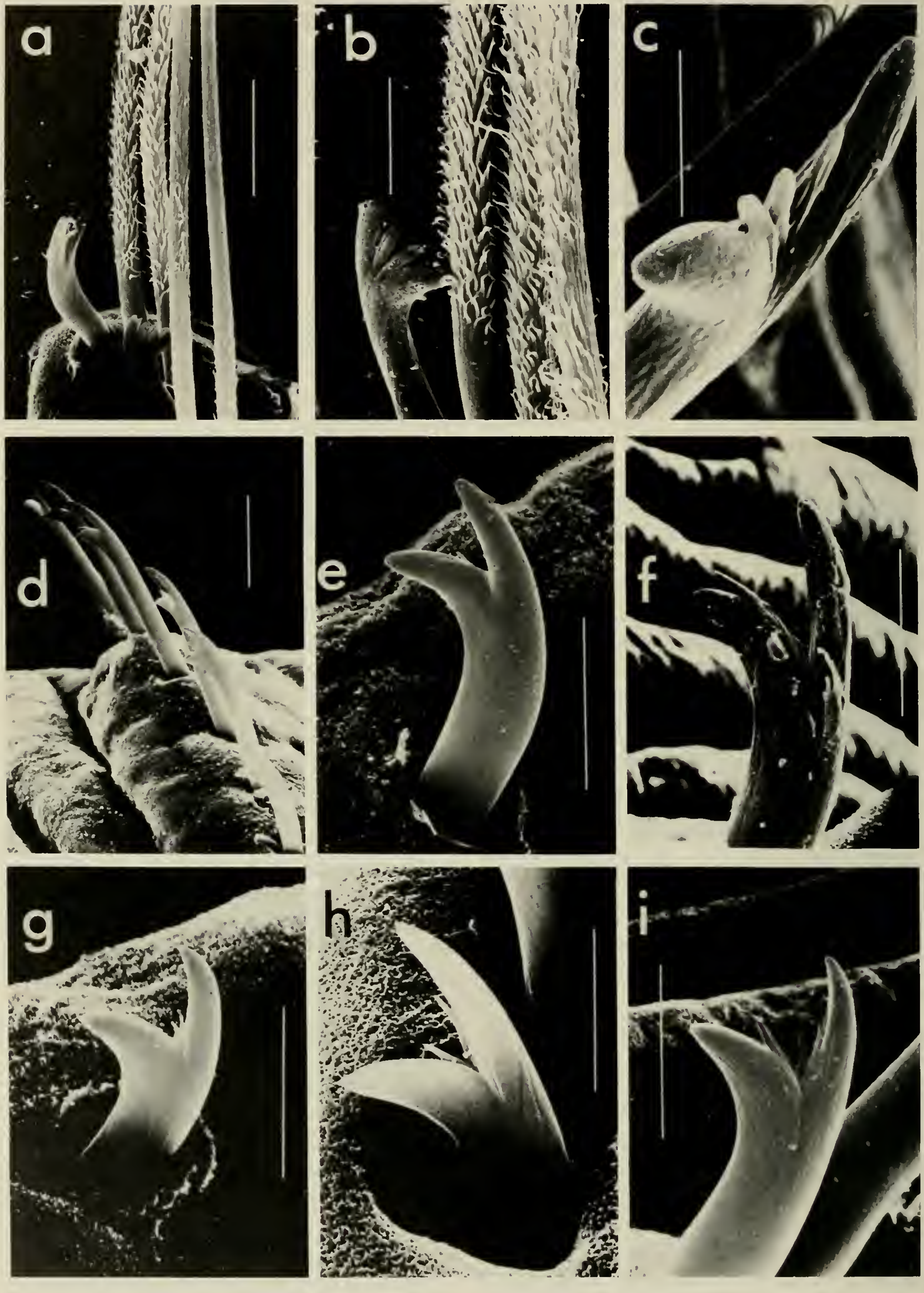
a
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Fig. 2. Details of setal morphology of *Ilyodrilus frantzi* (*capillatus*): a–b, Variable amounts of dorsal pectination, hairs show only traces of serrations; c, Detail of dorsal pectinate seta showing concave lower tooth (upper tooth is similar); d, Retracted, non-pectinate dorsal setae; e, Non-pectinate ventral setae; f, Pectinate ventral seta. Scale bars 10 μm for b and c, 20 μm for a and d to f.

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Fig. 1. Details of setal morphology of *Tubifex tubifex*: a–b, Variable amounts of serrations on dorsal hairs, note serrations begin around top of pectinate setae; c, Detail of dorsal pectinate seta; d–i, Ventral pectinations observed in various specimens. Scale bars 5 μm for c, 10 μm for a and d, 20 μm for b and e to i.

(Brinkhurst and Jamieson 1979; Brinkhurst 1982; Brinkhurst, 1986). The nature of these serrations, as documented in Fig. 1a–b, is variable even within a single dorsal bundle, which may simply reflect differential exposure to abrasion or other environmental factors causing shredding. SEM photographs indicate that the observed serrations are due to shredding; serrations generally begin immediately distal to the top of the dorsal setae, suggesting that the setae provide some measure of protection against abrasion. The hypothesis of serrations being formed through shredding was first advanced by Smith (1985), for *Dero* spp. Since serrations appear to be a variable characteristic, probably influenced by environmental conditions, their use in oligochaete taxonomy should be discontinued.

The nature of dorsal setal pectination is illustrated (Fig. 1a–c). Pectinations have approximately equal lateral teeth shorter in length than the upper and lower setal teeth.

The degree and variability of pectination possible on ventral setae is large (Fig. 1d–h). The degree of pectination can vary within a single bundle (Fig. 1d), and shows a range including single (Fig. 1e–f), bifid (Fig. 1g–h) and trifid pectinations (Fig. 1i). The degree of ventral pectination may approximate that seen dorsally (compare Fig. 1c and 1i) and is shown to be more extensive than that described by Brinkhurst and Jamieson (1971:455), "rarely with a single intermediate tooth," Brinkhurst (1982:40), "sometimes a few short intermediate teeth on ventral setae," or Brinkhurst (1986:149), "sometimes with a small intermediate tooth."

*Ilyodrilus frantzi (capillatus).*—Descriptions of *I. frantzi (capillatus)* have not included lateral serrations on hairs. This lack of serrations is confirmed by SEM (Fig. 2a–b).

Brinkhurst (1978) provided the first report of dorsal pectinate setae; Brinkhurst (1986:173) states that there are a "few pectinate setae" dorsally. Dorsal setae may have none, one (Fig. 2a), or two pectinations (Fig. 2b).

SEM reveals that the inner surfaces of the setae of *I. frantzi capillatus* have gutter-shaped (concave) upper and lower teeth (Fig. 2c, e–f). Apparently setal bundles can be retracted (Fig. 2d). These features have not previously been described for this or for any other aquatic oligochaete.

The presence of ventral pectinations was suspected by Brinkhurst (1978:2173) who noted that the ventral setae in some specimens "seem to be slightly ornamented, but this needs confirmation by scanning electron microscopy." Such confirmation is now provided. Ventral setae may be apectinate (Fig. 2e), or may have a single intermediate pectination (Fig. 2f).

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# *SERRABRYCON MAGOI,* A NEW GENUS AND SPECIES OF SCALE-EATING CHARACID (PISCES: CHARACIFORMES) FROM THE UPPER RÍO NEGRO

Richard P. Vari

*Abstract.*—*Serrabrycon magoi,* a previously undescribed genus and species of scale-eating tetragonopterin characid, is described from the black waters of the Río Negro system in the region of the Río Casiquiare, Venezuela. The genus and species are unique in the combination of the presence of a series of outwardly oriented teeth in the upper and lower jaws, the relatively low number of scales in a longitudinal series to the hypural joint, and in the limitation of pores for the laterosensory canal system of the body to the anteriormost scales of the lateral line.

Scale-eating (lepidophagy) has been described as a significant food habit in a variety of both freshwater and marine fishes inhabiting diverse regions of the world (see Sazima 1983 for a review). Within the freshwaters of the Neotropical realm, this specialized food habit has been described for a number of species belonging to the order Characiformes. Neotropical characiforms of the family Characidae for which lepidophagy has been previously described include *Catapríon mento* Müller and Troschel (Kner 1860:34; Gosline 1951:54, Géry 1964:460) and *Serrasalmus elongatus* Kner (Goulding 1980:162) of the subfamily Serrasalminae, *Exodon paradoxus* Müller and Troschel, *Roeboexodon guanensis* (Puyo), and the various species of the genus *Roeboides* (Breder 1927:127; Géry 1964:459–460) all presently assigned to the subfamily Characinae, and *Probolodus heterostomus* Eigenmann (Roberts 1970:384; Sazima 1977:510) and *Bryconexodon juruenae* Géry (1980:1) of the subfamily Tetragonopterinae. These taxa, with the exception of *Serrasalmus elongatus,* are characterized by specialized dentition, typically consisting of everted teeth, often mammilliform in overall shape, which form very irregular series along the outer margins of the jaws. The outwardly directed teeth function in dislodging scales from the host species, with the removed scales then being ingested directly if taken into the mouth, or gathered from the water column or substrate if knocked free (Sazima and Machado 1982). Although these dental modifications are characteristic for, and very similar in, the majority of lepidophagous Neotropical characiforms, such distinctive teeth have been implicitly hypothesized to have arisen independently in the diverse lineages of scale-eaters which are presently assigned to four different subfamilies of the Characidae (but see also comments under "Relationships").

Recent collecting activities in the upper portions of the Río Negro have revealed a previously undescribed genus and species of lepidophagous tetragonopterine characid described herein. This new form shares many of the dental modifications noted above as "typical" for lepidophagous Neotropical characiforms, but is quite distinctive in other attributes, most notably in its incompletely pored lateral line.

*Materials and methods.*—All measurements are given as proportion of standard length (SL) except for subunits of the head which are presented as proportions of head length. Vertebral counts were taken from radiographs, and cleared and counterstained specimens. This number includes the four vertebrae incorporated into the Weberian apparatus and considers the fused $PU_1+U_1$ as a single element. In the counts of median and pelvic fins, lower-case Roman numerals indicate unbranched fin rays, and Arabic numbers indicate branched fin rays. In the meristic values presented, the range for each measurement for the paratypes and holotype is presented first, with the value for the holotype indicated in brackets.

The following abbreviations are used for institutions: BMNH, British Museum (Natural History), London; MBUCV, Museo de Biología, Instituto de Zoología Tropical, Universidad Central de Venezuela, Caracas; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; and USNM, National Museum of Natural History, Smithsonian Institution , Washington, D.C.

## *Serrabrycon,* new genus

*Diagnosis.*—Tetragonopterine characid with mammilliform teeth in both jaws. Teeth of outermost tooth row of premaxilla directed anteriorly or anteroventrally rather than ventrally, forming irregular series. Second and fifth dentary teeth distinctly rotated anterodorsally. Lateral line pores present only on anterior seven or eight scales of laterosensory canal series. Scales in longitudinal series from supracleithrum to hypural joint 29 to 31.

The combination of an incompletely pored lateral line, the relatively low number of scales in a longitudinal series, and the noted modifications of the dentition in the upper and lower jaws distinguishes *Serrabrycon* in the Characiformes.

*Type species.*—*Serrabrycon magoi,* n. sp.

*Etymology.*—*Serrabrycon* from the Latin, *serra* for saw, and *Brycon* a genus of Neotropical characiforms, in reference to the saw-like appearence of the outwardly pointing teeth in the upper and lower jaws.

Table 1.—Morphometrics of *Serrabrycon magoi,* new species. Standard length is in millimeters; measurements 1 to 11 are proportions of standard length; 12 to 16 are proportions of head length.

| | Holotype | Paratypes (37) | |
|---|---|---|---|
| | | Range | Average |
| Standard length | 27.5 | 21.3–31.8 | |
| 1. Greatest body depth | 0.29 | 0.28–0.30 | 0.288 |
| 2. Snout to dorsal-fin origin | 0.53 | 0.53–0.57 | 0.540 |
| 3. Snout to anal-fin origin | 0.68 | 0.68–0.71 | 0.689 |
| 4. Snout to pectoral-fin origin | 0.30 | 0.29–0.33 | 0.319 |
| 5. Snout to pelvic-fin origin | 0.52 | 0.51–0.53 | 0.520 |
| 6. Origin of dorsal fin to hypural joint | 0.48 | 0.45–0.50 | 0.480 |
| 7. Pectoral-fin length | 0.20 | 0.19–0.22 | 0.207 |
| 8. Pelvic-fin length | 0.17 | 0.17–0.20 | 0.185 |
| 9. Length of base of anal fin | 0.23 | 0.21–0.24 | 0.223 |
| 10. Least depth of caudal peduncle | 0.12 | 0.11–0.12 | 0.115 |
| 11. Head length | 0.31 | 0.30–0.33 | 0.318 |
| 12. Snout length | 0.24 | 0.23–0.27 | 0.248 |
| 13. Orbital diameter | 0.39 | 0.36–0.40 | 0.375 |
| 14. Postorbital length | 0.41 | 0.39–0.43 | 0.401 |
| 15. Length of upper jaw | 0.46 | 0.45–0.48 | 0.466 |
| 16. Interorbital width | 0.32 | 0.29–0.33 | 0.305 |

## *Serrabrycon magoi,* new species

Figs. 1, 2, 3, Table 1

*Holotype.*—MBUCV 14270, 27.5 mm standard length (SL). Venezuela, Territorio Federal Amazonas, Departamento Río Negro, lower portion of Caño Manu, which drains into the Río Casiquiare about 250 m upstream of Solano (approx. 02°00′N, 66°57′W); collected by R. P. Vari, C. J. Ferraris, Jr., O. Castillo, and J. Fernandez; 7 Dec 1984.

*Paratypes.*—Taken with the holotype; 27 specimens: USNM 270260, 11 specimens, 21.5–27.5 mm SL (3 specimens cleared and

Fig. 1. *Serrabrycon magoi,* new species, holotype, MBUCV 14270, 27.5 mm SL.

counterstained for cartilage and bone); MBUCV 14271, 10 specimens, 21.3–25.4 mm SL; MZUSP 28749, 3 specimens, 23.5–24.6 mm SL; and BMNH 1985.4.9:4–6, 3 specimens, 21.3–23.5 mm SL. Venezuela, Territorio Federal Amazonas, Departamento Río Negro, drying lagoon northeast of airport at San Carlos de Río Negro (approx. 01°55′N, 67°02′W); collected by A. Machado-Allison, R. P. Vari, C. J. Ferraris, Jr., J. Fernandez and O. Castillo; 4 Dec 1984; 10 specimens: USNM 270259, 5 specimens, 24.9–31.8 mm SL; and MBUCV 14272, 5 specimens, 24.7–26.5 mm SL.

*Diagnosis.*—As for the genus.

*Description.*—Table 1 gives morphometrics of holotype and paratypes. Body relatively slender, moderately compressed laterally. Greatest body depth at origin of rayed dorsal fin. Dorsal profile of body gently curved from tip of snout to interorbital region, nearly straight from that point to insertion of rayed dorsal fin. Body profile at base of rayed dorsal fin straight, posteroventrally sloped. Dorsal profile of body slightly convex from rear of insertion of last dorsal fin ray to caudal peduncle. Ventral profile of head distinctly convex from tip of fleshy lower jaw to below opercle; nearly straight from that point to anus other than for slight convexity at insertion of pelvic fins. Ventral surface of body transversely flattened anterior to insertion of pelvic fins. Base of anal fin straight or very slightly convex. Ventral profile of caudal peduncle slightly convex.

Head obtusely pointed in profile; mouth terminal, lower jaw longer than upper. Upper jaw extending posteriorly to vertical through anterior third of pupil. Mammilliform teeth of outer row of premaxilla extending through fleshy covering of jaw. Nostrils approximate; anterior round, posterior crescent-shaped. Eye relatively large. Fronto-parietal fontanel extensive, completely separating parietals, frontals in contact only at epiphyseal bar. Fontanel wider posteriorly, extending onto dorsomedial portion of supraoccipital. No supraorbital present.

Four branchiostegal rays, three attached to anterior ceratohyal, one to posterior ceratohyal. Anterior cartilage of basihyal subdivided longitudinally into lateral halves. Pharyngeal teeth all unicuspidate; broad triangular patch of teeth on fifth ceratobranchial; smaller groupings of teeth on fourth and fifth upper pharyngeal tooth plates, and on tooth plate associated with third infrapharyngobranchial. Gill rakers elongate. Gill rakers on first gill arch 6 or 7+1+10 or 11.

Outer row of premaxillary teeth consisting of four mammilliform teeth, reoriented anteriorly or slightly anterodorsally (Fig. 2). Tips of teeth in very irregular line. Second tooth from midline distinctly oriented more anterodorsally than others. Teeth of inner row on premaxilla tricuspidate, somewhat anteroposteriorly flattened, not mammilli-

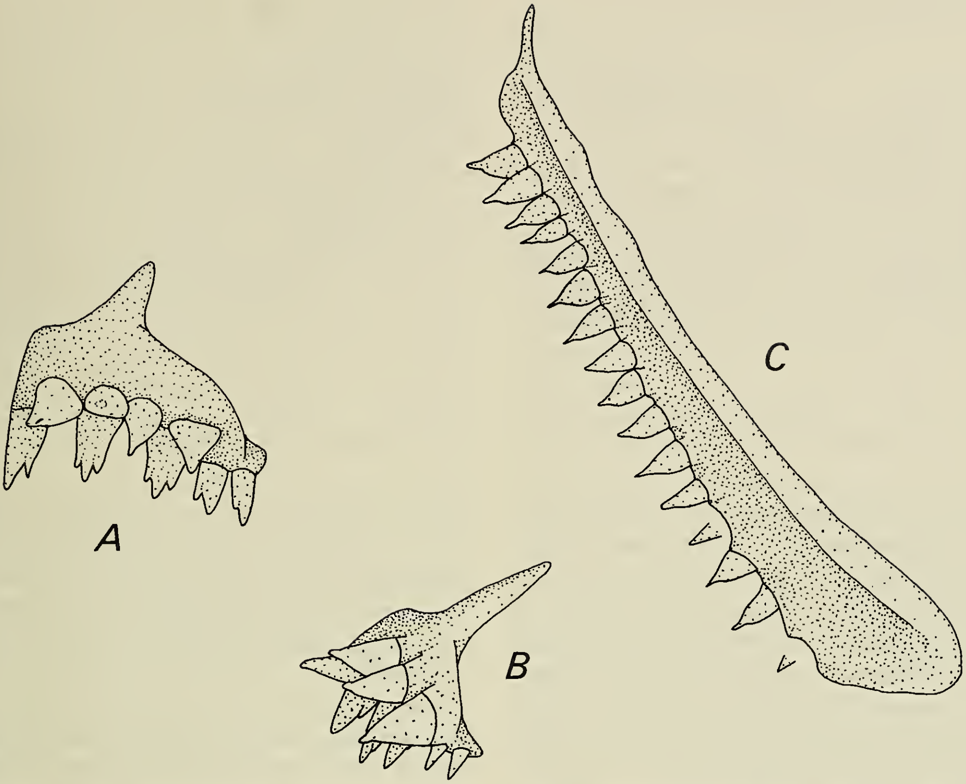

Fig. 2. *Serrabrycon magoi*: A, Left premaxilla, anterior view; B, Left premaxilla, lateral view; C, Left maxilla, lateral view, first and fourth teeth from bottom in process of replacement.

form; tips oriented ventrally or slightly anteroventrally. Five teeth in inner row. Maxilla with single series of 15 or 16 very slightly mammilliform teeth along entire anterior edge. Dorsalmost tooth in series somewhat mammilliform and laterally directed. Remaining teeth having typical tetragonopterin orientation, with tips approximately in plane of main body of maxilla; some very slightly mammilliform.

Lower lip very fleshy, forming distinct pad. Teeth on dentary becoming progressively smaller posteriorly (Fig. 3). First four or five dentary teeth tricuspidate; lateral cusps relatively small. Remaining dentary teeth slightly mammilliform or conical. Second tricuspidate tooth distinctly rotated laterally relative to primary axis of first and third teeth. Fourth dentary tooth more laterally oriented than third, fifth more than fourth; sixth through eighth teeth progressively less laterally aligned. Remaining dentary teeth vertically oriented.

Scales cycloid. Scales in longitudinal series between supracleithrum and hypural joint 29 to 32 [32]. Two or three series of scales extend beyond hypural joint onto base of caudal fin. Pores communicating with laterosensory canal system of lateral line developed only on anteriormost seven or eight scales of longitudinal series. Scales in transverse series from origin of rayed dorsal fin to ventral midline 12 or 13 [13].

Rayed dorsal fin obtusely pointed, first and second branched rays longest, last unbranched ray slightly shorter. Dorsal-fin rays

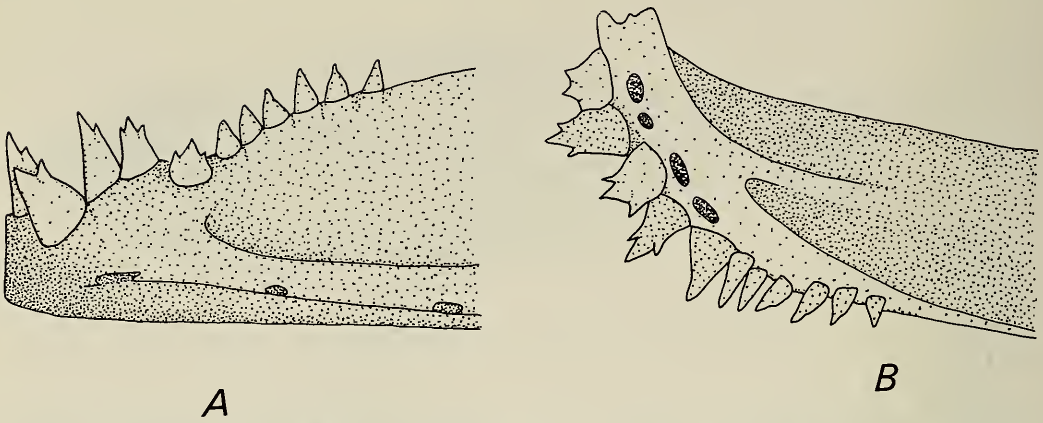

Fig. 3. *Serrabrycon magoi,* left dentary, anterior portion: A, Lateral view; B, Dorsal view.

ii,8 or ii,9 [ii,8]. Adipose dorsal fin relatively well developed, length about one-half diameter of orbit; unscaled. Anal-fin rays iii,15 or iv,15 or 16 [iv,15]; first two unbranched rays very short; last unbranched ray and first and second branched rays longest, subequal. Margin of anal fin falcate; posteriormost ten branched rays about one-third to one-half length of longest rays. Pectoral fin pointed, reaching to or slightly beyond origin of pelvic fin. Pectoral fin rays 12 to 14 [13]. Pelvic fin reaching to origin of anal fin. Pelvic fin rays i,6,i [i,6,i].

Vertebrae: 31 (6), 32 (18), 33 (1).

*Coloration in alcohol.*—Overall ground coloration of specimens fixed in formalin and preserved in alcohol light tan. Head with dense field of small chromatophores on upper lip, snout, and dorsal portion of head. Line of dark pigmentation along margin of lower lip. Lateral surface of head with scattered chromatophores, largest on opercle.

Body with diffuse field of chromatophores on lateral surface. Field more dense anteriorly, particularly in region of pored portion of lateral line. Chromatophore field extending to caudal peduncle, with discrete straight dorsal margin; field gradually thinning out ventrally in region between pectoral and anal fin origins; reaching to ventral margin of body along base of anal fin and ventral surface of caudal peduncle. Scales dorsal of lateral chromatophore field with margins distinctly outlined by relatively wide series of small chromatophores. Overall body pigmentation darkest along dorsal midline.

Caudal fin with well developed field of dark pigmentation at base of caudal fin rays. Pigmentation patch extending anteriorly on middle rays to slightly posterior of hypural joint; smaller chromatophores extending posteriorly from main portion of pigmentation patch to tips of those rays. Series of very small chromatophores outlining other caudal-fin rays. Dorsal-fin rays outlined by series of small chromatophores; fin dusky distally. Distal portion of anteriormost branched anal fin-rays dusky. Rays of pectoral and pelvic fins outlined by small chromatophores. Adipose dorsal fin covered with scattered small chromatophores.

*Relationships.*—Weitzman and Fink (1983) have recently summarized the difficulties and uncertainties associated with the present classificatory scheme applied to New World characiforms. *Serrabrycon* exemplifies many of the problems inherent in the present taxonomy of the group. Under the traditional classification the genus could be assigned to the *Hemigrammus-Pristella* grouping of tetragonopterines that is characterized, in part, by an incompletely pored lateral line. However, no member of that assemblage has the distinctive dental modifications characteristic of *Serrabrycon.* As noted by Fink and Weitzman (1974) and again by Weitzman and Fink (1983) an incompletely pored lateral line is a questionably valid character for delimiting hypothesized monophyletic lineages within characids. The relationships of *Serrabrycon* could also be hypothesized to lie with genera such as *Exodon, Roeboexodon,* and *Roeboides* that authors have placed in the characid subfamily Characinae. An alternative alignment of *Serrabryon* could be with *Probolodus* and *Bryconexodon* which have been assigned to the Tetragonopterinae. Although all of the genera just listed have completely pored laterosensory canal systems on the body, they are also characterized by mammilliform dentition similar to that of *Serrabrycon.* Furthermore the defining characters of the two subfamilies have not been based on derived characters supporting a hypothesis of their monophyly, and the present partitioning of the genera between the Characinae and Tetragonopterinae is open to reinterpretation (Menezes in Sazima 1983:88). Thus *Serrabrycon* together with *Exodon, Roeboexodon, Roeboides, Probolodus* and *Bryconexodon* may constitute a monophyletic group delimited, at least in part, by the presence of everted mammilliform dentition. On the other hand the assemblage may be polyphyletic with the mammilliform dentition homoplasiously present in two or more lineages.

Further research is necessary to resolve the above questions and to arrive at a hypothesis of the relationships between the contained species. Pending such a study and in light of the various uncertainties noted above, in particular the lack of a readily apparent sister group to the new species, a new genus of the Tetragonopterinae is proposed to contain the undescribed form.

*Etymology.—magoi,* in honor of Dr. Francisco Mago-Leccia of the Instituto de Zoología Tropical of the Universidad Central de Venezuela who has contributed significantly to our knowledge of the Venezuelan fish fauna.

*Food habits.—Serrabrycon magoi* has a very muscular stomach that is large relative to the remainder of the intestinal tract. Stomach content analysis of three individuals showed that the stomachs were completely and exclusively filled with series of scales of different sizes.

*Ecology.*—The holotype and 27 paratypes were collected in the lower portion of Caño Manu, a very slow-flowing black water tributary of the Río Casiquiare. The stream was well-shaded by rain-forest canopy, and had few small emergent plants and no floating vegetation. The remaining ten paratypes were collected in the shallow black waters of a small sluggish stream running through the center of a drying lagoon. That locality was characterized by large amounts of submerged logs and detritus. The site had numerous large emergent plants, but was distant from the rain-forest canopy and poorly shaded.

*Resumen.—Serrabrycon magoi,* un género y una especie no descritos anteriormente que comprende pequeños peces comedores de escamas pertenecientes a la subfamilia Tetragonopterinae, Characidae; son descritos a partir de muestras provenientes de aguas negras del sistema del Río Negro de la región del Río Casiquiare, Venezuela.

El género y especie son únicos en la combinación de los siguientes carácteres: la presencia de una serie de dientes en las mandíbulas superior e inferior orientados exteriormente; el número relativamente bajo de escamas en la serie longitudinal hasta la unión hipural y en la limitación de poros del sistema del canal laterosensorial a las escamas anteriores de la línea lateral.

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# *NEMATOCHARAX VENUSTUS,* A NEW GENUS AND SPECIES OF FISH FROM THE RIO JEQUITINHONHA, MINAS GERAIS, BRAZIL (TELEOSTEI: CHARACIDAE)

Stanley H. Weitzman, Naércio A. Menezes, and Heraldo A. Britski

*Abstract.*—*Nematocharax venustus,* a new genus and species, is described from the lower portion of the Rio Jequitinhonha in Minas Gerais, Brazil. The adult male of this species is distinguished from all known characins by the combination of elongate, filamentous dorsal, anal, and pelvic fins, and a nearly full series of maxillary teeth. The possible relationships of the new genus are briefly discussed but no corroborated hypothesis of relationship is advanced. The status of the knowledge of the fish fauna of the Atlantic forest of eastern Brazil is briefly discussed.

The description given below of a new species of characid from the Rio Jequitinhonha is a small contribution towards increasing the data base for studies of the biogeography of the small and modest-sized littoral streams of eastern and southeastern Brazil. Although the characid fish described herein is probably quite common in at least the middle and lower course of the Rio Jequitinhonha it apparently has been collected only twice, first in 1966 from the Rio Jequitinhonha at Itaobim, Minas Gerais and again in 1985 further east in the same river near Salto da Divisa. It was very common at both collecting sites. That a relatively common, distinctive, easy-to-capture fish of eastern Brazil is now being made known to science is a fact representative of our poor knowledge of the fish fauna of the region. Much future descriptive, phylogenetic, and faunal research must be published before adequate biogeographical studies of this region's fishes can be accomplished.

*Methods and materials.*—Counts and measurements are those described by Fink and Weitzman (1974:1–2). All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of the head which are expressed as a percentage of head length. Ranges and means of the meristics and morphometrics are given in the tables, with information for the holotype given separately. Ranges and means for counts in the tables are represented by one set of figures for both sexes combined except in cases of obvious sexual dimorphism where the information is given by sex. Logarithmic and square root transformed data were used in covariance analyses of sexual differences in measurements and counts respectively.

Specimens examined for this study are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), the National Museum of Natural History, Smithsonian Institution (USNM), Museum of Zoology, University of Michigan (UMMZ), the Academy of Natural Sciences of Philadelphia (ANSP), the British Museum (Natural History) (BMNH), Field Museum of Natural History (FMNH), and the Museu Nacional de Rio de Janeiro (MNRJ).

## *Nematocharax,* new genus

*Type species.*—*Nematocharax venustus,* new species.

*Diagnosis.*—A "tetragonopterine" characid distinguished from all other genera of American and African characids by having a combination of elongate branched dorsal-,

Table 1.—Morphometrics of *Nematocharax venustus,* Itaobim, Rio Jequintinhonha, holotype MZUSP 5131, paratypes from same locality, MZUSP 28480–28509, 28661–28689, and USNM 232955 and 232956. Standard length expressed in mm. Following 19 measurements are percentages of standard length and last 4 measurements are percentages of head length. Entries including both sexes and juveniles (n = 52 to 75) are for specimens 17.5 to 32.0 mm SL. Entries listed by sex include males (m) between 30.0 and 52.0 mm SL and females (f) between 33.0 and 40.5 mm SL.

| | Holotype | n | Low | High | $\bar{x}$ |
|---|---|---|---|---|---|
| Standard length | 50.5 | 75 | 17.7 | 52.0 | — |
| Depth at dorsal-fin origin m | 40.6 | 27 | 37.5 | 43.0 | 41.0 |
| Depth at dorsal-fin origin f | — | 30 | 36.0 | 40.4 | 38.6 |
| Snout to dorsal-fin origin | 53.7 | 75 | 50.8 | 55.8 | 53.4 |
| Snout to pectoral-fin origin | 26.5 | 75 | 24.7 | 31.5 | 27.4 |
| Snout to plevic-fin origin | 44.2 | 75 | 41.3 | 52.4 | 45.3 |
| Snout to anal-fin origin | 60.4 | 27 | 56.9 | 62.2 | 59.6 |
| Caudal peduncle depth | 13.1 | 75 | 10.8 | 13.5 | 12.1 |
| Caudal peduncle length | 11.3 | 75 | 9.9 | 13.5 | 11.2 |
| Pectoral-fin length | 23.8 | 74 | 14.7 | 26.2 | 23.2 |
| Pelvic-fin length m | 51.5 | 23 | 40.2 | 64.2 | 54.8 |
| Pelvic-fin length f | — | 30 | 20.0 | 30.9 | 23.2 |
| Dorsal-fin base length | 14.9 | 75 | 13.0 | 17.0 | 15.0 |
| Longest dorsal-fin ray length m | 73.3 | 24 | 59.9 | 78.8 | 68.2 |
| Longest dorsal-fin ray length f | — | 30 | 32.9 | 36.7 | 34.7 |
| Anal-fin base length m | 33.3 | 27 | 30.0 | 34.9 | 33.1 |
| Anal-fin base length f | — | 30 | 28.1 | 32.5 | 30.6 |
| Anal-fin lobe length m | 50.3 | 24 | 41.0 | 58.5 | 50.2 |
| Anal-fin lobe length f | — | 29 | 22.4 | 34.5 | 26.3 |
| Bony head length | 27.7 | 75 | 26.4 | 31.9 | 28.4 |
| Horizontal eye diameter | 35.9 | 75 | 34.8 | 43.0 | 38.4 |
| Snout length | 27.9 | 75 | 22.9 | 33.1 | 27.6 |
| Least width interorbital | 30.9 | 74 | 27.6 | 36.4 | 30.8 |
| Upper jaw length | 47.9 | 74 | 36.4 | 51.4 | 44.1 |

anal-, and pelvic-fin rays, two rows of premaxillary teeth in adults, and an almost complete row of teeth along the free ventral maxillary border.

The possible relationships of this genus to other characids are obscure and we recognize the genus *Nematocharax* because we are unable to hypothesize a particular relative of the single known species, *N. venustus* (see "Relationships.")

*Etymology.*—*Nemato* from the Greek for thread and *charax* from the Greek *characo* meaning a pointed stake, here used in reference to the characid genus *Charax,* hence a characid fish. *Nematocharax* thus means a thread-bearing characid fish in reference to the long threadlike extensions of the dorsal, anal, and pelvic fins.

## *Nematocharax venustus,* new species

Figs. 1–4, Tables 1, 2

*Holotype.*—MZUSP 5131, male, SL 50.5 mm, Brazil; Minas Gerais, Município Medina, Rio Jequitinhonha at Itaobim, about 16°40'S, 41°23'W, 25 Jun 1966, by Heraldo Britski and Naércio Menezes.

*Paratypes.*—1, MZUSP 28480, female (photographed), SL 35.4 mm.—29, MZUSP 28481–28509, SL 17.7–52.0 mm.—29, MZUSP 28661–28689, SL 33.0–51.5 mm.—80, MZUSP 28690 (data not taken).—6, USNM 232955, SL 34.0–51.7 mm.—7, USNM 232956, SL 34.7–52.0 mm.—4, UMMZ 213448, SL 34.7–51.9 mm.—2, ANSP 157373, SL 34.3–48.0 mm.—2, BMNH 1985.11.10.1–2, SL 37.5–

Table 2.—Meristics of *Nematocharax venustus,* Itaobim, Rio Jequitinhonha, holotype MZUSP 5131, paratypes from same locality, MZUSP 28480–28509, 28661–18689, and USNM 232955 and 232956.

| | Holotype | n | Low | High | $\bar{x}$ |
|---|---|---|---|---|---|
| Branched dorsal-fin rays | 9 | 73 | 9 | 10 | 9.0 |
| Branched pectoral-fin rays | 12 | 70 | 11 | 14 | 11.8 |
| Branched pelvic-fin rays | 6 | 73 | 7 | 7 | 7.0 |
| Branched anal-fin rays | 23 | 73 | 22 | 26 | 23.7 |
| Branched caudal-fin rays | 17 | 73 | 17 | 17 | 17.0 |
| Horizontal scale rows, between dorsal- and anal-fin origins | 13 | 73 | 11 | 13 | 12.7 |
| Predorsal scales | 11 | 68 | 10 | 12 | 10.8 |
| Perforated lateral-line scales | 10 | 66 | 8 | 12 | 9.7 |
| Lateral series scales | 34 | 66 | 32 | 35 | 33.9 |
| Horizontal scale rows around caudal peduncle | 14 | 52 | 13 | 14 | 14.0 |
| Dorsal limb gill rakers | 6 | 73 | 5 | 7 | 6.2 |
| Ventral limb gill rakers | 9 | 73 | 8 | 10 | 9.4 |
| Outer row premaxillary teeth | 4 | 73 | 2 | 4 | 3.1 |
| Inner row premaxillary teeth | 5 | 73 | 4 | 6 | 5.1 |
| Maxillary teeth m | 12 | 31 | 7 | 12 | 10.8 |
| Maxillary teeth f | — | 27 | 9 | 12 | 10.0 |
| Dentary teeth | 11 | 73 | 9 | 13 | 11.0 |
| Vertebrae | — | 36 | 33 | 34 | 33.7 |

50.3 mm.—2, FMNH 96633, SL 42.8–49.4 mm.—4, MNRJ 11.285, SL 33.6–49.6 mm. All preceding paratypes with same collection data as holotype.—15, USNM 270816, 29.5–41.7 mm, Brazil, Minas Gerais, Município Jequitinhonha, Rio Jequitinhonha, near km 205, road between Salto da Divisa and Jacinto, about 16°02′S, 40°00′W, 22 Mar 1985 by Naércio Menezes, Ricardo Castro, Marilyn Weitzman, and Stanley H. Weitzman.—18, MZUSP 28811, SL 23.0–41.5 mm, with same data as USNM 270816.

*Diagnosis.*—Since *Nematocharax* is monotypic, the species and the generic diagnoses are the same. See also discussion below under "Relationships."

*Description.*—See Tables 1 and 2 for morphometric values and counts. Body moderately deep, sides compressed, greatest depth at dorsal-fin origin. Predorsal body profile gently convex in females and juveniles, more steeply arched in males (compare Figs. 1 and 2). Body profile somewhat elevated at dorsal-fin origin, nearly straight along dorsal-fin base and continuing almost in straight line in females and juveniles to origin of adipose fin. In mature males, profile between posterior dorsal-fin base and adipose-fin origin slightly convex. Dorsal-fin origin about equidistant between caudal-fin base and snout tip. Dorsal-fin origin closer to posterior border of eye than to caudal-fin base. Ventral body profile gently convex to anal-fin origin in both sexes. Body profile along base of anal fin slightly convex to nearly straight in males, almost straight in females. Both dorsal and ventral profiles of body of distal to anal-fin border concave in both sexes.

Head and snout relatively deep. Jaws about equal, mouth terminal or lower jaw slightly included, ventral to upper jaw. Gape nearly horizontal. Maxilla extending posteriorly approximately to point on line drawn vertically at anterior one-third to one-half of pupil of eye.

Dorsal fin with last ray not split to its base. First to fourth branched dorsal-fin rays filamentous and much more elongate in males than females (see Table 1), rays ex-

Fig. 1. *Nematocharax venustus,* new species, holotype, MZUSP 5131, male, 50.5 mm SL; Brazil, Minas Gerais, Município Medina, Rio Jequitinhonha at Itaobim.

tending posteriorly beyond caudal-fin base. In females these rays occasionally reaching as far posteriorly as anterior origin of adipose fin. Branched rays two and three usually shorter than branched rays one and four; may occasionally equal rays two and three in length. Dorsal fin with no well-developed hooks but with small bony spinules scattered distally on branched rays two to six. Any given ray with more spinules on posterior borders of posterior branches than on anterior branch. (For example, a cleared and stained male, USNM 232955, 47.6 mm SL with 2 spinules on anterior branch, 10 on posterior branch of ray two; rays three and four damaged; ray five with 2 spinules on anterior branch, 3 on posterior branch; ray six with 2 on anterior branch and 4 on posterior branch; ray seven with 1 on anterior branch and 6 on posterior branch.)

Adipose fin present, situated at position bisected by or slightly anterior to imaginary line drawn vertically from posterior anal-fin base termination.

Posterior anal-fin ray split to its base. Anal fin of both sexes with broad anterior lobe (Figs. 1–3). Anal-fin rays of anterior lobe much longer in males than in females, reaching posteriorly beyond caudal-fin base. Males with fourth unbranched anal-fin ray and first to about sixth branched anal-fin rays forming major part of anal-fin lobe. Fifth branched anal-fin ray usually longest. See Table 1 and section on sexual dimorphism for comparison of anal-fin lobe lengths of males and females. Males with hooks present on third, fourth and/or fifth unbranched and on first to tenth or eleventh branched rays; see Fig. 3 of anterior unbranched and first six branched rays. Hooks small, 1 to 2 per ray segment. Hooks numerous (more than 10) on unbranched ray four or five and also on branched rays one to six or seven. Rays eight to eleven with 1 to about 3 hooks per ray, with 1 or 2 hooks on hook-bearing segments. Remaining rays may occasionally bear single spinule. Hooks occur near or on those divided, Y-shaped, segments forming initial branching point for each ray. Tiny spinules continuing on branched portions of rays five to six, especially one to four, most common on posterior branch of each ray.

Distal tips of pectoral-fin rays of males

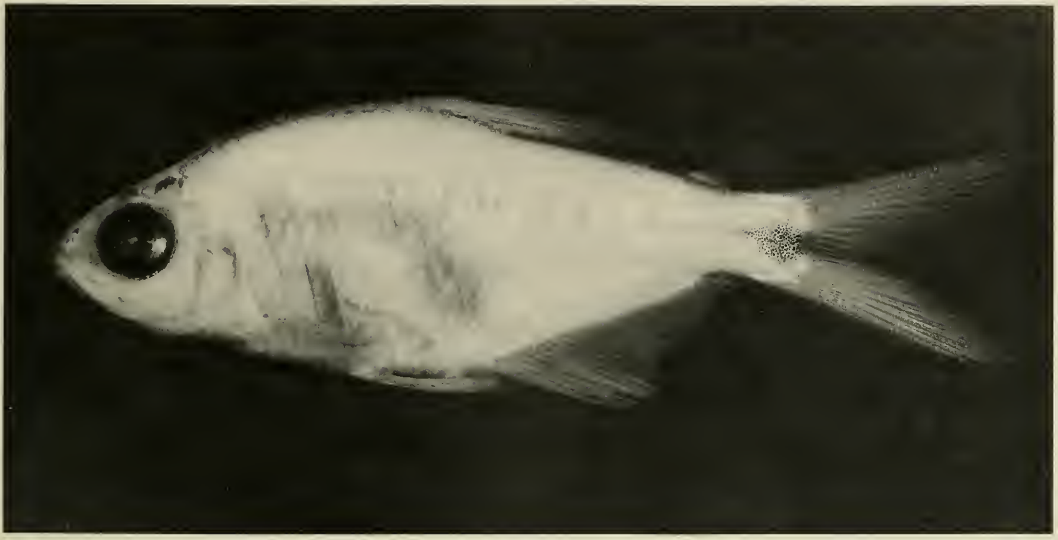

Fig. 2. *Nematocharax venustus,* new species, paratype, MZUSP 28480, female, 35.4 mm SL; Brazil, Minas Gerais, Município Medina, Rio Jequitinhonha at Itaobim.

and females extending posteriorly beyond pelvic-fin origin. Pelvic fin sexually dimorphic, with first unbranched ray greatly elongate in males. See discussion on sexual dimorphism below. Pelvic fin with about 1 to 5 spinules present distally on most branches of rays two to five. Principal caudal-fin rays 10/9 in all counted specimens (73). Hooks and spinules absent on caudal-fin rays.

Scales cycloid, lateral line complete. Predorsal scale series complete. See Table 2 for scale counts.

Premaxillary teeth in two distinct rows (Fig. 4). Two to four, usually three, teeth in outer row (see Table 2); first to fourth teeth of outer row cusped, with lateral most tooth having one to two cusps, and medial tooth up to four cusps. Four to six, usually five, teeth in inner row; inner row teeth with five or six, usually six, cusps. Outer row teeth circular in cross section, not compressed. Inner-row teeth compressed, especially distally along cusps. Maxillary teeth five to twelve, $\bar{x} = 9.5$ in 73 specimens 17.7 to 52.0 mm SL. Adult specimens over 33.0 mm SL, with seven to twelve teeth, $\bar{x} = 10.5$. Larger specimens usually having more teeth. See also discussion on sexual dimorphism. Anterodorsal four to five maxillary teeth with three or four cusps, remaining posteroventral teeth large, strong, and unicuspid. Dentary teeth nine to thirteen, in single row. Anterior six to eight teeth large, with three to five cusps; posterior five to seven teeth usually unicuspid and noticeably smaller than anterior teeth. See Figure 4 of jaws and teeth.

*Color in alcohol.*—See Figs. 1 and 2 for preserved color pattern of males and females respectively. Entire body pale yellowish brown (muscle tissue color) in specimens with guanine destroyed by formalin. Body silvery in specimens with guanine preserved. Series of small chevron-shaped marks occurring along horizontal junction of dorsal and ventral myomeres. These marks especially distinct in region posterior to middle of body cavity and anterior to dark shield-shaped caudal spot. Caudal spot extending posteriorly and terminating at distal tips of three or four middle caudal-fin rays. Caudal spot tapering anteriorly to narrow stripe and then terminating anterior to imaginary vertical line through posterior
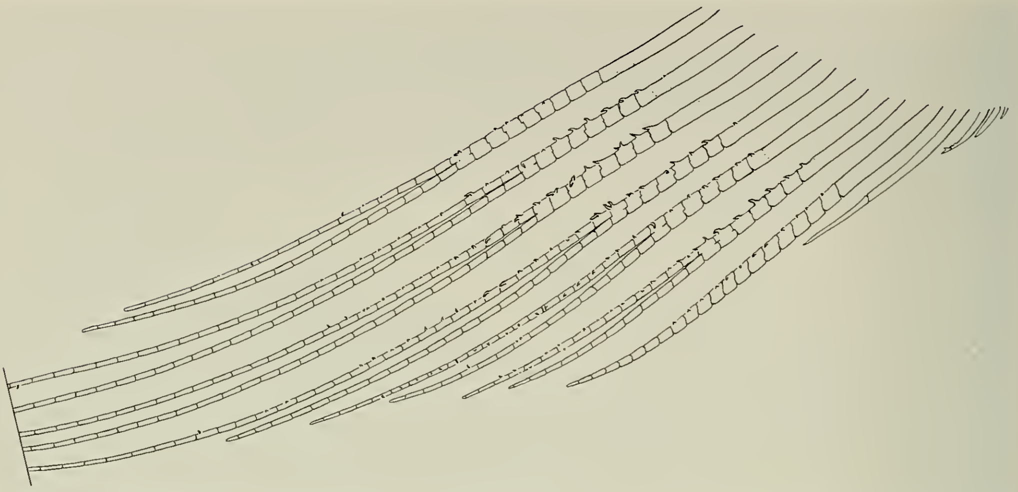
Fig. 3. *Nematocharax venustus,* USNM 232955, male, 47.6 mm SL, cleared and stained. Anal fin, lateral view, right side.

end of anal-fin insertion. Dorsal body surface dusky in area of predorsal scales, along base of dorsal fin, and along median part of back to base of dorsal caudal-fin lobe. Head dusky brown dorsally, pale ventrally, no dark markings. Dark crescent-shape mark on opercle in Figs. 1 and 2 formed by shadow within gill chamber, not from pigment. Belly pale, without dark marks.

Dorsal fin dusky in both sexes, with filamentous rays of males especially dark. Caudal fin dusky with pale brown chromatophores on fin rays. Anal fin dusky in both sexes with filamentous rays of males especially dark. Pelvic and pectoral fins slightly dusky, brown chromatophores few, scattered over rays.

*Color in life.*—Specimens taken from near Salto da Divisa in silty waters with very little visibility had body silvery with dark chevron-shaped marks pale, partly obscured by guanine pigment on body. Body with pale pink and greenish reflections on silvery sides. Back pale brown, top of head dark brown. Dorsal fin with same dark pattern as preserved specimens but with pale rosy color in fin rays. Adipose fin pale rosy. Dorsal caudal-fin lobe pale yellow distally and pale rosy proximally. Ventral caudal-fin lobe with similar color but somewhat yellowish throughout. Anterior lobe of anal fin in both sexes pale rosy, posterior part of anal fin pale yellow. Pectoral fin hyaline, pelvic fin pale rosy. Belly, sides, and side of head bright silvery flushed with small amount of rose color. Iris of eye silvery with rosy dark spot dorsally. In clear waters or in dark tea-colored waters which may have once been common in the tributaries of the lower regions of the Rio Jequitinhonha, the colors of this fish may have been darker and/or more intense.

*Sexual dimorphism.*—*Nematocharax venustus* is obviously sexually dimorphic in three characters. Table 1 shows gaps in ranges of ratios between males and females for the length of the longest dorsal-fin ray (measured between the origin of the fin and the distal tip of the longest ray), anal-fin lobe length, and pelvic-fin length. Measurements were taken from adult specimens between 33.3 to 52.0 mm SL for males and 33.3 to 40.5 mm SL for females.

Inspection of upper jaw length relative to head length in adult specimens shows a greater jaw length in males than in females.

The percent of upper jaw length relative to head length in 30 males (standard length 33.3 to 52.0 mm) from Itaobim ranged from 45.5 to 51.4, $\bar{x} = 47.7$. Twenty-seven females from the same locality (with standard lengths of 33.3 to 40.5 mm) ranged from 39.0 to 45.9, $\bar{x} = 42.5$. Analysis of covariance by sex using logarithmic transformations of original data for upper jaw and head lengths of the same population samples showed no significant difference in regression coefficients (slopes), $t = 0.696$, $P > 0.05$, determined in a two-tailed test but did show significant differences in the Y-intercepts (elevations), $t = 2.600$, $P < 0.001$, also determined in a two-tailed test. The upper jaw length differences in adult males and females may be due to a growth rate difference during sexual maturation since specimens of shorter standard length were not separable into two groups on the basis of upper jaw length.

Inspection of the population sample of *Nematocharax venustus* from Itaobim showed that ten juvenile specimens between 17.7 and 32.8 mm SL had 5 to 7 maxillary teeth, and a mean of 5.8. Twenty-seven adult males had 7 to 12, and a mean of 10.8 maxillary teeth. Thirty-one adult females between 33.3 and 40.5 mm SL had 9 to 12, and a mean of 10.0 maxillary teeth. Covariance analysis of the same two adult samples by sex using logarithmic transformations of upper jaw length measurements and square root transformations of maxillary tooth numbers showed a difference in regression coefficients (slope), $t = 2.117$, $P < 0.05$ and in the Y-intercept (elevations), $t = 2.003$, $P < 0.05$, both determined in a two-tailed test. In *Nematocharax venustus* there does seem to be some sexual dimorphism in maxillary tooth numbers.

Sexual dimorphism in maxillary (or other) tooth number is apparently rare in tetragonopterine characids, especially in those species with one to three or so teeth in each maxilla. When the count is higher, maxillary tooth count differences might be expected to display sexual dimorphism, especially if the maxilla is longer in males than in females. At some stage in the development of all tetragonopterines with maxillary teeth there are fewer teeth (or none) in the young than in older specimens. In species with many maxillary teeth and long maxillae the increase in tooth numbers and in maxillary length may continue evenly over a relatively long interval of growth and then differentiate during sexual maturation.

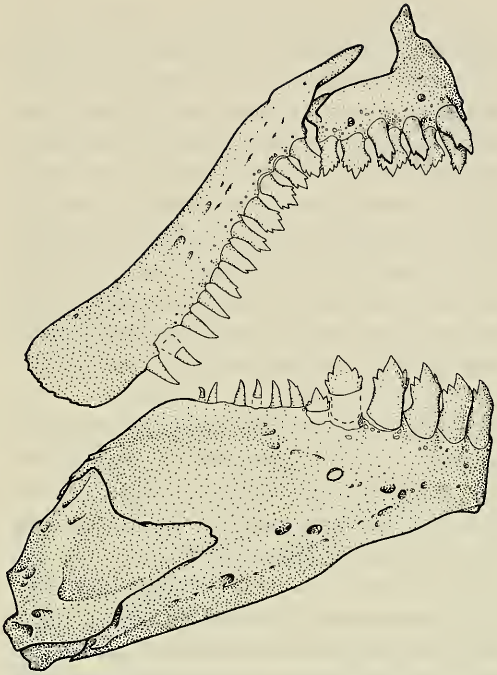

Fig. 4. *Nematocharax venustus,* USNM 232955, male, 47.6 mm SL, cleared and stained. Lateral view, right side of premaxillary, maxillary, and dentary bones.

Body depth in *Nematocharax venustus* increases at a greater rate relative to body length during growth. Males and females are evidently sexually dimorphic in the ratio of body depth to standard length. In the population from Itaobim, ten juveniles 17.7 to 32.0 mm SL had a body depth ratio of 33.0 to 37.3 percent of the standard length with a mean of 34.8 percent. In thirty-one females of 33.3 to 40.5 mm SL the rate ws 36.0 to 40.4, with a mean of 38.6 percent while in twenty-seven males of 33.3 to 52.0

mm SL the rate was 37.5 to 43.0, with a mean of 41.0 percent. Covariance analysis using logarithmic transformations of original measurements of these same males and females showed no differences in regression coefficients (slopes), $t = 0.000$, $P > 0.05$ and Y-intercepts (elevations), $t = 0.256$, $P > 0.05$. It would seem that differences are size related and that females appear to be less deep only because they do not reach as large a size as the males in the two population samples at hand (Itaobim and Salto da Divisa).

*Relationships.*—The phylogenetic relationships of *Nematocharax venustus* remain obscure. A combination of a compressed, relatively deep body form, long dorsal fin and a nearly fully toothed maxilla is also found in members of the Rhoadsiinae from western Ecuador, Colombia, Panama (an undescribed species), Costa Rica, and Lake Nicaragua in Nicaragua; see Eigenmann and Myers (1929:457), Dahl (1960:472), and Fink and Weitzman (1974: 26). These fishes, geographically distant from *Nematocharax,* lack the derived, elongate anal- and pelvic-fin rays of *Nematocharax.* Also, *Nematocharax* with a vertebral count of 33–34 differs from the higher vertebral count, 36–38, of species of the Rhoadsiinae [based on specimens of *Rhoadsia altipinna* Fowler (FMNH 83870), *Parastremma sadina* Eigenmann (FMNH 56023), *Carlana eigenmanni* (Meek) (USNM 272646) and specimens of an undescribed species of *Carlana* collected recently in Panama (USNM uncatalogued)]. Furthermore, *Nematocharax venustus* does not have the "cheirodontine" teeth (flattened and with a single series of several more or less subequal cusps) found in young specimens and as at least partly present in adults of the Rhoadsiinae, Eigenmann and Myers (1929:457), Fink and Weitzman (1974:25). Small specimens, down to 17.7 mm SL, of *Nematocharax venustus* have teeth similar to those of adults, relatively elongate, rather flattened and with cusps of different sizes on each tooth. The geographical distance between *Nematocharax* and members of the Rhoadsiinae make it unlikely that *Nematocharax venustus* is most closely related to members of Rhoadsiinae, but the possibility cannot be ignored.

If *Nematocharax* is most closely related to the Rhoadsiinae it is less derived in having fewer conical teeth in the maxilla than members of the Rhoadsiinae, having no "cheirodontine"-like teeth at any life history stage, and possibly in vertebral numbers as described above. *Nematocharax* does have its own derived features relative to the Rhoadsiinae. These are the elongate anal and pelvic fins.

The color pattern of *Nematocharax* appears less derived, having a caudal spot and chevron-shaped marks along the midsides similar to those of many tetragonopterine characids. It lacks the bright red color of some (all?) of the Rhoadsiinae and the large midside blotch (posterior humeral spot?) in life of some of the Rhoadsiinae. At this time, little phylogenetic information can be gathered from the color patterns of characid fishes since so little of that system has been cladistically analyzed. Only in those cases where a species or a group of species have a unique (not found in any other taxa) color pattern as in *Paracheirodon* (see Weitzman and Fink 1983:354) can color pattern currently be used in a cladistic analysis of characids.

Another fish, *Hyphessobrycon elachys* M. Weitzman (1985) from Paraguay, has elongate dorsal- and pelvic-fin rays. This fish differs from *Nematocharax venustus* in having a different color pattern, derived anterior jaw teeth in which the central cusp extends in an opposite plane from the lateral cusps, and a small adult standard length of nearly 20.0 mm. The only evidence suggesting a possible relationship with *N. venustus* are the elongate dorsal and pelvic fins, a character we suspect is convergent. Again, phylogenetic studies are necessary to examine possible relationships between the two species.

Other "tetragonopterine characids" have long fins. The glandulocaudine characid *Gephyrocharax martae* Dahl (1942:4) from northern Colombia has an elongate anterior anal-fin lobe that becomes filamentous. Other species of glandulocaudines such as *Corynopoma riisei* and *Pseudocorynopoma doriae* tend to have fin rays produced or to have entire fins elongate. There is no evidence that *Nematocharax venustus* is a glandulocaudine characid since it lacks the glandular tail structure of these fishes. Some species of "rosy" tetras in the genera *Megalamphodus* Eigenmann (1915:50), and *Hyphessobrycon,* Weitzman (1977:335) have relatively elongate dorsal and anal fins which are not, however, filamentous as in *Nematocharax venustus.* Sometimes specimens of *Hyphessobrycon bifasciatus* also have a somewhat elongate dorsal fin and somewhat filamentous anterior pelvic-fin rays, but these are never as long as in *Nematocharax venustus.* It is our opinion that elongate fins in characids probably evolved independently several times and that for such fins to be utilized as synapomorphies relating species and genera, the morphological similarity of the fins should involve homologous rays. Such characters would be best used when they are congruent with other synapomorphies indicating the monophyletic relationships of particular taxa.

Two genera, *Hollandichthys* Eigenmann (1910) and *Rachoviscus* Myers (1926) have species which, like *Nematocharax venustus,* bear well-toothed maxillae. Since these species are part of the Atlantic forest fish fauna, relatively close geographically to the known localities for *N. venustus,* they should be considered as possible candidates for relationships with *Nematocharax.*

Weitzman and Cruz (1981:999) briefly discussed some possible relationships of *Rachoviscus* and concluded that the species were "tetragonopterine" rather than "cheirodontine" characids as suggested by Myers (1926:1). Weitzman and Cruz (1981:1003) were unable to corroborate any phylogenetic hypotheses of the relationships of *Rachoviscus* to specific "tetragonopterine" genera. In addition to a rather heavily toothed maxilla, the two species of *Rachoviscus* have a deep red adipose fin. The adipose fin of *Nematocharax venustus* is a pale rosy color but has none of the deep red pigment found in the species of *Rachoviscus.* Considering the differences in these pigments we cannot consider the adipose fin color of *Rachoviscus* and *Nematocharax* a synapomorphy based on similar color pattern, although the rosy color could be considered a transition state between no red color and deep red.

The details of the jaw morphology of *Nematocharax* are different from those of *Rachoviscus. Nematocharax venustus* has the mouth horizontal, not angled. Both species of *Rachoviscus* have somewhat upturned mouths with the gape angled posteroventrally (Weitzman and Cruz 1981:1005, 1009). The condition in *Rachoviscus* is probably more derived and may represent a synapomorphy for the species of that genus, although it must be kept in mind that an angled jaw is not uncommon in other "tetragonopterine" characids. The maxilla of *Nematocharax venustus* is well toothed ($\bar{x}$ = 10 teeth) (Fig. 3 and Table 2), while *Rachoviscus graciliceps* Weitzman and Cruz has 3 to 8 teeth and *Rachoviscus crassiceps* Myers has 8 to 14 teeth. Evolution of a well-toothed maxilla may have taken place within *Rachoviscus crassiceps* and *Nematocharax* independently. We have at present no way of evaluating the cladistic significance of maxillary teeth in these genera since the character appears in several other "tetragonopterine" genera and we have found no other synapomorphies possibly indicative of a close relationship between *Nematocharax* and *Rachoviscus.*

The monotypic *Hollandichthys multifasciatus* Eigenmann and Norris (1900:358) might be related to *Nematocharax venustus,* both having well-toothed maxillae. Because of its nearly fully toothed maxillae *Hollandichthys multifasciatus* was considered a species of *Pseudochalceus* by Schultz (1966:26) and Géry (1972:30). The relationships of *Hollandichthys* and putatively related characids assigned to *Pseudochalceus* were reviewed by Schultz (1966:26), and Géry (1972a:24–25; 1972b:933–942). We here make no comment on these reviews pending a cladistic treatment of these and other, possibly related fishes. *Hollandichthys multifasciatus,* apparently confined to Atlantic coastal streams between and including the states of São Paulo and Santa Catarina, has a maxilla with up to 17 teeth. There are several differences between *Hollandichthys* and the other species assigned to *Pseudochalceus,* Géry (1972a:37; 1972b:942; 1977:414). Considering these differences and the geographical isolation of *Hollandichthys* (southeastern Brazil) from other species assigned to *Pseudochalceus* (western Ecuador and Colombia) we propose to retain the name *Hollandichthys* until a cladistic phylogenetic study demonstrates monophyly of these geographically disparate genera. At present we see no more reason to relate *Nematocharax venustus* to *Hollandichthys multifasciatus* or to any species of *Pseudochalceus* than to relate *Nematocharax* to the species of *Rachoviscus.* The only possible synapomorphy found by us relating these genera and species is a high maxillary tooth count. For some taxa, a high maxillary tooth count is undoubtedly a synapomorphy indicating monophyly of a group formed by these taxa; for example, the species of *Pseudochalceus* from Ecuador recorded by Géry (1972). But high maxillary tooth counts have appeared a number of times in characids, for example in *Rachoviscus* Weitzman and Cruz (1981:1000) and xenurobryconin characids subgroup C, Weitzman and Fink (1985:55). Because of the possibility that *Nematocharax* may have evolved its maxillary teeth independently and especially because we have been unable to find any other synapomorphies common to *Nematocharax* and other characid genera with high maxillary tooth counts we are unable to accept a hypothesis that *Nematocharax* forms a sister group with any of them.

Without extensive and detailed morphological and phylogenetic research, we have no fully tested hypotheses concerning the relationships of *Nematocharax venustus.* It appears to be a "tetragonopterine" characid but that group itself is not currently defined by synapomorphies (see Weitzman and W. Fink (1983:342) and Weitzman and S. Fink (1986) for our opinions about the monophyly of the Tetragonopterinae).

*Etymology.*—The name *venustus* is from the Latin Venus, meaning like Venus, hence beautiful, elegant, or graceful. The name is given in reference to the graceful flowing shape of the dorsal, anal, and pelvic fins of this fish.

*Remarks.*—The yet-to-be-accomplished studies of fish biogeography and fish species composition of the streams in areas formerly occupied by the Atlantic forests of eastern and southeastern Brazil have now been made more difficult by inadequate sampling in the past and by much habitat alteration within the last eighty years and especially within the last thirty years. It is no surprise that new species of fishes have been collected and described from many of the Atlantic forest areas in recent years. For example, see Britski and Ortega (1983), Buckup (1981), Garavello (1977), Nijssen and Isbrücker (1976, 1980), and Weitzman and Cruz (1981).

The Rio Jequitinhonha, a relatively large coastal river, has been very little explored ichthyologically, and unfortunately for systematic and biogeographic ichthyological research, in part has been long subject to habitat alteration by man's agricultural activities. Arising in the cerrado area of the Serra do Espinhaço of Minas Gerais, the

Rio Jequitinhonha flows north then east through Minas Gerais and Bahia to the Atlantic Ocean. In parts of Minas Gerais and in Bahia this river originally traversed the Atlantic forest. Only about two percent of the forest area remains, the rest is now essentially replaced by agriculturally developed land. A combination of cattle grazing, farming, and pulpwood plantations of pine and eucalyptus trees constitute most of the land use along the coastal plain. The ecology of the middle and lower Rio Jequitinhonha drainage is greatly altered from its preagricultural condition and this has undoubtedly greatly affected the composition of the fish fauna. At the present time this river bears a heavy silt load, at least during the rainy season. Furthermore, in 1985 two of us (Menezes and Weitzman) observed an introduced species of the African cichlid genus *Tilapia* to be common in the vicinity of Salto da Divisa and we suspect this fish is common in most parts of the river. *Tilapia,* just as other factors influencing the altered ecology, undoubtably has affected the relative composition of the fish fauna in the Rio Jequitinhonha. We will never know the preagricultural composition of the fish fauna of this river. Some species, less adaptable to the altered ecology of the river, may have become rare or extinct. Other species, not impacted by *Tilapia,* adaptable to a heavy silt load, increased sunlight and probably to higher water temperatures, and to a non-forest water chemistry, especially in the small tributaries in the lower courses of the river, may now be far more common than formerly. Eventually some presumptive measure of the original fish fauna of middle and lower parts of the Rio Jequitinhonha and its tributaries may be discerned by sampling the shorter coastal rivers in adjacent areas where some forest remains, such as those flowing within and from the Parque Nacional de Monte Pasqual just to the south. However, the shorter coastal rivers now have and probably formerly had a poorer fish fauna than the Rio Jequitinhonha because they lacked access by stream capture to the richer ichthyofauna of more interior water courses such as the Rio São Francisco drainage further to the west. Furthermore, the larger Rio Jequitinhonha may have had a longer geological history than the shorter coastal rivers, allowing the evolution of more endemic species. Thus the fish faunas of the short adjacent coastal rivers that drain only the Atlantic forest are unlikely to represent fully the original fauna of the Rio Jequitinhonha.

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# ADDITIONAL RECORDS FOR *CALLIANASSA RATHBUNAE* SCHMITT, 1935, FROM FLORIDA AND THE BAHAMAS (CRUSTACEA: DECAPODA: CALLIANASSIDAE)

Raymond B. Manning and Richard W. Heard

*Abstract.*—*Callianassa rathbunae* Schmitt is far more abundant in shallow water habitats than suggested by records in the literature. More than 40 specimens are recorded from localities in the Bahamas and the Indian River, Florida.

The mud shrimp *Callianassa rathbunae* was described by W. L. Schmitt (1935:15) from two male specimens, 59 mm and 61 mm long, that had washed ashore at Bluefields, Jamaica [18°10′N, 78°03′W], in 1899. Biffar (1971:699) redescribed the species from two other specimens, one male, 95 mm long, and one female, 82 mm long, dredged in an undisclosed depth off the east coast of Key Biscayne, Miami, Florida, in 1969. Suchanek (1985) reported the results of investigations of the biology of *C. rathbunae* and three other species of *Callianassa* at three localities on St. Croix, U.S. Virgin Islands: Tague Bay, 17°46′N, 64°36′W; Great Pond Bay, 17°43′N, 64°39′W, in depths to 5 m; and Salt River Canyon, 17°47′N, 64°45′W, in depths to 40 m. So far as we are aware, there are no other records in the literature for this species.

Independent collections by each of us has uncovered much additional material of this species. On 2 October 1980, one of us (RWH) found this species on a silt and coralline sand bottom in 10 to 15 feet of water north of the seaplane ramp on the west side of the channel at Bimini, Bahamas [25°44′N, 79°15′W]. A total of 19 specimens was taken with a suction pump: 10 ♂, carapace lengths (cl) 11.0–17.8 mm (total lengths (tl) 37–68 mm); 5 non-ovigerous ♀, cl 11.5 to 15.4 mm (tl 42–57 mm); and 4 ovigerous ♀, cl 11.7 to 19.0 mm (tl 42–57 mm) [1 ♂, 1 ovigerous ♀, GCRL I80:1107; 2 ♂, 2 ♀ (1 ovigerous), USNM]. One specimen of *Callianassa branneri* (Rathbun), one of the commonest shallow water species in the tropical western Atlantic, and two specimens of an undescribed species, closely related to *Callianassa quadracuta* Biffar, were taken at the same time.

Twenty-four other specimens have been collected by one of us (RBM) at two localities in the southern Indian River, Florida, one just inside the St. Lucie Inlet, Martin County, the other just inside the Fort Pierce Inlet, St. Lucie County. All of these collecting sites were on sand flats exposed at low tide; that on the south side of the Fort Pierce Inlet was on a sand bar with scattered seagrass, most abundant on the edges of the bar where the bottom became muddier, whereas the site on the north side of the Fort Pierce Inlet and the St. Lucie site lacked vegetation. The following specimens were taken in the Indian River (unless otherwise indicated, all specimens are in the collection of the Smithsonian Institution, USNM):

Florida, Martin County, flat just inside St. Lucie Inlet, 27°10.3′N, 80°10.4′W, clean sand: Sta RBM FP-82-8, R. B. Manning, M. E. Rice, J. Piraino, H. Reichardt, 16 Jul 1982: 1 ♂, cl 16.3 mm (tl ca. 64 mm).—Sta RBM FP-83-2, R. B. Manning, W. D. Lee, H. Schiff, 11 Feb 1983: 1 ♂, cl 10.1 mm (tl 33 mm), 1 ♀, cl 8.9 mm (tl 30 mm).

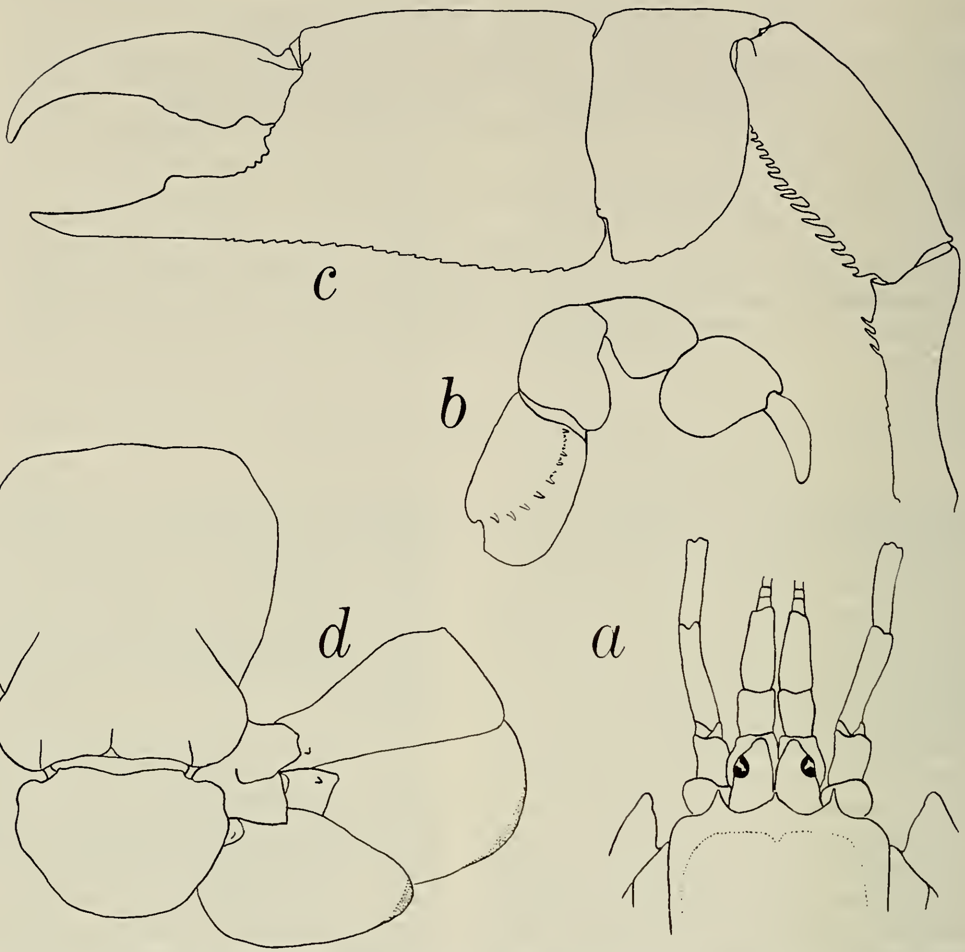

Fig. 1. *Callianassa rathbunae* Schmitt. Male, cl 16.3 mm, Sta RBM FP-82-8: a, Front; b, Inner face of third maxilliped; c, Chela; d, Sixth abdominal somite, telson, and uropod (stippled areas distally on uropods mark regions of dense setation).

St. Lucie County, south side of Fort Pierce Inlet, 27°27.7′N, 80°18.7′W, sand flat with sparse seagrass: Sta RBM FP-83-5, R. B. and L. K. Manning, 12 Jul 1983: 1 ♀, cl 14.5 mm (tl 51 mm).—Sta RBM FP-84-8, R. B. Manning, D. L. Felder, 14 Jul 1984: 1 ♂, cl 15.8 mm (tl 65 mm), 8 ♀, cl 16.1–20.5 mm (tl 69–81 mm).—Sta RBM FP-85-1, R. B. Manning, D. L. Felder, 17 Jul 1985: 6 ♀ (2 ovigerous), non-ovigerous cl 17.2–21.1 mm (tl 62–76 mm), ovigerous specimens damaged, cl ca. 17 mm (tl ca. 62 mm) [1 specimen to Indian River Coastal Zone Museum, Fort Pierce; 1 specimen to Gulf Coast Research Laboratory (GCRL)].—Sta RBM FP-85-4, R. B. Manning, D. L. Felder, 23 Jul 1985: 1 ♂, cl 19.1 mm (tl 81 mm), 1 ovigerous ♀, damaged (female taken with 2 specimens of *Pinnixa retinens* Rathbun).—Sta RBM FP-85-8, R. B. Manning, M. L. Reaka, W. D. Lee, B. Tunberg, 15 Aug 1985: 2 ♂, cl 18.8–19.0 mm (tl 76–80 mm).

St. Lucie County, north side of Fort Pierce Inlet, south side of Coon Island, 27°28.2′N, 80°18.3′W, muddy, hard packed sand near shore: Sta RBM FP-85-2, R. B. Manning,

D. L. Felder, W. D. Lee, 18 Jul 1985: 1 ♀, cl 19.0 mm (tl 74 mm).

The specimens from both the Indian River (Fig. 1) and Bimini were pink overall in color, with deeper pink to red on the claws. Unlike many callianassids, which appear to be listless when taken from their burrows, the smaller specimens taken at the St. Lucie Inlet site were very active and tried to escape capture.

All of the specimens reported here were taken with a suction or yabby pump. Those from Bimini were taken with an open ended pump, as described by Manning (1975), which can be used by divers as well as from shore, whereas those from the Indian River were collected with a closed-end Australian commercial yabby pump (Hailstone & Stephenson 1961), which can only be used with the lower part of the tube under water. Use of either kind of suction pump greatly simplifies the collection of callianassids and other burrowing crustaceans.

These samples demonstrate that *C. rathbunae* is far more abundant and widespread than suggested by records in the literature, and that it occurs in intertidal habitats as well as in shallow, sublittoral habitats. Curiously, whereas Biffar's collections from shallow water dredging operations off Miami (Biffar 1971:704) yielded about 40 specimens of *C. branneri* and two specimens of *C. rathbunae,* our collections from Bimini yielded 19 specimens of the latter and only one *C. branneri.*

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# PSEUDOJANIRIDAE (CRUSTACEA: ISOPODA), A NEW FAMILY FOR *PSEUDOJANIRA STENETRIOIDES* BARNARD, 1925, A SPECIES INTERMEDIATE BETWEEN THE ASELLOTE SUPERFAMILIES STENETRIOIDEA AND JANIROIDEA

George D. F. Wilson

*Abstract.*—The South African marine isopod *Pseudojanira stenetrioides* is redescribed because characters of its male copulatory structures may be intermediate between the asellote superfamilies Stenetrioidea and Janiroidea. Specifically, the endopod of pleopod II has a stylet similar to that of the Janiroidea, but it lacks a sperm tube; pleopod I is similar to the stenetrioid condition but has distal stylet guides as in the Janiroidea. The female copulatory structure, the cuticular organ, is not on the anterodorsal surface as in most janiroideans, and has special auxiliary structures not described from any other asellotan. The species and genus is assigned to a new family, Pseudojaniridae, but its superfamily designation is left undecided.

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*Pseudojanira stenetrioides* Barnard (1925) is a small isopod from South Africa, recently redescribed by Kensley (1977) and classified by that author as a member of the family Janiridae, superfamily Janiroidea. This species showed a stenetrioid habitus and male pleopods I–II that display similarities with both the Stenetrioidea and the Janiroidea (Kensley 1977: his figures 9–10). An examination of two specimens of this species from the South African Museum confirmed these observations and, in addition, revealed a new type of female genital organ. The discovery of unusual female and male copulatory organs in *Pseudojanira stenetrioides* Barnard (1925) made it necessary to prepare a redescription of this unique species. Because of the possibly transitional characters found in *P. stenetrioides,* the new family Pseudojaniridae is erected for the genus *Pseudojanira.* The superfamilial classification, however, is left undecided; proper determination of the superfamilies must be based on a complete morphological survey of all the families of the "lower" Asellota. This paper adds to and corrects information in Kensley (1977) for the purpose of providing the data on *P. stenetrioides* for such a morphological survey. A survey of asellotan female copulatory organs and other characters (manuscripts in preparation) will extend the results reported here.

## Materials and Methods

M. G. van der Merwe, Marine Biology Technical Officer of the South African Museum (SAM) kindly loaned the holotype female and male specimen of *Pseudojanira stenetrioides* (catalogue numbers SAM A6295 and SAM A15345, respectively). The illustrations in this paper were inked from pencil drawings made using a Wild M20 microscope fitted with a camera lucida drawing tube. To study the reproductive organs of the female specimen, it was stained with methylene blue dissolved in lactic acid. Previous discussion of the evolution of the Asellota has typically relied on simple outline drawings of limbs for comparison. The fine details of asellotan construction, however, are often phylogenetically important

(Wägele 1983). For example, an outline of the endopod of male pleopod II would not show the difference between the stylet of *Pseudojanira* and that of the Janiroidea. Therefore, this paper will provide more pictorial information than has been typically offered in the past. In the illustrations of body parts, anterior is toward the top of the page, mouthparts and pleopods are shown in ventral view unless noted otherwise.

### Order Isopoda Latreille, 1817
### Suborder Asellota Latreille, 1803
### Superfamily *Incertae Sedis*
### Pseudojaniridae, new family
Figs. 1–3

*Type genus.*—*Pseudojanira* Barnard, 1925, by original designation.

*Previous assignments of type.*—Jaeridae: Barnard, 1925:406. Janiridae: Wolff, 1962: 252; Kensley, 1977:251. Ianiridae: Kensley, 1977:252.

*Diagnosis.*—Asellota with broad pereonal tergites extending laterally and ventrally, hiding coxae from dorsal view. Cephalon with dorsal eyes, broad lateral lappets, and large frontal rostrum. Pleotelson with only 1 free pleonite visible dorsally, 2 ventrally. Pereopod I robust, with enlarged setose propodus; prehension between dactylus and propodus; carpus short, quadrangular, setose, not participating in grasping. Male first pleopods with basal segments fused, distal rami separate; distolateral corners with dorsal grooves; distal margins truncate, with simple setae. Male pleopod II basal segment enlarged, with endopod and exopod projecting medially; posterior end of basal segment enlarged, thickened, with transverse distomedial groove supplied with fine setae; endopod distal segment stylet-shaped, with open ventral groove and distolateral barbs; endopod proximal segment with thickened cuticular ridge; exopod comprising only single short, robust segment, with thickened dorsal hook on setose anterodistal corner. Male pleopods I and II together not opercular. Female second pleopods (not seen by me) fused into single opercular segment lacking setae on margins. Pleopod III exopod broad, rounded, with fringe of simple setae; endopod with 3 large plumose setae; in male, exopod opercular. Uropods short, biramous, setose, barely extending beyond posterior margin of pleotelson.

### *Pseudojanira stenetrioides* Barnard
Figs. 1–3

*Pseudojanira stenetrioides* Barnard, 1925: 406–407.—Kensley, 1977:251–253.

*Holotype.*—Adult female, 2 poorly preserved fragments (cephalon and pereon), pleotelson missing, original reported length 3 mm, width 1.3 mm, SAM 6295. Type locality: "Zululand coast, in a coral (H. W. Bell-Marley, 1920) . . ." (verbatim from original description, Barnard 1925).

*Additional material.*—Partially dissected adult male, with removed limbs on a slide, length (including rostrum) 2.8 mm, width at sixth pereonite 1.4 mm, SAM A15345. Locality: ". . . 24°53'S, 34°56'E, 55 metres, from fine gray sand" (verbatim from Kensley 1977).

*Description (in addition to Kensley 1977).*—Body characters (Fig. 1A, B): Lateral margins of pereonites oval. Body surfaces covered with fine setae. Body dorsoventrally thin but highly vaulted: tergites extending beyond main part of body and angling sharply downward. Pereonite 1 sexually dimorphic, longer and more robust in males than in females.

Female cuticular organ (Fig. 1B, 3): Described below in the section on the female copulatory organ.

Cephalon (Fig. 1A, D): Rostrum: anteriorly rounded; thin, broad, nearly as long as short antennulae; projecting anteriorly from frons, below anterior margin of cephalic dorsum. Lateral margins broad, flattened, with small anterior spine. Eyes projecting dorsolaterally from domed central

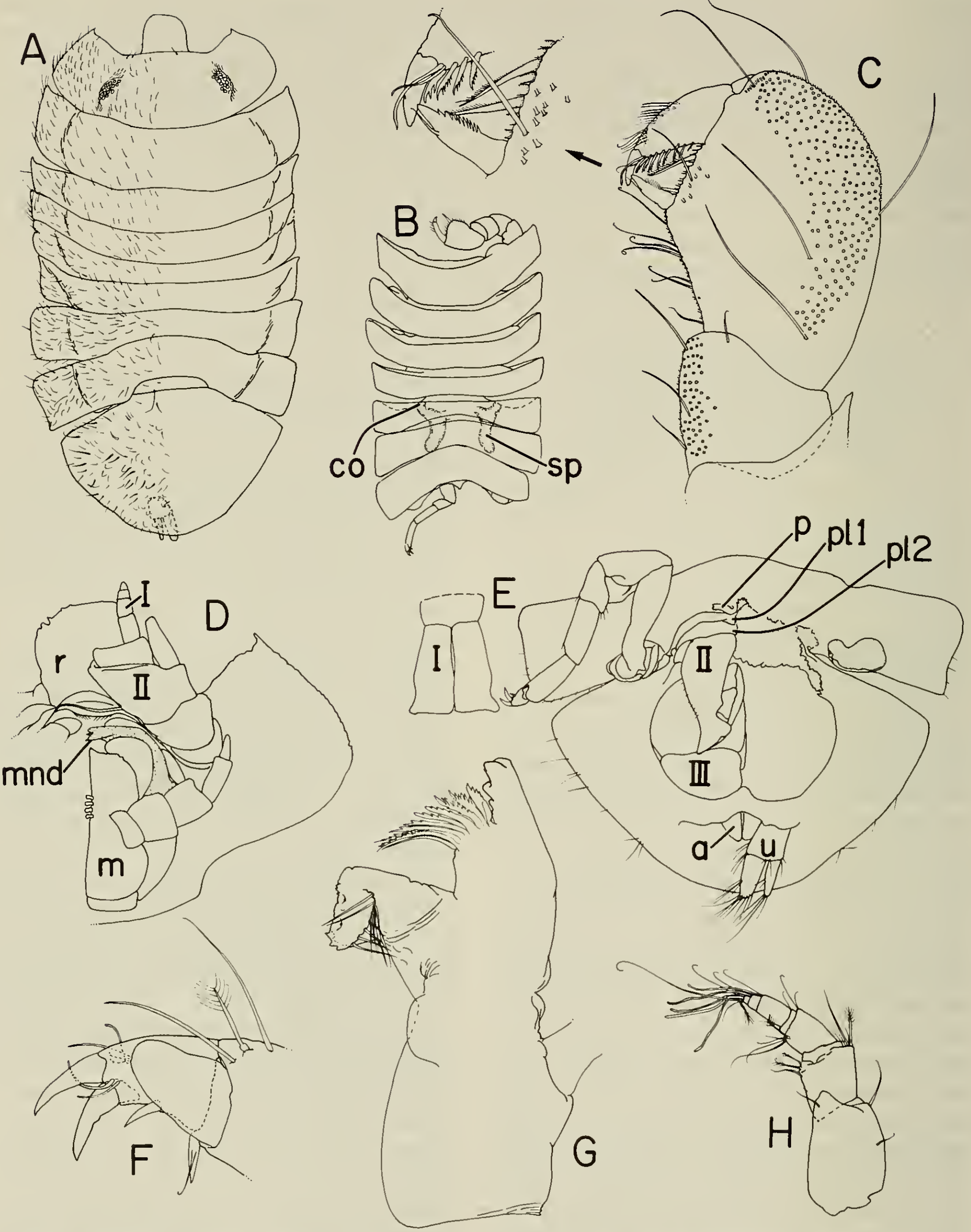

Fig. 1. *Pseudojanira stenetrioides.* A, C–H, Male, 2.8 mm; B, Holotype female, reported intact length 3 mm; A, Dorsal view, setae on right side omitted; B, Dorsal view of female pereonal fragment, co—position of cuticular organ seen through dorsal cuticle, sp—spermatheca seen through dorsal cuticle; specimen was stained in lactic acid and methylene blue to make this possible; C, Pereopod I of male, distal segments only, with enlargement of opposing setation on propodus and dactylus (carpus and propodus have many long tubular setae; setal insertions are indicated by 'u' or circular marks, and a few are drawn in to show an approximate length of the ones omitted. Some of the setae in the enlargement are illustrated in the same manner.); D, Ventral view of left side of cephalon

portion of cephalon, positioned roughly halfway between midline and lateral margins.

Pleotelson (Fig. 1A, E): Broader than long. Pleopodal cavity small, width half width of pleotelson, cavity separate from anus. Lateral margins entire, smoothly curving.

Antennula (Fig. 1H): Very short, length approximately length of antennal segments 1–4, basal segment largest. Broom setae on segments 2 and 3; aesthetascs on distal 3 segments.

Antenna (Fig. 1D): Basal segment 3 with large, basally articulated scale (or squama) extending beyond segment 4.

Right mandible (Fig. 1G): Spine row with 10 members. Articular condyle on dorsal surface distinctly shorter than length of robust molar process. Molar process with approximately 9 setae on posterior part of denticulate circumgnathal surface.

First pereopod (Fig. 1C): Claw of dactylus opposing large spine-like serrate seta on propodus. Row of small tapering setulate setae leaning toward more posterior large spine-like seta. Opposing margin of dactylus armed with row of short multiply-toothed setae. Carpus and propodus with several dense groups of long, thin setae.

Dactylar claws of walking legs (Fig. 1F): Distal tips of walking legs with 2 robust claws of similar size, and more proximal small claw-like accessory seta.

Male Pleopod I (Fig. 2A, B): Length 0.42 pleotelson length, distal segments covering rami of pleopod II. Basal segments quadrate, fused medially. Distal rami separate, distally truncate with fringe of simple setae posteriorly and laterally. Dorsal side of distolateral corners with stylet grooves (sg in Fig. 2B).

Male pleopod II (Fig. 2C, D): Length of basal segment subequal to pleopod I, with endopod and exopod inserting in center of medial margin. Basal segment distally broad, curving laterally to subacute angle, with setose groove in medial part of margin. Lateral margin of basal segment with row of simple setae. Endopod proximal segment robust, with pronounced ridge on ventromedial edge; distal segment styliform, with distally tapering groove on ventral surface and 4 small denticles on distolateral margin. Exopod robust, powerfully muscled, with rounded hook and fine setae on anterodistal edge.

Pleopod III (Fig. 2E): Exopod broad, fringed with simple setae, covering pleopods IV and V; endopod somewhat less broad, dorsal to exopod.

Pleopod IV (Fig. 2F): Endopod broader than exopod. Exopod with 2 free, laterally rounded segments, and 7 plumose setae on distal tip.

Pleopod V (Fig. 2G): Endopod longer and broader than endopod of pleopod IV. Basal segment and endopod fused, exopod absent.

## Discussion

*Characters important to the classification of the Asellota.*—Because the current classification of the superfamilies of the Asellota is based on the pleopods (Wolff 1962), the unique combination of the male pleopod characters (Fig. 2A–D) in *Pseudojanira stenetrioides* make it difficult to place in the accepted superfamilies. I will not discuss all the superfamilies here because the Pseu-

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(right side had been dissected); I—antennula, II—antenna, r—rostrum, m—maxilliped, mnd—mandible; note how the rostrum is nearly as long as the antennula, the tip of which is protruding past the basal articles of the antenna; E, Ventral view of male pereonite 7 and pleotelson, with pleopod I shown at the same scale; I—pleopod I, II—pleopod II, III—pleopod III, p—penile papillae, pl.1—presumed pleonite 1, pl.2—presumed pleonite 2, a—anus, u—uropod; F, Dactylus of pereopod mounted on slide, possibly pereopod VII as in Kensley (1977); note presence of 2 subequal claws and a more proximal accessory seta on dactylus; G, Right mandible, dorsal view, palp omitted; H, Right antennula, ventral view.

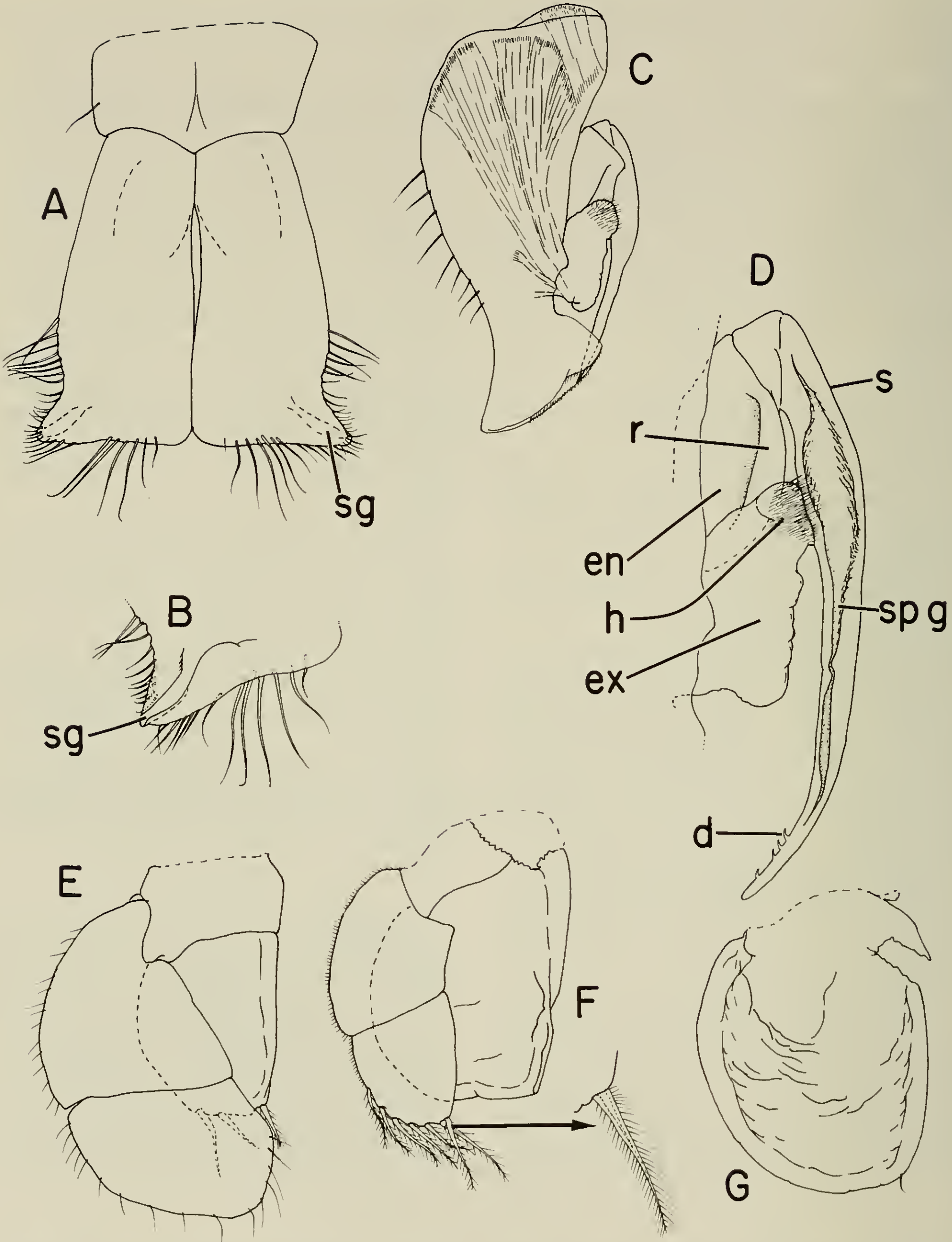

Fig. 2. *Pseudojanira stenetrioides.* Dissected parts on slide from male paralectotype. A, Pleopod I, ventral view; B, Pleopod I, dorsal (interior) view of distolateral corner; sg—stylet groove; C, Pleopod II, ventral view, exopodal musculature shown through cuticle; D, Pleopod II rami, d—denticles, en—endopod, ex—exopod, h—position of dorsally directed hook on exopod, r—ridge on proximal segment of endopod, s—stylet (distal segment of endopod), spg—sperm groove (note the ridge on proximal segment of the endopod; if homologous to the janiroidean condition, this ridge may allow the well-muscled exopod to hook onto the endopod during copulation); E–G, Pleopods III–V respectively, plumose seta on pleopod IV enlarged.

dojaniridae, the Stenetrioidea, and the Janiroidea will be shown in another paper to form a monophyletic group in exclusion to all the other asellote taxa. The primary synapomorphies of this group are a short, single-articled exopod of male pleopod II and a cephalon with a frontal projection. The following discussion is nonphylogenetic and is only meant to highlight the intermediate nature of *Pseudojanira.* The unique female copulatory organs, also of taxonomic significance, are described below.

The first male pleopod of *Pseudojanira* has a mixture of janiroidean and stenetrioid characters. As in *Stenetrium,* the basal segment is large, quadrate, and medially fused. The two sides of the distal segment are free from each other. In contrast, all janiroideans have highly reduced basal segments of the male pleopods I and their distal rami are medially fused forming a central sperm tube. However, the distal tips of the first pleopod in *Pseudojanira* are setose, and their distolateral corners have deep, laterally-curving grooves on the dorsal surfaces, homologous to the same structures in the Janiroidea that function as guides for the stylet of the second pleopod. This determination of homology is made on the basis of the position and presumed functional relationships of the stylets in both taxa.

The male second pleopod is interesting not only in its similarity to the janiroidean condition, but also for specializations that are seen only in this species. Derived characters shared with the Janiroidea are the pointed endopodal stylet, the ridge on the proximal segment of the endopod, and the club-like and hooked form of the exopod with its enlarged musculature and distal group of fine setae. The stenetrioid endopod is club-shaped and lacks the proximal coupling groove, and the exopod, although short, is not stout and hooked. Unlike any janiroidean, however, the stylet of *Pseudojanira* has only a ventral groove and terminates with tiny barbs. The distal end of the basal segment is also unusual and does not occur in either the Stenetrioidea or the Janiroidea: it narrows just posterior to the exopod, and then becomes broad more distally. The distal end is curved, grooved, and covered with tiny, fine setae. The distal part of the stylet rests in the groove of the basal segment's tip. It may function as an auxiliary stylet guide, or perhaps as the top part of an enclosed sperm channel.

The diagnosis (above) of the Pseudojaniridae states that one free pleonite is visible dorsally (Fig. 1A), and two ventrally (Fig. 1E). This observation is made with some misgivings because the only whole specimen had been damaged by Kensley's dissection in the region of the ventral pleonites. If more specimens come to light, the pleonites should be re-examined. If this observation is correct, *Pseudojanira* possesses another intermediate character between the Janiroidea (1 free pleonite) and the Stenetrioidea (2 free pleonites, 1 reduced). I agree, however, with Fresi et al. (1980) that the number and fusion of free pleonites is less important than other characters in the classification, simply because the reduction of characters may recur independently, without apparent differences in unrelated taxa.

The chaetotaxy and form of the first pereopod require special mention: in many respects, both features are similar to those of *Stenetrium.* The typical janiroidean first pereopod has fewer setae, a larger carpus, and a smaller propodus. Wägele (1983) makes a strong case for the similarity of the chaetotaxy of the Stenasellidae, Atlantasellidae, and Microcerberidae of the superfamily Aselloidea (see his figure 1, p. 253), asserting that the microcerberids belong in the Aselloidea based on these similarities. Although I don't doubt his overall conclusions on the placement of the Microcerberidae, these setal similarities may be primitive characters at the level of the Asellota, because many of the same types of setae are also seen in *Pseudojanira, Stenetrium,* and *Gnathostenetroides,* all "out groups" to the Aselloidea.

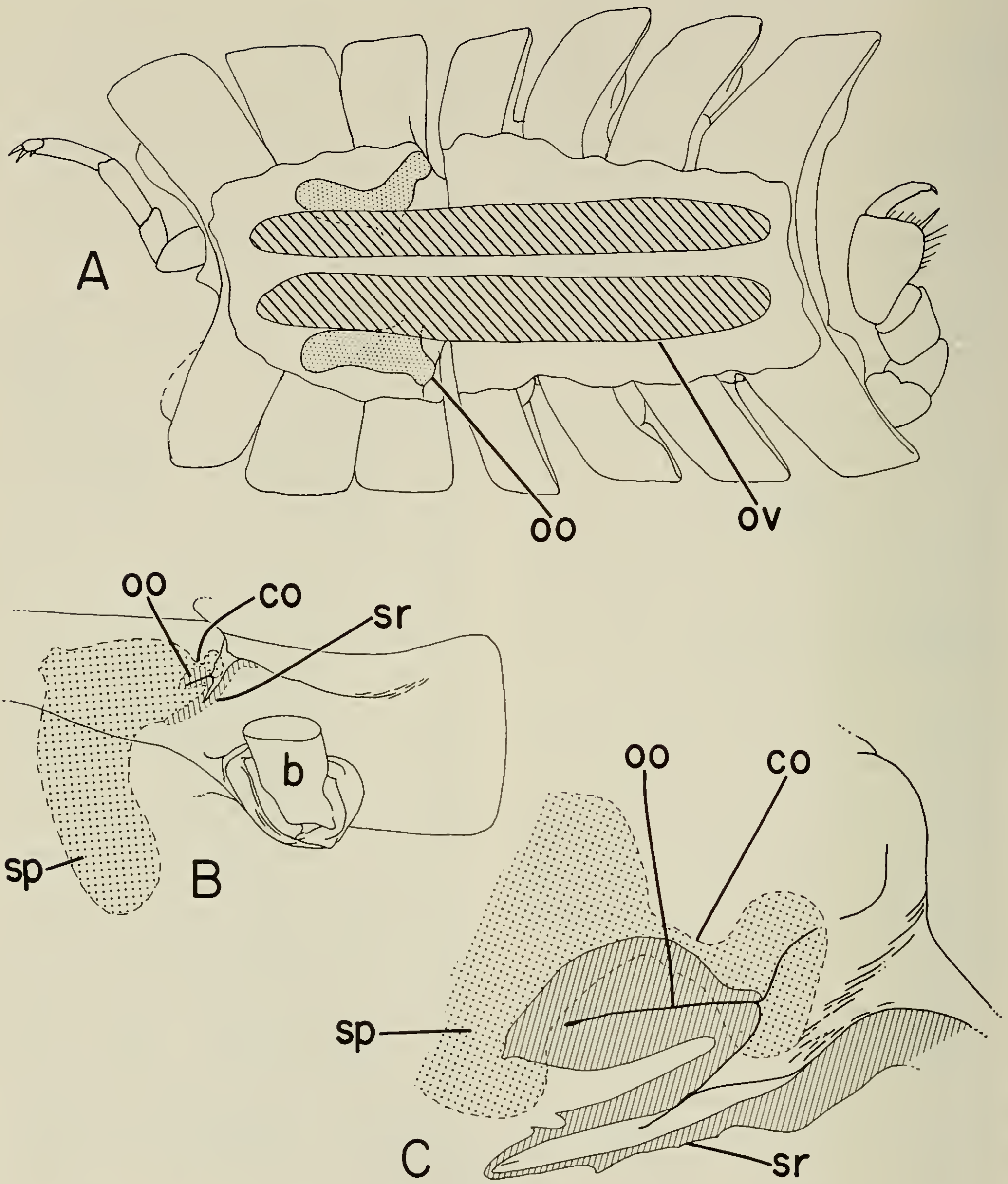

Fig. 3. Female reproductive system of *Pseudojanira*, preparatory female. A, Semi-diagrammatic dorsal view of the reproductive organs, showing what they would look like if the dorsal surface of the pereon were removed (anterior is to the right, cephalon and pleotelson broken off); B, Ventral view of pereonite 5, left side, showing oopore region and spermatheca through the ventral surface; C, Enlargement of oopore region showing structures beneath the cuticle, ov—ovary, oo—oopore, co—cuticular organ, sp—spermatheca, sr—stylet receptacle, b—basis of pereopod V truncated (shown only partially).

The accessory seta on the dactyli of pereopods II–VII is close in position to the third accessory claw found in the janiroidean family Janiridae and also in the Protojaniridae, and is nearly identical in position to an accessory seta on the dactyl of the Stenasellidae (see Magniez 1974:33). This seta is presumed to be homologous to the third "claw" of the Janiridae, and could well be common to all of the Asellota.

*The female copulatory organ.*—Because only the preparatory female holotype of *Pseudojanira stenetrioides* was available, no specimens were macerated in potassium hydroxide (a useful technique for studying cuticular structures). The female did stain well in lactic acid and methylene blue, allowing inspection of the cuticular organ (see Veuille 1978 for a description of the homologous structure in *Jaera*) close to the ventral surface. The cuticular organ opens on the anterior edge of the attachment of the oviduct to the ventral cuticle, and is adjacent to a cuticular fold that continues posteriorly into a blind tube just below the ventral surface. This closed tube opens anteriorly to a broad groove in the anteroventral edge of the fifth pereonite that curves dorsally. The opening of the cuticular organ is surrounded by a bulbous, thickened funnel that appears to open almost directly into a large spermathecal sac. The cuticular organ is also positioned anterior to the oopore and is almost separate from it. The spermatheca protrudes posteriorly into the sixth pereonite and was observed to contain translucent, heavily staining material similar to sperm masses seen in other species of Asellota. A pocket-like structure protrudes internally and dorsally from the external position of the oopore.

*The systematic position of* Pseudojanira.—Much of the unusual nature of *P. stenetrioides* derives from its possession of unique characters or characters seemingly intermediate between two superfamilies of the Asellota. This taxon is assigned to the Pseudojaniridae n. fam. because it cannot be effectively placed in any of the existing asellote families without diluting the potential recipient family's or superfamily's concept. Moreover, *Pseudojanira* has reproductive specializations that are unique to the Asellota, thereby warranting the new family for the genus. Its higher classification, however, can be stated no more accurately than "Isopoda Asellota superfamily *incertae sedis.*" Conceivably a new superfamily could be created as well, but this would result in continued 'superfamily inflation' with the perceived differences between the superfamilies becoming smaller and more difficult to reconcile. Note, for example, Schultz's (1978) ill-fated (Sket 1979; Wilson 1980) attempt to create a new asellotan superfamily based on the presence of a free coxa on the first pereopod.

The male pleopods I and II define the superfamily Janiroidea extremely well: all the diverse members of that taxon have male copulatory structures identical in their general form. The homologous structures in all the remaining families of the Asellota, on the other hand, show radical variations, with differences in the endopod of male pleopod II often characterizing species and genera, rather than superfamilies (e.g. species of the asellid genus *Caecidotea,* Lewis and Bowman 1981; genera of the Stenasellidae, Magniez 1974, his figure 11). This variation heralds a need for a re-evaluation of the current classification. Describing the second pleopod's endopod of the janiroidean male as "stylet-like" provides insufficient data because the detailed structure of the stylet is different between the Janiroidea, the Pseudojaniridae, and the Protojaniridae (Fresi et al. 1980). More morphological data must be collected on all the major groups of the Asellota to allow effective comparisons. A study of the female copulatory organs may be of considerable value, but other features require attention. *Pseudojanira stenetrioides* will provide a useful datum in this evolutionary discourse.

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# TRANSFER OF *QUADRASIA* FROM THE PLANAXIDAE TO THE BUCCINIDAE (MOLLUSCA: GASTROPODA: PROSOBRANCHIA)

Richard S. Houbrick

*Abstract.*—*Quadrasia hidalgoi* Crosse, previously assigned to the Planaxidae, is herein transferred to the genus *Clea* H. and A. Adams, family Buccinidae, on the basis of anatomical characters. The animal has a long muscular inhalant siphon, closed pallial gonoducts, a pleurembolic proboscis, and a rachiglossate radula.

The poorly known genus *Quadrasia* Crosse, 1886, has been cited by Crosse (1886), Cossmann (1906:197), Thiele (1929: 204), and Wenz (1940:722) as the only freshwater representative of the family Planaxidae Gray, 1850. Very few references to this monotypic genus occur in the literature, and despite a thorough search of major museum collections throughout the world only three specimens were found, one of which was the holotype. A single, alcohol-preserved specimen, from which soft parts were extracted, was studied. Anatomical examination showed that *Quadrasia hidalgoi* Crosse, 1886, is not a planaxid as originally suggested, but should be allocated to the genus *Clea* H. and A. Adams of the family Buccinidae. A redescription of this genus and species follows with a discussion of the evidence placing them in the Buccinidae.

## Genus *Clea* H. and A. Adams, 1855

*Clea* H. and A. Adams, 1855:119. Type species: *Clea nigricans* A. Adams, 1855, by monotypy and original designation; 1858:623; Thiele, 1931:316–317.

*Quadrasia* Crosse, 1886:159–161. Type species: *Quadrasia hidalgoi* Crosse, 1886, by monotypy; Cossmann, 1906:197; Thiele, 1929:204; Wenz, 1940:722, fig. 2090.

*Diagnosis.*—Shell solid, ovate, moderately elongate with 5–6 convex, inflated, transversely striated whorls of overall smooth aspect. Protoconch large, smooth, usually missing. Aperture large, about one-half the shell length, fusiform. Outer lip smooth, convex. Columella concave, abruptly truncate with basal fold. Anterior canal short. Shell cream-colored but with horny, dark brown periostracum. Operculum corneous, ovate, with subterminal nucleus. Radula rachiglossate, buccinid.

*Remarks.*—This little-known taxon has been found in the Philippines, Borneo, and in parts of Indonesia. It is noteworthy in being a freshwater representative of the largely marine Buccinidae.

## *Clea hidalgoi* (Crosse), new combination
Figs. 1, 2

*Quadrasia hidalgoi* Crosse, 1886:161–163, pl. 8, fig. 7; (Holotype: MNHNP).—Cossmann, 1906:197.—Thiele, 1929:204.—Wenz, 1940:722, fig. 2090.

*Description.*—Shell moderate in size (holotype 13.4 mm in length), solid, moderately elongate with overall smooth aspect, comprising about 6 inflated whorls. Shell sculptured with minute axial riblets and spiral threads producing wrinkled look under

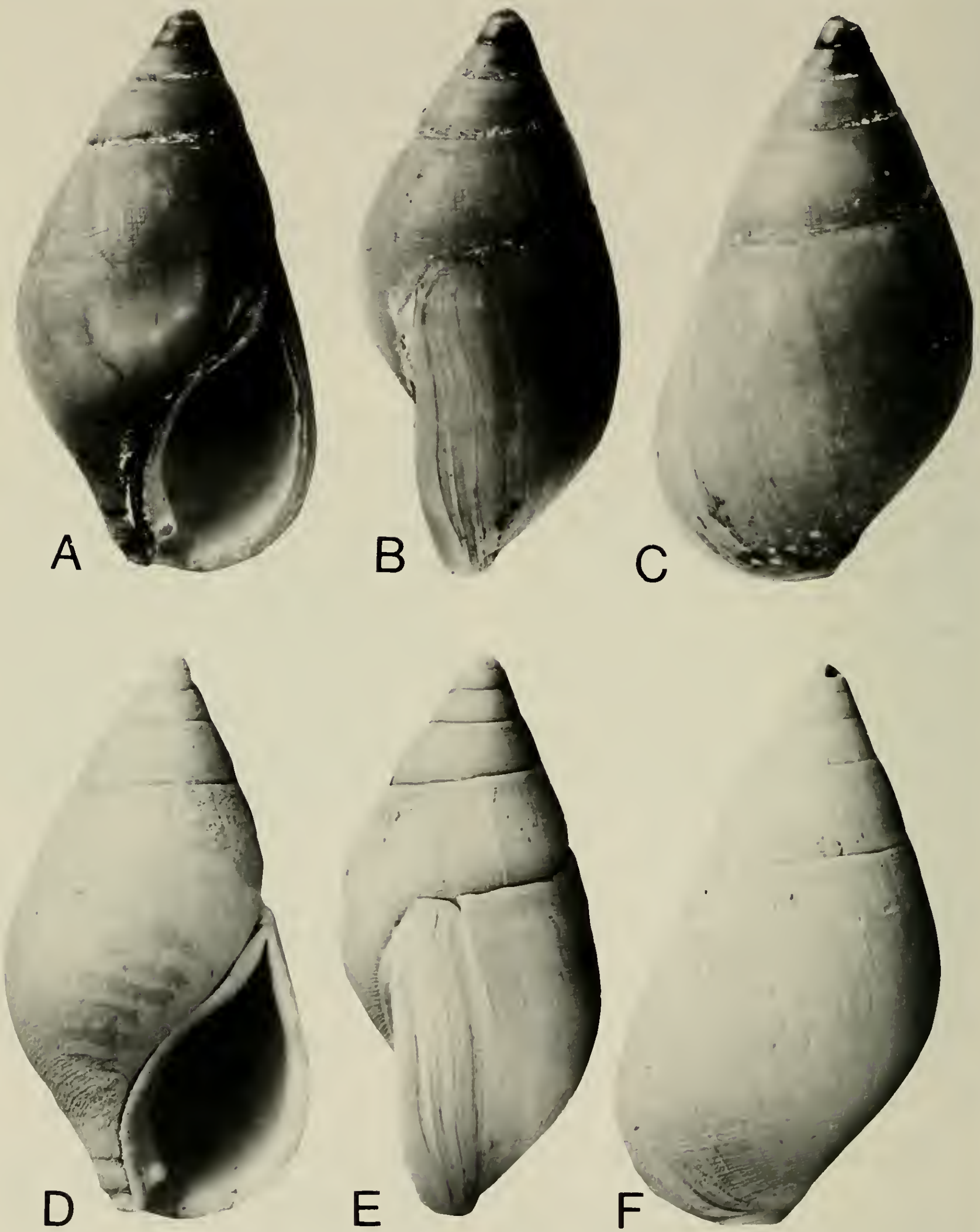

Fig. 1. A–F. Apertural, side, and dorsal views of holotype of *Quadrasia hidalgoi* Crosse, 1886 (MNHNP, no number, 13.5 mm length). Bottom row shows holotype whitened with ammonium oxide to enhance sculptural details.

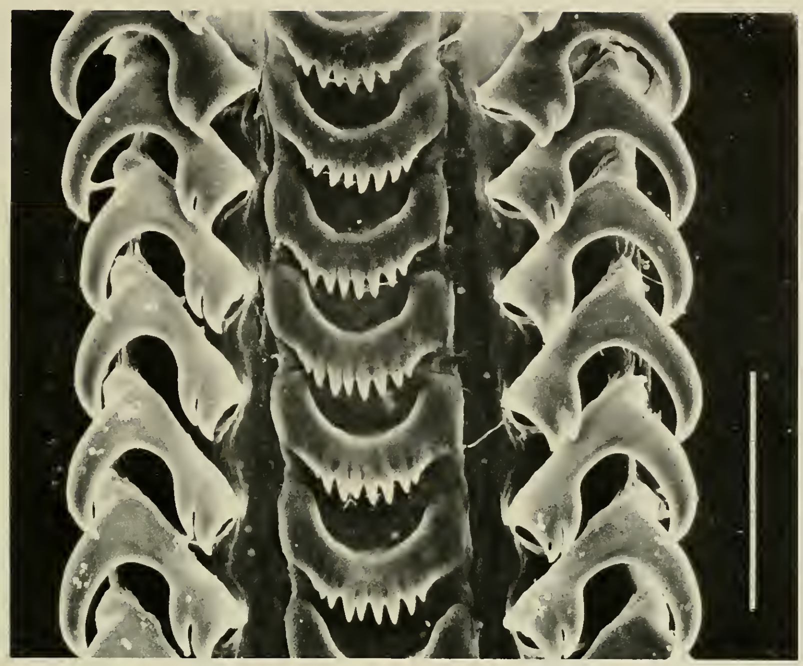

Fig. 2. Radula of *Clea hidalgoi* from Palawan, Philippines (bar = 110 μm).

magnification. Protoconch large, 1.5 whorls, smooth. Large body whorl with elongate, fusiform aperture spanning about one-half of shell length. Anal canal elongate. Anterior siphonal canal short, but well-developed. Outer lip smooth, slightly sinuous. Columella concave with prominent basal tooth and slight columellar callus. Suture moderately impressed, slightly overhung by each consecutive whorl. Shell flesh-colored, early whorls dark purple-brown. Periostracum well-developed, wrinkled, light brown, giving shell overall tan color. Operculum corneous, elongate-ovate, paucispiral with subterminal nucleus. Radula (Fig. 2) rachiglossate, long and narrow. Rachidian tooth strongly arched with cutting edge of 7–8 tiny, sharp denticles and expanded lateral extensions. Lateral teeth large, angular in outline, and tricuspid with 2 sharp, curved inner basal cusps and large sickle-shaped distal cusp. On basal radular membrane, laterals slightly separated from rachidian teeth. Animal with long muscular inhalant siphon, closed pallial gonoducts, and pleurembolic proboscis.

*Remarks.*—*Quadrasia hidalgoi* was described from freshwater streams on the island of Balabac, Philippine Islands. The original description (Crosse 1886:160) stated that according to the observations of Quadras, it lives on sandy bottoms in quiet streams.

Both the shell and radula of *Quadrasia* are similar to those of some buccinids which have been described from freshwater habitats in this region. Among these freshwater buccinid genera the genus *Clea* H. and A. Adams best matches the description of *Quadrasia*. Crosse (1886:161–162) referred *Quadrasia hidalgoi* to the Planaxidae, but this allocation was based on shell characters only. He pointed out that other marine prosobranch families also had freshwater representatives, specifically referring to *Canidia* H. Adams, 1862 (not Thompson, 1857), which is a synonym of *Anentome* Cossmann, 1901, a ribbed, buccinid genus closely related to *Clea.* Crosse (1886) was apparently unaware of the description of *Clea* by H. and A. Adams in 1855. Had he been familiar with the type species of this genus, *Clea nigricans,* he would have noted the close resemblance of it to *Quadrasia hidalgoi.* Thiele (1931:317) considered *Canidia* to be a subgenus of *Clea.* H. and A. Adams subsequently (1858:623) referred *Clea* to the subfamily Melanopsidae (superfamily Cerithiacea).

The radula of *Quadrasia* is very similar to that of *Clea nigricans* as depicted by Thiele (1931:317) and also to *Macron* (Thiele 1931:316). The tricuspid lateral teeth of *Quadrasia* clearly distinguish it from the similar radulae of nassariids, which have bicuspid laterals (Cernohorsky 1984:12–13).

As may be seen in the above discussion, *Quadrasia hidalgoi* was previously allocated to the Planaxidae and Melanopsidae, both in the superfamily Cerithiacea. Examination of the anatomy of *Quadrasia* revealed a long, tubular inhalant siphon, closed pallial gonoducts, a pleurembolic proboscis, and a rachiglossate radula. These anatomical and radular features exclude *Quadrasia* from the Cerithiacea and point to the Buccinidae as the proper taxonomic assignment. Within this family, the genus *Clea* appears best to fit the shell and radular characters seen in *Quadrasia,* which is here considered to be conspecific with *Clea. Quadrasia hidalgoi* is herein transferred from the Planaxidae and assigned to the genus *Clea* in the family Buccinidae.

## Acknowledgments

I thank Dr. Philippe Bouchet of the Museum National d'Histoire Naturelle, Paris, for loans of the type specimen and the preserved material. Mr. Victor Krantz of the Smithsonian's Photographic Services kindly supplied the photographs. Drs. David Reid and M. G. Harasewych critically reviewed the manuscript.

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99(2), 1986, pp. 363–365

# PRELIMINARY DESCRIPTIONS OF FOUR NEW SPECIES OF DORIPPID CRABS FROM THE INDO-WEST PACIFIC REGION (CRUSTACEA: DECAPODA: BRACHYURA)

Raymond B. Manning and L. B. Holthuis

*Abstract.*—The following species are diagnosed: *Dorippe irrorata,* from the Andaman sea; *Dorippoides nudipes,* from the western Indian Ocean; *Nobilum arachnoides,* from the Inland Sea of Japan; and *Paradorippe cathayana,* from China.

Since our review of the west African brachyuran crabs was published (Manning and Holthuis 1981), we have been working on a revision of the crabs of the subfamily Dorippinae, family Dorippidae, from the Indo-West Pacific region. The two Atlantic representatives of this subfamily were revised by us in 1981. Publication of our revision of the Dorippinae has been delayed much longer than anticipated, and several colleagues have inquired about the status of our new species, some of which have been labelled as new in museum collections (British Museum (Natural History), London; Muséum National d'Histoire Naturelle, Paris; Zoological Museum, Copenhagen; and our institutions as well) for several years. We take this opportunity to make available the names of these new taxa.

The diagnoses given below will differentiate the new species from others in their respective genera, defined in Manning and Holthuis (1981:30, 31). The following abbreviations are used: BM(NH), British Museum, Natural History, London; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; USNM, National Museum of Natural History, Smithsonian Institution, Washington; cb and cl, carapace breadth and carapace length, respectively, in mm.

## *Dorippe irrorata,* new species
Fig. 1a, b

*Holotype.*—Andaman Sea, south of Mergui Archipelago; 09°54'N, 97°42'E; 73 m; International Indian Ocean Expedition, *Anton Bruun* (Cruise I, Sta AB-21; 24 Mar 1963: 1 male, cl 21.5, cb 22.0 (USNM 172495).

*Diagnosis.*—Carapace broader than long, with distinct tubercles dorsally and with distinct lateral branchial tooth. Anterolateral margin of carapace, between bases of exorbital teeth and cervical groove, smooth. Inner dorsal margin of exorbital tooth smooth. Lower orbital margin with teeth and denticles mesially. Carpus of cheliped with granules, palm of chela with granules over most of surface. Teeth on second and third somites of male abdomen very low, distinctly granular.

*Remarks.*—This species differs from the three species of *Dorippe* now recognized as follows: It can be distinguished from *Dorippe frascone* (Herbst, 1785) in having the carpus of the chelipeds granular and in having granules on the teeth of the male abdomen. It differs from *D. sinica* Chen, 1980, in having tubercles or denticles on the anterolateral margin of the carapace, behind

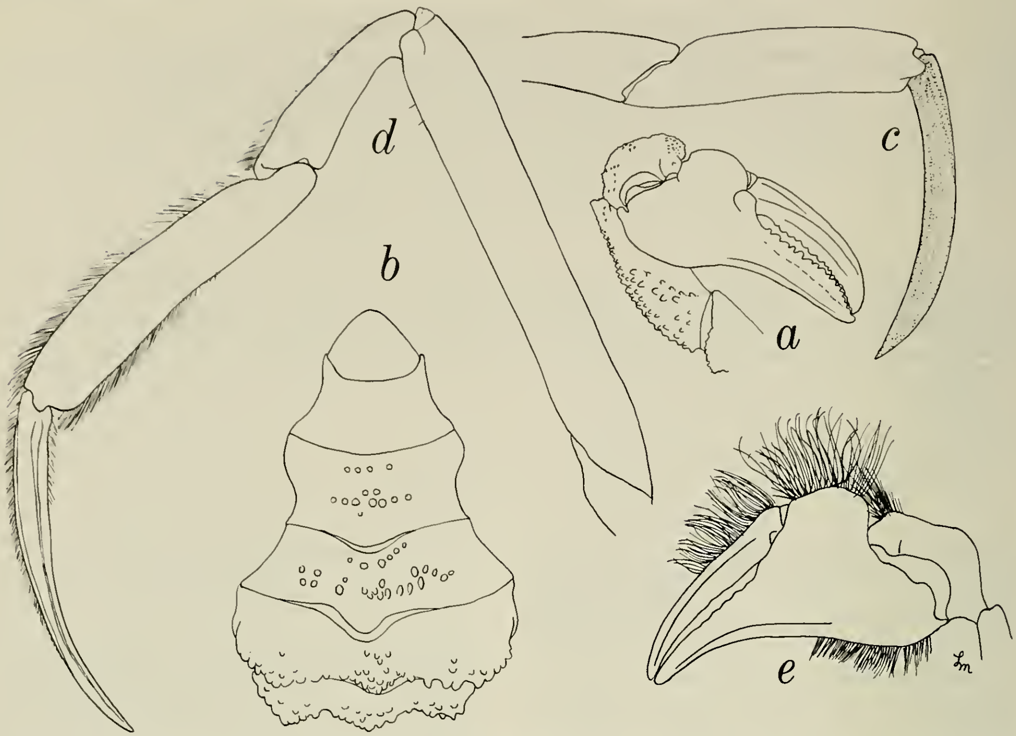

Fig. 1. a, b, *Dorippe irrorata,* male holotype, Andaman Sea: a, Cheliped; b, Abdomen; c, *Dorippoides nudipes,* female paratype, Harkiko Bay, Ethiopia, Red Sea, propodus and dactylus of third pereopod; d, *Nobilum arachnoides,* male holotype, Inland Sea of Japan, third pereopod; e, *Paradorippe cathayana,* male holotype, Jimei, Fujian Province, China, cheliped.

the anterolateral spine, and differs from *D. tenuipes* Chen, 1980 [=*D. miersi* Serène, 1981] in having shorter walking legs, with the merus of the second pereopods only five rather than six times as long as high in males.

*Etymology.*—The specific name is from the Latin, "irroratus," covered with granules.

### *Dorippoides nudipes,* new species
Fig. 1c

*Holotype.*—Massawa, Ethiopia, Red Sea; Israel South Red Sea Expedition no. E62/4115; trawled: 1 male, cl 17 mm, cb 19 mm (RMNH no. D.35530).

*Diagnosis.*—Carapace broader than long, lacking both dorsal tubercles and distinct lateral branchial tooth. Surface distinctly granular laterally on branchial region. Exorbital teeth overreaching frontal teeth. Dactyli of second and third pereopods broad throughout their lengths, broadest in distal fourth.

*Remarks.*—Differs from the only other species in the genus, *Dorippoides facchino* (Herbst, 1785), in having the carapace more granular and in having the dactylus of the second and third pereopods broadest in distal fourth rather than at midlength.

*Etymology.*—The name is from the Latin, "nudus," naked, and "pes," foot.

### *Nobilum arachnoides,* new species
Fig. 1d

*Holotype.*—Japan, Inland Sea, near Kobe; 34°38′N, 135°01′E; dredged in 8–50 fms (15–

92 m); sand; *Challenger* Sta 233A; 19 May 1875: 1 male, cl 15.8, cb 16.7 (BM(NH) 84.44).

*Diagnosis.*—Carapace wider than long, surface lacking erect tubercles, grooves well defined. Exorbital teeth falling short of front. Posterior margin of orbit lacking erect spine on outer side of orbital fissure. Gastric region lacking erect prominences. Merus of second and third pereopods about 7 times longer than high.

*Remarks.*—This species agrees with *Nobilum japonicum* (von Siebold, 1824) and differs from *N. histrio* (Nobili, 1903) in lacking a tooth on the exorbital margin and five prominences on the gastric region. It differs from both of these species in length and slenderness of the second and third pereopods.

*Etymology.*—The name is from the Greek, "arachnes," spider, and "-oides," like.

### *Paradorippe cathayana,* new species

Fig. 1e

*Holotype.*—China, Jimei, Fujian Province; S. F. Light, coll.; 24 Jun 1923: 1 male, cl 16.8, cb 18.2 (USNM 57762).

*Diagnosis.*—Carapace wider than long, surface lacking erect tubercles or prominences, appearing smooth, grooves well defined. Orbital fissure narrow, closed. Carpus of chelipid smooth. Propodus of third leg less than 3 times longer than high.

*Remarks.*—This species differs from *Paradorippe australiensis* (Miers, 1884) in smoothness of carapace and in having the carpus of the cheliped smooth, not granular, and it can be distinguished from *P. polita* (Alcock and Anderson, 1894) in having the orbital fissure closed and the propodus of the third pereopod less than three times longer than high.

*Etymology.*—The name is derived from Cathay, the name used for China in the Middle Ages.

## Acknowledgments

We thank Lilly King Manning for preparing the figure.

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# NOTES ON *GERYON* FROM BERMUDA, WITH THE DESCRIPTION OF *GERYON INGHAMI,* NEW SPECIES (CRUSTACEA: DECAPODA: GERYONIDAE)

Raymond B. Manning and L. B. Holthuis

*Abstract.*—Two species of the deep water crab genus *Geryon,* taken in commercial traps, *G. fenneri* Manning and Holthuis and *G. inghami,* n. sp., are reported from Bermuda. *Geryon incertus* Miers, 1886, originally described from Bermuda, is shown to be a junior synonym of the portunid *Bathynectes longispina* Stimpson, 1871.

Commercial trapping operations in depths in excess of 400 fathoms (732 m) around the Bermuda Islands [32°20′N, 64°45′W] by John P. Ingham in 1984 have revealed the occurrence of two distinct species of *Geryon.* One of these, *G. fenneri* Manning and Holthuis, 1984, was originally described from localities around Florida. The second species proves to be undescribed and is named below. Luckhurst (1985) has provided a preliminary account of the fishery.

There are two previous records of a species of *Geryon* from Bermuda. The first is that by Miers (1886:224), who described *Geryon incertus* from an immature specimen taken off Bermuda. As both Chace (1940:39) and Manning and Holthuis (1984:666) pointed out, the status of Miers' species has remained uncertain since its description. We believe that *G. incertus* is the juvenile of a portunid described by Stimpson in 1871, *Bathynectes longispina.* Although adults of *B. longispina* have not yet been recorded from Bermuda (Markham and McDermott 1981), we provide records of adults taken in traps off Bermuda.

The second record was given by Markham and McDermott (1981), who included *G. quinquedens* Smith in a checklist of Bermuda decapods. We tentatively identify their material with *G. fenneri,* as we have found neither records in the literature nor material of *G. quinquedens* from Bermuda.

## Species of *Geryon* from Bermuda

### *Geryon fenneri*
### Manning and Holthuis, 1984
### Figs. 1a, 2a

?*Geryon quinquedens.*—Markham and McDermott, 1981:1274 [not *G. quinquedens* Smith, 1879].

*Geryon fenneri* Manning and Holthuis, 1984:666, figs. 1, 2a, b, 3a–c, 4a, b.—Soto, 1985:482, 483, 486, 487.

*Material.*—Off Bermuda [32°20′N, 64°45′W], 430–450 fms (787–824 m), traps, Oct 1984, John P. Ingham, Eugene Lambe, R. B. Manning, D. L. and J. Felder, and B. Luckhurst, collectors, from vessel *Trilogy*: 2 males, 8 females (3 ovigerous), 3 dry carapaces (USNM 205334, 205335; 2 females to Rijksmuseum van Natuurlijke Historie, Leiden; 2 females to British Museum (Natural History), London).—Off south shore of Bermuda, 500 fms (915 m), 5 Nov 1984, John P. Ingham, collector: 1 male (USNM).—Same, ca. 550 fms (1007 m), 27 Dec 1984: 1 male, 1 female (USNM).—Off Bermuda, 1985: 2 females (1 with sacculinid) (USNM).—Same, 1985: 8 males, 10 females (2 ovigerous) (USNM).

*Measurements.*—Carapace lengths (cl) of examined males 57 to 160 mm, of nonovigerous females 68.5 to 116 mm, of ovigerous females 91 to 118 mm, of unsexed

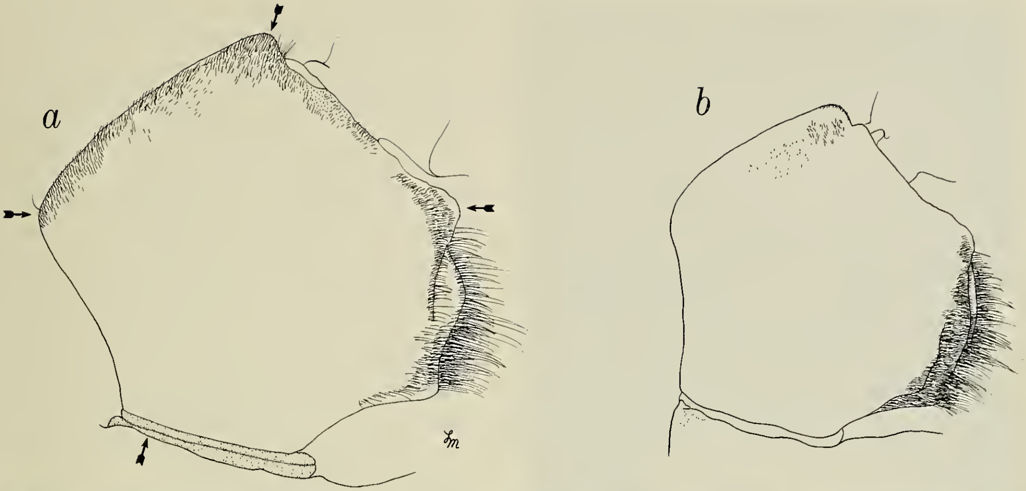

Fig. 1. Merus of third maxilliped of: a, *G. fenneri,* male, cl 160 mm, Bermuda (arrows indicate points of measurement of height and width); b, *G. affinis,* male, cl 134 mm, off Scotland (USNM 210904).

dry carapaces 97 to 98 mm. Carapace widths (cb) of examined males 81 to 190 mm, of non-ovigerous females 89 to 146 mm, of ovigerous females 113 to 146 mm, of unsexed dry carapaces 121 to 124 mm.

Luckhurst (1985) reported that 73 specimens examined by him in October and November 1984 had carapace widths ranging from 108 to 177 mm, and that all of the largest crabs he examined were males.

*Remarks.*—These specimens agree well with the original account. The carapace length ranges from 0.76–0.84 times the width. The distance between the first and third anterolateral teeth of the carapace is 0.93 to 1.10 times the distance between the third and fifth anterolateral teeth. The orbit is narrower than the front in most specimens. On the fifth leg, the merus is about half as long as the carapace and its length is 4.1 to 5.1 times its height; and the propodus is 3.5 to 4.3 times longer than high.

The third maxilliped of the largest male (cl 160 mm) differs from that of *G. affinis* A. Milne Edwards and Bouvier (male, cl 134 mm), from off Scotland, as shown in Fig. 1. In *G. affinis* the merus of the third maxilliped is slightly longer than high, whereas in *G. fenneri* it is slightly wider than high. The outer angle differs in the two species.

As we noted above, we tentatively assign Markham and McDermott's (1981) record for *G. quinquedens* to this species, the more abundant of the two species of *Geryon* now known with certainty from Bermuda.

Soto (1985) reported this species from the Straits of Florida, on mud bottoms in depths of 322 to 470 m. He characterized it as one of the species taken only on the continental side of the Straits.

### *Geryon inghami,* new species
Figs. 2b, c, 3, 4, 5a

*Material.*—Off Bermuda [32°20′N, 64°45′W], 1400 fathoms (2562 m), traps, summer 1984, John P. Ingham, collector: 2 males, 1 female (USNM: largest male is holotype, USNM 205336, other specimens are paratypes, USNM 205333); 2 males (Rijksmuseum van Natuurlijke Historie, Leiden, paratypes); 1 male (British Museum (Natural History), paratype); 5 males (Bermuda Division of Fisheries, paratypes).—Bermuda, off south shore, 500–550 fms (915–

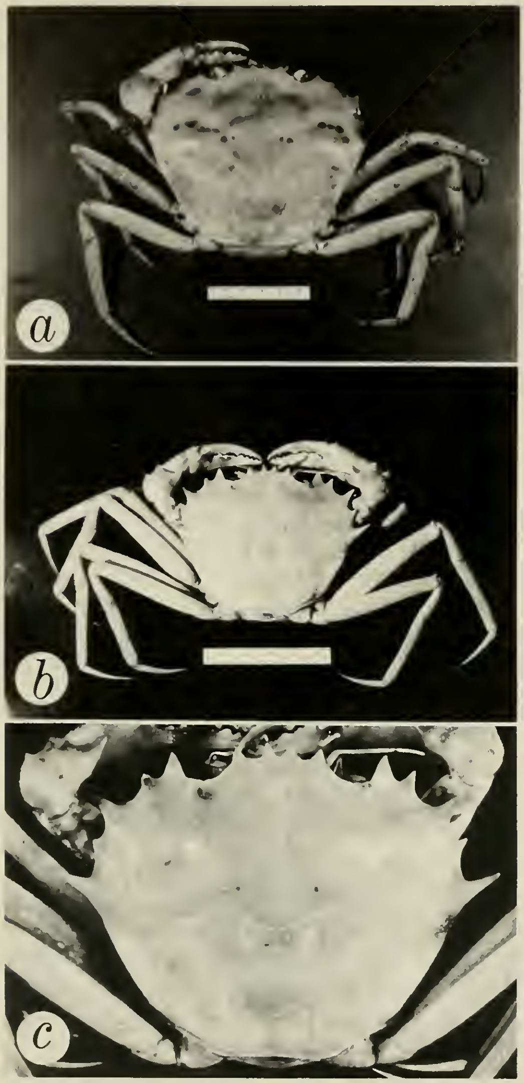

Fig. 2. Dorsal view of: a, *G. fenneri,* ovigerous female, cl 91 mm, Bermuda; b, c, *G. inghami,* male holotype, cl 64 mm, Bermuda (carapace enlarged in c to show detail).

1007 m), 25 Feb 1985, J. P. Ingham, collector: 1 male (paratype, USNM 228196).—Off Bermuda, 1985: 1 male (USNM 228197, paratype).

*Diagnosis.*—A small *Geryon,* cl to 82 mm in adults. Carapace broader than long, length 0.68 to 0.77 (mean 0.72) times width. Median pair of frontal teeth large, overreaching larger lateral frontal teeth, separated by median V-shaped sinus, latter usually posterior to level of acute, pointed lateral frontal teeth. Distance between submedian frontal teeth variable, usually more than half distance from each to lateral frontal tooth, but much less in largest male. Anterolateral teeth 5, first, third, and fifth strongest, second and fourth smaller but well developed, all sharp. Distance between first and third teeth subequal to distance from third to fifth (less in some specimens, more in others). Suborbital spine large, extending to level of apex of lateral frontal teeth. Carapace with curved ridge extending mesially from lateral tooth. Posterolateral margin of carapace irregularly granular. Cheliped rather rough, surface distinctly granular, with sharp subdistal and smaller distal spine dorsally on merus; carpus with distinct outer spine, anterior margin with small, sharp granules and large inner spine; propodus with distinct dorsal spine. Meri of second to fifth pereopods with distinct distal dorsal spine. Fifth leg: merus slender, length 6.1 to 6.9 times height, with erect distal dorsal spine; carpus with distinct line of granules dorsally; propodus slender, length 5.5 to 6.0 times height, with sharp dorsal granules proximally; dactylus 0.74 to 0.87 times as long as propodus, compressed laterally, height at midlength greater than width, longitudinally channelled dorsally. Telson triangular, 1.3 to 1.6 times broader than long. Gonopod as figured.

*Size.*—Carapace lengths of males 40 to 82 mm, of single female examined 44 mm; carapace widths of males 55 to 110 mm, of female 64.5 mm.

*Color.*—In life this species is dark red.

*Remarks.*—*Geryon inghami* shares many features with *G. gordonae* Ingle (1985:90) from the northeastern Atlantic, but a comparison of specimens from the two areas reveals that *G. inghami* differs as follows: overall the body is much more coarsely granulated, especially on the chelae and the anteroventral surfaces of the carapace; the suborbital teeth are stronger, and there is a

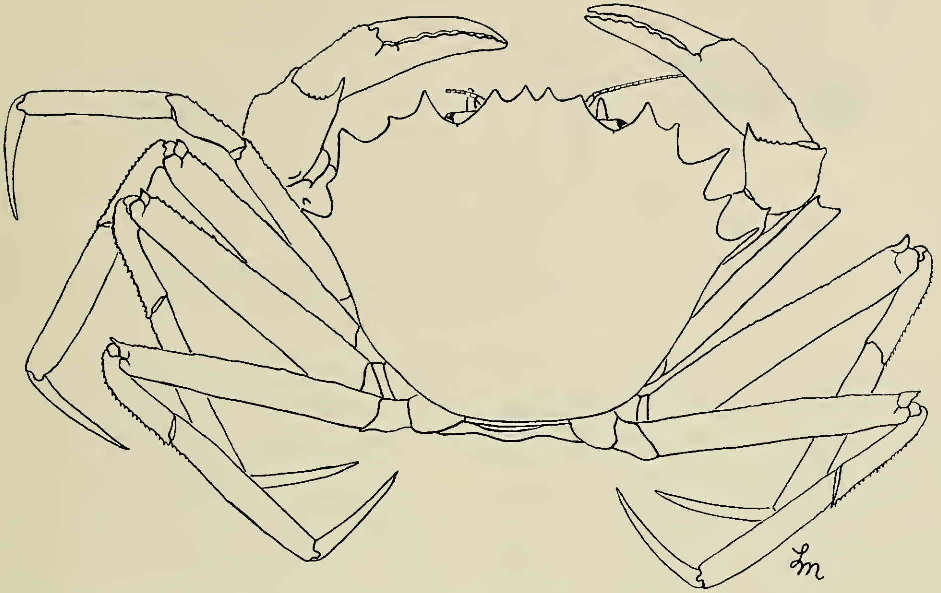

Fig. 3. *Geryon inghami,* male holotype, cl 64 mm, dorsal view.

distinct line of tubercles on the suborbital margin; the frontal teeth are larger; the fourth anterolateral tooth is much larger; the second and fifth anterolateral teeth are stronger; the longitudinal carina on the outer surface of the palm of the cheliped is more distinct, and, in the female, the inner surface of the palm is much more granular. Ingle (1985:95) noted that in *G. gordonae* the anterolateral spines of the carapace are smaller and blunter with increasing size; this trend is not at all apparent in the available material of *G. inghami.* All of the anterolateral spines of the carapace are present and well developed, even in the largest male examined.

In *G. gordonae* the fourth lateral tooth is very small even in small specimens; it may be essentially obsolete in adults.

The holotype of *G. inghami,* the illustrated specimen, has the fourth anterolateral tooth of the left side damaged; in other specimens it is as large as shown for the right fourth tooth in Fig. 3.

This species, apparently less common off Bermuda than *G. fenneri,* was found in depths between 430 and 1900 fms (787–3477 m) (Luckhurst 1985).

*Etymology.*—This species is named for Mr. John P. (Sean) Ingham of Bermuda, whose interest in deep-water trapping in Bermuda led to its discovery.

## The Status of *Geryon incertus* Miers (Fig. 6)

Miers (1886:224, pl. 16, fig. 3) described *Geryon incertus* from off the Bermudas (32°21′30″N, 64°35′55″W) in 435 fms (796 m). Miers's account was based on an immature specimen with a carapace length and width of 5 mm. Miers noted (1886:224) that "It [*G. incertus*] may belong to a genus of the Portunidae, near to *Bathynectes,* where I originally placed it." The status of Miers's species has remained uncertain since it was described. Chace (1940:39) remarked that "it obviously does not belong in this genus."

*Geryon incertus,* although characterized by Miers as having four anterolateral teeth, actually has but three primary teeth on each side, as shown in Miers's original figure (pl.

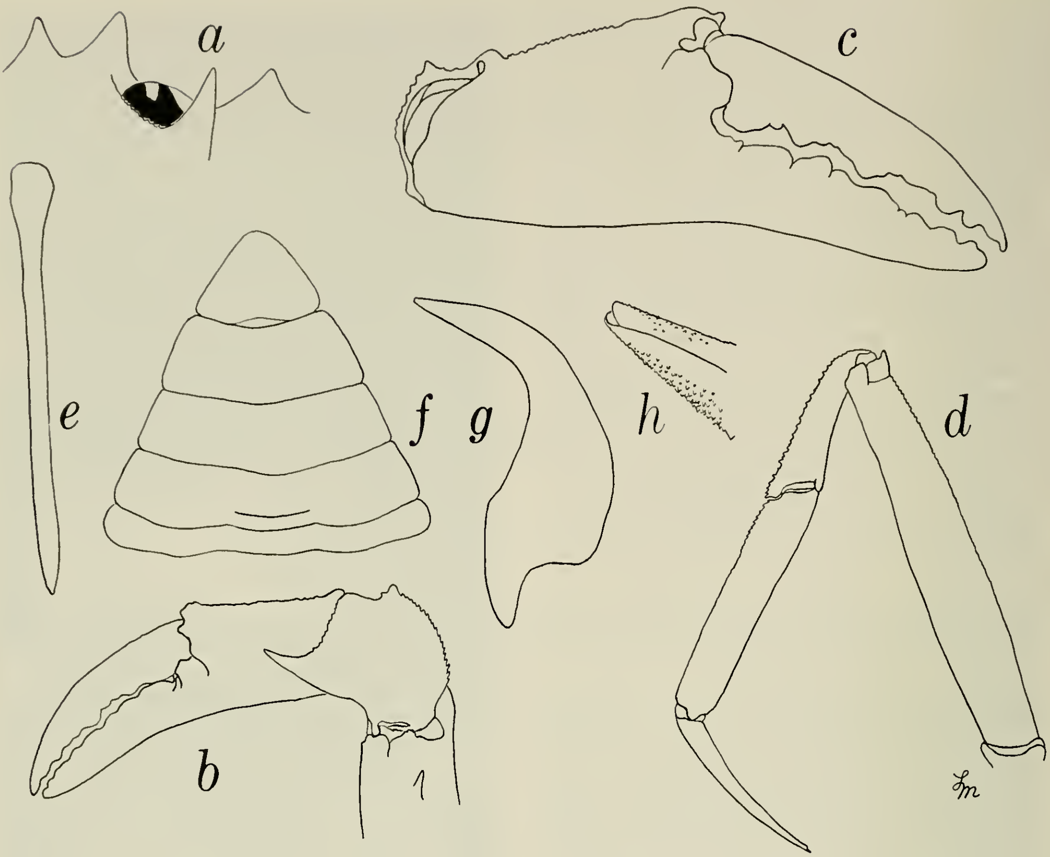

Fig. 4. *Geryon inghami,* male holotype, cl 64 mm: a, Suborbital margin; b, Cheliped; c, Chela; d, Fifth pereopod; e, Dactylus of fifth pereopod, dorsal view; f, Telson; g, Gonopod; h, Tip of gonopod.

16, fig. 3), parts of which are reproduced here in Fig. 6. The posteriormost two teeth have a small denticle between them. This denticle is shown on both sides in Miers's figure, but was described as occurring on one side and being obsolete on the other.

In his original account, Miers remarked (1886:225): "From all the described species of this genus, *Geryon incertus* is distinguished by the form of the front, and from the typical species of *Bathynectes,* Stimpson, not only by this character, but also by the structure of the basal antennal joint, which is free and not united with the lateral subfrontal process." The basal joint of the antenna also is free in specimens of *B. longispina* Stimpson from off New Jersey and in our material of *Geryon* (Fig. 5) as well.

R. W. Ingle of the British Museum (Natural History) (in litt.) examined the type of *Geryon incertus* at our request, and pointed out similarities between it and juveniles of *B. longipes* (Risso, 1816), reported in Ingle and Rice (1984). A comparison of the figure of the carapace of the type of *G. incertus* in the collections of the British Museum (Natural History) (Fig. 6a) with that of a juvenile of *B. longispina* (Fig. 7) from off New Jersey reveals that they share many similarities, even to the pattern of granulation on the carapace. At the size figured by Miers, the lateral spine of the carapace has not yet be-

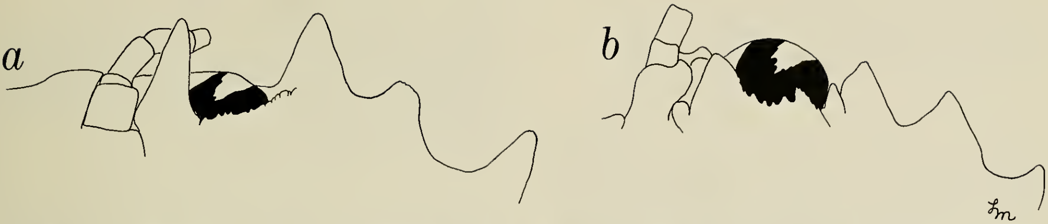

Fig. 5. Ventral view of orbit and antenna in: a, *G. inghami,* male holotype, cl 64 mm; b, *Bathynectes longispina,* male, cl 45 mm, off New Jersey (USNM 185422).

gun to enlarge in relation to the other spines. We consider *Geryon incertus* Miers, 1886, to be a subjective junior synonym of *Bathynectes longispina* Stimpson, 1871.

Until recently, *Bathynectes longispina* was identified with the East Atlantic species then known as *B. superbus* (Costa, 1853). Manning and Holthuis (1981:80) pointed out that the East Atlantic *B. superbus* was a junior synonym of *B. maravigna* (Prestandrea, 1839) and that material from the West Atlantic until then identified with *B. superbus* actually should be known as *B. longispina* Stimpson, 1871.

*Bathynectes longispina* has not been recorded from Bermuda as an adult. Williams and Wigley (1977:11) noted that it was known from Martha's Vineyard to the Yucatan Channel. Two specimens were sent to one of us (RBM) for identification by W. Sterrer, then Director of the Bermuda Biological Station. They were taken a few miles south of Bermuda in May 1981, in about 500 meters. Both specimens are males, with carapace lengths of 32.7 and 41.5 mm and carapace widths of 59.6 and 72.9 mm, respectively. A second lot of this species from Bermuda was found in the Smithsonian collections (USNM 169237). It comprises two females with carapace lengths of 28.5 and 37.2 mm and carapace widths of 52.0 and 68.2 mm, respectively. These latter specimens were collected in 400 fathoms (732 meters) by R. T. Abbott on 26 September 1974.

*Bathynectes longispina* recently has been recorded from localities off North Carolina (Williams, McCloskey, and Gray 1968), in the Chesapeake Bight (Lewis and Haefner 1977), the Middle-Atlantic Bight (600 spec-

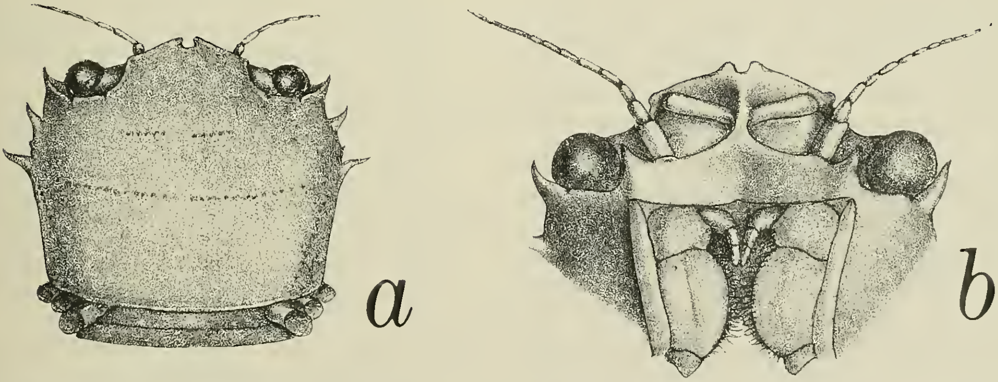

Fig. 6. Holotype of *Geryon incertus* Miers, cl ca. 5 mm: a, Dorsal view; b, Suborbital margin. (From Miers 1886: pl. 16, fig. 3, 3a).

Fig. 7. Carapace of juvenile *B. longispina*, cl 5.0 mm, off New Jersey (USNM 185623).

imens at 33 stations in depths between 90 and 751 meters; Wenner and Boesch 1979), the middle Atlantic shelf (Bowen et al. 1979), and the Straits of Florida in 174 to 403 m (Soto 1985). It apparently is fairly common in moderate depths off the eastern United States (see Rathbun 1930:28, for earlier records), and its occurrence in Bermuda is not too surprising.

## Acknowledgments

Our studies of members of the crab genus *Geryon* have been supported by the Food and Agriculture Organization of the United Nations (FAO); that support is gratefully acknowledged. Our studies of Atlantic species of *Geryon* were initiated with the support of the Smithsonian Marine Station at Fort Pierce; this is contribution number 160 from that station and contribution number 1070 from the Bermuda Biological Station. We thank Roy Kropp for taking the photographs, Lilly King Manning for preparing the figures, and Austin B. Williams, Systematics Laboratory, National Marine Fisheries Service, for reviewing the manuscript. R. W. Ingle, British Museum (Natural History), examined the type of *G. incertus* and pointed out the similarity between it and juveniles of *Bathynectes*. This work would not have been possible without the support and cooperation of John P. Ingham and Eugene Lambe of Bermuda, and Brian Luckhurst, Bermuda Division of Fisheries.

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# *SPELEOBREGMA LANZAROTEUM*, A NEW GENUS AND SPECIES OF SCALIBREGMATIDAE (POLYCHAETA) FROM A MARINE CAVE IN THE CANARY ISLANDS

Rodney Duane Bertelsen

*Abstract.*—*Speleobregma lanzaroteum*, a new genus and species of polychaete in the family Scalibregmatidae, is described from a marine lava tube cave, Jameos del Agua, on Lanzarote Island, Canary Islands. It differs from all scalibregmatid genera by possessing hirsute hooded geniculate setae. Its placement within the family is discussed.

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During a recent cave-diving expedition on Lanzarote in the Canary Islands (Fig. 1), a new genus and species of scalibregmatid was collected by Dennis Williams. The expedition was part of an ongoing study of insular aquatic cave fauna (Iliffe et al. 1984).

Although only one specimen was found, it is in excellent condition due to careful collection and gentle handling. The specimen contains unique and important systematic characters that warrant a description. Due to the difficulties of cave diving and potential scarcity of material, additional specimens may not be available in the

Fig. 1. Map of Lanzarote, Canary Islands. The "×" indicates location of Jameos del Agua, the collection site of *Speleobregma lanzaroteum*. The inset shows the relationship of the Canaries to the coast of Africa and Europe. Lanzarote is the darkened island.

foreseeable future. The holotype is deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

### *Speleobregma*, new genus

*Etymology.*—"Speleo" referring to cave, "bregma" from the stem of the family. Gender: Neuter.

*Type species.*—*Speleobregma lanzaroteum*, new species

*Diagnosis.*—Body elongate, slender, and cylindrical. Prostomium blunt, entire, with lateral horns. Acicular setae and furcate setae lacking; branchiae absent; capillary setae in both rami with hirsute hooded geniculate setae in neuropodia.

### *Speleobregma lanzaroteum*, new species
Figs. 2, 3

*Material examined.*—Jameos del Agua lava tube cave, Lanzarote, Canary Islands, 4 Mar 1984, 29°12′N, 13°38′W, 20 m, SCUBA, coll. D. Williams, holotype, USNM 98275.

*Diagnosis.*—Neuropodial hirsute hooded geniculate setae present on all setigers. Parapodia with neuropodial postsetal lamellae and interramal papillae. Pygidium lacking anal cirri; with 2 ventral spherical papillated lobes.

*Description.*—Holotype 8 mm in length, 0.8 mm in width, 23 setigers. Body colorless, elongate, cylindrical and slender; setigers 7–11 slightly inflated (reduced arenicoliform). Dorsal surface of anterior segments weakly biannulate and areolated.

Prostomium (Fig. 2a) triangular, anteriorly blunt with a pair of tapered lateral horns, eyes absent. Nuchal organs not evident. Proboscis ventral, forming soft, smooth, eversible pouch. Buccal segment apodous and achaetous.

Each parapodium with single spherical interramal organ and cylindrical neuropodial postsetal lamella (Fig. 2b). Lamellae conspicuous on all but last 2 setigers. Branchiae and cirri absent.

All notosetae simple capillaries inserted in single row; up to 20 per fascicle. Neurosetae inserted in 2 rows. Anterior row shorter than posterior row, consisting of 5 to 9 hirsute, distally abruptly tapered, hooded geniculate setae (Fig. 3b). Posterior row all capillaries.

Pygidium with 2 heavily papillated ventral spherical lobes. Lobes with anteroventral groove extending halfway across ventral surface (Fig. 3a). Anal cirri lacking.

*Distribution.*—Known only from type locality, Jameos del Agua Cave, Lanzarote, Canary Islands.

*Etymology.*—The specific epiphet is taken from the type locality, Lanzarote Island.

## Discussion

Lanzarote and its large marine lava tube cave, Jameos del Agua, are noted for their unusual fauna (Dinkins 1969; Iliffe et al. 1984). This species, typical of many cave organisms, is eyeless and lacks pigment. The thickened areolated epidermis, common among scalibregmatids, is reduced in this species. Staining with fast-blue aided in revealing this character.

Following the organization of the family Scalibregmatidae proposed by Blake (1981), *Speleobregma* belongs to body type I (arenicoliform with T-shaped prostomium) and parapodial type D (dorsal and ventral cirri absent; prolonged postsetal lamellae present). This classification includes the genera *Scalibregmides* (Hartmann-Schröder 1965) and an undescribed genus (for *Asclerocheilus californicus* Hartman, 1963). *Speleobregma* differs from them in having long postsetal lamellae only on the neuropodia and in lacking furcate setae.

The only other species lacking furcate setae is *Kebuita minuta* Hartman, 1967. *Speleobregma* differs in body form in that *Kebuita minuta* is maggotlike.

*Speleobregma* differs from all scalibregmatid genera by possessing hirsute hooded geniculate setae.

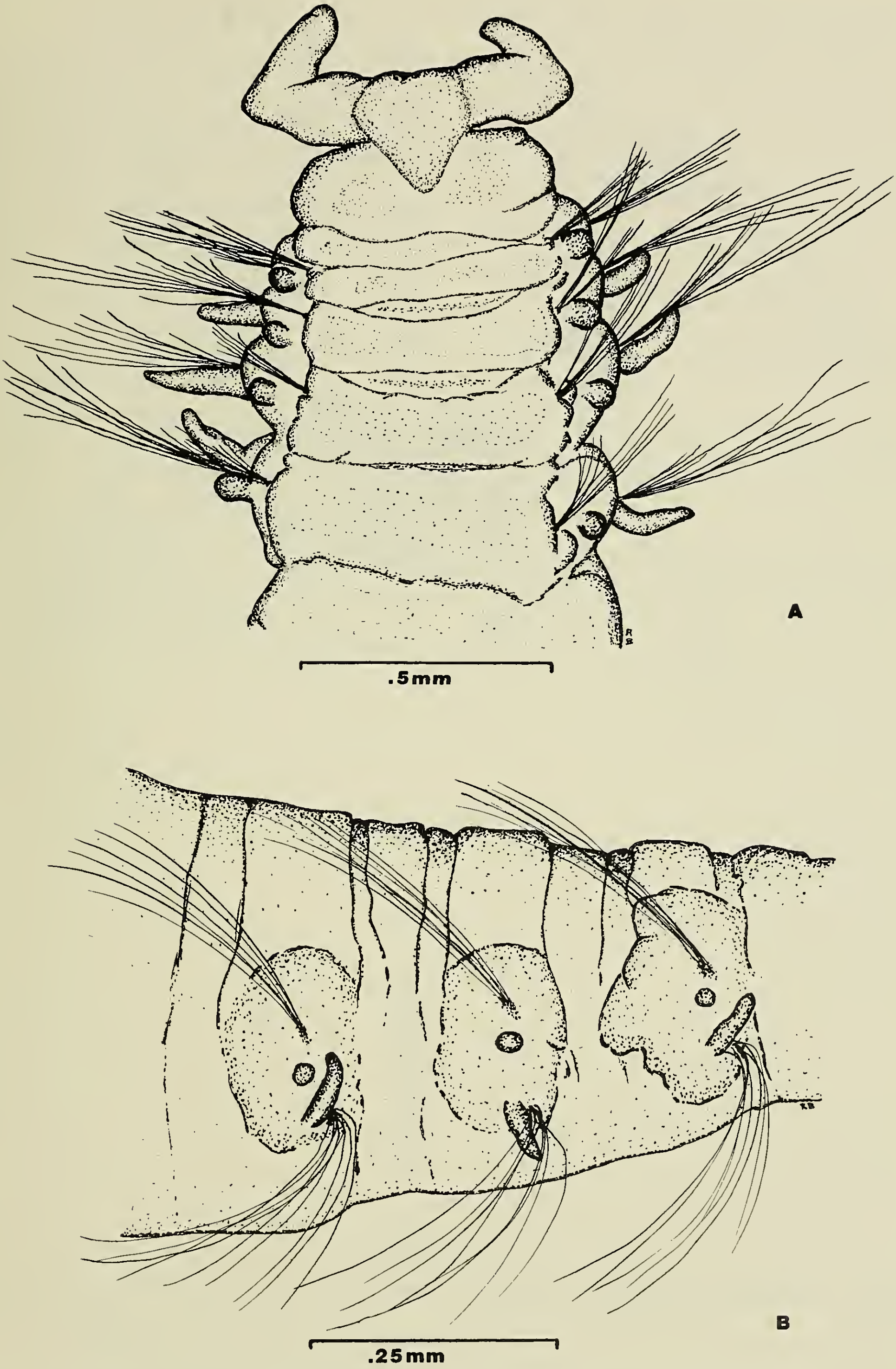

Fig. 2. *Speleobregma lanzaroteum*: A, Anterior end, dorsal view; B, Setigers 3–5, lateral view.

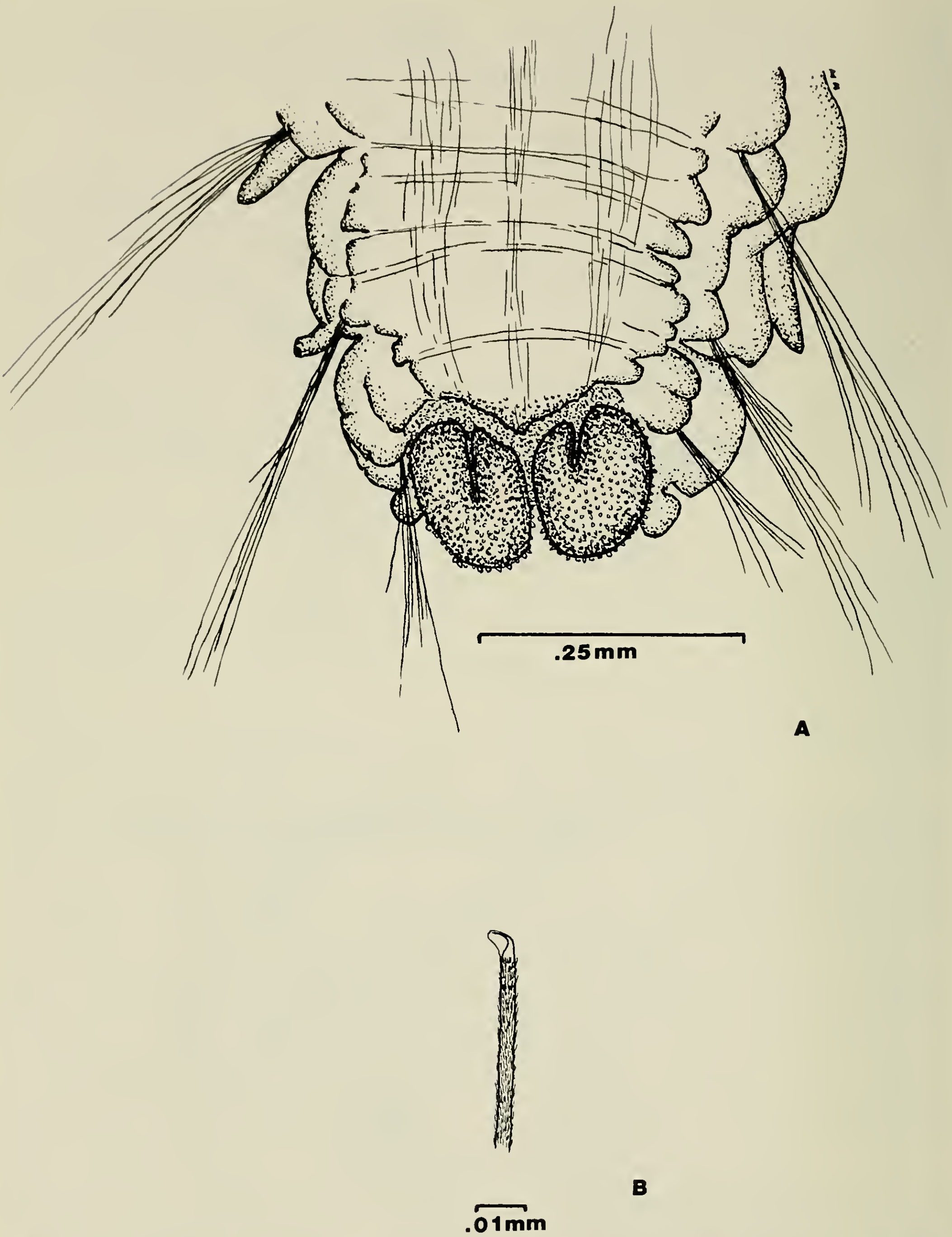

Fig. 3. *Speleobregma lanzaroteum*: A, Pygidium, ventral view; B, Neuropodial hirsute hooded geniculate seta.

## Acknowledgments

I wish to thank Jill Yager and Dennis Williams for permission to examine their collection of marine cave polychaetes and for helpful discussions about their research. Drs. John R. Holsinger and Marian Pettibone gave valuable support and advice. Dr. Kristian Fauchald examined the specimen. The manuscript benefitted from reviews by Dr. Fauchald and an anonymous reviewer. The collection of material studied is supported by a grant from the National Science Foundation to Dr. Thomas M. Iliffe (BSR-8215672).

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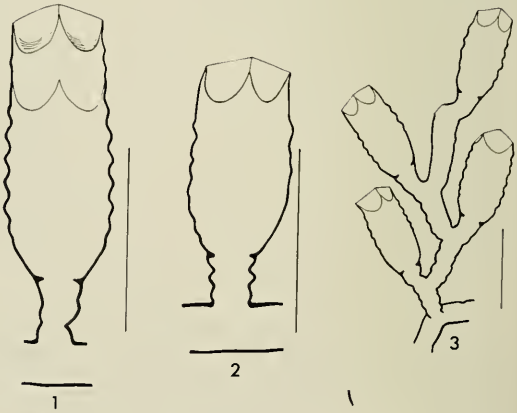
# *SYMMETROSCYPHUS*, A NEW GENUS OF THECATE HYDROID (FAMILY THYROSCYPHIDAE) FROM BERMUDA

Dale R. Calder

*Abstract.*—A new genus, *Symmetroscyphus*, is proposed for the single species *Thyroscyphus intermedius* Congdon, 1907, a shallow water hydroid of the family Thyroscyphidae Stechow, 1920, from Bermuda. Unlike the closely allied genus *Thyroscyphus* Allman, 1877, with its erect hydroid colonies and bilaterally symmetrical hydrothecae, *Symmetroscyphus* typically has stolonial colonies and radially symmetrical hydrothecae. *Symmetroscyphus intermedius* is superficially similar to but morphologically distinct from *Calamphora parvula* Allman, 1888, *Sertularella solitaria* Nutting, 1904, and *Sertularella campanulata* Warren, 1908.

*Thyroscyphus intermedius* Congdon, 1907, is a small thecate hydroid presently known only from Bermuda, where it is common to abundant in shallow water on turtle grass (*Thalassia*). Colonies are brownish in color when alive due to the presence of algal symbionts in the coenosarc. Hydroids of this species superficially resemble those of *Calamphora parvula* Allman, 1888, *Sertularella solitaria* Nutting, 1904, and *Sertularella campanulata* Warren, 1908, in their colony form, which is typically stolonial, and in having hydrothecae with annulated walls and four marginal teeth. Because of the similarity of these species, *T. intermedius* has been included as a synonym of *C. parvula* (as *Sertularella parvula*) by Vervoort (1968) and as a questionable synonym of *S. campanulata* by Stechow (1919). Specimens of *T. intermedius* from Bermuda differ from type material of both *Calamphora parvula* and *Sertularella campanulata*, as well as *Sertularella solitaria*, in having radially rather than bilaterally symmetrical hydrothecae, a centrally located rather than an excentric hydropore, an annular fold about the hydranth base instead of an abcauline diverticulum, perisarc of uniform thickness around the perimeter of the hydrothecal wall instead of thicker perisarc on the side opposite the excentric hydropore, and clusters of large nematocysts in an intrathecal sheath of ectoderm. Unlike *C. parvula*, the hydrothecal orifice of *T. intermedius* is perpendicular to the axis of the hydrotheca, and intrathecal teeth are lacking. Based on such major differences, *T. intermedius* cannot be retained in the synonymy of either *C. parvula* or *S.*



Figs. 1–3. *Symmetroscyphus intermedius*: 1, Hydrotheca with renovated margin, ROMIZ B313; 2, Hydrotheca, ROMIZ B314; 3, Erect colony, ROMIZ B314. Scale bars equal 500 μm.

Fig. 4. Large nematocysts from ectodermal sheath lining hydrothecal cavity of *Symmetroscyphus intermedius,* ROMIZ B314. Scale bar equals 20 μm.

*campanulata,* nor can it be assigned to *Calamphora* Allman, 1888, *Sertularella* Gray, 1848, *Thyroscyphus* Allman, 1877, or any other described genus. A new genus, *Symmetroscyphus,* is established for the species in this report.

Institutional abbreviations used in this paper are: BMNH—British Museum (Natural History); NM—Natal Museum; ROMIZ—Royal Ontario Museum, Department of Invertebrate Zoology.

## Materials and Methods

Type materials of *Calamphora parvula* (BMNH 1888.11.13.65A) from Bass Strait, Australia, and *Sertularella campanulata* (NM 751) from Natal, were obtained on loan and compared with specimens of *Thyroscyphus intermedius* (ROMIZ B186, ROMIZ B205, ROMIZ B313, ROMIZ B314) from Bermuda. Nematocysts of formalin-preserved materials of *T. intermedius* (ROMIZ B314) were examined in unstained tissue squashed under a coverslip. All observations were made using brightfield microscopy.

## *Symmetroscyphus,* new genus
Figs. 1–4

*Diagnosis.*—Hydroid colonies occasionally with erect hydrocauli, but typically stolonial. Hydrothecae pedicellate in both stolonial and erect colonies, radially symmetrical, barrel-shaped, margin with 4 teeth, submarginal teeth absent. Operculum pyramid-shaped, composed of 4 triangular valves. Diaphragm present, with centrally located hydropore. Hydranth with annular fold basally, abcauline diverticulum absent, with large nematocysts in body wall. Inner surface of hydrothecal wall lined to some extent with ectoderm, ectodermal layer with aggregation of large nematocysts beneath each marginal tooth.

Gonophores unknown.

*Type species.*—*Thyroscyphus intermedius* Congdon, 1907, designated herein.

*Etymology.*—The name is derived from the Latin (originally Greek) words *symmetria* (symmetry) and *scyphus* (goblet) in allusion to the radial symmetry of the hydrotheca; the gender is masculine.

*Remarks.*—In being stolonial, *Symmetroscyphus* superficially resembles the genera *Calamphora* and *Sertularella* of the family Sertulariidae Fleming, 1828, but differs in having hydrothecae that are radially instead of bilaterally symmetrical, a hydropore that is centrally located instead of excentric, an annular fold about the hydranth base rather than an abcauline diverticulum, and large nematocysts of an undetermined category (Fig. 4) in the ectoderm. *Symmetroscyphus* is most closely allied to *Thyroscyphus* Allman, 1877, of the family Thyroscyphidae Stechow, 1920, from which it differs in having a stolonial instead of an erect colony form, and in having symmetrical hydrothecal walls instead of a more protuberant adcauline than abcauline wall.

The gonophores of *Symmetroscyphus* are unknown. Gonothecae were present in hydroids identified by Leloup (1935) as *Thyroscyphus intermedius* forme *peculiaris.* However, Leloup's specimens are regarded here as belonging to a species other than *S. intermedius,* and in fact correspond with diagnoses of the genus *Sertularella* rather than *Symmetroscyphus.*

*Symmetroscyphus* is a monotypic genus, referable to the family Thyroscyphidae. The only species assigned here to the genus is its type species, *Thyroscyphus intermedius.*

## Acknowledgments

I am indebted to Dr. P. F. S. Cornelius and Mr. S. J. Moore of the British Museum (Natural History) for loan of the type material of *Calamphora parvula,* and to Dr. Londt of the Natal Museum for loan of the type material of *Sertularella campanulata.* This study was supported by funds from the Royal Ontario Museum, the Canadian Associates of the Bermuda Biological station, and the Exxon Corporation. The paper is contribution number 1103 from the Bermuda Biological Station for Research, Inc.

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# THE STATUS OF THE OPHIDIID FISHES *OPHIDIUM BREVIBARBE* CUVIER, *OPHIDIUM GRAELLSI* POEY, AND *LEPTOPHIDIUM PROFUNDORUM* GILL

C. Richard Robins

*Abstract.*—*Ophidium brevibarbe* Cuvier is shown to be the oldest valid name for a common and wide-ranging species of *Lepophidium,* of which *Ophidium graellsi* Poey is a junior synonym and *Lepophidium profundorum* auctorum is a common misattribution. *Leptophidium profundorum* Gill, type species both of *Leptophidium* (preoccupied) and of *Lepophidium,* its replacement name, is a senior synonym of *L. cervinum* (Goode and Bean), a common species in shelf waters along the eastern seaboard of the United States and southeastern Canada.

Several nomenclatural problems have delayed a revision of the ophidiid genus *Lepophidium,* now nearing completion. The answers to these problems are important because they involve: a) the most common shallow-water species which ranges from the southeastern United States and the Northern Gulf of Mexico to the southern coast of Brazil, b) the earliest name in the genus, and c) the type species of the genus. The solution of these problems is the object of this paper. Because the names of two common species are changed as a result, this information is being made available separately so that they will be available to regional works and checklists now in preparation. Counts and measurements used in this paper (Table 1) are as defined by Robins (1962:487–488).

## *Ophidium brevibarbe* Cuvier, 1829

Cuvier (1829:359) simply stated "Nous en connaissons une troisième espèce du Brésil (*Oph. Brevibarbe* N.) brune, a barbillons plus courts; . . ." This species cannot be identified with any particular species on the basis of this statement alone. However, type material of the species exists. We have examined MNHM 5772, the type material of *Ophidium brevibarbe.* There are two specimens. One, the *Lepophidium* illustrated by Kaup (1856a:95; 1856b:154, pl. 16, fig. 4) clearly shows the rostral spine and head squamation which uniquely define the genus *Lepophidium.* The other is a specimen of *Ophidion holbrooki* (Putnam). *Lepophidium brevibarbe* and *Ophidion holbrooki* are the most common and widespread species of their respective genera, occurring together from the southeastern and Gulf coasts of the United States to the southern coast of Brazil. Both are species of the inner shelf. They are common "jar mates" in museums because early collectors commonly preserved one specimen of each type of organism which they obtained. It also was common practice to describe one specimen as a new species and return it to its jar which contained other species. Nothing in Kaup's description suggests a second specimen, and, since *Ophidion holbrooki* has very long pelvic rays, it could well be that Cuvier paid no attention to the second, smaller specimen. Kaup (1856a:95) recorded the length of the specimen as 200 mm. I measure it at 202 mm, but it is now quite soft. There is little question but that this is the specimen described by Kaup. If both specimens in MNHM 5772 are regarded as syntypes, we may regard Kaup (1856a, b) as having restricted the name *brevibarbe* to the larger specimen, which becomes the lectotype, the specimen of *Ophidion holbrooki* becoming a paralectotype of *L. brevibarbe.* Alternatively, one can regard the largest specimen as the holotype, and the smaller specimen as lacking type status as it did not enter into the description. I have followed the first course here. Counts and measurements of both specimens are given in Table 1. That *brevibarbe* was a *Lepophidium* was correctly noted long ago by Gill (1863:210).

### *Ophidium graellsi* Poey, 1861

Poey (1861:425–426) described *Ophidium graëllsi* in some detail, based on a specimen 230 mm long (=total length). He noted that the head was scaled except for the very tip of the snout. He also said that it lacked pyloric caeca. His later accounts (1868:402; 1876:137) added nothing, the latter being a mere listing of the name. Jordan and Evermann (1898:2488) correctly emended the spelling to *graellsi* and redescribed the species based on a small specimen from Havana, sent to them by Poey. They noted six developed gill rakers on the lower limb of the first gill arch (*O. holbrooki* has only four), a sharp spine at the snout tip, and a lanceolate swimbladder. Poey also sent a drawing of his type and a description, a short translation of the original, which Jordan and Evermann included in their account. Apparently two specimens of cusk-eels were sent to the Museum of Comparative Zoology as *Ophidium graellsi* and I consider them to be Poey's original material. They are now catalogued as MCZ 12440 and 12441 and bore Poey's original numbers 729 and 720 respectively. MCZ 12440 is a specimen of *Lepophidium brevibarbe* (Cuvier) 216 mm standard length. It is gutted as expected if Poey has removed the gut for description. The specimen agrees with all of the salient features noted by Poey (1861) and Poey (in Jordan and Evermann 1898), except that one cannot attest to the pyloric caeca. All species of *Lepophidium* always have at least a few small pyloric caeca. These could have been overlooked or the statement could have been based on MCZ 12441, a specimen of *Ophidion holbrooki* (Putnam). It also is gutted but all species of this genus lack pyloric caeca. Although it bears a label "Poey's orig.," it cannot be the type as it is too small and lacks scales on the head and a forward-projecting rostral spine. MCZ 12440, the specimen of *L. brevibarbe* (Cuvier), is the holotype as Poey mentioned only one specimen. Poey commonly described species from one specimen stored with other, not necessarily related, species. There is no reason, except for the statement concerning the absence of pyloric caeca, to regard the specimen of *Ophidion holbrooki* (=MCZ 12441) as a paralectotype. *Ophidium graellsi* Poey is therefore a junior synonym of *Lepophidium brevibarbe* (Cuvier). Counts and measurements of both specimens are given in Table 1.

### *Leptophidium profundorum* Gill, 1863

Gill described this species from a single specimen collected by Commodore Rogers off the east coast of Florida in 60 fms (277 m). It is the type species, by monotypy, of *Leptophidium* Gill, 1863 (preoccupied) and also of the replacement genus *Lepophidium* (Gill, 1895). This name, which represents a valid species, has commonly been misapplied to the common shallow-water species whose correct name is *L. brevibarbe.* Counts and measurements of the holotype (USNM 6247), are given in Table 1. Its gill chamber and gill bars are blackish, the peritoneum is silvery, and the esophagus is black. All these structures are without pigment in *L. brevibarbe.* The specimen is badly faded so that no external pigment pattern is evident. The counts, proportions, and the internal pigment noted above are identical with those of *Lepophidium cervinum* (Goode and Bean, 1885), a common shelf species characterized by a row of pale spots on a tan back-

Table 1.—Morphometric data for the type and other relevant specimens of *Ophidium brevibarbe* (MNHN 5772). *Ophidium graellsi* (MCZ 12440, 12441); *Leptophidium profundorum* (USNM 6742) and *Leptophidium cervinum* (USNM 28764, 274258). Proportions are expressed in percent standard or (*) head length.

|  | MNHM 5772 1† | MNHM 5722 2†† | MCZ 12440† | MCZ 12441 | USNM 6472† | USNM 28764† | USNM 274258†† |  |
|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  |  | 1 | 2 |
| Standard length (mm) | 202 | 123 | 216 | 160 | 168 | 232 | 220 | 218 |
| Head length | 20 | 21 | 19 | 18 | 17 | 17 | 16 | 17 |
| Predorsal distance | 23 | 26 | 22 | 27 | 21 | 22 | 22 | 23 |
| Preanal (fin) distance | 40 | 41 | 38 | 31 | 34 | 34 | 32 | 36 |
| Snout tip to occiput | 14 | 14 | 14 | 14 | 12 | 11 | 11 | 12 |
| Snout tip to end of lateral line | 85 | — | — | 89 | 89 | 95 | 92 | 98 |
| Depth of body |  |  |  |  |  |  |  |  |
| 1) At dorsal-fin origin | 11 | — | 11 | 12 | 10 | — | 98 | 93 |
| 2) At anal-fin origin | 10 | 11 | 11 | 11 | 10 | 85 | 83 | 84 |
| 3) At occiput | 11 | 13 | 14 | 12 | 10 | 90 | 82 | 86 |
| Pectoral-fin length | 92 | 97 | 79 | 14 | 70 | 91 | 79 | 85 |
| Caudal-fin length | — | — | 4.0 | — | 4.8 | 4.6 | 4.1 | 5.5 |
| Pelvic ray length |  |  |  |  |  |  |  |  |
| 1) Anterior (outer) | 7.6 | 14 | 6.3 | 13 | 4.9 | 5.4 | 4.0 | 5.0 |
| 2) Posterior (inner) | 5.4 | 8.8 | 4.0 | 5.0 | 3.3 | 3.7 | 3.0 | 3.7 |
| Snout length* | 21 | 20 | 21 | 21 | 22 | 22 | 23 | 24 |
| Postorbital length* | 56 | 56 | 59 | 55 | 54 | 56 | 53 | 55 |
| Snout tip to end of maxilla* | 52 | 46 | 45 | 40 | 36 | 36 | 38 | 37 |
| Orbit diameter* | 23 | 24 | 30 | 27 | 27 | 27 | 25 | 26 |
| Bony interorbital* | 16 | 13 | 18 | 14 | 17 | — | 16 | — |
| Pyloric caeca |  | 0 | — | — | 3 | 3 | — | 3 |
| Dorsal-fin rays | 126 | 134 | 131 | 140 | 136 | 134 | 135 | 137 |
| Anal-fin rays | 107 | 106 | 109 | 114 | 115 | 114 | 117 | 117 |
| Pectoral-fin rays | 19-19 | 22-22 | 22-22 | 21-20 | 22-22 | 23-23 | 23-24 | 22-22 |
| Vertebrae (precaudal + caudal) | 15/56=71 | 16/50=66 |  | 15/53=68 | 17/58=75 | 16/58=77 | 15/60=75 | 16/60=76 |
| Gillrakers | 3+6=9 | 2+4=6 | 3+7=10 | 2+4=6 | 2+5=9 | 2+7=9 | 2+6=8 | 2+7=9 |

† Lectotype or holotype.
†† Paralectotype (see text).

ground, which ranges from Florida to eastern Canada. Although the probable identity of *profundorum* has been known to me for years, new species in the genus were being encountered regularly, and I wished to be certain that there was not a very similar, but unpatterned species, in the region. That no other species shares this combination of characters is now clear. *Lepophidium cervinum* (Goode and Bean) is, therefore, a junior synonym of *Lepophidium profundorum* Gill. Goode and Bean (1885:422) designated one specimen, USNM 28764, 262 mm total length, as the type. The jar bearing this number contained three specimens, the smaller two of which are recataloged as paratypes, USNM 274258. Counts and measurements of these three specimens are given in Table 1. *Lepophidium cervinum* is not of sufficient importance under guidelines laid down by the International Commission of Zoological Nomenclature, to merit a request to the Commission for conservation of the name.

The use of *Lepophidium brevibarbe* by Robins (1958: fig. 1d) for a species with short pelvic fins and a dark gill chamber was in error. That species lacks a name and is being described elsewhere.

## Acknowledgments

Many persons have supplied information and loaned material relevant to this study, or made facilities available to me at their institutions. In particular, I am indebted to Marie-Louise Bauchot (Muséum National d'Histoire Naturelle, Paris; the late Henry B. Bigelow, Myvanwy Dick, and Karsten Hartel (Museum of Comparative Zoology, Harvard University); Giles W. Mead and Daniel M. Cohen (then of the Systematics Laboratory, National Marine Fisheries Service); and Leonard P. Schultz, Ernest A. Lachner, Robert H. Kanazawa, and Susan L. Jewett (National Museum of Natural History). Aspects of this study were discussed with the late Luis Howell-Rivero and, most thoroughly, with Robert N. Lea, California Department of Fish and Game, to whom I am especially indebted. Catherine H. Robins commented on the manuscript. Some of this work was done with grant support through NSF-G-7116, G105. The Maytag Chair of Ichthyology has supported me throughout.

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# A REDESCRIPTION OF *COLOBOMATUS MYLIONUS* FUKUI FROM AUSTRALIAN *ACANTHOPAGRUS* (SPARIDAE) (CRUSTACEA: COPEPODA: PHILICHTHYIDAE)

Thomas Byrnes and Roger Cressey

*Abstract.*—*Colobomatus mylionus* Fukui has been recollected from Australian *Acanthopagrus.* The original description was based on a single female from a Japanese *Acanthopagrus macrocephalus.* The species is unique because of the presence of rings of fine processes on the surface of the lateral processes of the female. The male is described for the first time.

In 1965 Fukui described a new species of *Colobomatus* from the sparid fish *Acanthopagrus macrocephalus* from Japan. This description was based on a single damaged female. Recently, the first author, as part of a survey of the parasitic copepods of Australian bream, collected several specimens of the same species from three species of *Acanthopagrus.* This paper is based on that additional material including the first description of the male.

## *Colobomatus mylionus* Fukui, 1965
Figs. 1–15

*Material examined.*—51 females and 2 males collected from the cephalic canal system adjacent to the nasal cavity of *Acanthopagrus australis* (Gunther), *A. berda* (Forsskål), and *A. latus* (Houttuyn) from off Eden, Newcastle, Brisbane, Yeppoon (all east coast Australia), and Point Sampson (west coast Australia).

*Description.*—Female: Body form as in Figs. 1 and 2. Length of body, including processes, 4.75 mm (3.37–5.71 mm). Greatest width 0.94 mm (0.61–1.1 mm) measured near base of posterior thoracic process. Measurements based on 10 specimens from Point Sampson. Color in life yellowish with or without black gut contents visible in vivo.

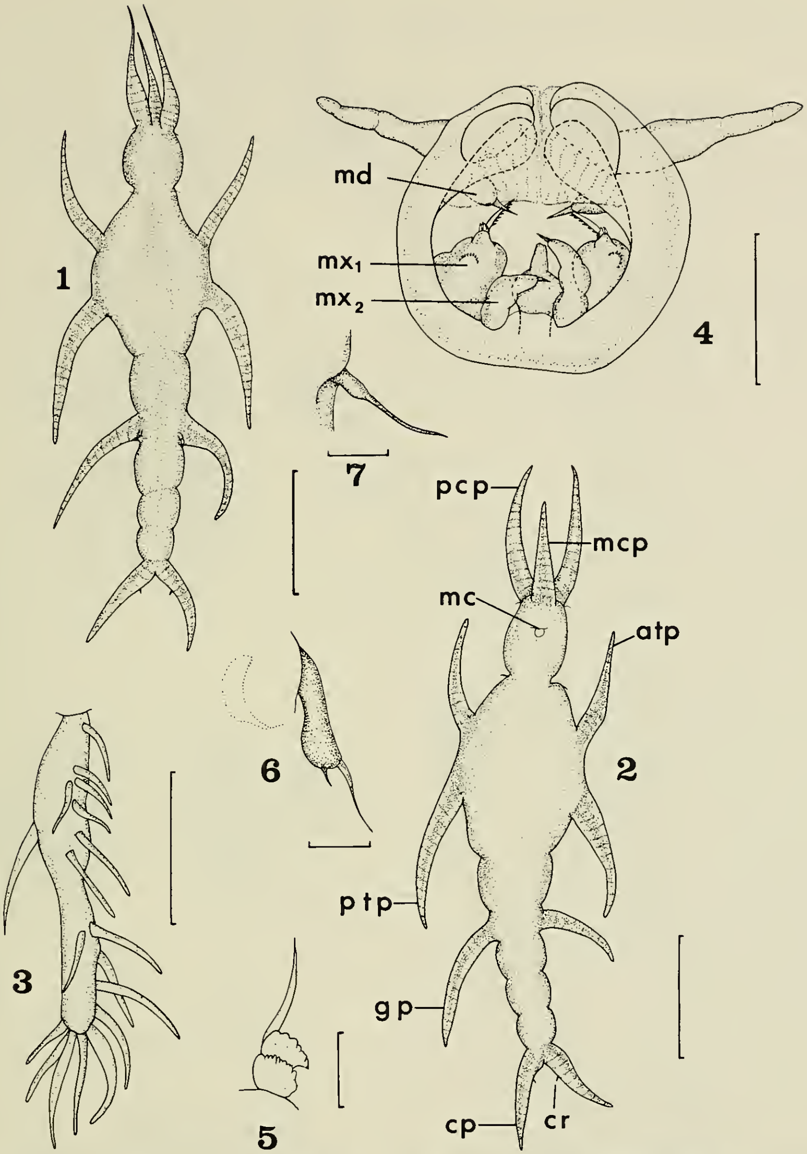
Cephalon bearing 2 dorsolateral processes and shorter ventromedial process. First antenna (Fig. 3) indistinctly segmented, bearing naked, blunt setae as figured. Mouth ventral, with mandibles, first maxillae, and second maxillae within. Mandible armed with single blade. First maxilla with robust base bearing row of spinules and 3 spines at base of distal process (process with row of denticles along inner edge). Second maxilla with globose basal segment and short naked terminal process. Maxilliped absent (see Fig. 4). Single anteriorly directed process arising from center of posterior margin of mouth cone.

Leg 1 (Fig. 5) 2-segmented with single naked seta on last segment. Legs 4–5 absent.

Genital segment bearing 2 lateral, posteriorly directed processes. Small genital process bearing 1 short and 1 long setae (Fig. 6) on dorsolateral posterior margin of genital segment near origin of lateral processes. Abdomen indistinctly 3-segmented. Each caudal process bearing small seta-like process (Fig. 7), possibly representing caudal ramus.

Egg sacs typical of genus and loosely attached (often dropping off when specimens handled).

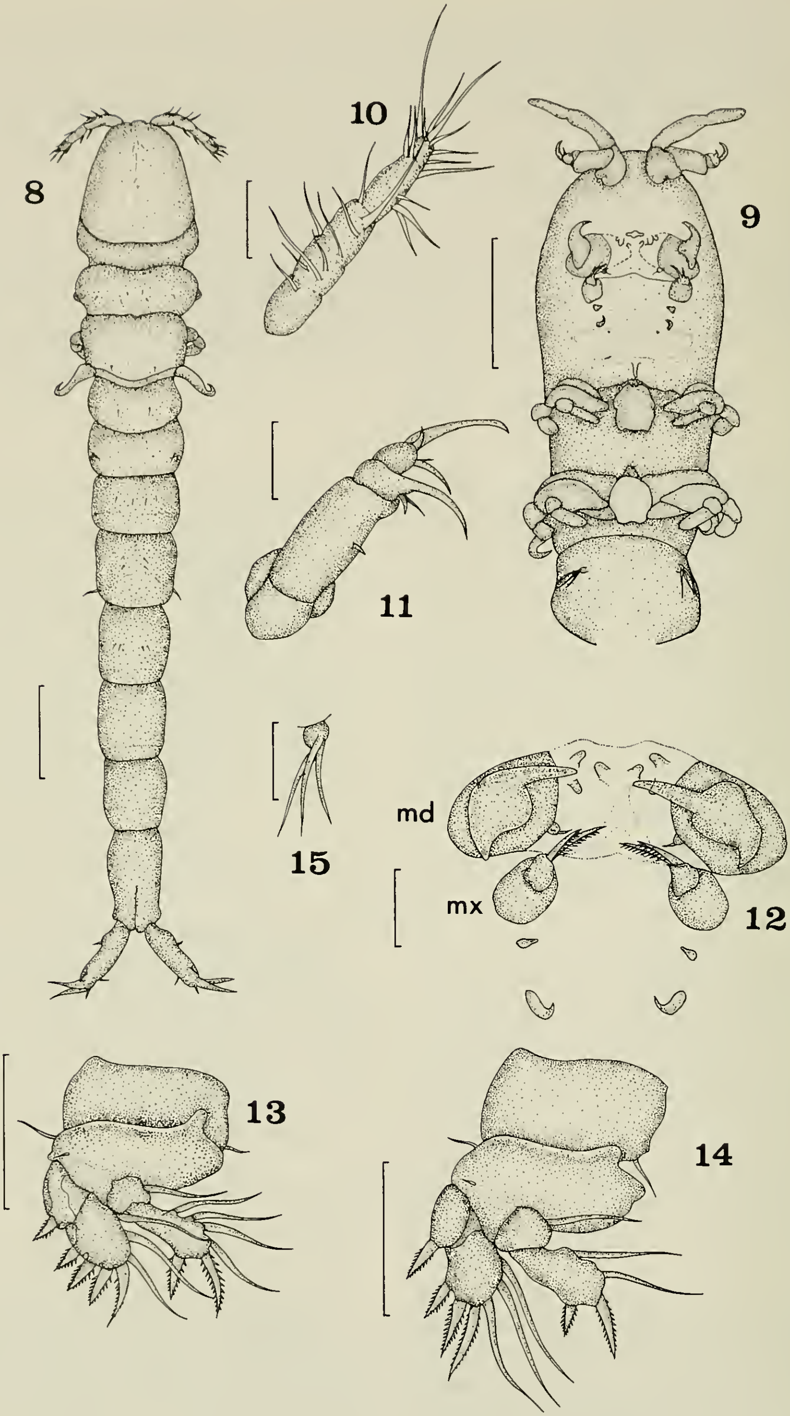
Male: Body form as in Fig. 8. Total length 0.95 mm, greatest width 0.14 mm, based on single specimen. Cephalothorax indistinct.



Figs. 1–7. *Colobomatus mylionus* Fukui, female: 1, Dorsal; 2, Ventral; 3, First antenna; 4, Oral area; 5, Leg 1; 6, Leg 2; 7, Leg 3.

First and second antennae separated from oral area (Fig. 9). First antenna 5-segmented, armed with setae as in Fig. 10. Second antenna (Fig. 11) 4-segmented, last 2 segments bearing spines and setae as in figure. Remaining oral appendages as in Fig. 12.

Leg 1 (Fig. 13) coxopod with inner naked seta; basipod with outer naked seta; exopod first segment with outer stout spine; second segment with 4 outer stout spines and 3 inner setae (all spines barbed along both margins); endopod first segment with inner



Figs. 8–15. *Colobomatus mylionus* Fukui, male: 8, Dorsal; 9, Cephalon and leg bearing thoracic segments, ventral: 10, First antenna; 11, Second antenna; 12, Oral area; 13, Leg 1; 14; Leg 2; 15, Leg 3.

seta; second segment with 2 outer barbed spines and 4 inner setae (all setae naked). Leg 2 (Fig. 14) as in leg 1 except exopod with 1 less spine on last segment and endopod last segment with 2 less setae. Leg 3 (Fig. 15) represented by 3 naked setae (Fig. 9).

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We wish to thank Mr. K. Izawa of Mie University for opinions relative to the taxonomic status of the new material from Australia and for suggesting the collaborative arrangement with the second author that resulted in the above redescription of *C. mylionus*.

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# NEOTROPICAL MONOGENEA. 9. STATUS OF *TRINIGYRUS* HANEK, MOLNAR, AND FERNANDO, 1974 (DACTYLOGYRIDAE) WITH DESCRIPTIONS OF TWO NEW SPECIES FROM LORICARIID CATFISHES FROM THE BRAZILIAN AMAZON

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

*Abstract.*—The generic diagnosis of *Trinigyrus* Hanek, Molnar, and Fernando, 1974, is emended to incorporate the following characters: presence of confluent intestinal caeca, overlapping gonads (testis dorsal or dorsoposterior to ovary), a ventral anchor/bar complex, and a haptor with 4 pairs of appendages on which hook pairs 2, 3, 4, 6, and 7 are located. The genus is transferred from the Dactylogyrinae to the Ancyrocephalinae based on the presence of the ventral anchor/bar complex, the absence of hook pair 4A, and its relationship to *Hamatopeduncularia* Yamaguti, 1953. Two new species of *Trinigyrus* are described from the gills of Loricariidae: *T. acuminatus* from *Acanthicus hystrix* Spix, and *T. tentaculoides* from *Hypoptopoma thoracathum* Günther.

Hanek, Molnar, and Fernando (1974) proposed *Trinigyrus* for their new species, *T. hypostomatis,* infesting the gills of *Hypostomus robinii* (Valenciennes), Loricariidae, in Trinidad. The genus was originally placed in the Dactylogyrinae of the Dactylogyridae presumably because of the presence of a single anchor/bar complex in the haptor. Gussev (1978) postulated that members of this subfamily would be rare or absent in the native Neotropical fauna since their primary hosts (cyprinid fishes) do not occur naturally in the region. Gussev (1978), who felt the types of *T. hypostomatis* were probably damaged specimens in which the second anchor/bar complex had been torn away, suggested that *Trinigyrus* belongs to the Ancylodiscoidinae Gussev, 1961, based on the morphology of the anchors and bar and on the reported host. However, he did not formally make the transfer. In the present study, *Trinigyrus* is emended and reassigned at the subfamily level, and two new species of the genus are described.

Hosts were collected from the environs of Manaus, Amazonas, Brazil, during September and November 1984. Methods of host and parasite collection, preparation of helminths for study, measurement, and numbering of haptoral hook pairs are those used by Kritsky, Thatcher, and Boeger (1986). Measurements are in micrometers; averages are followed by ranges in parentheses. Cirrus length was approximated using a Minerva curvimeter on camera lucida drawings. Type specimens are deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia (INPA), the U.S. National Museum Helminthological Collection (USNM), and the University of Nebraska State Museum (HWML) as indicated below.

## *Trinigyrus* Hanek, Molnar, and Fernando, 1974

*Emended diagnosis.*—Dactylogyridae, Ancyrocephalinae. Body divisible into cephalic region, trunk and haptor (peduncle absent). Tegument thin, smooth. Cephalic lobes, head organs, cephalic glands present. Eyes absent. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short or absent; intestinal caeca 2, confluent posterior to gonads, lacking diverticula. Gonads intercaecal, overlapping; testis dorsal or dorsoposterior to ovary. Vas deferens looping left intestinal caecum; seminal vesicle a dilation of vas deferens; prostatic reservoirs 2; copulatory complex comprising accessory piece and tubular cirrus. Oviduct short; uterus delicate or well developed; vagina dextral; seminal receptacle lying diagonally to right of midline. Genital pore midventral. Vitellaria consisting of 2 bilateral bands in trunk and anterior portion of haptor. Haptor with variable number of glandular reservoirs, ventral anchor/bar complex, 7 pairs of similar hooks. Haptor exhibiting 4 pairs of hook-bearing appendages: 2 bilateral pairs bearing hooks pairs 2, 7; single posteroventral pair branched, bearing hook pairs 3, 4; pair of posterodorsal appendages bearing hook pair 6; hook pairs 1, 5 sessile. Parasites of gills of Loricariidae, Siluriformes.

*Type species, host, and locality.—Trinigyrus hypostomatis* Hanek, Molnar, and Fernando, 1974, from *Hypostomus robinii* (Valenciennes), Talparo River near Talparo, Trinidad.

*Other species.—Trinigyrus acuminatus,* n. sp. from *Acanthicus hystrix* Spix, Rio Negro near Manaus, Amazonas, Brazil; *T. tentaculoides,* n. sp. from *Hypoptopoma thoracathum* Günther, Rio Solimões near Marchantaria Island, Manaus, Amazonas, Brazil.

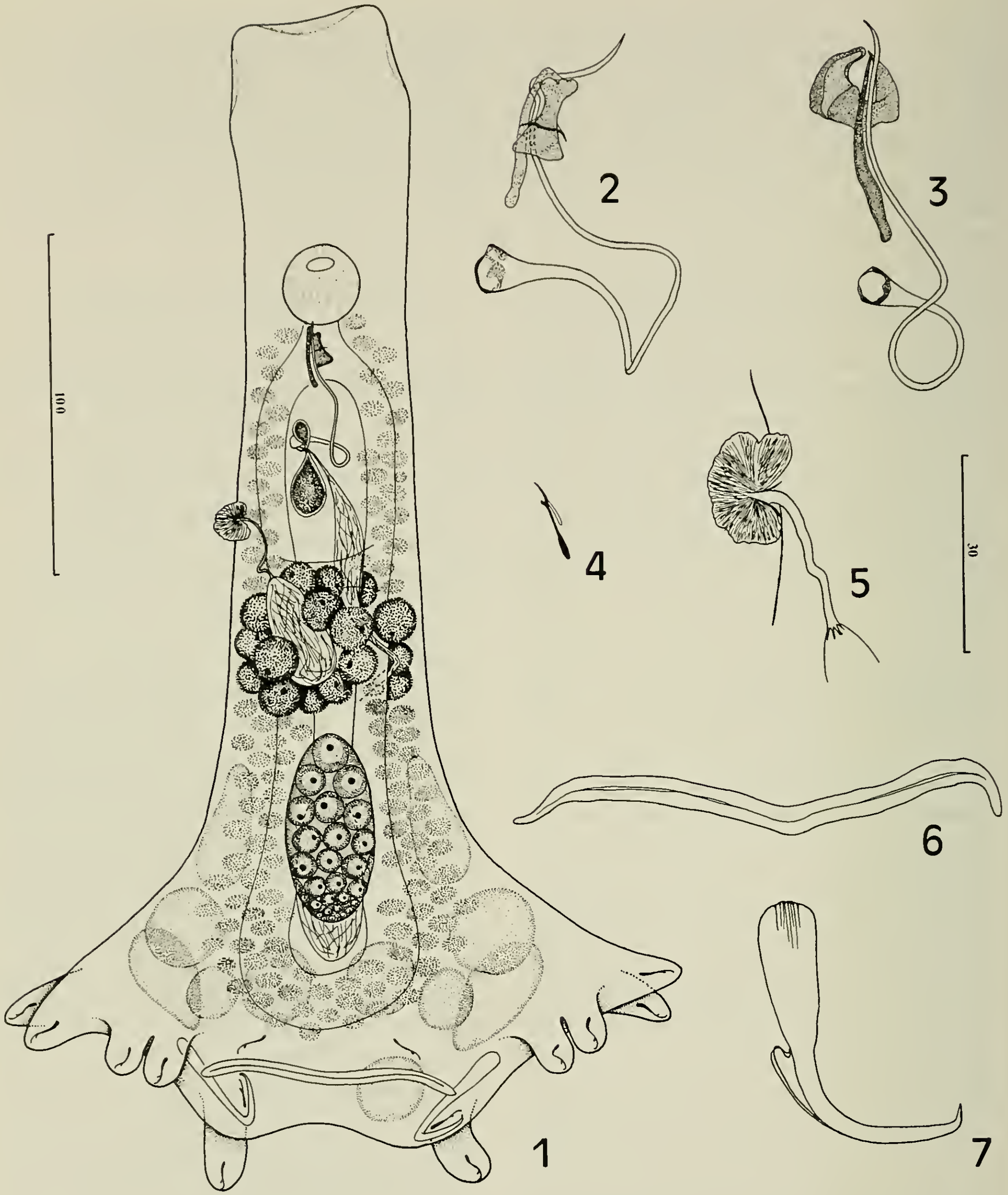
*Remarks.*—In adults of *Trinigyrus* species described below, we observed that the testis is seldom developed, although the ovary exhibits large oocytes and the seminal vesicle and receptacle are filled with spermatozoa. These observations suggest that some form of protandry exists in *Trinigyrus,* though we could not determine the developmental sequence from available specimens. The occurrence of spermatozoa in the seminal vesicle of specimens apparently lacking a testis implies that this gonad develops and subsequently regresses before the ovary matures. Bychowsky (1957) reports that the testes form prior to the ovary in *Microcotyle spinicirrus,* but that both gonads apparently remain in the fully developed adult. Protandry has also been reported in hexabothriids by Brinkmann (1952) and Mayes, Brooks, and Thorson (1981).

### *Trinigyrus acuminatus,* new species
Figs. 1–7

*Host and locality.—Acanthicus hystrix* Spix, Loricariidae; Rio Negro near Manaus, Amazonas, Brazil, 1 Nov 1984.

*Type specimens.*—Holotype, INPA PA 284-1; paratypes, INPA PA 284-2 + PA 284-4, USNM 79139, HWML 23306.

*Description* (based on 32 specimens).—Body subconical, 320 (190–407) long; greatest trunk width immediately anterior to haptor. Cephalic region elongate, with 2 terminal lobes and subterminal dilation; head organs poorly developed, present in cephalic lobes and expanded cephalic area; cephalic glands indistinct, lying posterolateral to pharynx. Pharynx spherical, 26 (16–33) in diameter. Haptor 164 (110–196) wide, 93 (63–129) long, an expanded portion of body; haptoral appendages short; glandular reservoirs variable, conspicuous. Anchor 41 (33–45) long, with short shaft, elongate point, sharply recurved tip, base lacking roots; base 9 (7–11) wide; anchor filament double. Bar 66 (60–79) long, with ventral longitudinal groove, tapered ends. Hooks similar, delicate; each 13 (11–16) long, with erect thumb, enlarged proximal shank; FH loop ½ shank length. Cirrus 98 (94–101) long, an elongate slender tube with sinistral loop, base reduced; accessory piece 24 (19–36) long, comprising a proximal rod, distal dumbbell-shaped appendage. Gonads subovate. Testis 25 (21–30) wide, 46 (39–53) long; seminal vesicle elongate, fusiform; prostatic reservoirs ovate, with thick walls. Ovary 52–53 wide, 26–27 long; oviduct, ootype, uterus not observed; numerous conspicuous glands surrounding presumed



Figs. 1–7. *Trinigyrus acuminatus*: 1, Composite drawing of whole mount (ventral); 2, 3, Copulatory complexes; 4, Hook; 5, Vagina and distal portion of seminal receptacle; 6, Bar; 7, Anchor. All figures are reproduced to the same scale (30 micrometers) except Fig. 1 (100 micrometers).

ootype; vagina with exterior flower-like appendage, short internal sclerotized tube directed posteriorly; seminal receptable ovate, ventral in trunk, extending posteriorly to midline. Vitellaria coextensive with intestinal caeca, vitelline commissure indistinct.

*Remarks.—Trinigyrus acuminatus* differs notably from *T. hypostomatis* Hanek, Molnar, and Fernando, 1974, and *T. tentaculoides* by possessing an elongate cirrus and a complex accessory piece. In *T. hypostomatis* and *T. tentaculoides,* the cirrus comprises a short curved tube associated with a simple rod-shaped accessory piece. Based on the morphology of the haptoral armament, *T. acuminatus* is most closely related to *T. hypostomatis* in that the anchor/bar complexes are similar.

*Etymology.*—The specific name is from Latin (*acumin/o* = pointed) and refers to the elongate anchor point with recurved tip.

### *Trinigyrus tentaculoides,* new species
Figs. 8–14

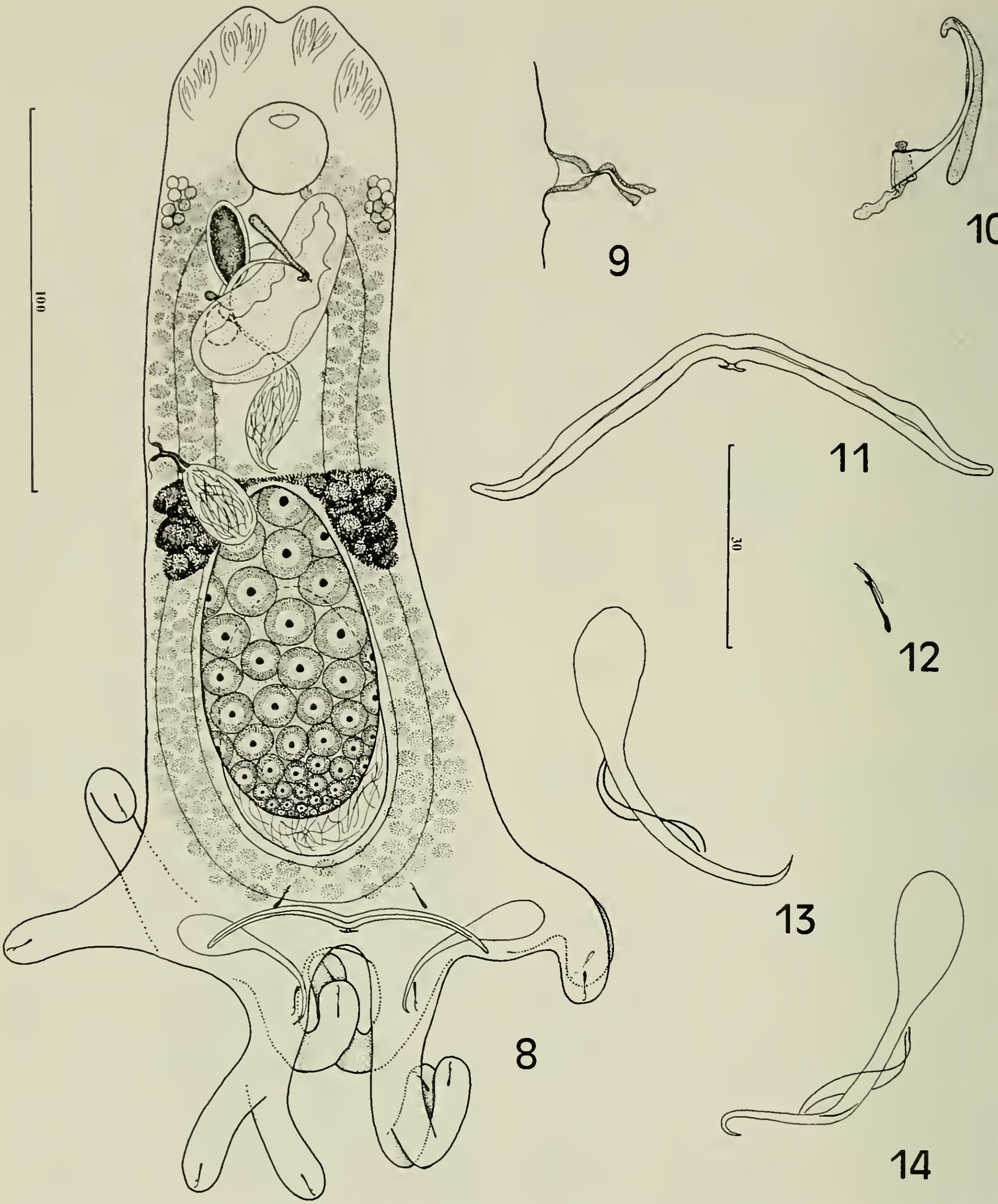
*Host and locality.—Hypoptopoma thoracathum* Günther, Loricariidae; Rio Solimões near Marchantaria Island, Manaus, Amazonas, Brazil, 13 and 26 Sep 1984.

*Type specimens.*—Holotype, INPA PA 285-1; paratypes, INPA PA 285-2, PA 285-3, USNM 79138, HWML 23305.

*Description* (based on 19 specimens).—Body robust, stout, 222 (165–307) long; greatest trunk width immediately anterior to haptor. Cephalic margin rounded or with 2 terminal, 2 bilateral cephalic lobes; head organs well developed in lobes and adjacent cephalic area; cephalic glands comprising small spherical cells posterolateral to pharynx. Pharynx subspherical, 21 (16–30) in diameter. Haptor 110 (81–145) wide, 59 (42–73) long; posteroventral appendages conspicuously bifurcated; glandular reservoirs poorly developed. Anchor 47 (43–50) long, easily distorted by coverslip pressure (Fig. 14), roots absent, base tear-drop shaped, shaft and point a continuous smooth curve, tip of point recurved; base 10 (8–11) wide; anchor filament delicate. Bar 75 (60–93) long, with tapered ends, ventral longitudinal groove, flat posteromedial projection. Hooks 10 (7–12) long, delicate; each with erect thumb, proximal dilation of shank; FH loop ½ shank length. Cirrus 29–30 long, a curved shaft arising from simple base; accessory piece 28 (22–33) long, rod-shaped, recurved distally. Gonads ovate. Testis 33 (30–36) wide, 41 (40–43) long; seminal vesicle fusiform, lying medially anterior to gonads; prostatic reservoirs subovate, with thick wall. Ovary 35 (27–45) wide, 49 (36–57) long; oviduct, ootype not observed; well-developed glands surrounding presumed ootype; uterus with thick muscular wall distally; vagina comprising a small funnel and irregularly sclerotized tube reaching to ovate seminal receptable; vitellaria coextensive with intestinal caeca, commissure indistinct. Egg distorted, with exceptionally elongate proximal filament.

*Remarks.*—Based on comparative morphology of the haptoral sclerites and copulatory complex, *T. tentaculoides* is most similar to the type species, *T. hypostomatis* Hanek, Molnar, and Fernando, 1974. These species are easily differentiated by *T. tentaculoides* possessing conspicuous haptoral appendages, which are short in *T. hypostomatis.*

*Trinigyrus tentaculoides* also shares features of the haptoral armament with several species of the marine genus *Hamatopeduncularia* Yamaguti, 1953. A flat posteromedial projection of the bar similar to that of *T. tentaculoides* occurs in *H. arii* Yamaguti, 1953 of Bychowsky and Nagibina (1969), and *H. thalassini* Bychowsky and Nagibina, 1969. Glandular reservoirs in the haptor have been described in most *Hamatopeduncularia* species. These features and the fact that all species of *Hamatopeduncularia* and *Trinigyrus* occur on siluriform fishes suggest a close relationship of the two genera (see discussion).



Figs. 8–14. *Trinigyrus tentaculoides*: 8, Ventral view of whole mount (composite); 9, Vagina; 10, Copulatory complex; 11, Bar; 12, Hook; 13, Anchor; 14, Typically distorted anchor as a result of coverslip pressure. All figures are drawn to the 30-micrometer scale except Fig. 8 (100 micrometers).

*Etymology.*—The specific name is from Neolatin (*tentacul/o* = tentacle + *oides* = like) and refers to the well-developed haptoral appendages.

## Discussion

*Trinigyrus* was briefly diagnosed by Hanek, Molnar, and Fernando (1974) based on observations of unstained specimens of the type species, *T. hypostomatis.* Our discovery of two new species of the genus from Loricariidae in the Brazilian Amazon, some specimens of which were prepared for study of the internal anatomy, provided new information which necessitated an emended generic diagnosis. Findings that supplement the original diagnosis include: (1) the presence of a bifurcated gut with intestinal caeca confluent posterior to the gonads (not observed by Hanek et al. 1974); (2) overlapping gonads with the testis lying dorsal or dorsoposterior to the ovary (described as tandem by the original authors); (3) an anchor/bar complex that is ventral in the haptor with the bar lying on the superficial (ventral) surface of the anchor bases (anchors and bar are said to be dorsal by Hanek et al. 1974) and (4) a haptor with short to well-developed appendages on which hook pairs 2, 3, 4, 6 and 7 are located (haptoral appendages were not reported in the type species). We examined a paratype of *T. hypostomatis* (USNM 73183) and have verified the presence of short haptoral appendages and a ventral anchor/bar complex in this species. The cleared, unstained and highly contracted paratype precluded determination of the position of the gonads and the pattern of the haptoral appendages.

Although reduced hooks (pair 4A of Mizelle and Price 1963) are absent, Hanek, Molnar, and Fernando (1974) considered *Trinigyrus* a member of the Dactylogyrinae apparently because of the presence of a single anchor/bar complex. Our finding that the complex is ventral in the haptor, along with the fact that 4A hooks are absent, suggests that the genus belongs in the Ancyrocephalinae as a group expressing derived characters which include the loss of the dorsal anchor/bar complex and eyes, and the development of haptoral appendages. Thus, *Trinigyrus* is the only genus of Ancyrocephalinae characterized by species possessing a single anchor/bar complex.

The transfer of *Trinigyrus* from the Dactylogyrinae to the Ancyrocephalinae is further supported by the apparent relationship of *Trinigyrus* species with those of the ancyrocephaline genus *Hamatopeduncularia* Yamaguti, 1953. As far as we are aware, the characteristic flat posteromedial projection of the bar in *Trinigyrus tentaculoides* is also found only in species of *Hamatopeduncularia* (*H. arii* of Bychowsky and Nagibina 1969, and *H. thalassini* Bychowsky and Nagibina, 1969). Although not unique to the genus, nearly all *Hamatopeduncularia* species have been described with conspicuous glandular reservoirs (usually four) in the haptor. These structures seem similar to those we report from *T. acuminatus* and *T. tentaculoides,* in the former of which they are well developed. The relationship is further substantiated by the fact that species of both genera possess haptoral appendages and parasitize fishes of the Order Siluriformes.

"Fahrenholz Rule" states that the natural classification of some parasite groups usually corresponds directly with the natural relationships of their hosts (Eichler 1948). The Ariidae include primarily marine catfishes believed derived from freshwater siluriform ancestors (Darlington 1957); and the *Hamatopeduncularia* are known only from marine ariid hosts. Our conclusion that the species of *Trinigyrus* and *Hamatopeduncularia* are related suggests that the *Hamatopeduncularia* and species of related marine genera (*Chauhanellus* Bychowsky and Nagibina, 1969; and *Hargitrema* Tripathi, 1959) represent derived taxa whose common ancestors secondarily invaded the marine environment. This invasion likely occurred concomitantly with the same event for their hosts. The *Hamatopeduncularia* apparently retain more of the primitive characters of their ancestor than do the *Trinigyrus* species. For example, the loss of the dorsal anchor/bar complex and eyes and the development of confluent intestinal caeca in *Trinigyrus* likely occurred after isolation of the two ancestral populations. Divergence in the marine population appears less dramatic, although it has also progressed to the generic level as expressed in the related genera *Hamatopeduncularia, Chauhanellus,* and *Hargitrema.*

## Acknowledgments

The authors are grateful to Dr. J. Ralph Lichtenfels, USNM, for providing the paratype of *Trinigyrus hypostomatis*; and Lucia Py-Daniel, INPA, for identifying the fish hosts. The Max Planck Institute, Plon, Germany, kindly provided financial and technical support for the collection of fish hosts, and the Conselho Nacional de Desenvolvimento Científico e Tecnológico provided a study grant (20.0115/84) to WAB.

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# REDESCRIPTION OF *ECHINODERES PILOSUS* (KINORHYNCHA: CYCLORHAGIDA)

Robert P. Higgins

*Abstract.*—*Echinoderes pilosus* Lang is redescribed from a paratypic male and female collected from kelp washed onto a beach at South Georgia Island in the southwestern Atlantic. The presence of lateroventral adhesive tubes on the fourth segment, patterns of cuticular hairs, scars, and sensory spots, and the morphological differences between the sexes are noted. The species is compared with other species having the same spine formula.

Although the phylum Kinorhyncha generally is associated with marine benthic sediment, several species have been found in association with either other invertebrates or plants (mostly algae). *Echinoderes dujardinii* Claparéde, 1863 was discovered in washings of estuarine algae and oysters by the French zoologist Felix Dujardin (1851). In his "Monographie der Echinodera," Zelinka (1928) again reported *E. dujardinii* and added *E. ferrugineus* Zelinka, 1928, several additional juvenile cyclorhagids, and a homolorhagid, *Pycnophyes rugosus* Zelinka, 1928 to the list of algal inhabitants.

Karl Lang (1936) found *P. kielensis* Zelinka, 1928 and *P. flaveolatus* Zelinka, 1928 in "red algae associated with stone and mud"; 13 years later, he described *E. pilosus* Lang, 1949 "from washings of old kelp cast up on shore. S. Georgia. Grytviken." Pallares (1966), apparently studying the plankton associates with red algae along the southeastern coast of Argentina, also found Lang's species. The only other published record of kinorhynchs in association with algae is that of Moore (1973) who found *Campyloderes macquariae* in samples of kelp holdfast fauna from several localities in the British Isles.

The precise relationship between these kinorhynchs and their algal habitat remains a matter of conjecture. Since all of the kinorhynchs reported from algae also are known from sediments, it is most probable that their presence, in most instances, has been a matter of their being washed into intertidal algae or transferred to the algae as it is washed along the sediment.

At the time of its description, *E. pilosus* needed only to be compared with three other species having the same or at least similar spine formula: *E. dujardinii, E. ferrugineus,* and *E. worthingi* Southern, 1914. Since its description, ten additional species with this same spine formula have been described. In the genus *Echinoderes,* the presence or absence of one spine in particular, the lateral spine or adhesive tube on the fourth segment (L-4), is often difficult to determine. In some species such as one most recently described, *E. nybakkeni* Higgins, 1986, it is a robust spine equal to the other lateral spines in its cuticularization as well as dimensions. In others, such as *E. brevicaudatus* Higgins, 1966, it may be smaller and less cuticularized. In *E. bookhouti* Higgins, 1961 and a few others, only a round cuticular scar, possibly a pore, may replace the L-4 spine or adhesive tube. Some species appear to have neither the L-4 spine or any vestige of it. In some cases such as *E. ferrugineus,* the presence of this spine is mentioned in the description (Zelinka 1928) but not shown in the illustration. In other cases such as *E. pilosus,* the L-4 spine was neither mentioned in the description nor indicated in the illustration (Lang 1949). The apparent absence of the L-4 spine and the exact nature of several other taxonomic characters prompted the re-examination of this species which is the subject of this report.

Suborder Cyclorhagae Zelinka, 1896
Family Echinoderidae Butschli, 1876
*Echinoderes* Claparéde, 1863
*Echinoderes pilosus* Lang, 1949
Figs. 1–10

*Echinoderes pilosus* Lang, 1949:17, fig. 4a, b (type locality: Grytviken, South Georgia Island).—Karling, 1954:189.—Higgins, 1960:88; 1964:491; 1966:518.—Pallares, 1966:103, pl. 1: figs. A–D; pl. 2 (Puerto Deseado to Sorrel, Argentina).—Kozloff, 1972:121.—Schmidt, 1974: 189.—Higgins, 1977a:12; 1977b:353; 1983:9; 1986:267.

*Diagnosis.—Echinoderes* with middorsal spines on segments 6–10, lateral spines on segments 4, 7–12; middorsal spines 36–74 μm long, becoming longer in posterior progression; lateral spines 36–48 μm long; lateral terminal spines 175–184 μm long, 43–46% of trunk length, with serrulate lateral margins; trunk length 400–408 μm (400–460 μm, Lang's data); lateral terminal accessory spine (of female) 55 μm long, 29% of lateral terminal spine; pectinate fringe very fine; perforation sites abundant, pattern distinctive but not well defined, cuticular hairs appear more abundant than perforation sites suggest; trichoscalid plates large ventrally, very small dorsally.

*Redescription.* —Paratypic adult male (Figs. 1, 2, 5, 6, 8–10) trunk length 408 μm; MSW-8 (maximum sternal width, at segment 8), 84 μm, 20.5% of trunk length; SW (standard width, =sternal width at segment 12), 78 μm, 19.1% of trunk length; cuticle with many hairs, perforation sites not uniformly distinct; posterior margins of trunk segments finely striated with very fine pectinate fringe.

Segment 2 with 16 placids, about 24 μm long, widest posteriorly, narrowest anteriorly; midventral placid wider (22 μm) than others (14 μm); trichoscalid plates of head region (segment 1) overlapping alternate placids, ventral trichoscalid plates larger (12 μm × 15 μm) than dorsal trichoscalid plates (8 μm × 5 μm), modified midventral scalid prominent, 12 μm long, pointed at posterior end, overlapping midventral placid.

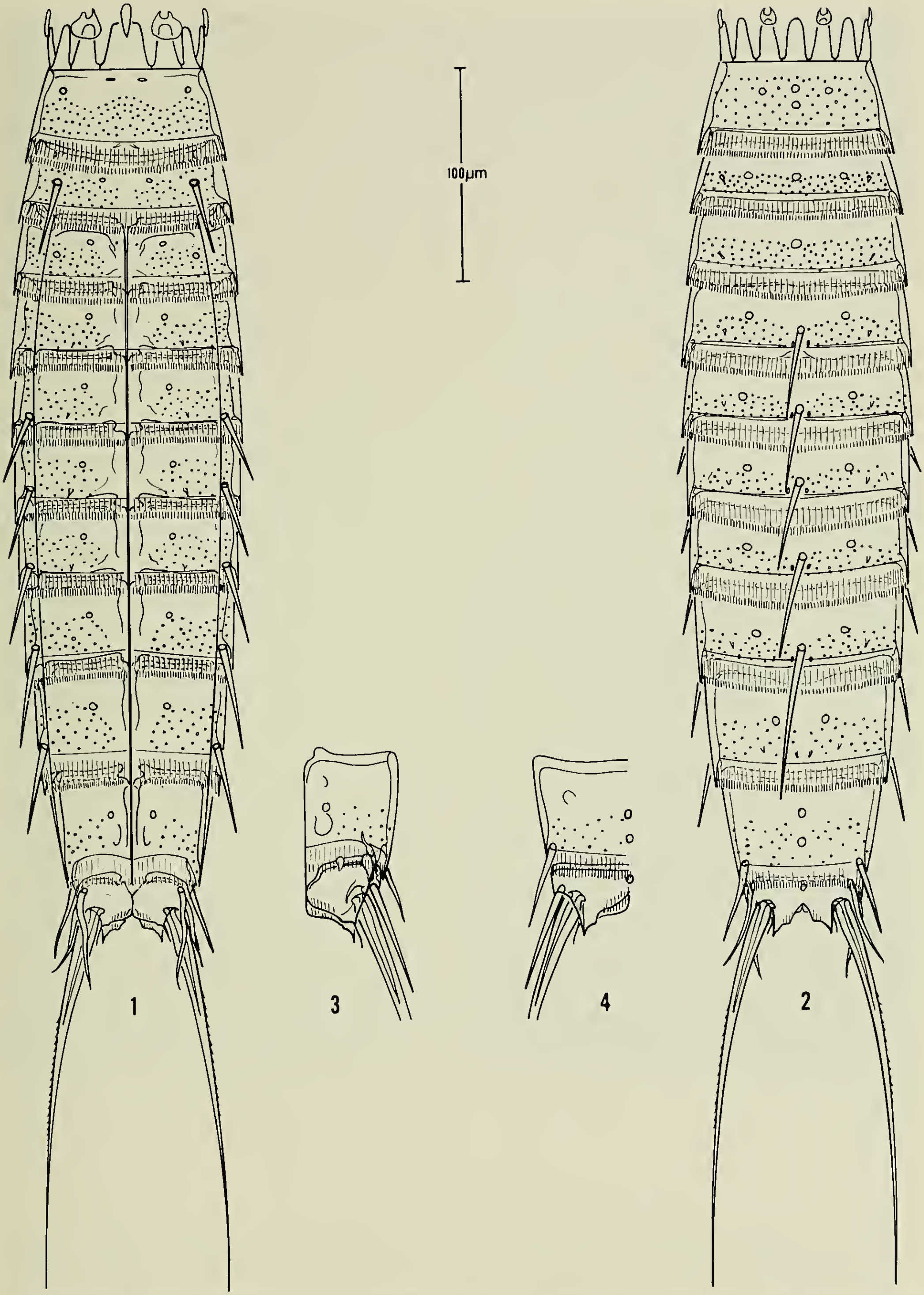
Segment 3, 44 μm long (at lateral optical view); sternal width (measured along anterior pachycycli) 76 μm; two middorsal cuticular scars at midline, subdorsal cuticular scar on either side; single cuticular scar near anterolateral margins on ventral surface.

Segment 4, 42 μm long; pachycyclus moderately developed, no evidence of cuticular thickening along midventral line; middorsal and more lateral (than on segment 3) subdorsal cuticular scars; small angular muscle scar lateral to each dorsolateral cuticular scar; single cuticular scar on either side of ventral midline, near anterior margin; prominent lateral spines (adhesive tubes), 38 μm long, midway in segment, in line with ventrolateral articulation zones of remaining segments.

Segment 5, 44 μm long; sternal width 80 μm; pachycyclus well developed, midventral articulation of sternal plates clearly visible, well cuticularized; middorsal cuticular scar only, small angular muscle scar more lateral, in line with previous scar; single cuticular scar on either side of ventral midline, near anterior margin, additional cuticular scar near each lateral margin of ventral plates.

Segment 6, 48 μm long; sternal width 82 μm; pachycyclus similar to preceding one; middorsal spine, 42 μm long, sensory spots laterally adjacent and slightly posterior to middorsal spine; dorsolateral cuticular scars and small angular muscle scar similar to those of segment 4; cuticular scar near middle of ventral plate, in line with those of previous segments.

Segment 7, 48 μm long; sternal width 83 μm; pachycyclus similar to preceding one;



Figs. 1–4. *Echinoderes pilosus*: 1, Adult male, neck and trunk segments, ventral view; 2, Same, dorsal view; 3, Adult female, segments 12, 13, ventral view; 4, Same, dorsal view.

middorsal spine, 42 μm long, with adjacent sensory spots, cuticular scars and muscle scars as in segment 6; lateral spine 36 μm long (probably adhesive tube) on tergal plate adjacent to junction with each ventral plate; cuticular scar near middle of ventral plate as in previous segment, slight evidence of small angular muscle scar slightly more lateral, near origin of arthrocorium where marginal striation begins.

Segment 8, 50 μm long; maximum sternal width (MSW) 84 μm; middorsal spine, 46 μm long; lateral spine 36 μm long; otherwise similar to segment 7.

Segment 9, 50 μm long; sternal width 84 μm; middorsal spine 50 μm long; lateral spine 40 μm long; otherwise similar to segment 8.

Segment 10, 60 μm long; sternal width 83 μm; middorsal spine 74 μm long; lateral spine 46 μm long; no evidence of small, angular muscle scar on each ventral plate; otherwise similar to segment 9.

Segment 11, 60 μm long; sternal width 80 μm; without middorsal spine; lateral spine 42 μm long; subdorsal cuticular scars closer to midline, small, angular muscle scars less distinct, otherwise dorsal and ventral morphology similar to segment 10.

Segment 12, 61 μm long; SW-12 78 μm; lateral spine 40 μm long, more flexible in appearance than preceding lateral spines, more dorsally elevated on tergal plate; 2 middorsal cuticular scars, no subdorsal cuticular scars or evidence of small, angular muscle scars, perforation sites weak, sparsely distributed near posterior half of segment both dorsally and ventrally; ventral cuticular scars similar to those on preceding segments.

Segment 13, 35 μm long; sternal width 50 μm; lateral terminal spines 175 μm long; serrulate on lateral margins beginning about one-fourth the distance from base; ventral plates with slightly pointed margins, somewhat conforming to margin of tergal plate, with hair-like projection; pachycycli widely divergent at anterior margin; tergal plate with single middorsal cuticular scar, plate bifurcated into two pointed tergal extensions; 3 pairs of penile spines (P-1, 45 μm long, dorsally displaced; P-2, 28 μm long, with blunted tip, ventrolateral; P-3, 50 μm long, adjacent to P-2).

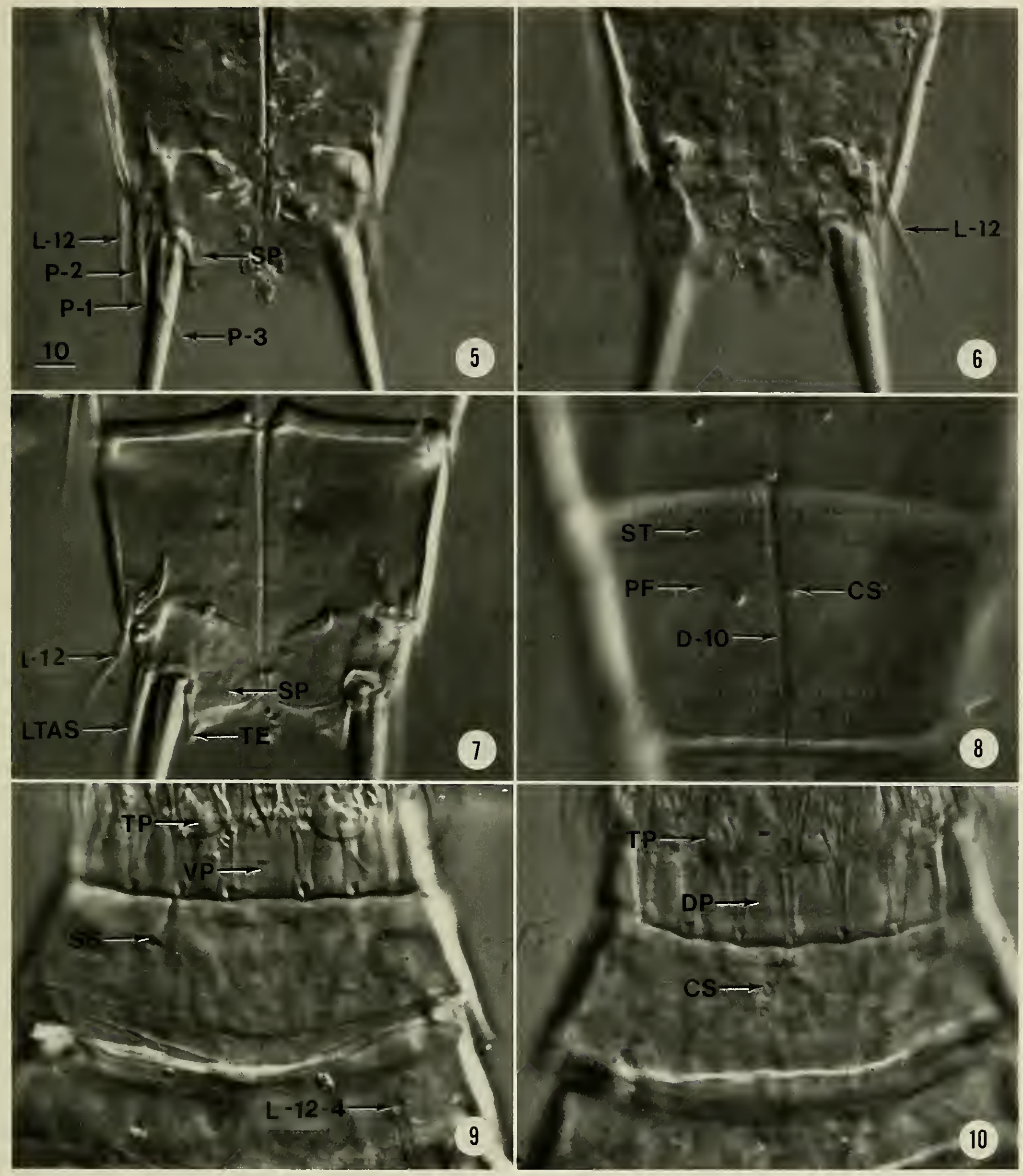
Mean length of middorsal spines (D 6–10) 50.8 μm, 12.5% of trunk length; mean length of lateral spines (L 4, 7–12) 39.7 μm, 9.7% of trunk length.

Paratypic female (Figs. 3, 4, 7) TL about 400 μm (broken specimen); MSW-8 86 μm, 21.5% of trunk length; SW 80 μm, 20.0% of trunk length; middorsal spine lengths: D-6 36 μm, D-7 42 μm, D-8 44 μm, D-9 52 μm, D-10 74 μm; mean length of middorsal spines (D 6–10) 49.6 μm, 12.2% of trunk length; lateral spine lengths: L-4 34 μm, L-7 38 μm, L-8 34 μm, L-9 38 μm, L-10 48 μm, L-11 42 μm, L-12 40 μm; mean length of lateral spines (L 4, 7–12) 39.1 μm, 9.7% of trunk length; lateral terminal spines 184 μm long, 46.0% of trunk length; lateral terminal accessory spines (female only) 54 μm long, 13.5% of trunk length, 29.3% of lateral terminal spine length.

With exception of minor morphological differences in the structure of the last two segments, the female (Figs. 3, 4, 7) closely resembles the male.

*Material examined.*—1 paratypic male and 1 paratypic female (broken specimen), permanently mounted (by Higgins) in Cobb aluminum slide frames with modified Hoyer's medium (Higgins 1983), material from the Swedish South Pole Expedition (1901–1903), 23 May 1902, Grytviken, South Georgia Island, "Sample 11." Repository: Swedish Natural History Museum (Section of Invertebrate Zoology), Stockholm.

*Remarks.*—Forty-two species of *Echinoderes* are based on adult specimens and identifiable on the basis of their description. Three others are so poorly described that I consider them species inquirenda; 27 others are based on juvenile states which are not likely to be reconciled with any adult. Within this genus, the most common middorsal



Figs. 5–10. *Echinoderes pilosus*: 5, Adult male, segments 12, 13, ventral view; 6, Same, dorsal view; 7, Adult female, ventral view; 8, Adult male, segments 10 (partial), 11, dorsal view; 9, Same, segments 2–4, ventral view; 10, Same, dorsal view. (Interference contrast photographs.)

spine formula is D 6–10; it is shared by 23 species, 12 of which have lateral spines on segments 4, 7–12. Two of these have an additional lateral accessory spine (LA-10) dorsally adjacent to the L-10 spine and two others differ only by the absence of the L-4 spine or adhesive tube, a character that can be difficult to see. The current re-examination of *E. pilosus,* in large part, was to determine whether or not this spine was absent as indicated in the original description, or present as has now been established.

Of the 12 species having the same spine formula, *E. dujardinii,* from northern European coasts, and its sibling species, *E. gerardi* Higgins, 1978, from the Mediterranean, have a lateral accessory spine on segment 10 leaving only nine remaining species to compare with *E. pilosus.* The L-4 spine or adhesive tube is not present in either *E. truncatus* Higgins, 1983 or *E. bookhouti,* although the latter species has either a pore or a cuticular scar in the L-4 position.

Several distinctive as well as unique characters in the recently described *E. nybakkeni* separate it from *E. pilosus*; the former species is very small, 185 μm long, has a midventral cuticularization on segment 4, extremely prominent pectinate fringe, and very prominent spines, including a D-7 spine which is twice the length of those on adjacent segments. Similarly, *E. krishnaswamyi* Higgins, 1985 is equally distinctive in having very long, flexible spines and a unique perforation site pattern of one or two transverse rows. This species is the only other with the same spine formula that has serrulate lateral margins on the lateral terminal spines as in *E. pilosus.*

*Echinoderes ferrugineus* is not as well described as the remaining species closely related to *E. pilosus.* Lang (1949) separated *E. pilosus* from *E. ferrugineus* on the basis of differences "in the size of the 3rd and the shape of the last zonite." *Echinoderes ferrugineus* females, at least, have a prominent seta adjacent to the L-12 spine, and the lateral terminal accessory spine is only 13.5–16.4% of the lateral terminal spine length as contrasted with 29.3% in *E. pilosus.* Although the significance of total length is questionable because of annual variation (Higgins and Fleeger 1980), *E. ferrugineus,* from European coasts, is much smaller (TL 210–220 μm) than *E. pilosus* (TL 400–408 μm; or by Lang's measurements, 400–460 μm). In addition, Lang's species appears to have relatively shorter lateral terminal spines (42.9–46.0% of the trunk length) in contrast with the longer (up to 71% of the trunk length) in *E. ferrugineus.*

Lang also compared his species with *E. worthingi* (redescribed by Higgins 1985). The latter northern European species also is smaller (242–265 μm) than *E. pilosus,* has relatively longer lateral terminal spines (60.3–72.7% of the trunk length), distinctly longer terminal tergal extensions, and a D-10 spine twice the length of the D-9 spine.

Distinctive brace-shaped muscle scars on certain ventral plates of *E. kozloffi* Higgins, 1977, *E. ehlersi* Zelinka, 1913, *E. imperforatus* Higgins, 1983, *E. pacificus* Schmidt, 1974, and *E. sublicarum* Higgins, 1977, separate them from *E. pilosus.*

*Echinoderes pilosus* has been reported only once since its original description. Pallares (1966) found numerous specimens of this species, including juvenile stages as small as 149 μm long, mostly in various collections of red algae made between 1949–1965 along the southeastern coast of Argentina. Pallares reported the presence of red eyespots in the animals but, like Lang, did not observe the L-4 spines. As in the case of Lang, Pallares' measurements of body length are not defined. Using the standard trunk length measurement (from the anterior margin of the first trunk segment to the posteriormost margin of the last segment) and the measurement scales or other information provided by each of these authors I would suggest that their reported length measurements are excessive. The lengths and relative proportions of various body regions and spines that can be obtained through Pallares' illustrations agree remarkably well with those I have derived from the two paratypes used in the redescription. Similar data derived from Lang's illustrations tend to be much less compatible.

In addition to confirming the presence of the L-4 spine in *E. pilosus,* Lang's (1949) original description requires two additional emendations. His notation on the presence of "a ring of extremely fine 'hair' quite close to the anterior border of the zonite," refers to the very fine pectinate fringe along the posterior margin of each segment which overlaps the anterior part of the posteriorly adjacent segment. Lang also was in error in his interpretation of placid morphology. Correctly noting the presence of 16 placids comprising segment 2, he stated: "Neither of the two ventro-median placids is perceptibly wider than the others." There is, in *E. pilosus,* as in all known species of this genus, a single midventral placid which is wider than the laterally adjacent placids. In this case, the midventral placid of *E. pilosus* is nearly twice as wide as the others, morphology which also escaped notation by Pallares (1966).

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# SEPARATION OF *HABER SPECIOSUS* (HRABĚ) (OLIGOCHAETA: TUBIFICIDAE) FROM ITS CONGENERS, WITH A DESCRIPTION OF A NEW FORM FROM NORTH AMERICA

Michael R. Milligan

*Abstract.*—The diagnosis of *Haber* Holmquist is expanded to include species of previously questionable position. The members of this genus are unique among the Tubificinae in possessing similar penial and spermathecal setae and have characteristic genital morphology. *Haber* now includes eight species: *H. speciosus* (Hrabě), *H. dojranensis* (Hrabě), *H. monfalconensis* (Hrabě), *H. amurensis* (Sokolskaja and Hrabě), *H. pyrenaicus* (Juget and Giani), *H. turquini* (Juget and Lafont), *H. hubsugulensis* (Semernoi and Akinshina), and *H. svirenkoi* (Lastockin). *Haber simsi* (Brinkhurst) is confirmed to be a synonym of *H. speciosus.* Based on setal morphology, *H. speciosus* is separated into four forms: speciosus, zavreli, simsi and fluminialis. This complex is compared to all congeners.

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Until Brinkhurst (1981) recorded the first appearance of *Haber* in the state of New York, this genus was only known from localities in Europe. Subsequent material from Maryland, South Carolina, and Florida indicates that this genus, represented by a single species, is well established in extreme upper estuarine locations along the eastern seaboard and Gulf of Mexico in North America. Eight species have been incorporated into the genus *Haber,* some based on incomplete descriptions. The species are: *H. speciosus* (Hrabě, 1931), *H. svirenkoi* (Lastockin, 1939), *H. dojranensis* (Hrabě, 1958), *H. monfalconensis* (Hrabě, 1966), *H. amurensis* (Sokolskaja and Hrabě, 1969), *H. pyrenaicus* (Juget and Giani, 1974), *H. turquini* (Juget and Lafont, 1979), and *H. hubsugulensis* (Semernoi and Akinshina, 1980). Holmquist (1978) established the genus (*Haber*) to accommodate those Tubificinae previously identified as either *Peloscolex* or *Tubifex* sharing the unique combination of similarly shaped penial and spermathecal setae, and an "apparent" penis sheath. Early descriptions of many of these species described a "cuticular penis sheath." Holmquist (1978) has shown, through the analysis of serial sections, the structure actually to be a thickened basement membrane, not of cuticular origin, surrounded by epithelial cells, which acts as an attachment for the musculature of the penial apparatus. Two forms of *H. speciosus* (zavreli and simsi) were once regarded as distinct species, but Hrabě (1981) regarded zavreli as a subspecies of *speciosus*; he placed both in the genus *Tubifex.* Brinkhurst and Jamieson (1971) had synonymized both plus the subspecies *monfalconensis* with *H. speciosus.* The most recent account by Brinkhurst and Wetzel (1984) suggests that some species in the genus (including *zavreli* and *simsi*) would not survive a revision, but their status was left in doubt. Holmquist (1979) elevated *monfalconensis* to specific rank, along with *speciosus* and *zavreli,* but she indicated a possible relationship between *simsi* and *speciosus* based on the single specimen of *simsi* available at that time. She listed other possible *Haber* species as *dojranensis* Hrabě, *amurensis* Hrabě and *svirenkoi* Finogenova.

The North American forms are herein described and compared with their congeners.

## Materials and Methods

Samples were collected from the Head Springs region of the Crystal River as part of a study of estuaries on the west coast of Florida sponsored by the Southwest Florida Water Management District. Samples were taken using a 12.5 × 12.5 × 20 cm diver operated core. A 15% solution of magnesium sulfate was added to narcotize the animals. The samples were subsequently sieved through a 0.5 mm mesh screen, fixed in formalin with Rose Bengal stain, then transferred to 70% isopropyl alcohol. The preserved worms were sorted from the residue and mounted on microscope slides in Amman's lactophenol. Additional specimens were stained in Grenacher's alcohol borax carmine, cleared in terpineol, and either dissected or mounted whole in Canada balsam. Measurements referred to in the description were taken from fixed, mounted worms. Representative material has been deposited in the United States National Museum of Natural History, Washington, D.C. (USNM).

Specimens of *Haber* from South Carolina collected by Dr. Dale Calder were supplied to me courtesy of Dr. R. O. Brinkhurst. These worms were stained with Rose Bengal and mounted whole in Canada balsam. Material from Maryland was received courtesy of Mr. Michael T. Barbour (EA Engineering, Science and Technology, Inc.). Specimens from New York identified as *Haber* cf. *speciosus* by Dr. Brinkhurst were received courtesy of the USNM. The Maryland and New York material was mounted whole and cleared in CMC-10. Specimens of *Haber* from England were mounted in polyvinyl lactophenol and provided by Dr. Michael Ladle (Freshwater Biological Association, England).

## Systematics

### *Haber* Holmquist, 1978

*Definition* (modified).—Limnetic tubificids. Dorsal bundles include smooth or hispid hair setae, and bifid or pectinate crotchets. Somatic ventral setae all bifid crotchets. Body wall usually smooth, without adherent foreign particles. Male and spermathecal pores paired. Coelomocytes absent or inconspicuous. Modified spermathecal and penial setae present: thin and hollow-tipped, inserted in glandular sacs. Vas deferens long, bipartite in some species, entering ental portion of atrium apically. Glandular prostate present, attached to atrium medially in most species. Ectal region of atrium often modified into narrow ejaculatory duct. Penial pouch present. Cuticular penis sheath absent. Thick basal membrane resembling a penis sheath lining internal canal of penis. Male pore and penial setal sac with common opening. Spermathecae bipartite: ectal narrow canal; entally, elongate ampullae. Spermatozeugmata vermiform.

*Type species.*—*Tubifex speciosus* Hrabě, 1931.

*Remarks.*—The presence of modified penial setae has been reported in only two tubificine species, *Tubifex nerthus* Michaelsen, and *T. thompsoni* Southern, other than those now considered in the genus *Haber.* Brinkhurst and Baker (1979:1554) determined the penial setae reported in a single specimen of *T. nerthus* from Europe probably to be "no more than broken somatic setae." *Tubifex thompsoni,* synonymized with *T. costatus* by Brinkhurst (1963), has been reported as having unmodified penial setae according to Holmquist (1979). However, the morphology of the male efferent duct and the presence of palmate setae precludes any relationship to the *Haber* group, and the penial setae may simply be bifids retained. *Tubifex costatus* was described as lacking penial setae (Brinkhurst and Baker 1979).

*General Remarks.*—Eight species are included in this genus as suggested by Holmquist (1978) and Brinkhurst (1981, 1984) based on the presence of penial and spermathecal setae inserted in a glandular sac. These species are separated primarily by the morphology of the male genitalia. Secondary characters are setal morphology, position of the spermathecal pore, and modifications of the body wall.

*Distribution.*—North America, Europe.

### *Haber speciosus* (Hrabě, 1931)

*Tubifex* (*Tubifex*) *speciosus* Hrabě, 1931: 24–27; 1964:108.

*Peloscolex zavreli* Hrabě, 1942:23–26.—Brinkhurst, 1963:41, (equals *Peloscolex speciosus* (Hrabě), Brinkhurst, 1971:514).

*Peloscolex speciosus* (Hrabě), Brinkhurst, 1962:304–305; 1963:43; 1966:735 (partim).—Brinkhurst and Jamieson, 1971: 514–515.

*Peloscolex simsi* Brinkhurst, 1966:735–736 (equals *Peloscolex speciosus* (Hrabě), Brinkhurst, 1971:514).

*Tubifex speciosus speciosus* (Hrabě), Hrabě, 1966:68–70.

?*Peloscolex zavreli* Hrabě, Kasprzak, 1973: 421–422.

*Haber speciosus* (Hrabě), Holmquist, 1978: 188, 191, 193, 195, 196, 200, 201, 203, 204, 206; 1979:51, 52, 58.—Brinkhurst, 1984:52.

*Haber simsi* (Brinkhurst), Bird and Ladle, 1981:493–498.

*Haber* cf. *speciosus* (Hrabě), Brinkhurst, 1981:1062–1064.

*Tubifex speciosus zavreli* Hrabě, Hrabě, 1981:87.

*Type material.*—1593-10-P-II Hrabě Oligochaeta collection, from Ochrida Lake, Yugoslavia.

*Material examined.*—NEW YORK: One wholemounted specimen from Susquehanna River, 4.6 kilometers upstream of railroad bridge, above Gaudey Generating Station, Binghamton, New York, shallow riffle, large cobbles, USNM 065223; collector, Kurt Stimpson, 2 Aug 1976. MARYLAND: 7 wholemounted specimens from Piscataway Creek, tributary of Potomac River south of Washington, D.C., 1 m, tidal freshwater marsh, sandy silt; collector, Michael T. Barbour, May–June 1983. SOUTH CAROLINA: 9 wholemounted specimens; 7 from upper estuarine region of Black River, 5 m, sand, 5 Apr 1977, 2 from upper estuarine region of Pee Dee River, 3 m, sand, collector, Dr. Dale Calder; 5 Jan 1977. FLORIDA: 30 wholemounted specimens, 3 dissected specimens, Head Springs region of Crystal River off Banana Island, Crystal River, 1 m, medium clean sand; collector, Michael R. Milligan, Feb–Nov 1984. ENGLAND: 2 wholemounted specimens from Bere Stream, tributary of River Piddle, Dorset, stream bed with corase flint gravel and sand; collector, Michael Ladle, 27 Oct 1980.

*Diagnosis* (combined from literature and current studies).—Length (fixed, wholemounted, complete specimens) 10–15 mm, width at clitellum 0.15–0.4 mm (Table 1). Body wall generally naked. Clitellum covering X–XII. Preclitellar dorsal bundles with 1–3(4) smooth or hispid setae 150–290 μm, and 1–4(5) pectinate setae 25–65 μm with maximally 8 intermediate teeth, nodulus distal. Postclitellar dorsal bundles with 1(2) hair setae 95–442 μm, and 1(2,3) bifid or pectinate setae 35–52 μm (Table 2). Pectinate setae with maximally 3 intermediate teeth. All somatic ventral setae bifid. Preclitellar ventral setae with upper tooth as long as or longer, and thinner than, lower tooth, 3–8 per bundle 35–65 μm (Table 2). Postclitellar ventral setae generally with upper tooth as long as, and thinner than, lower tooth, 1–3 per bundle 43–62 μm (Table 2). Spermathecal and penial setae thin, hollow-tipped, embedded in glandular sac, gener-

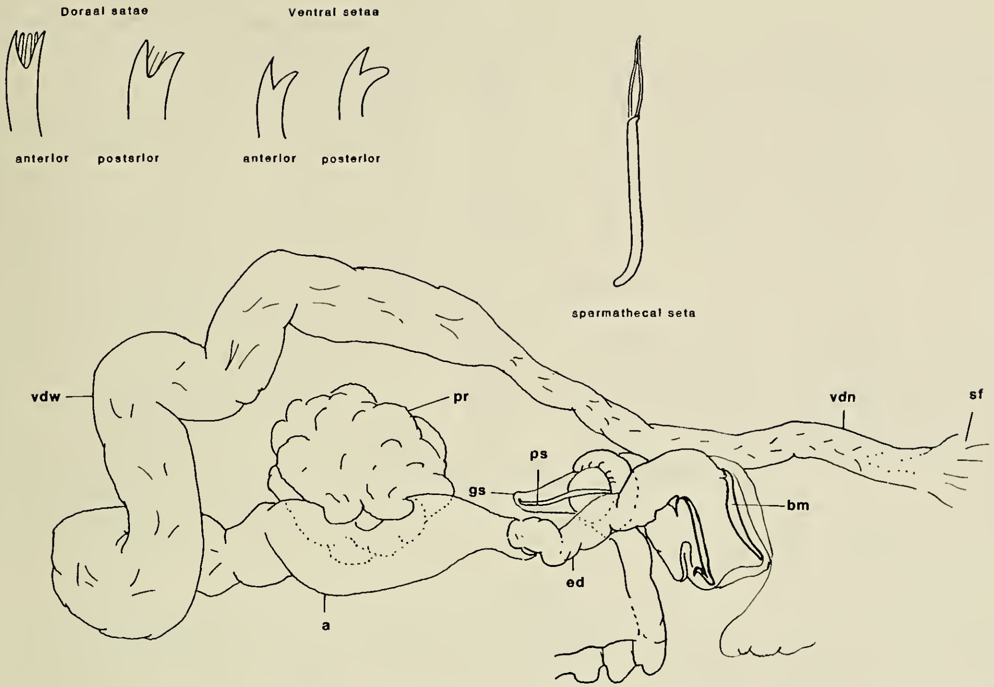

Fig. 1. Male efferent duct and characteristic setae of *Haber speciosus,* simsi form, from Florida. Abbreviations: a, atrium; bm, basement membrane; gs, glandular sac; pr, prostate gland; ps, penial setae; sf, sperm funnel; vdn, vas deferens, narrow part; vdw, vas deferens, wide part.

ally of equal length 42–70 μm (Fig. 1). Spermathecal pore dorsal to ventral seta. Male funnel small. Vas deferens, long, bipartite. Thinner ental half 16–25 μm wide, ciliated, distinctly separated from wider ectal half 38–45 μm wide. Ectal region partly or wholely ciliated, enters atrium of similar width. Glandular prostate attached medially to relatively elongate, spindle-shaped atrium (Figs. 1–2). Ejaculatory duct present, terminating in bulb-like penial apparatus. Basal membrane lining the penial canal forming a tube longer than wide. Canal of spermatheca c. 20 μm wide and c. 100 μm long; ampulla c. 100 μm wide, length variable.

*Remarks.*—This species can be divided into four distinct "forms" based on setal morphology: speciosus, zavreli, simsi, and fluminialis form. Differences between the male efferent ducts of the different forms are insufficient to warrant separation as distinct species. The differences are summarized in Tables 1 and 2. The term "subspecies" usually refers to a geographic race differing slightly from another group of the same species (Steen 1971). Form is more appropriately applied to the variants of *H. speciosus* since the variations observed may be attributable to changes in the environment, primarily conductivity (Brinkhurst, pers. comm.), not necessarily due to geographic isolation.[1]

Two of these forms have only been collected from Europe: the speciosus form from

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[1] According to Article 45g(i) of the 1985 International Code of Zoological Nomenclature adopted by the XX General Assembly of the International Union of Biological Sciences, a new name proposed as a form after 1960 is infrasubspecific and not officially recognized.

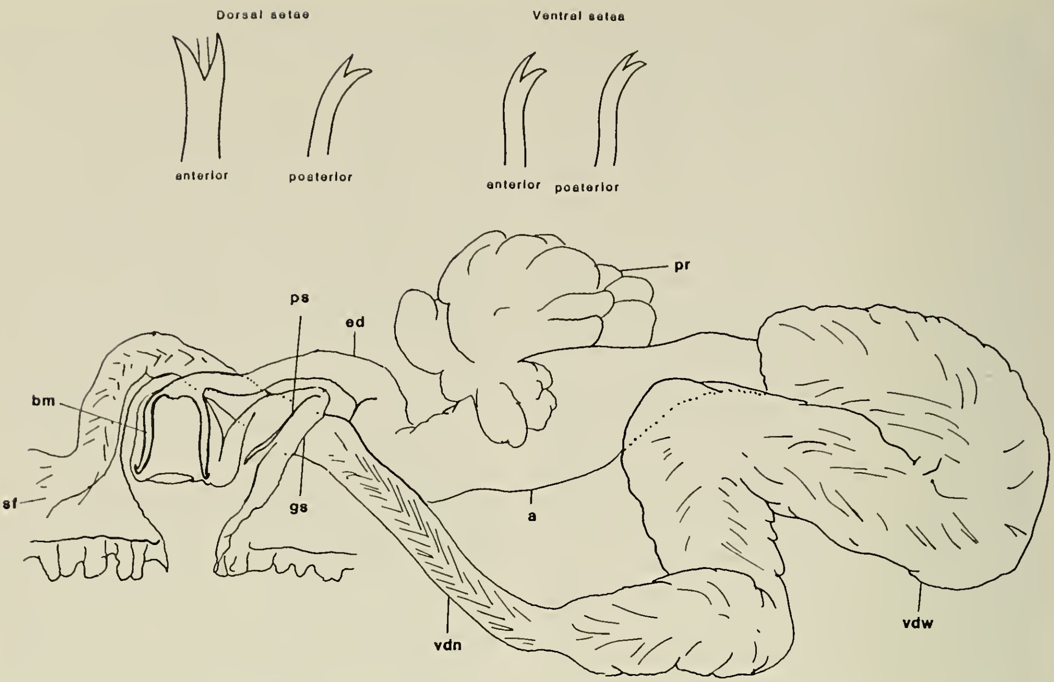


Fig. 2. Male efferent duct and characteristic setae of *Haber speciosus,* fluminialis form, from South Carolina. Abbreviations as in Fig. 1.

Ochrida Lake, Yugoslavia, and the zavreli form from Poland and Slavakia. In the original description of *Haber speciosus* (Hrabě, 1931) Hrabě referred to glandular hypodermal swellings on the body wall. This character was absent from the types Holmquist (1979) examined. However Holmquist (1979) does report the body of *H. speciosus* and *H. zavreli* to be finely ringed post-clitellarly. Hrabě (1981) regarded the latter to be a subspecies of *H. speciosus.*

The simsi form has been found on both sides of the Atlantic: two streams in Dorset, England, and the Head Springs region in Crystal River, Florida. Brinkhurst (1966) described *simsi* as a separate species of *Peloscolex,* synonymized it with *speciosus* in 1971, and subsequently transferred it to the genus *Haber* (Brinkhurst 1981) as one of a string of possible species. Bird and Ladle (1981) redescribed *H. simsi.* None of the previous references described the male efferent ducts. Bird and Ladle (1981) cleared their material in polyvinyl lactophenol. Consequently, a description of the internal male genitalia is not possible. However, from examination of their specimens, all observable characters agree with the specimens from Florida, which have been determined to be a separate form of *H. speciosus* (Fig. 1). A few specimens from Florida and England have been found with hispid hair setae.

The fluminialis form of *Haber speciosus* was previously described as *Haber* cf. *speciosus* (Brinkhurst 1981). Examination of subsequent material from Maryland and South Carolina has determined it to be another form of *H. speciosus* (Fig. 2) unique to the east coast of the United States. The term fluminialis refers to the streams from which it has been collected.

Table 1.—Body size and setal length of the forms of *Haber speciosus.*

| | speciosus | zavreli | simsi (England) | simsi (Florida) | fluminialis (New York) | fluminialis (Maryland) | fluminialis (South Carolina) |
|---|---|---|---|---|---|---|---|
| Number of segments | 70 | 50–68 | 42 | 94–107 | 19* | 74–80 | 70 |
| Length (mm) | 10 | 12 | 11 | 12 | * | c. 15 | NA |
| Width (mm) | 0.16 | 0.3 | 0.4 | 0.24–0.64 | 0.15 | 0.30–0.47 | 0.22–0.29 |
| Spermathecal setae (μm) | NA | 62–67 | >35 (broken) | 46–54 | 60 | 50–72 | 47–67 |
| Penial setae | NA | 62–67 | 62 | 47–62 | 63 | 54–70 | 46–64 |
| Dorsal crotchets (anterior) (μm) | NA | NA | 65 | 46–59 | 54 | 55–70 | 44–65 |
| Dorsal crotchets (posterior) (μm) | NA | NA | 38 | 40–60 | 43 | 37–52 | 40–45 |
| Hair setae (anterior) (μm) | 290 | 448 | 300 | 157–250 | 200 | 205–245 | 137–232 |
| Hair setae (posterior) (μm) | 290 | NA | 362 | 287–442 | 142 | 147–215 | 95–170 |
| Ventral setae (anterior) | NA | 90 | 55 | 40–53 | 54 | 55–63 | 45–51 |
| Ventral setae (posterior) | NA | c. 90 | 49 | 40–50 | 43 | 44–62 | 43–48 |

* = incomplete.
NA = not available.

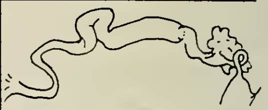
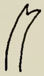
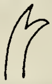
The fluminialis form is most similar to the speciosus form, but differs in number and morphology of anterior pectinate and ventral bifid setae (Table 2). It differs from the zavreli form by having an equal or slightly subequal lower tooth on all ventral setae, fewer intermediate pectinate teeth, and bifid posterior dorsal crotchets. It may be separated from the simsi form by possessing bifid crotchets instead of pectinate setae and shorter hair setae in posterior dorsal bundles.

## Discussion

Separation of species within the genus *Haber* is difficult because of the extensive intraspecific morphological variation of setae. Brinkhurst and Chapman (pers. comm.) have demonstrated that a change in the conductivity of the water can alter the degree of pectination of dorsal crotchets in two unrelated tubificid species, can change the length of hair setae and cause them to have a hispid appearance, and can even remove hair setae altogether. Additional experiments have indicated that setal variations have been associated with salinity and ionic concentrations (Giere and Pfannkuche 1982). The relative length of the teeth on the crotchets may also be subject to variation due to wear (Brinkhurst 1971). Consequently, the basic criteria for distinguishing *Haber speciosus* from its congeners should be based primarily on the configuration of the male efferent ducts and secondarily on the setal shape and distribution, the latter characters being most useful in the separation of "forms" or distinct populations exhibiting the same genital morphology.

The two largest species of *Haber* are notable exceptions, because their setae are so distinct from their congeners. *Haber svirenkoi* and *H. dojranensis* are the only members of this genus lacking pectinate setae, and having the upper tooth of dorsal and ventral bifid setae much shorter than the lower. *Haber svirenkoi,* the only species (in mature specimens) lacking preclitellar hair setae, has a greater number of anterior dorsal crotchets, and is the largest (Tables 3 and 4). Although these characters distinctly separate *H. svirenkoi* from the other seven congeners, comparison of the vas deferens will further distinguish this species from *H.*

Table 2.—Distinguishing characters of the species of *Haber.*

| Haber Holmquist, 1978 | dorsal crotchet setae per bundle | | dorsal hair aetae per bundle | | ventral bifid setae per bundle | | morphology of male efferent ducts |
|---|---|---|---|---|---|---|---|
| | anterior | posterior | ante-rior | poste-rior | anterior | posterior | |
| *svirenkoi* Lestokin, 1937 | 3-7  | 3-7  | 1 (2) (from IX in immeture forms) | 1 (from XIII in mature forms) | 3-8  | NA  |  |
| *dojranensis* Hrabe, 1958 | 3-5  | 3-5  | 1 | 0-1 | 3-6  | 2  |  |
| *monfalconensis* Hrabe, 1966 | 1-2 (3)  | 1  | 1-2 | 1 | 3 (4)  | 3-2  |  |
| *amurensis* Sokolskaja and Hrabe, 1969 | NA  | NA  | 1-3 | NA | 3  | 2-3  | NA |
| *pyrenaicus* Juget and Giani, 1974 | (1) 2-5  | 2-3  | 2-3 | 2-3 | (1,2)3-5 (6)  | 3-5  |  |
| *turquini* Juget and Lafont, 1979 | 1  | 1 NA | 1(2) | 1(2) | 1,2,3 (4)  | 1,2,3,(4) NA | NA |
| *hubsuglensis* Semernoi and Akinshina, 1980 | 3-4  | 2  | 2-3 | 1-2 | 4-6  | 3-4  |  |
| 'Peloscolex sp.' Giani and Martinez-Ansemil, 1981 | 1  | NA | 1 | 1 | 1-2  | 1-2  | NA |

NA = NOT AVAILABLE

*speciosus.* The ental portion of the vas deferens in *H. svirenkoi* is narrower (c. 12 μm vs. c. 20 μm), and the ectal region is much greater (c. 40 μm vs. >65 μm) and lacks ciliation. Whereas Finogenova (1972) describes a chitinous tubular structure at the male sexual orifice, further investigation may reveal it to actually be synonymous with the basal membrane of *H. speciosus,* as indicated by Holmquist (1979).

The shape of the male efferent duct can also be used to differentiate *H. speciosus* from *H. dojranensis.* The vas deferens of the latter is of uniform width, not distinctly set off from the very narrow atrium (Table 4).

*Haber speciosus* can be distinguished most reliably from the remaining taxa by comparing the position of the spermathecal pore in relation to the ventral seta, and the shape

Table 3.—Size, position of spermathecal pore and type-locality of the species of *Haber.*

| Species | Segment number | Length (mm) | Width at clitellum (mm) | Spermathecal pore | Type-locality |
|---|---|---|---|---|---|
| *speciosus* | 70–170 | 10–12 | 0.16–0.47 | in lateral line | Lake Ochrid, Yugoslavia |
| *svirenkoi* | 180 | 22–38 | NA | in line of ventral setae | Dnepr River, U.S.S.R. |
| *dojranensis* | 140–150 | 20–25 | NA | in line of ventral setae | Lake Dojran, Yugoslavia |
| *monfalconensis* | NA | NA | 0.28 | in line of ventral setae | Timova River, Europe |
| *amurensis* | NA | NA | 0.44 | in line of ventral setae | Amur River, U.S.S.R. |
| *pyrenaicus* | 50–70 | 9–15 | 0.4–0.5 | in line of ventral setae | Mountain Lakes, High Pyrenees |
| *turquini* | 13–27 | 1–3 | 0.14–0.32 | in line of ventral setae | Puits de Rappe, France |
| *hubsugulensis* | 38 | 10 | 0.36 | in line of ventral setae | Lake Khubsugul, Mongolia |

NA = not available.

of the male efferent duct. The spermathecal pore is located in the line of the ventral setae in all species except *H. speciosus,* where it lies in the lateral line dorsal to the ventral seta (Table 3).

*Haber monfalconensis* was originally described as a subspecies of *H. speciosus* (Hrabě 1966), but Brinkhurst and Jamieson (1971) synonymized it with *H. speciosus* along with *Peloscolex simsi* and *P. zavreli.* Holmquist (1979) elevated it to species status because the position of the spermathecal pore is in line with the ventral setae. The narrow region of the vas deferens is also shorter as is the ejaculatory duct which enters the atrium more gradually (Table 4). A further separation is based on the shape of the pectinate setae. In *H. monfalconensis* the lateral teeth are acute and very long, the upper tooth longer than the lower (Hrabě 1966) (Table 4). In *H. speciosus* the lateral teeth are obtuse and of equal length (Table 3).

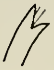
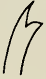
Somatic setae of *H. speciosus* and *H. pyrenaicus* are very similar. Conversely, the genital setae are distinctive. Penial setae are rarely present in *H. pyrenaicus,* and the spermathecal setae are more than twice as long (120–130 $\mu$m) as those observed in *H. speciosus.* The male genitalia of *H. pyrenaicus* are also considerably different: the vas deferens is of uniform width, the prostate is attached posteriorly on the atrium, and the ejaculatory duct is absent (Table 4). As in *H. svirenkoi,* the basal membrane of the penis may have been misinterpreted as a cuticular sheath.

The only way to separate reliably *H. speciosus* from *H. hubsugulensis* is to compare the morphology of the male genitalia. The vas deferens of the latter species is similar in shape to that of *H. speciosus,* but is approximately one-half the width. The atrium is sacciform, leading directly into a cone-shaped penis and the ejaculatory duct is absent (Table 4). Semernoi and Akinshina (1980) describe the penis of *H. hubsugulensis* as being covered by a thickened cuticle, but without a separate penial case.

Descriptions of *H. turquini* and *H. amurensis* were derived from poorly preserved material and are here only tentatively considered as distinct species. Sokolskaja (1961) briefly described *H. amurensis* as *Tubifex* sp. No. 1 from the examination of a single incomplete specimen in poor condition. The subsequent conflicting description by Hrabě (1969) as *Tubifex amurensis* was based on a single series of damaged longitudinal sections. Although the description is adequate enough to commit it to the genus *Haber,* I agree with Brinkhurst (1971) that a specific designation should be reserved until additional specimens of better quality are examined. At present, the location of the spermathecal pore in line with the ventral setae of *H. amurensis* is the only definitive character to separate it from *H. speciosus.*

The description of *H. turquini* (Juget and Lafont, 1974) omits the morphology of the

Table 4.—Distinguishing characters of the forms of *Haber speciosus.*

| Haber speciosus forms | dorsal crotchet setae per bundle | | dorsal hair setae per bundle | | ventral bifid setae per bundle | | morphology of male efferent ducts |
|---|---|---|---|---|---|---|---|
| | anterior | posterior | anterior | posterior | anterior | posterior | |
| speciosus | 1-2  | 1-2  | 2-3 | 1 | 3-4  | 1-2 |  |
| simsi (England) | 1-3  | 1  | 1-2 | NA | 3-4 (5)  | 2  | NA |
| zavreli | 1  | 2-3 | 2 | 0 | 2-3  | NA  |  |
| simsi (Florida) | 2-4  | 1-2  | 1-2<br>(3) | 1 | 3-6  | (1) 2-3  |  |
| fluminialis (Maryland) | 2-4  | 1  | 2-3 | 1 | 4-7  | (1) 2-3  | NA |
| fluminialis (South Carolina) | 4 (5)  | 1 (2)  | 2-4 | 1 | 4-8  | 2  |  |
| "possible congener" (New York) | 1-2  | 1  | 1-2 | 1 | 4-5  | 2  | NA |
| fluminialis (New York) | 2-3  | 1  | 1-3 | 0-1 | 3-6  | 2-3  | NA |

NA = NOT AVAILABLE

genitalia (other than the presence of modified spermathecal and penial setae) because of poorly preserved material, but somatic characters are distinctive enough to separate it from *H. speciosus. Haber turquini* is the smallest species in this group, and the only one to have a papillate cuticle reminiscent of *Peloscolex.* The shape of the "gaine cuticulisée" covering the penis is of the form characteristic of the basal membrane in other species of *Haber,* and may prove to be the same structure upon further examination of additional material.

Two specimens of indeterminable status have been described in the literature and tentatively referred to this genus (Brinkhurst 1981; Brinkhurst and Wetzel 1984). Giani and Martinez-Ansemil (1981) collected a mature specimen, identifying it as "*Peloscolex* sp." They compared it to *H. speciosus* and *H. zavreli.* Penial setae are absent, but the penis is enclosed by a "cuticular sheath" similar to *H. zavreli.* The shape of the spermatheca and spermatophore also conform to the genus *Haber.* Until conspecifics can be more thoroughly examined, this species is best left undesignated.

Brinkhurst (1981) mentioned a "possible congener" from the Hudson River, New York, of a species he referred to as *Haber* cf. *speciosus* described from the Susquehanna River, New York. The specimen was deposited in the United States National Museum of Natural History (USNM 65224) and identified as *Peloscolex speciosus.* The specimen was mounted in a clearing medium. Consequently, the genital morphology cannot be determined. However, the presence of spermathecal and penial setae suggests its placement in the genus *Haber.* The morphology of the somatic setae is different from any form thus far encountered in North America (Table 2). Examination of additional specimens will probably establish it as either a new species of *Haber* or as an additional "form" within the complex of *Haber speciosus,* most similar to the zavreli form.

As Bird and Ladle (1981) indicated, immature specimens of *H. simsi,* confirmed herein as a synonym of *H. speciosus,* may be confused with *Tubifex ignotus.* They presented a comparison between the setae of the two species, and used this character as a basis for separation. Unfortunately, due to the plasticity of the setal morphology, this distinction is unreliable. Care must be exercised when referring to the taxonomic key prepared by Stimpson and Klemm (1982) on the Tubificidae of North America. An immature specimen of *H. speciosus* will be misidentified as *T. ignotus.* Careful examination of mature specimens is essential for accurate identification.

## Summary

The genus *Haber* is newly reported from eastern North America. Specimens were examined from New York, Maryland, South Carolina, and Florida, and have been determined to be the same species, *Haber speciosus,* based on similar morphology of the male efferent duct. The eight species of *Haber* are separated, primarily by differences within the male genitalia, and secondarily by setal morphology and modifications of the body wall. Four distinct forms of *H. speciosus* can be distinguished on the basis of their setal morphology. Two of these forms are represented in the North American fauna, the fluminialis form and simsi form. The former has been found only on the east coast of North America. The latter has been collected from the Gulf of Mexico, Florida, and from England. The material from England was originally described as a distinct species, *P. simsi.* The remaining two forms, zavreli and speciosus, have only been reported from Europe.

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# REDESCRIPTION OF THE OLIGOCHAETE GENUS *PROPAPPUS,* AND DIAGNOSIS OF THE NEW FAMILY PROPAPPIDAE (ANNELIDA: OLIGOCHAETA)

Kathryn A. Coates

*Abstract.*—Examination of type material of *Propappus glandulosus* Michaelsen, 1905, and *P. volki* Michaelsen, 1916, as well as other material of the latter, led to a reconsideration of the classification of *Propappus* Michaelsen, 1905, within the Enchytraeidae. Species included in *Propappus, P. volki, P. glandulosus,* and *P. arhyncotus* Sokolskaja, 1972, possess character-states that are unique. They have sigmoid, nodulate, bifid setae; large epidermal glands posterior to each setal bundle; spermathecal pores at septum 3/4; and glandular parts of the vasa deferentia located posterior to 11/12. Another significant, unique character state is the location of the single pair of ovaries in XIII, except in *P. arhyncotus,* rather than in the male pore segment, XII. This character, in addition to the others, warrants the removal of *Propappus* from the Enchytraeidae. The new, monotypic family Propappidae is erected for species of *Propappus.* The genus *Propappus* is redefined. *Propappus glandulosus* and *P. volki* are redescribed, and a description of *P. arhyncotus* is given.

*Propappus* Michaelsen, 1905, has been accepted as being nearest the stem form of the Enchytraeidae (Michaelsen 1916a, 1923; Stephenson 1930; Cernosvitov 1937a; Timm 1981). These authors thought that *Propappus* exhibited a high number of ancestral states for the Enchytraeidae, reminiscent of a freshwater origin of the family. All species of the genus, *P. glandulosus* Michaelsen, 1905, *P. volki* Michaelsen, 1916, and *P. arhyncotus* Sokolskaja, 1972, are known from temperate, fresh waters. The presence of both *P. glandulosus* and *P. volki* in Lake Baikal, an ancient lake, enhanced the view of the genus as, itself, relatively ancient. *Propappus volki,* the species most studied, is regarded as characteristic of pure waters with sandy bottoms, and strong or moderate currents (Bird 1982).

Michaelsen (1905) established the genus *Propappus* and described its type species (by monotypy), *P. glandulosus.* In his diagnosis of this genus he noted that one characteristic was unique for the Enchytraeidae: the setae on all the segments were distinctly double-pointed (now see also *Barbidrilus* Loden and Locy, 1980). His species description included other character states anomalous for Enchytraeidae: 1) each setal bundle was associated with a large, glandular organ; 2) setae occurred ventrally in the male pore segment; 3) the sperm funnel was not glandular, but the ental part of the vas deferens, posterior to 11/12, was thickened and glandular; and 4) the ovary was located on the posterior of 12/13, in the segment posterior to the male pore segment. According to the latter character state the species of *Propappus* were plesiopore, like all other enchytraeids, but had a sterile segment between the two fertile segments, as in many earthworms (Lumbricida Brinkhurst, 1982) and some Haplotaxidae and Lumbriculidae.

Michaelsen (1916a, b) described a second species, *Propappus volki.* It differed from *P. glandulosus* in that it was slightly larger and possessed a well-developed, finger-like, prostomial proboscis. Michaelsen (1916a) noted that the ectal pore of the spermatheca was anterior to the setae of IV, as ("wie auch bei . . .") in *P. glandulosus*. This was, in fact, an amendment to the original description of *P. glandulosus* in which the spermathecal pore had been described in the usual enchytraeid position, at 4/5. In his early papers on *Propappus*, Michaelsen (1905, 1916a) described the ovaries in XIII, with the egg cell string extending from 12/13, and clearly recognized (Michaelson 1905) that this was not the usual enchytraeid condition. He did not include the location of the ovaries in the diagnosis of *Propappus*. Later, Michaelsen (1923) described the ovaries in *P. volki* as lying on the posteroventral part of 11/12. He reported that he had never clearly seen the female funnel or female pore but thought that both were in 12/13. Material from the Volga River was used for these (Michaelsen 1923) amendments to the description of *P. volki*.

Michaelsen (1916a) suggested that, because of the double-pointed setae, the lack of integrity of the pharyngeal glands, the loose structure of the nephridial postseptale, and the structure of the sperm funnel (=the preseptal part of the male duct), *Propappus* was very likely near the stem form of the Enchytraeidae. Cernosvitov (1937a) stated categorically that *Propappus* was the most primitive genus of the Enchytraeidae. This, he thought, was most clearly shown by the setal form and the structure of the sperm funnels. He also suggested that a number of character states pointed to a close affinity between *Propappus* and a subgroup of *Mesenchytraeus* Eisen, 1878, including nephridial form, structure of the pharyngeal glands, development of the sperm funnel, and structure of the longitudinal muscles. Nielsen and Christensen (1959) suggested that *Propappus* was rather doubtfully placed in the Enchytraeidae at all. At no time was the diagnosis of that family amended to include the gonadal arrangement originally described in *Propappus*, nor were derived character states unifying *Propappus* with other Enchytraeidae recognized. Instead, many of the derived character states possessed by *Propappus* are unique and those states that are shared with Enchytraeidae can only indicate some more remote common ancestor.

## Materials and Methods

Cotype material was borrowed from the British Museum (Natural History). All material was examined under a compound microscope. Drawings were made with the aid of a drawing tube (camera lucida). Photographs were made using a Zeiss-Universal photo-microscope. The means of the lengths of the probosces of *Propappus volki* in different populations were compared using the two-sample *t* test for two-tailed hypotheses, all means were tested for significant difference from 0 and the samples were compared by a non-parametric Mann-Whitney U test (Zar 1974).

## Propappidae, new family

*Type genus.*—*Propappus* Michaelsen, 1905.

*Diagnosis.*—As for type genus.

*Distribution.*—Palearctic.

*Discussion.*—Species of the genus *Propappus* do not exhibit apomorphies shared with other Enchytraeidae. A group Enchytraeidae, including *Propappus*, cannot be diagnosed. The few, obviously derived character states of *Propappus* do not allow an immediate, intuitive choice for the precise position of *Propappus* within the existing classifications of the Oligochaeta. A new family of Oligochaeta, the Propappidae with type genus *Propappus*, is established here for the single genus and its included species *P. glandulosus*, *P. volki*, and *P. arhyncotus*.

The family Propappidae is phylogenetically near both the Enchytraeidae and some species of Haplotaxidae (Coates MS). Those species of Haplotaxidae from which the lineage of the family Propappidae is not yet clearly resolved include *Metataxis americanus* (Cernosvitov 1939) and *M. brink-*

*hursti* (Cook 1975) in the recently recognized genus *Metataxis* Righi, 1985. Along with at least some Enchytraeidae, species of Propappidae are in a monophyletic lineage including *Metataxis falcifer* (Omodeo 1958). The initial implications of this are that *Metataxis* is paraphyletic. Characteristic of all these nominal taxa is the presence of a pair of testes in at least segment XI, and, with the exception of Enchytraeidae, the occurrence of paired ovaries only in segment XIII. In order to conserve a consistent taxonomy of the sistergroup Enchytraeidae, and to avoid attenuating the diagnosis of that family, the new family Propappidae is erected for the genus *Propappus.* The outgroup criterion for determining relative polarity of character states should be applied and phylogenetic analyses performed to resolve these genealogical problems.

The primary distinguishing characteristics of this monotypic family are discussed following the diagnosis of *Propappus.*

### *Propappus* Michaelsen, 1905

*Propappus* Michaelsen, 1905:24–25; 1916a: 51–55; 1923:37–42.—Stephenson, 1930: 765–766.—Cernosvitov, 1937a:264–267, 269–270, 277, 279.—Nielsen and Christensen, 1959:29–30.—Cekanovskaja, 1962:370–377.

*Palpenchytraeus* Michaelsen, 1916b:1; 1916a:52; nomen nudum.

*Type species.*—*Propappus glandulosus* Michaelsen, 1905, by monotypy.

*Diagnosis.*—Setae in 4 bundles per segment, including genital segments; bundles ventrolateral and dorsolateral. Three setae, rarely 2, per bundle; setae sigmoid, bifid, nodulate. Setal gland present immediately posterior to each setal bundle (Figs. 1a, g; 2a & 2b). Head and other dorsal pores absent. Prostomium with or without proboscis. Clitellum single-layered, usually extending over XII–XIV. Pores of male and female reproductive systems paired. Spermathecal pores anterolateral in IV. Male pores (Fig. 1a, m) anterior to ventral setal bundles and setal glands of XII. Female pores ventral, in or just posterior to 13/14. Anus opening dorsally. Cavity of prostomium almost filled by elongate, glandular, epidermal cells (Fig. 1a, pg). Brain deeply cleft posteriorly, divided into almost separate, lateral lobes. Dorsal pharyngeal pad (Fig. 1a, p) slightly thickened, protrusile. Bodies of glandular cells of pharyngeal pad not organized into compact pharyngeal glands. Gut without appendages or diverticula; expansion at intestinal origin may be abrupt. Holonephridial, preseptal parts of nephridia small (Fig. 1b), including funnel only; postseptal parts lobed, with little interstitial tissue. Spermathecae paired (Fig. 1a), originating in IV, not communicating with gut; ectal duct thick-walled, aglandular; ampulla abruptly expanded, thin-walled, extending posteriad through a few segments. One pair of testes (Fig. 1a, t) ventrolateral on posterior of 10/11. Seminal vesicle (Fig. 1a, sv) unpaired, extending as far anteriad as VI. Sperm funnels (Fig. 1a, sf) simple, on 11/12; vasa deferentia confined to XII, anteriorly thickened (?glandular). Atria, prostates and other copulatory glands lacking. One pair of ovaries (Fig. 1a, o) ventrolateral on the posterior of 12/13 (see *P. arhyncotus*). Female ducts simple, on 13/14 (as above).

*Distribution.*—Palearctic. Central and eastern USSR; England; France; Austria; West Germany; Finland; and Norway. Lakes or running waters with moderate to strong currents; in sand or gravel.

*Discussion.*—The Enchytraeidae can be characterized by their possession of a number of shared character states: discrete, well-developed pharyngeal glands; testes only in XI, male pores and ovaries in XII; preseptal, glandular sperm funnels in XI; dorsal setal bundles, when present, (usually) in a mid-lateral position; spermathecal pore/pores at or just posterior to 4/5; and, frequently, modified glandular structures at the penial pore.

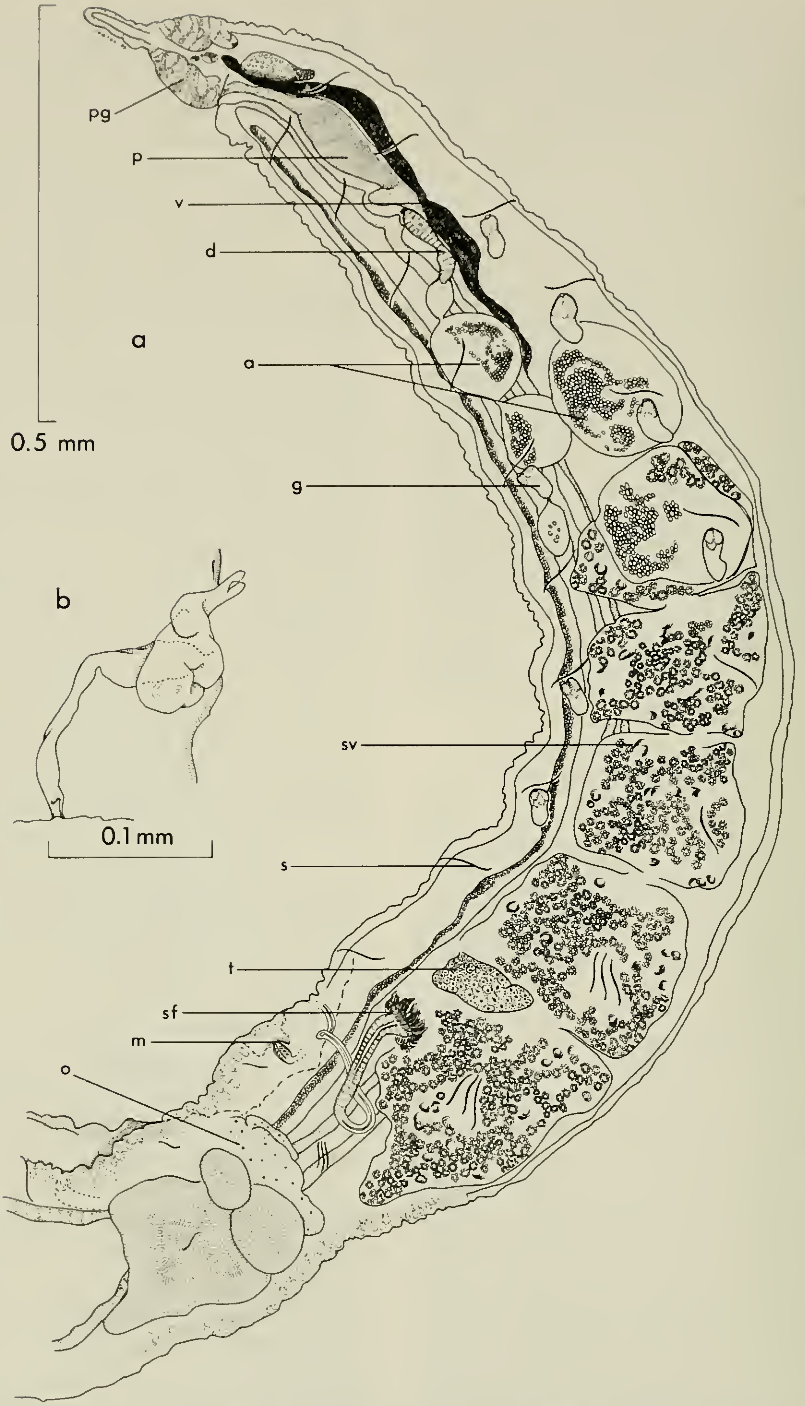

Fig. 1. *Propappus volki*: a, Drawing of anterior of whole-mount, to segment XIV; b, Nephridium from postclitellar segment; specimens from southern England. Abbreviations—a, spermathecal ampulla; d, spermathecal duct; g, setal gland; m, male pore; o, ovary; p, pharynx; pg, prostomial glandular epidermis; s, seta; sf, sperm funnel; sv, seminal vesicle; t, testis; v, dorsal blood vessel.

The species of *Propappus* share a set of character states distinct from those of the Enchytraeidae: setae with bifid ectal ends, usually three per bundle; setal glands in association with every setal bundle; spermathecal pores at or near 3/4; thickened vasa deferentia in XII; and ovaries only in XIII with female funnels on 13/14.

The species of *Achaeta* Vejdovsky, 1877, a genus of the Enchytraeidae, lacking setae entirely, may possess sac-like organs in positions similar to those occupied by either the setal follicles of setate genera or by the setal glands of species of *Propappus.* The homologies of the organs in *Achaeta* have been debated by several authors (Michaelsen 1923, Stephenson 1930, Nielsen and Christensen 1959). In megadrile and some haplotaxid oligochaetes various glandular appendages of setal follicles, which may not all be homologous structures (Stephenson 1930), have also been termed setal glands.

The organs of *Achaeta* were first described (Vejdovsky 1879) as homologues of the setae, possibly as the empty follicles. Michaelsen (1923) did not think that it was possible to distinguish the setal follicles of *Achaeta* from the setal glands of *Propappus*; the organs in *Propappus* were just composed of fewer, larger cells. Thus the glands were not a unique character of *Propappus.* Both Stephenson (1930) and Cekanovskaja (1962) also saw the structures of *Achaeta* as setal glands but Nielsen and Christensen (1959) referred to these as setal follicles or setal sacs for which the true homology ("nature") was doubtful.

In sectioned and whole-mounted specimens of *Achaeta* that I have examined using a compound light microscope, cellular structure inside the cuticular sac of the setal gland could not be discerned. The contents of the cuticular sacs were granular and not densely packed. The internal cellular structure of the organs of *Propappus* is easily discernible at similar magnifications, although it does not stain with borax carmine in whole mounts. The cells of the gland do stain with haematoxylin and are quite obvious in sectioned material. A cuticle-like outer layer can be distinguished in both whole-mounts and in sections. There appear to be two types of secretory cells present in each gland, distinguished by the stained color and by the coarseness of the granular inclusions. Such a glandular-type complement is common in invertebrate adhesive-gland systems. Cekanovskaja (1962) observed that specimens of *P. volki* adhere to stone and sand grains by means of some secretion from the setal glands of the posterior segments.

With the present information it is not possible to establish the probable homologies of the setal glands of either *Propappus* or *Achaeta.* Their distribution in *Propappus* specimens, co-occurring with all setal bundles, is unique among the microdrile oligochaetes.

Other characteristics of *Propappus* are not regarded as derived. These are the presence of unmodified, ventral setae in the male pore segment; dorsolateral location of the dorsal setal bundles; unmodified gut; diffusion of the pharyngeal gland cell bodies; and the lack of interstitial tissue associated with the postseptal part of the nephridia. These characteristics are considered "primitive" for the class Oligochaeta (Jamieson 1978; Brinkhurst 1982, 1984).

### *Propappus glandulosus* Michaelsen, 1905
Figs. 2a, 2c & 2d

*Propappus glandulosus* Michaelsen, 1905: 25–28, figs. 4–5.—Cernosvitov, 1937b: 273–274, figs. 3–4.—Cekanovskaja, 1962: 371–272, fig. 187.

?*Propappus volki.*—Sokolskaja, 1968:21.

?*Propappus arhyncotus* Sokolskaja, 1972: 83–85, fig. 5; 1973:64–66, fig. 8.

*Material examined.*—Syntypes of *Propappus glandulosus,* BMNH 1949.3.1.226, mature whole-mount; BMNH 1949.3.1.227, a mature, sagittally sectioned specimen; and BMNH 1949.3.1.228, a mature, transverse-

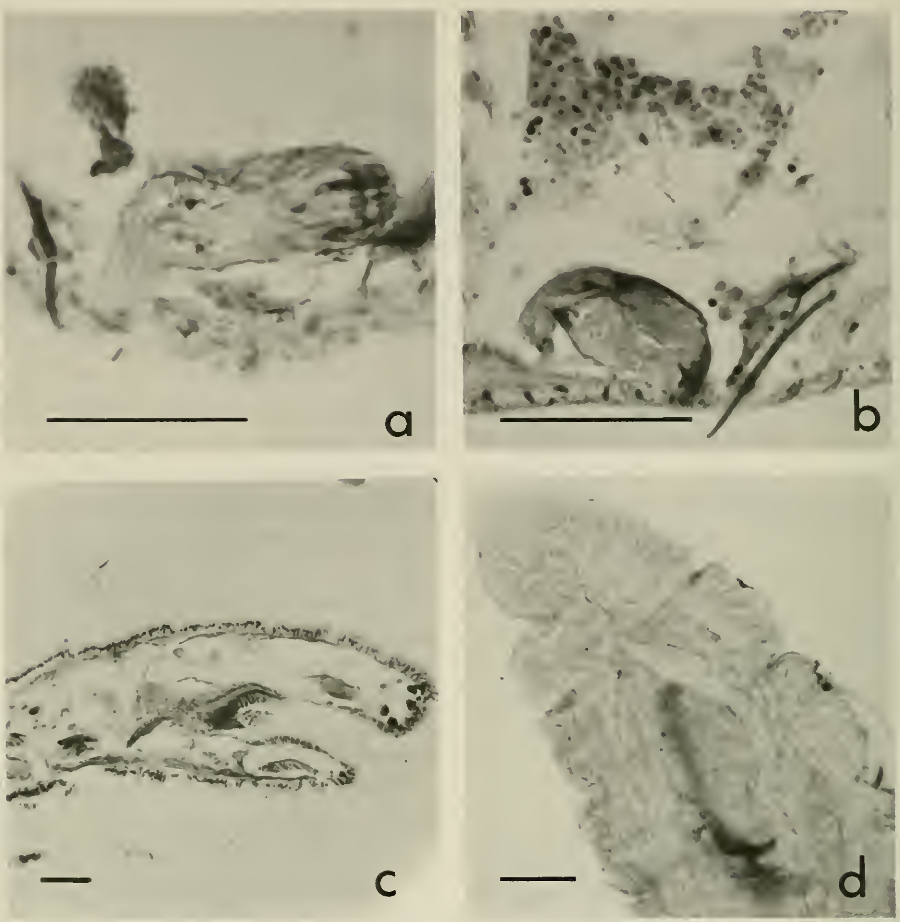

Fig. 2. a, *Propappus glandulosus,* setal gland from sectioned cotype specimen BMNH 1949.3.1.227; b, *Propappus volki,* setal gland and seta from sectioned cotype specimen BMNH 1949.3.1.230; c, *Propappus glandulosus,* sagittal section of prostomium and pharyngeal pad of cotype BMNH 1949.3.1.227; d, *Propappus glandulosus,* prostomium of whole-mounted cotype specimen BMNH 1949.3.1.226. Scale bar = 50 μm.

ly sectioned specimen. Collected in 1901 or 1902.

*Type locality.*—Lake Baikal, middle and southwest side, in sand or gravel at 2–8 meters depth.

*Description of material examined.*—Four to 5 mm long, with 28–32 segments; body diameter at IV–V (specimens slightly compressed) 175–224 (175, 219, 224) μm, at IX about 300 (301, 307) μm. Prostomium short and rounded, without proboscis (Figs. 2c & 2d). Spermathecal pores at 3/4. Setae 55–73 (59-dorsal, 55, 73-ventral) μm up to 90 μm long (according to Michaelsen 1905); nodulus in distal one-third of seta; upper tooth much shorter and thinner than lower; ventral and dorsal setae alike in size. Female pore at 13/14. Setal glands (Fig. 2a) 80, 106 μm long, 22–32 (22, 26, 32, 32) μm in diameter, flask-shaped with narrow ectal neck; entire gland appearing filled with secretions. Pharyngeal gland cells ventral in V–VIII. First pair of nephridia at 7/8 or 8/9, nephridia absent in clitellar and most of more posterior segments. Dorsal vessel origin at abrupt transition from esophagus to intestine, in VIII or IX. Thick-walled ental parts of vasa deferentia about 120 μm long, 14, 24 μm in diameter; ectal part 2–3 times as long as ental, only 6–12 (6, 8, 7.5, 12) μm in diameter. Diameter of vas deferens at male pore may be slightly greater, about 13 μm, canal sometimes with short, abrupt widening just ental to pore. Spermathecal duct extending to one-half IV, ampulla extending into VI or more posteriad; duct narrowing gradually from pore to ampulla, from about 22 μm to 8–10 μm, then widening slightly at ampulla (according to Cernosvitov 1937b).

*Remarks.*—The cotype specimens of *Propappus glandulosus* examined here came from the collections of L. Cernosvitov held at the BMNH. This material was originally held in Hamburg and is from the type series (Cernosvitov 1937b).

*Discussion.*—Although Michaelsen (1923), in redescribing *Propappus volki,* amended the position of the ovaries from 12/13 to 11/12 he did not include this characteristic in a formal generic diagnosis. In fact, *P. glandulosus* was never redescribed with the "new" ovarial position.

Michaelsen (1905) reported that the origin of the dorsal blood vessel and the abrupt widening of the esophagus to the intestine was in VIII. This was the condition seen here in *P. glandulosus* and also in the new material of *P. volki* from Lake Baikal. Further comments on the determination of the intestinal origin are made following the description of *P. arhyncotus.*

*Propappus arhyncotus,* also aproboscidial, may be a synonym of *P. glandulosus,* as indicated. Three characteristics possibly distinguish the species. In *P. arhyncotus* the origin of the intestine is reported to be postclitellar, the diameters of the vasa deferentia are greater ectally than entally, and the ovaries are located in the anterior of XII (Sokolskaja 1972, and pers. comm.). These characteristics are discussed following the description of *P. arhyncotus.*

*Distribution.*—Lake Baikal, shallow (Michaelsen 1905) to abyssal (820 m) (Semernoj 1983); Yenisey River from the mouth of the Angara River to Igarka (Cekanovskaja 1962). As *Propappus arhyncotus*: Kamchatka Peninsula, Zhupanova River basin, Karymai Reach inflow to Bol'shaya River, and Kamchatka River basin (Sokolskaja 1972). On sand and gravel bottoms.

### *Propappus volki* Michaelsen, 1916
Figs. 1, 2b & 3

*Palpenchytraeus volki.*—Michaelsen, 1916b: (in Michaelsen, 1916a) 1. [nomen nudum].

*Propappus volki.* Michaelsen, 1916a:51–55; 1923, 37–42; 1926:4.—Cernosvitov, 1937b:273, figs. 1–2.—Chekanovskaja, 1962:372–373, fig. 188.—Wachs, 1967: 322, fig. 9.—Bird, 1982:67–75. Non Sokolskaja, 1968:21.

*Material examined.*—Cotypes from the Cernosvitov collection, BMNH 1949.3.1.230, mature, sagittally sectioned specimen, and BMNH 1926.927.1-5, 3 specimens in fluid, collected by W. Michaelsen, in the Lower Elbe River, near Hamburg; Nov 1915 to Jan 1916. Nineteen mature specimens collected from gravel at East Burton on the River Frome, Dorset, England, during period Jan 1979 to Dec 1980. All stained in alcoholic borax carmine. Fifteen specimens subsequently mounted whole in Canada balsam; 3 specimens sectioned transversely and 1 specimen sectioned sagittally, at 7 μm intervals. Twenty mature and 15 immature specimens collected from River Tarn, tributary of Garonne River, Massif Central near Albi, France; 17 Oct 1979. Four specimens attributed to *Propappus volki* from Lake Baikal. Two with developing gonads, one also with developing spermathecae and vasa deferentia. All mounted whole, as above.

*Type locality.*—Elbe River, near Hamburg, at 3–5 m depth.

*Description of material examined.*—Four to 7 mm long, with 29, 33–43 segments;

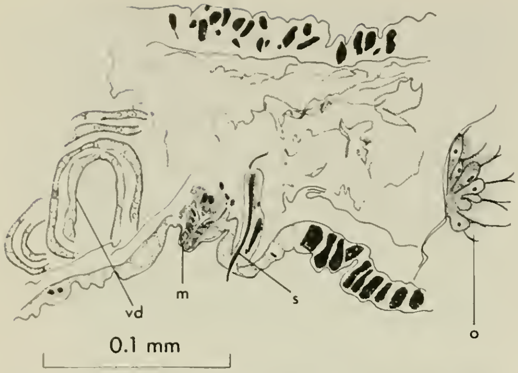

Fig. 3. *Propappus volki*, segment XII with male pore and anterior of XIII with part of an ovarial strand; drawn from a sagittally-sectioned specimen from southern England. Abbreviations—m, male pore; o, ovary; s, seta; vd, vas deferens.

body diameter at IV–V about 150–300 $\mu$m, at XI about 300–400 $\mu$m; body of mature specimens usually constricted through XII and XIII. Prostomium with annulate, nonretractile proboscis (Fig. 1a), up to 97 $\mu$m long; proboscis with distinct lumen. Setae (Fig. 1a, s; 3, s) 40–80 $\mu$m long, ventrals (preclitellar: $\bar{x} = 69.6 +/- 6.7$ $\mu$m [n = 17]; postclitellar: $\bar{x} = 60 +/- 12.4$ $\mu$m [n = 5]) on average just longer than dorsals (preclitellar: $\bar{x} = 64.0 +/- 14.0$ $\mu$m [n = 14]; postclitellar: $\bar{x} = 56.0 +/- 8.0$ $\mu$m [n = 8]); preclitellar setae slightly longer than postclitellar setae; upper tooth much thinner and shorter than lower. Epidermal papillae in transverse ring at level of setae; other epidermal glands in 12–15 transverse rows per segment. Spermathecal pores just posterior to 3/4. Clitellar gland cells small, scattered over XII through ½ XIV. Male pores each on small, conical papilla (Fig. 6, m), body wall usually depressed around papillae. Brain with median, anterodorsal projection. Anterior dorsal blood vessel dividing in front of brain, vessel originating in VII (Fig. 1a, v) or in clitellar segments. Abrupt expansion of gut in VII or XIV to XV. Setal glands (Figs. 1a, s; 2b) flask-shaped, with narrow ectal neck; glands in anterior segments with maximum diameter about 17–25 $\mu$m ($\bar{x}$ = 20.1 +/− 3.1 $\mu$m [n = 10]), about 40–70 $\mu$m ($\bar{x} = 57.4 +/- 8.8$ $\mu$m [n = 9]) long. Ectal end filled by large cells with dense, finely or coarsely granular contents. Gland enclosed by cuticle-like layer. Nephridia (Fig. 1b) from 5/6. Seminal vesicle (Fig. 1a, sv) extending as far anteriad as VI or VII and posteriad into XII. Testes (Fig. 1a, t) large, compact. Vas deferens sometimes with bit of thicker-walled ental part appearing to protrude into XI; ental part 20–52 $\mu$m ($\bar{x}$ = 40 +/− 10 $\mu$m [n = 15]) in diameter, 154, 171, 186 $\mu$m long; ectal part of vas about 7–16 $\mu$m ($\bar{x}$ = 12 +/ − 3.4 $\mu$m [n = 17]) in diameter, widening to 14–23 $\mu$m ($\bar{x}$ = 18.6 +/− 4.2 $\mu$m [n = 5]) at pore (Fig. 3, m), 2–4 times as long as ental part. Segment XII criss-crossed by muscular strands (Fig. 3). As many as 3 maturing eggs in XIII, extending into XII and/or XIV. Spermathecal ectal duct (Fig. 1a, d) bulbous just ental to pore, 21–29 $\mu$m ($\bar{x}$ = 26 +/− 3.2 $\mu$m [n = 12]) in diameter at pore to 11–17 $\mu$m ($\bar{x}$ = 13 +/− 1.7 $\mu$m [n = 12]) between expansion and ampulla. Ampulla (Fig. 1a, a) extending from 4/5 as far as XII, walls very thin.

*Remarks.*—As for *Propappus glandulosus*, the specimens of *P. volki* held at BMNH are cotypes. The comprehensive description of *P. volki* by Michaelsen (1923) included specimens from the Volga River but none of these could be obtained for this study. The Volga material and additional cotypes are held at the Zoologisches Museum Universität Hamburg.

*Discussion.*—The ovarial segment in the material examined was always XIII, and there was no evidence for lability of this character in *Propappus volki* (Michaelsen 1916a, 1923).

The origin of the dorsal blood vessel and gut transition in *Propappus volki* are consistently (Michaelsen 1916a, 1923) described as in postclitellar segments, XIV or XV. In the new material from Lake Baikal, none of which was fully mature, an abrupt expansion of the gut (?transition from esophagus to intestine) was located in VII or VIII, as for *P. glandulosus,* and the dorsal blood vessel origin was at the expansion or just anterior to it. The esophageal wall immediately posterior to the pharyngeal pad was highly folded in all specimens of *P. volki,* perhaps facilitating the eversion of the pad.

In many specimens, the ental part of the setal glands appeared empty. Here the cuticular layer was collapsed forming a "tail" (Fig. 2b) on the gland. The glands appeared to be larger and full in more mature specimens.

The length of the proboscis in specimens of *Propappus volki* obtained from England, France and Lake Baikal varied from 29 μm to 97 μm. Statistical comparisons of the proboscideal length for each population by the *t* test showed that the mean probosces lengths of the French and English populations were not significantly different at the 95% level (mean lengths were 56.2 +/− 11.2 μm [n = 26] and 64.6 +/− 15.9 μm [n = 15], respectively). The mean length of probosces (38.5 +/− 5.4 μm [n= 4]) for Baikal specimens was significantly different from the mean lengths of both French and English populations. The Mann-Whitney U test gave the same results. All mean lengths of probosces were significantly different ($P \ll 0.001$) from a mean of 0 when compared by a *t* test. The presence of a prostomial proboscis may be the only character state that can be used easily to distinguish *P. volki* from *P. glandulosus.* These species differ little in size or in the size and shape of various taxonomic characters including setae, spermathecae and male ducts.

Both *Propappus volki* and *P. glandulosus* are recorded from Lake Baikal. However, *P. glandulosus* is known from only a few additional locations near Lake Baikal, whereas *P. volki* is recorded from numerous, widespread locations in the USSR and Europe.

*Distribution.*—Widely distributed in western Europe: Germany (Michaelsen 1916a, Stephenson 1930, Wachs 1967); Austrian Tyrol (Bird 1982); France (Juget 1980, 1984); and northwest Spain (Martinez-Ansemil 1982). Britain, southern England (Ladle and Bird 1980, Bird 1982). Central and eastern Europe: rivers of the Baltic Sea Basin (Parele 1983); Latvia (Cekanovskaja 1962); Estonia (Bird 1982); Ukraine and Moldavia (Grigelis 1980); Poland: Tatra and Carpathian Mountains (Bird 1982), Welna and other Polish rivers (Kasprzak 1980); Czechoslovakia (Bird 1982); and Romania (Bird 1982). Central USSR: large rivers, especially Volga and tributaries, and reservoirs (Michaelsen 1923, 1926; Cekanovskaja 1962; Grigelis 1980; Bird 1982); Lakes Baikal, Chud and Pskov (Cekanovskaja 1962). In springs and phreatic waters (moving ground waters); small stony streams, on sand beds in large rivers, in the sandy substrates of lakes and reservoirs (Bird 1982).

### *Propappus arhyncotus* Sokolskaja, 1972

*Propappus arhyncotus* Sokolskaja, 1972:83–85, fig. 5; 1973:64–66, fig. 8.
*Propappus volki.*—Sokolskaja, 1968:21.

*Type material.*—No. 1001 in the Zoological Museum of Moscow University (not seen). Collected 11 Aug 1964 by V. Ya. Lavanidov.

*Type locality.*—Kamchatka, Lake Azabach'e at 7 cm depth; gravel substrates.

*Description from the literature.*—Six to 12 mm long, maximum diameter 300–400 μm; with 29–40 segments. Prostomium large, without proboscis. Setae commonly 3–4, rarely 5–6 per bundle in preclitellar segments, usually 3 posteriorly. Dorsal setae 55–71 μm long, ventral setae 59–76 μm long; length of setae increasing slightly from anterior to posterior segments; upper tooth much shorter and thinner than lower; nodulus distal. Spermathecal pores approximately lateral at or in 3/4. Small epidermal tubercles irregularly distributed on prostomium and peristomium, in more regular rings in following segments. Male pores on cone-shaped papillae. Setal glands flask-shaped, about 55 μm by 27 μm at segments VII–X. Most anterior nephridia in V (? at 5/6). Esophagus widening to intestine at XV. Vasa deferentia about 310 μm long, widening from about 17 μm in diameter entally to 29 μm near pore, distal end further widened to 34–38 μm but with narrow channel. Ovaries paired in anterior of XII. Spermathecal duct about 160 μm long, extending through IV, ampulla may extend into VI.

*Remarks.*—It has not been possible to borrow or otherwise obtain specimens of *Propappus arhyncotus,* and some questions concerning its structure could not be resolved.

*Discussion.*—Sokolskaja (1972) recorded that bundles of three through six setae were present; however, she consistently depicted (1972, fig. 5A, obviously schematic) only three setae per bundle. Other species of *Propappus* have only two or three setae per bundle. As in some enchytraeids, replacement setae may be present at the same time as the seta or the bundle being replaced. This was observed here in *P. volki.* The entire bundle complement can be replaced simultaneously, leading, in *Propappus* species, to bundles appearing to have four or six and possibly five setae.

The condition of the male duct described by Sokolskaja (1973) for *Propappus arhyncotus* is quite different from that found in either *P. volki* or *P. glandulosus.* In the former the vas deferens widens from the ental to the ectal end whereas in the latter two species the ental part (about one-quarter of the total length of the vas deferens) is notably wider and the walls more "glandular" than in the ectal part. In *P. arhyncotus* there is a considerable widening of the vas deferens at the male pore, to about 34–38 μm. In *P. volki* and *P. glandulosus* the terminal part of the vas deferens is either not measurably wider or may be a few micrometers wider than the ectal part, with a maximum diameter of 23 μm in *P. volki.*

It was originally stated (Sokolskaja 1972), and has been confirmed (Sokolskaja, pers. comm.) that the ovaries are in segment XII in *Propappus arhyncotus.* It would seem that little doubt could remain about this character state. However, the same character state has erroneously persisted in the literature regarding both *P. glandulosus* and *P. volki* for more than 60 years. Other shared characters point to a very close relationship of all three species and similarity of the gonadal condition seems probable.

Sokolskaja (1972) pointed out four categories of differences of *Propappus arhyncotus* from *P. volki*: 1) the shape of the prostomium and absence of proboscis; 2) the thickness and sculpturing of the cuticle; 3) the location of the spermathecal pores in 3/4; and 4) the structure of the spermatheca, with a short ampulla extending only into V. Michaelsen (1923) mentioned that the cuticle in *Propappus* was very thick and that there were rings of prominent epidermal cells around the segments. The epidermal papillae are similarly described by Sokolskaja (1972). The location of the spermathecal pore in all the specimens of *Propappus* examined was in or very near the furrow marking 3/4. Sokolskaja (1973) modified the description of the spermatheca of *P. arhyncotus* to indicate that the ampulla was more sac-like and extensive in mature specimens. Apparently only the proboscidial (and ovarial) character state separates *P. arhyncotus* from *P. volki.*

*Propappus arhyncotus* was distinguished (Sokolskaja 1972) from *P. glandulosus* by the postclitellar location of the esophageal-intestinal transition in the former. This is a character that may be difficult to determine without examination of the cellular structure of the gut. In much of the fixed material examined here the location of the gut transition was, in fact, difficult or impossible to observe. Present estimations of the location of the gut transition are not consistently reliable.

This species remains a systematic problem. If the ovaries are in XIII, then *Propappus arhyncotus* probably should be synonymized with *P. glandulosus.* However, the condition of the male ducts also requires examination. If the ovaries are in XII, *P. arhyncotus* may differ from the other species of *Propappus* at the generic or even familial level. Only re-examination of specimens of *P. arhyncotus* can resolve its specific, generic and familial relationships and consequent classification.

*Distribution.*—Kamchatka Peninsula: Zhupanova River basin, inflow of Bol'shaya River, Kamchatka River basin, including Lakes Azabach'e and Klyuchevskoe.

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# CARIDEAN SHRIMPS OF THE GULF OF CALIFORNIA. V. NEW RECORDS OF SPECIES BELONGING TO THE SUBFAMILY PONTONIINAE (CRUSTACEA: DECAPODA: PALAEMONIDAE)

Rubén Ríos

*Abstract.*—Extensions in the known distribution of three species of pontoniine shrimps are presented. The first known male of *Neopontonides dentiger* has been collected in Bahía Kino, Sonora, some 800 km northwestward from its previously recorded range. Two other species of Panamic pontoniine shrimps are reported for the first time from the Gulf of California: *Periclimenaeus hancocki* and *P. spinosus* were found in two different sponges in Bahía Concepción, B.C.S. The male holotype is the only previous record of the latter species. Diagnoses and illustrations of all three species are provided.

*Resumen.*—Se incrementa el rango de distribución conocida de tres camarones pontoninos. Las especies panámicas *Periclimenaeus hancocki* y *P. spinosus* han sido colectadas por vez primera en el Golfo de California: en Bahía Concepción dentro de dos esponjas diferentes. De *P. spinosus* sólo se conocía el holotipo macho. En Bahía Kino, Sonora, fué hallado el primer macho conocido de *Neopontonides dentiger*; ésto significa un incremento de unos 800 km hacia el NW, en el área de su distribución conocida. Se incluyen diagnosis e ilustraciones de las tres especies mencionadas.

Because of their small size and typical associations, pontoniine shrimps are very likely to go unnoticed. Detailed examination of sponges collected in Bahía Concepción (25°40'N, 11°50'W) has provided several specimens of two species of *Periclimenaeus.* Another specimen available through the kindness of Prof. Marco Escalante, from the Escuela de Ciencias del Mar (University of Sinaloa at Mazatlán) has proved to be the first male specimen known of *Neopontonides dentiger.* All specimens are deposited in the reference collection of the Centro de Investigación Científica y Educación Superior de Ensenada (CICESE).

### *Neopontonides dentiger* Holthuis, 1951
Fig. 1

*Neopontonides dentiger* Holthuis, 1951:193, pl. 61; 1952:18.—Hendrickx, Wicksten, and van der Heiden, 1983:70.—Wicksten, 1983:20.

*Material examined.*—One male (carapace length 1.6 mm), Bahía Kino, Sonora (28°45' N, 111°55'W), 4 m, macroalgae, coll. M. Escalante, 1983.

*Previous records.*—Cabo San Francisco (Ecuador); Mazatlán and Punta Piaxtla in Sinaloa (Mexico).

*Diagnosis.*—Carapace smooth, only antennal spines present. Rostrum laterally expanded in proximal portion and laterally compressed in distal part; 9 to 11 dorsal teeth, ventral margin unarmed. Basal segment of antennular peduncle armed with spine on anterolateral border. Stylocerite sharply pointed, reaching middle of basal segment. Scaphocerite well developed, with lateral spine overreached by lamella. Second and third maxillipeds without exopods,

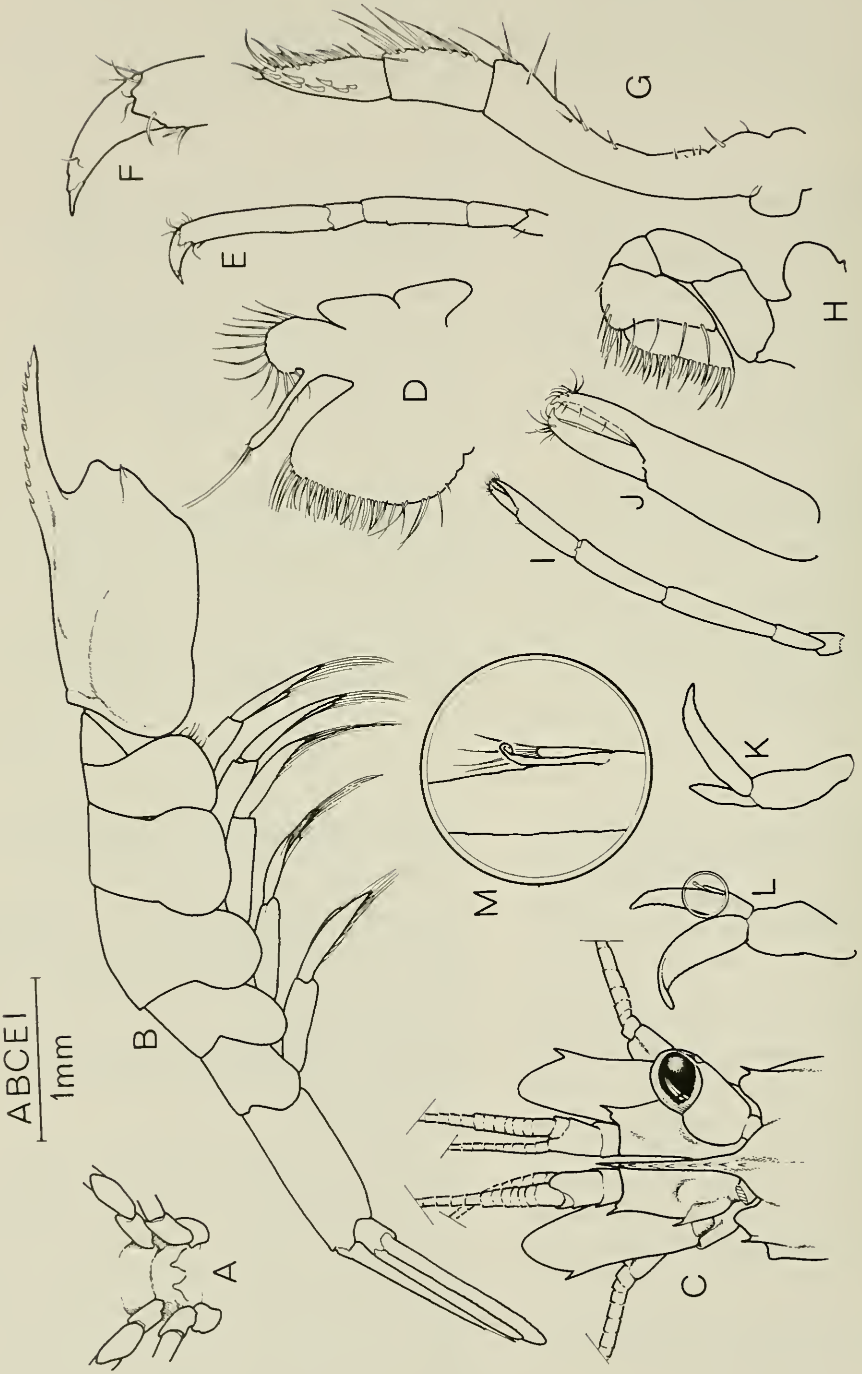

Fig. 1. *Neopontonides dentiger*, male: A, Base of first and second pereiopods, ventral view; B, Carapace and abdomen, lateral view; C, Anterior region, dorsal view; D. First maxilliped; E. Third pereiopod; F, Same, dactyl; G, Third maxilliped; H, Second maxilliped; I, First pereipod; J, Same, chela; K, First pleopod; L, Second pleopod; M, Same, detail of appendix interna and appendix masculina.

widely separated at base. Ventral two-pointed process between coxae of first and second pereiopods. Third pereiopod with dactylus simple, without basal protuberance. Second pleopod with appendix masculina reaching beyond middle of appendix interna and armed with 3 apical setae.

*Remarks.*—Holthuis (1951) described *N. dentiger* from a single incomplete ovigerous female. Apparently, the specimens examined by Wicksten (1983) are those reported in Hendrickx, Wicksten and van der Heiden (1983): an ovigerous female and an undetermined specimen. This is the first report of a male of the species, unfortunately lacking both second pereiopods. The most conspicuous differences with the holotype description are the number of rostral teeth and the ventral mesial spiniform bifurcate process between pereiopods I and II. *Neopontonides dentiger* was previously collected in mud and rocks (Holthuis 1951) and on sandrock and muddy bottoms with gorgonians on stones (Hendrickx, Wicksten and van der Heiden 1983, Wicksten 1983). It is now recorded along with macroalgae. Proper host identity remains to be established.

### *Periclimenaeus hancocki* Holthuis, 1951
Fig. 2

*Periclimenaeus hancocki* Holthuis, 1951:97, pl. 29.—Abele, 1975:70, Fig. 28; 1976: 270—Wicksten, 1983:8.

*Material examined.*—One male (c.l. 2.9 mm), one female (c.l. 3.5 mm), one ovigerous female (c.l. 3.5 mm); Bahía Concepción, Baja California Sur, 2.3 m, sponge; coll. H. Licón, 10 May 1981.

*Previous records.*—Bahía Piñas, Pacific coast of Panama; Malpelo Island.

*Diagnosis.*—Carapace smooth, only antennal spines present. Rostrum laterally compressed, longer than eye, reaching beyond first antennular peduncle; 4 or 5 dorsal teeth, ventral margin entire. Scaphocerite shorter than antennular peduncle; anterolateral spine overreached by lamella. First pereiopods with fingers a little shorter than palm. Second pereiopods unequal, larger with fingers almost half as long as palm; smaller with palm almost 3 times as long as fingers. Larger second pereiopod with fingers obliquely inserted on palm. Posterior pereiopods with dactylus strongly biunguiculate. Second pelopod of male with appendix masculina not reaching middle of appendix interna, armed with 2 apical and 2 subapical setae.

*Remarks.*—The holotype of this species came from soft mud (Holthuis 1951). Abele (1976) found it in what he called "*Pocillopora damicornis* habitat". Specimens from Bahía Concepción were taken from a noncalcareous sponge with acicular spicules. A male and a female were living together, which suggests that *P. hancocki* occurs in pairs as in other sponge associate species. Wicksten (1983) included *P. hancocki* in a list of four species that may occur in the Gulf of California because of its presence on the southwestern Mexican coast. Unfortunately I did not find any precise records from that region. Abele (1975) refers to the holotype as being a male, while Holthuis (1951) in the original description mentions a female as the only specimen examined. Dr. Raymond B. Manning of the Smithsonian Institution kindly examined that specimen and found that Prof. Holthuis was correct.

### *Periclimenaeus spinosus* Holthuis, 1951
Fig. 3

*Periclimenaeus spinosus* Holthuis 1951:113, pl. 35.

*Material examined.*—One male (c.l. 1.8 mm), one ovigerous female (c.l. 2.3 mm), Bahía Concepción, B.C.S.; sponge, coll H. Licón, 10 May 1981.

*Previous records.*—South Viradores Islands off Pacific coast of Costa Rica.

*Diagnosis.*—Carapace smooth with supraorbital and antennal spines. Rostrum laterally compressed and directed slightly

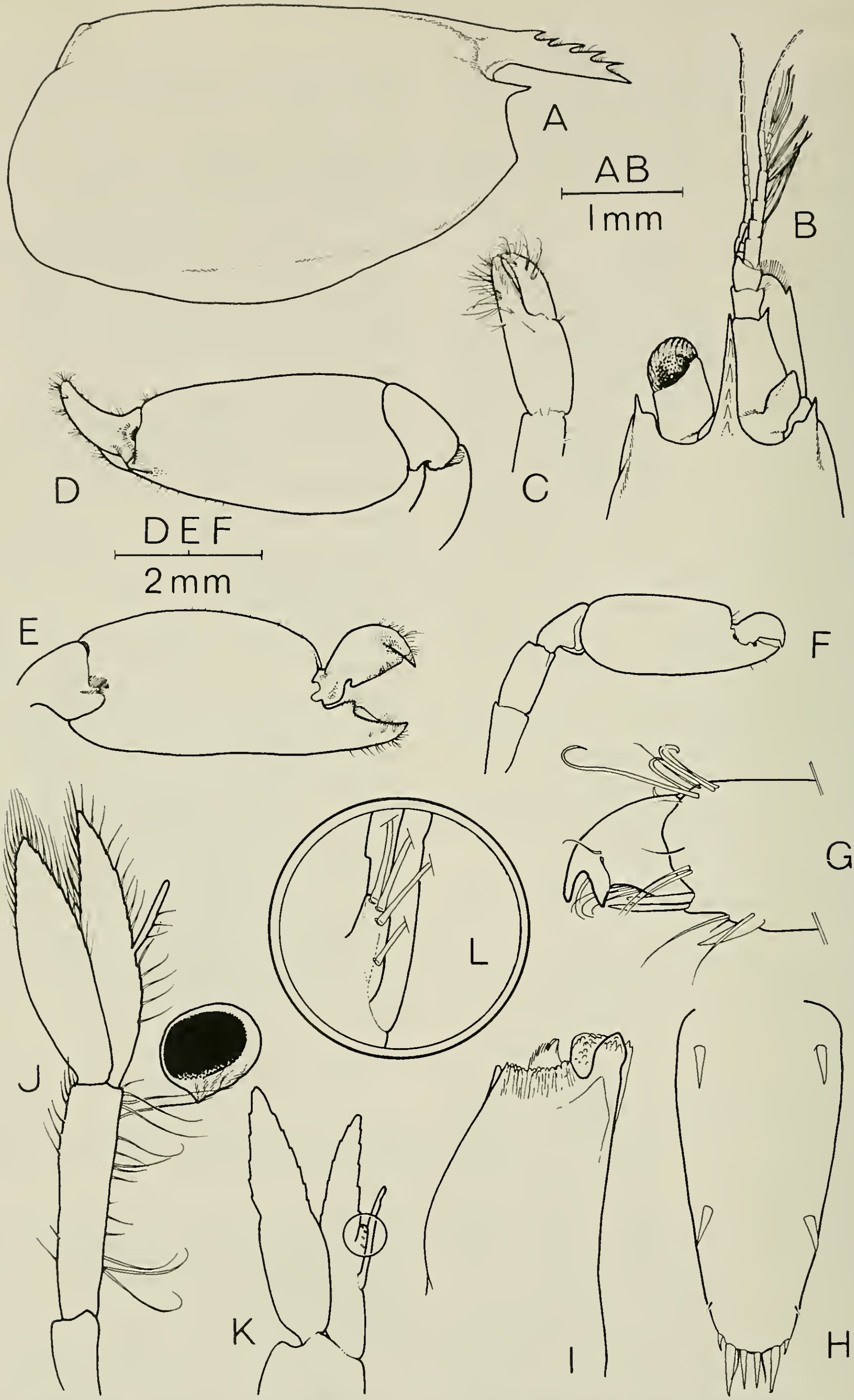

Fig. 2. *Periclimenaeus hancocki* A–J, ovigerous female: A, Carapace, lateral view; B, Anterior region, dorsal view; C, Chela of first pereiopod; D, Left second pereiopod, outer view; E, Same, inner aspect; F, Right second pereiopod, outer view; G, Dactyl of third pereiopod; H, Telson; I, Mandible; J, Second pleopod with egg attached. K–L, male: K, Second pleopod; L, Same, detail of appendix masculina.

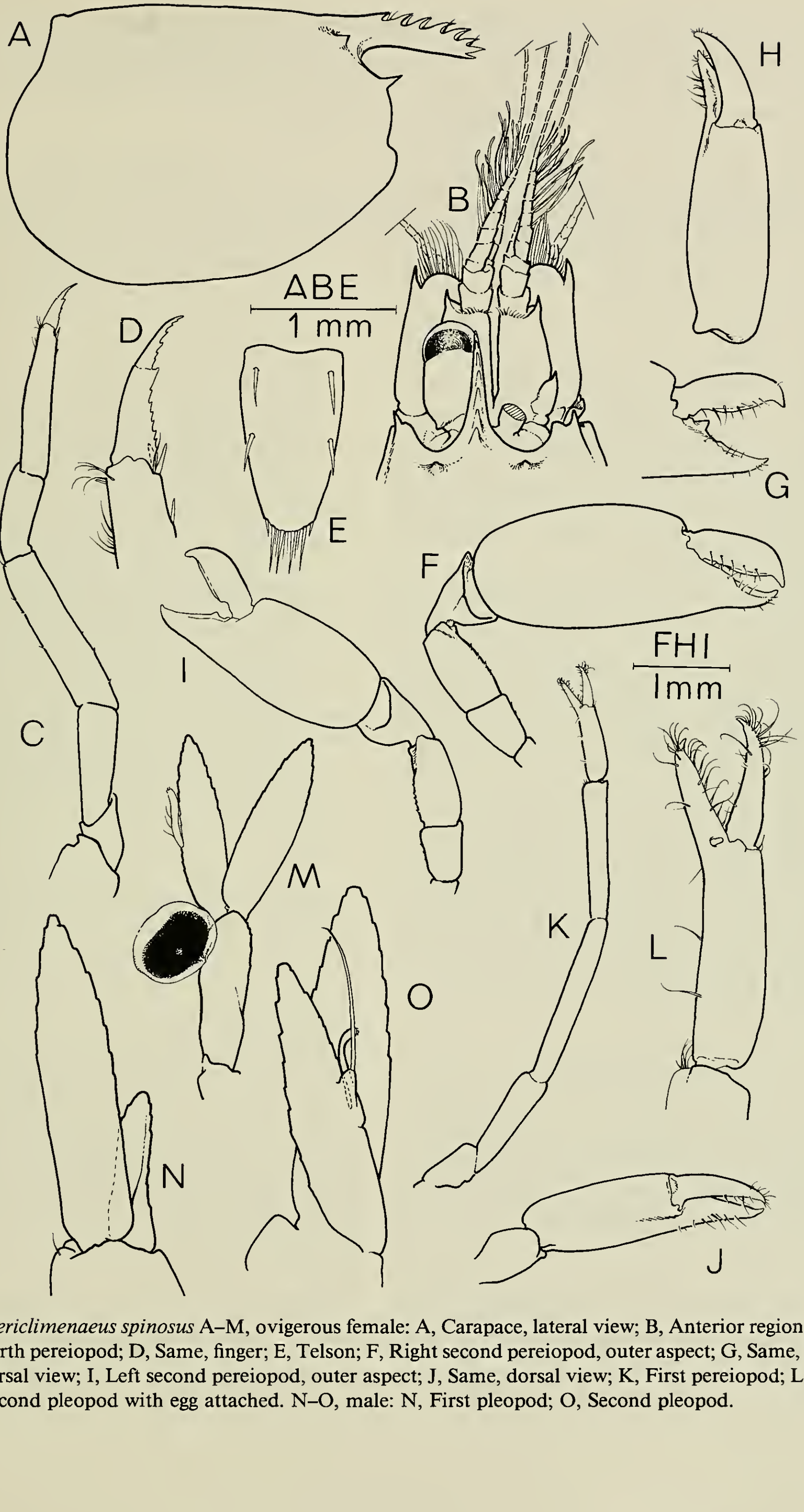

Fig. 3. *Periclimenaeus spinosus* A–M, ovigerous female: A, Carapace, lateral view; B, Anterior region, dorsal view; C, Fourth pereiopod; D, Same, finger; E, Telson; F, Right second pereiopod, outer aspect; G, Same, fingers; H, Same, dorsal view; I, Left second pereiopod, outer aspect; J, Same, dorsal view; K, First pereiopod; L, Same, chela; M, Second pleopod with egg attached. N–O, male: N, First pleopod; O, Second pleopod.

downwards, armed with 5 or 6 dorsal and one subterminal ventral teeth. Basal segment of antennular peduncle with a spine on anterolateral margin. Stylocerite sharp-pointed, reaching middle of basal segment. Scaphocerite well developed, with lateral spine overreaching lamella. First pereiopods with slender chela and small round tooth on proximal margin of fixed finger. Second pereiopods different in size but subequal in shape. Posterior legs with dactylus biunguiculated and accessory spinules on ventral margin. Accessory spinules also present on posterior margin of propodus and merus of third leg and propodus of fourth and fifth legs. Second pleopod of male with appendix masculina reaching beyond middle of appendix interna and furnished with single long apical seta.

*Remarks.—Periclimenaeus spinosus* was known only from the male holotype from Costa Rica. Specimens examined showed the following small differences with the description of the holotype: third maxilliped does not reach middle of scaphocerite; second pereiopods with small spinules on posterior margin of merus and ischium; carpus of larger second pereiopod is about one fourth as long as chela. *Periclimenaeus spinosus* has been collected with corals (Holthuis 1951). Both specimens from Bahía Concepción were drawn from conspicuous channels of a small sponge with a loosely reticular mesenchima.

## Acknowledgments

Prof. Alberto Carvacho critically reviewed the manuscript. Mme. Clara Yáñez made the drawings. Dr. Raymond B. Manning from the Smithsonian Institution, checked the sexual identity of the holotype of *Periclimenaeus hancocki* and kindly reviewed the final manuscript. Marco Escalante provided the specimen from Bahía Kino.

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Note added in proof:

Another record of *Neopontonides dentiger* has recently appeared: Heard, R. W. 1986. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. I. The genus *Neopontonides* Holthuis, 1951, with the description of *N. chacei*, new species, and the erection of *Pseudopontonides*, new genus, to receive *N. principis* Criales, 1980.—Journal of Crustacean Biology 6:471–484.

PROC. BIOL. SOC. WASH.
99(3), 1986, pp. 435–436

# TWO HITHERTO UNNAMED POPULATIONS OF *AECHMOPHORUS* (AVES: PODICIPITIDAE)

Robert W. Dickerman

*Abstract.*—The Mexican nesting populations of *Aechmophorus occidentalis* are named *A. o. ephemeralis,* and the larger birds of the northern populations of *Aechmophorus clarkii* in the United States and Canada are named *A. c. transitionalis.*

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The Western Grebe (*Aechmophorus occidentalis*) was named as *Podiceps occidentalis* by Lawrence (1858:892, 894), from "Pacific coast from Washington Territory to California" (=Fort Steilacoom, Washington, fide American Ornithologists' Union Checklist, 6th Edition [1983]). On the following page Lawrence described *Podiceps clarkii.* These were dark-backed, dark-lored and pale-backed, white-lored forms, respectively. Two of the three specimens of *clarkii* listed by Lawrence were wintering birds from California of the large, pale morph that occurs throughout the range of the species in the United States and Canada. Deignan (1961:7–8) pointed out that the third specimen, from Laguna Santa Maria, Chihuahua, should be considered the type of *P. clarkii,* and Dickerman (1963) redundantly so restricted the type locality. The critical differences between the two morphs are the yellow-orange bill and white face of the pale morph, and darker bill and black face of the dark morph (Storer 1965); but all color characters are highly variable (Storer and Nuechterlein 1985).

*Podiceps clarkii* was considered a synonym of *A. occidentalis* until 1963, when Dickerman (1963) demonstrated the lack in overlap in wing chord measurements (and very little overlap in bill length) between northern and Mexican populations, and recognized *clarkii* as a small subspecies with pale and dark morphs as in nominate *occidentalis.* Mayr and Short (1970:29) overlooked or ignored the 1963 paper, stating "no races are recognized."

Later, Dickerman (1973) further characterized the small Mexican subspecies. He also pointed out that there was a degree of geographical segregation of the two morphs, in that more specimens from the central plateau and northern Mexico were of the pale type, while more from the western and southern portions of the plateau were of the dark morph. However, the trenchant characteristic of the Mexican versus northern populations is the small size of Mexican birds.

In the ensuing years, studies of the breeding behavior of northern populations (see review in Storer and Nuechterlein 1985) indicated than an apparently significant degree of assortative mating occurs between the two morphs. Based on this, the American Ornithologists' Union Committee on Classification and Nomenclature (AOU 1985) concluded that the two color morphs should be recognized by the specific names *Aechmophorus occidentalis* and *A. clarkii.* This decision was made in the absence of studies of the critical Mexican populations, and is contrary to recommendations published earlier in the same volume of the Auk (Storer and Nuechterlein 1985). Further, starch gel electrophoresis revealed no significant difference between the two color morphs in preliminary studies (Ratti 1979).

In view of the AOU Committee's decision, and in view of the great size disparity between birds of the northern and southern populations, it now becomes necessary to name the large pale northern population and the small dark southern population. These may now be known as:

### *Aechmophorus occidentalis ephemeralis*, new subspecies

*Holotype.*—Adult male, American Museum of Natural History 708,559, collected at Laguan de San Pedro Lagunillas, Nayarit, Mexico, 25 May 1962 by Robert W. Dickerman; field number RWD 10650. Additional data: with a large young; weight 1050 gms.; pectoral muscles 17 and 16.3 gms.; moderately to rather fat; extent 851 mm.; wing chord 179 mm., culmen (from anterior edge of nostril) 56.7 mm., tarsus 70.4 mm.

*Diagnosis.*—Small, inseparable in size from the co-existing population of *A. clarkii*, but dark-lored as in nominate *occidentalis*.

*Distribution.*—Specimens recorded to date from Nayarit, western Jalisco, Puebla and Guererro (Dickerman 1973).

### *Aechmophorus clarkii transitionalis*, new subspecies

*Holotype.*—Adult male, National Museum of Natural History 158016, collected at Silver Lake, Lake County, Oregon, 22 Jun 1897 by Vernon Bailey; original number 20. Additional data: wing cord 194 mm., culmen (from anterior edge of nostril) 63.4 mm., tarsus 77.5 mm.

*Diagnosis.*—Large, similar in size to nominate *A. occidentalis*, but coloration pale as in *A. clarkii*.

*Distribution.*—Sympatric with *A. o. occidentalis* in western North America, north of the Mexican border, becoming rarer northwards.

*Discussion.*—For detailed size comparison of nominate *A. o. occidentalis* and *A. clarkii transitionalis* see Storer and Nuechterlein (1985).

## Acknowledgments

I thank M. Ralph Browning for his selection and measurement of the type of *A. clarkii transitionalis*, and Kenneth C. Parkes and Robert W. Storer for their comments on the manuscript.

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# THE STATUS OF THE CALLIANASSID GENUS *CALLICHIRUS* STIMPSON, 1866 (CRUSTACEA: DECAPODA: THALASSINIDEA)

Raymond B. Manning and Darryl L. Felder

*Abstract.*—The callianassid genus *Callichirus* Stimpson is redefined and restricted to its type species, *Callianassa major* Say, 1818, and three other species.

The callianassid genus *Callichirus* was established by Stimpson (1866:47) with *Callianassa major* Say, 1818, from the southeastern United States, as its type species. Since then, *Callichirus* has been treated in various ways, including: (1) as a subgenus of *Callianassa* Leach, 1814 (e.g., by Borradaile 1903; De Man 1928a, b; Schmitt 1935; Rodrigues 1971); (2) as a distinct genus, comprising numerous species formerly assigned to *Callianassa* (e.g., by de Saint Laurent 1974, Le Loeuff and Intès 1974, De Saint Laurent and Le Loeuff 1979); or (3), as a synonym of *Callianassa* (e.g., by Biffar 1971, Poore and Griffin 1979). We disagree with all of these interpretations for reasons discussed below, and we give here characters that distinguish *Callichirus* from all other genera of the Callianassidae.

Part of the problem has been that most authors, at least up to de Man (1928a:30), had seen *no* material of *Callianassa major,* and that until very recently the only available illustrations of the species were photographs (Hay and Shore 1918:pl. 29, fig. 10; De Man 1928a:fig. 14c, d). De Man had examined and figured two chelipeds (1928a: fig. 14–14b), but had studied no complete specimens. The species was not well figured until specimens from Brazil were studied by S. A. Rodrigues (1971:192, figs. 1–20).

In his original account of *Callichirus,* Stimpson (1866:47) noted that the cheliped was elongate ("carpus and hand of the greater cheliped very long"), that the uropodal endopod was narrow ("very narrow, almost styliform"), and that the telson was short and broad, with a posterior emargination. We suggest that these features and the distinctive ornamentation of the third to fifth abdominal somites (Figs. 1f, 2e, 3e) are diagnostic for the genus *Callichirus,* and will serve to distinguish its members from all other callianassids.

De Saint Laurent (1974:513) divided the family Callianassidae into two subfamilies, the Callianideinae and the Callianassinae. She assigned eight genera, including *Callichirus* Stimpson, 1866, to the Callianassinae. Refinement of diagnoses for most of these genera was attempted later by Le Loeuff and Intès (1974) and by de Saint Laurent and Le Loeuff (1979).

However, not all of the genera recognized by de Saint Laurent have been accepted by other workers. Poore (1975:205) commented on the limitations of de Saint Laurent's genera, and Poore and Griffin (1979:245) noted, "We have had some difficulty in placing some of the Australian callianassid species in the new genera erected by Saint Laurent (1973) . . . and therefore prefer not to follow her arrangement. The exception is her new genus *Gourretia* which forms a relatively homogeneous group of species clearly distinct from the remainder of the family." Rabalais, Holt, and Flint (1981:98) abandoned use of de Saint Laurent's genera because "the distinctions proposed . . . were not clear cut for Western Hemisphere callianassids." Williams (1984:180) commented, "According to de Saint Laurent, the

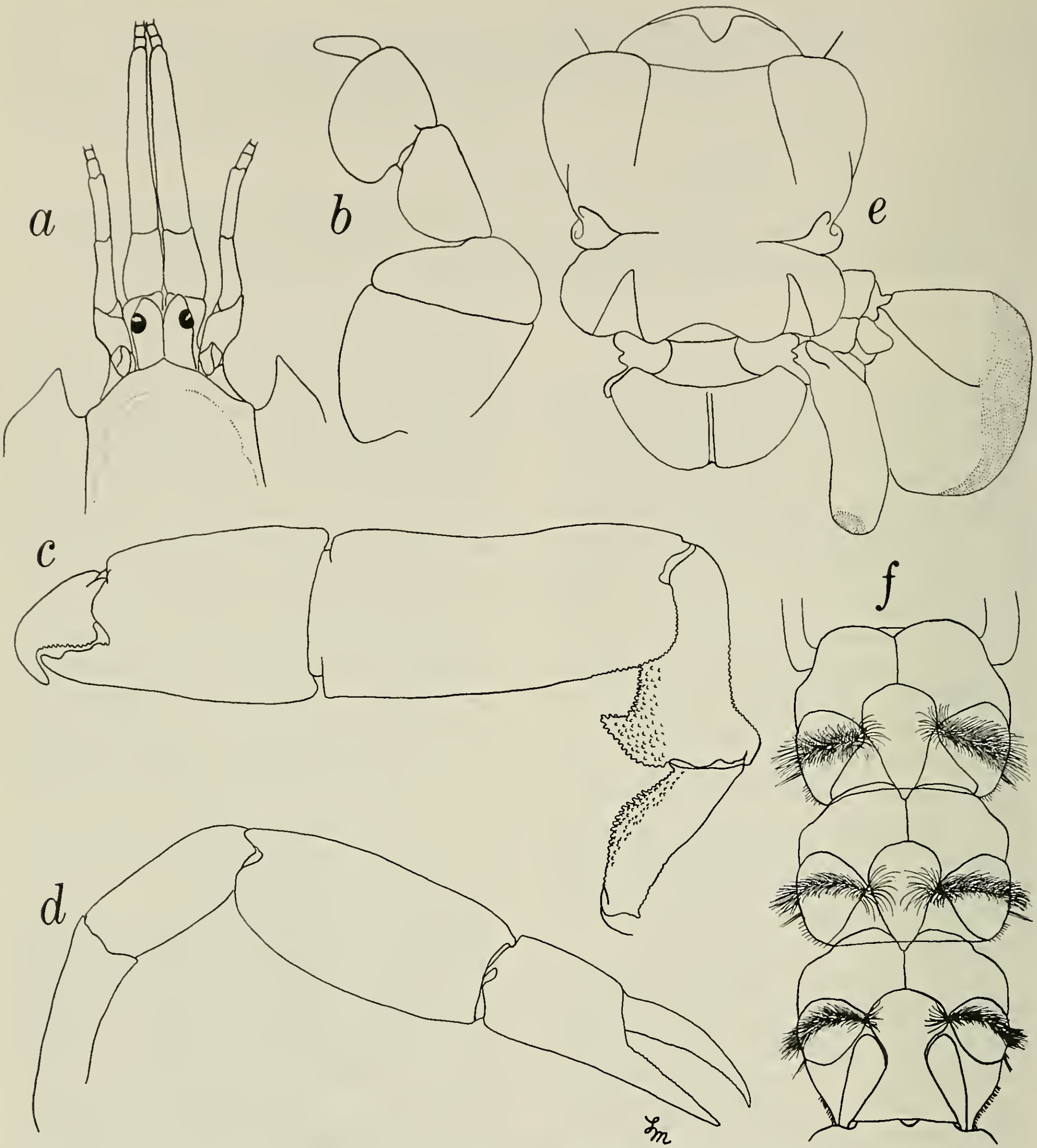

Fig. 1. *Callichirus major* (Say), male, tl 77 mm, Indian River, Florida (USNM 228086): a, Front; b, Third maxilliped; c, Major cheliped; d, Minor cheliped; e, Sixth abdominal somite, telson, and uropod (stippled areas on uropod show areas of dense setation). Male, tl 56 mm, Indian River, Florida (USNM 228087): f, Third to fifth abdominal somites (top is anterior).

known species from the western Atlantic formerly placed in *Callianassa* belong in *Callichirus.* The differences between *Callianassa* and *Callichirus* depend upon mouthparts and seem somewhat overlapping. For the time being, therefore, I am retaining the well-known name *Callianassa* for these species, awaiting further research which may place de Saint Laurent's system on a firmer basis."

We redefine *Callichirus,* as follows:

### Genus *Callichirus* Stimpson, 1866

*Callichirus* Stimpson, 1866:47.

*Definition.*—Ocular peduncles elongate, either in precorneal region or as postcorneal spine. Major chela of adult male greatly enlarged, with 3 distal segments equal to 2 or more times middorsal carapace length. Third to fifth abdominal somites with distinctive ornamentation, visible dorsally, each somite with midlateral patch of setae. Telson much shorter than uropods, much wider than long, with medial emargination. Uropodal endopods strap-shaped, very slender, 2.5 to 4 times longer than wide, with setae most concentrated in apical patch.

*Type species.*—*Callianassa major* Say, 1818, by original designation and monotypy.

*Included species.*—Four, as follows:

1. *Callichirus major* (Say, 1818:238) (Fig. 1), from the southeastern United States, Gulf of Mexico, and Brazil.
2. *Callichirus islagrande* (Schmitt, 1935: 5) (Fig. 2), from the northern and western Gulf of Mexico.
3. *Callichirus seilacheri* (Bott, 1955:47) (Fig. 3), from El Salvador.
4. *Callichirus adamas* (Kensley, 1974: 266), from West Africa and South Africa.

*Remarks.*—We believe that these four species comprise a distinctive group of species within the Callianassidae recognizable as a distinct genus, *Callichirus.* The ornamentation of the third to fifth abdominal somites alone will distinguish these species from all other species assigned to *Callianassa* or other genera of the Callianassidae.

Preliminary anatomical studies of the third to fifth abdominal somites suggest that the dorsal sculpture and setation may comprise the exoskeletal components of an abdominal glandular apparatus, perhaps related to cementing of burrow walls. If so, this apparatus would represent a unique anatomical specialization among the thalassinideans. A previous study (Thompson 1972) has demonstrated that cement production is centered in a hindgut gland in *Upogebia pugettensis* (Dana) and in glands at the bases of mouthparts in *Callianassa californiensis* Dana. Additional histological studies are planned to resolve the function of these abdominal glands in *Callichirus.*

Our corrected definition of *Callichirus* also is corroborated in part by recent ecological and physiological studies. Osmoregulatory capacities and habitat preferences in *C. major* and *C. islagrande* are very similar; neither species can osmoregulate and both can tolerate limited reductions in salinity (Felder 1978). This is in striking contrast to the case in *Callianassa jamaicensis* Schmitt and *Callianassa kraussi* Stebbing, both of which are euryhaline, hyperosmotically regulate at and tolerate low salinities, withstand abrupt changes of salinity, and show marked regulation of volume (Forbes 1974, Felder 1978). But the four above species were treated as congeneric in the broadly defined *Callichirus* of de Saint Laurent and Le Loeuff (1979). In fact, the tendency for osmoconformation and limited tolerance of reduced salinity, characteristic of *Callichirus major* and *Callichirus islagrande,* bears the greatest similarity to those features in *Callianassa californiensis, Callianassa filholi* A. Milne Edwards, and *Callianassa affinis* Holmes (see Gross 1957, Thompson and Pritchard 1969), Felder 1978), none of which

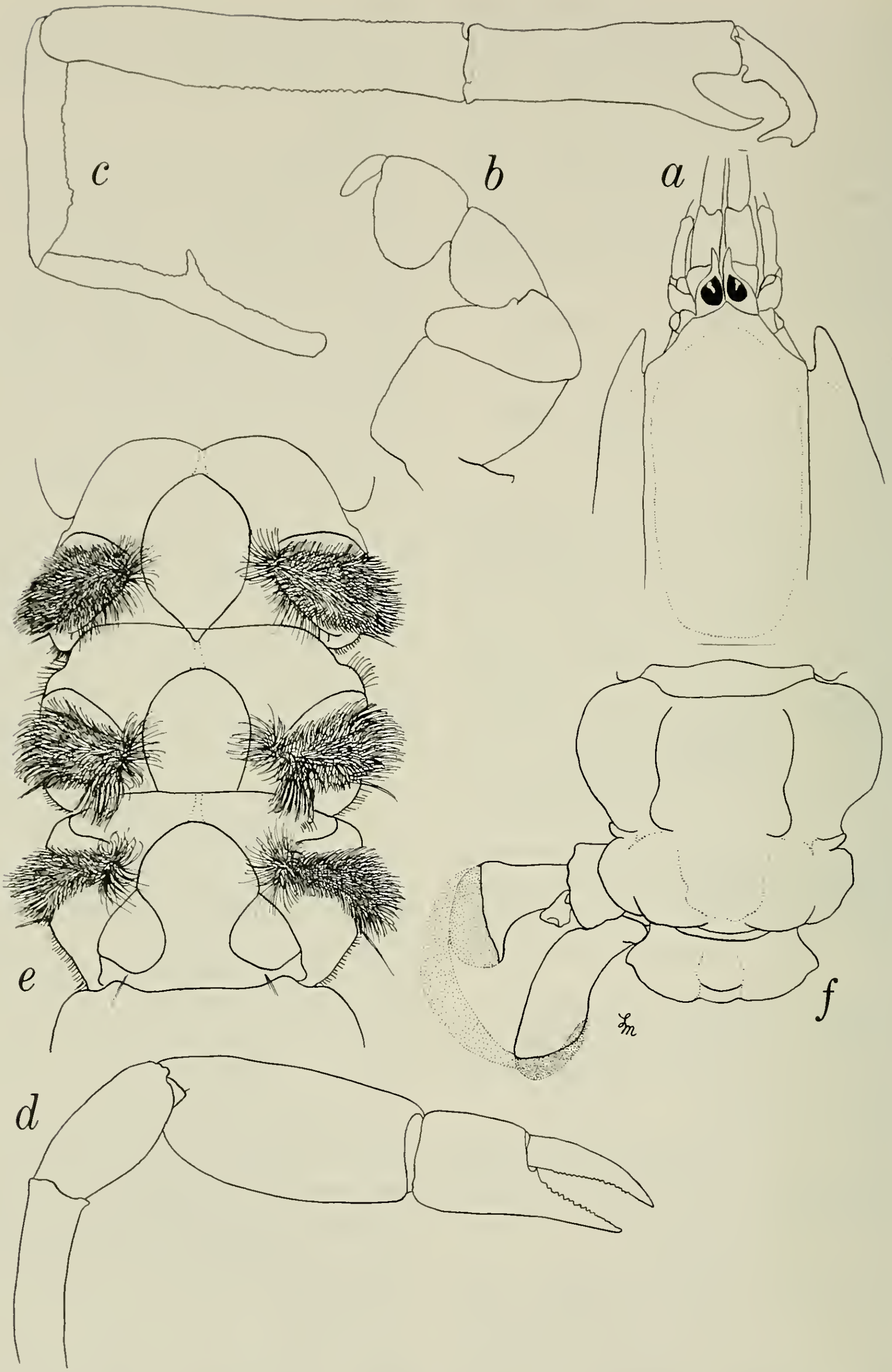

Fig. 2. *Callichirus islagrande* (Schmitt), male holotype, TL 87 mm, Grand Isle, Louisiana (USNM 69369): a, Front; b, Third maxilliped; c, Major cheliped; d, Minor cheliped; e, Third to fifth abdominal somites (top is anterior); f, Sixth abdominal somite, telson, and uropod (stippled areas on uropod show areas of dense setation).

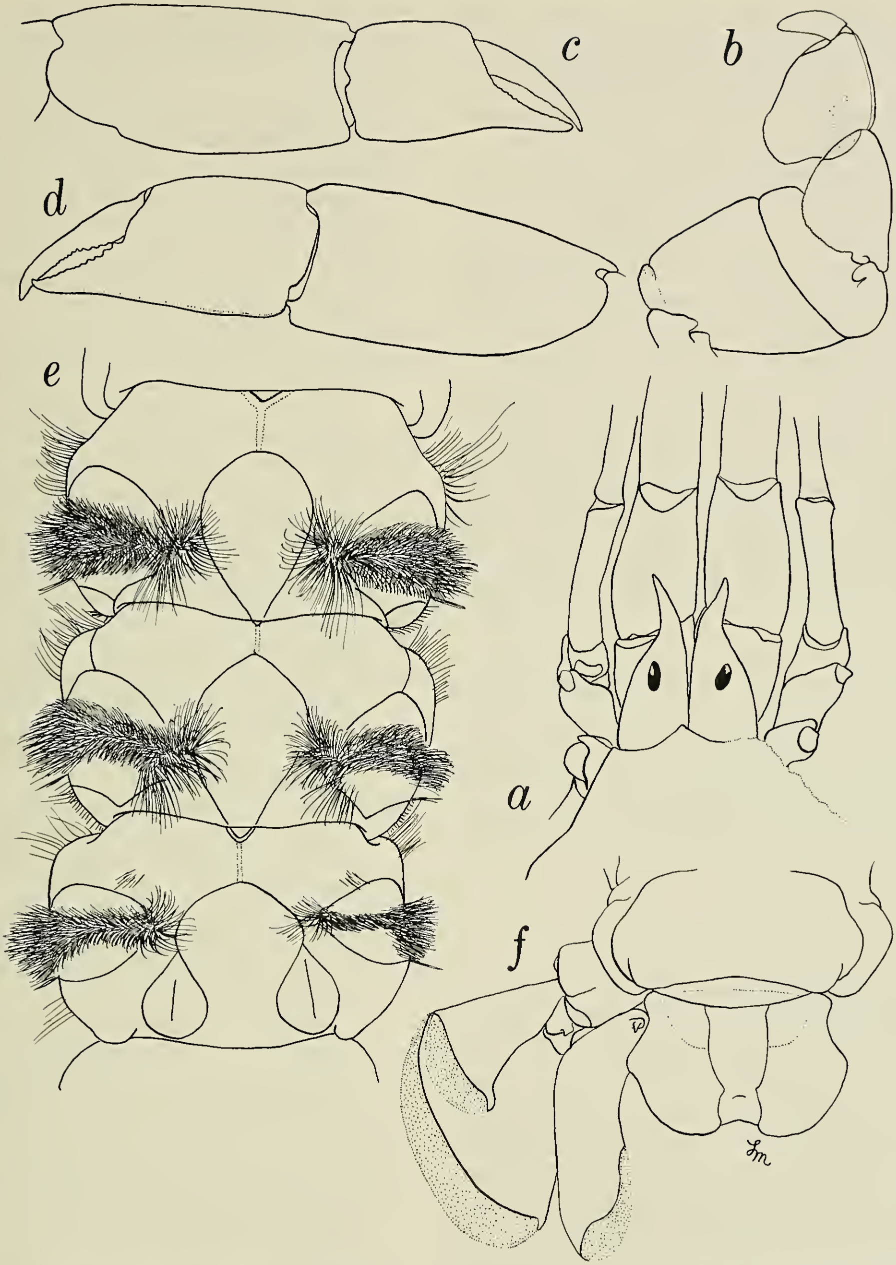

Fig. 3. *Callichirus seilacheri* (Bott), male holotype, tl 85 mm, Los Blancos, El Salvador (Forschungsinstitut Senckenberg no. 2184): a, Front; b, Third maxilliped; c, Right first cheliped; d, Left first cheliped; e, Third to fifth abdominal segments (top is anterior); f, Sixth abdominal segment, telson, and uropod (stippled areas on uropod show areas of dense setation). Note that both first chelipeds are of minor form.

is assignable to *Callichirus.* We believe that this evidence from the physiology of these organisms suggests an artificial and heterogeneous grouping within *Callichirus* sensu de Saint Laurent and Le Loeuff (1979).

We provide here original sketches (Figs. 1–3) of three of the species that we assign to *Callichirus.* We have not seen material of *Callichirus adamas,* but the accounts and figures of this species provided by Kensley (1974:266, figs. 1, 2), who first pointed out the resemblance between *C. adamas, C. major,* and *C. islagrande,* and by de Saint Laurent and Le Loeuff (1979:67, figs. 14f, 16a, 17a, 19f, 20e–g, 23f–i), clearly identify *C. adamas* as a member of *Callichirus.* The characteristic ornamentation of the abdomen in *C. adamas* is clearly shown by de Saint Laurent and Le Loeuff (1979) in their figure 17a.

Of the species assigned to or described in *Callichirus* by Le Loeuff and Intès (1974) and de Saint Laurent and Le Loeuff (1979), only those four listed above can be assigned to *Callichirus* sensu stricto. We consider all of the other species assigned to *Callichirus* by those authors to be members of *Callianassa.*

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We thank Austin B. Williams, Systematics Laboratory, National Marine Fisheries Service, for reviewing this paper. M. Türkay, Forschungsinstitut Senckenberg, Frankfurt-am-Main, West Germany, loaned us the holotype of *Callianassa seilacheri.* The figures were prepared by Lilly King Manning. This paper is contribution number 163 from the Smithsonian Marine Station, Fort Pierce, Florida, and contribution number 2 from the Center for Crustacean Research, University of Southwestern Louisiana.

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# A NEW SCALE-WORM COMMENSAL WITH DEEP-SEA MUSSELS IN THE SEEP-SITES AT THE FLORIDA ESCARPMENT IN THE EASTERN GULF OF MEXICO (POLYCHAETA: POLYNOIDAE: BRANCHIPOLYNOINAE)

Marian H. Pettibone

*Abstract.*—Some polynoid polychaetes found living commensally in mantle cavities of deep-sea mussels at the seep-sites near the Florida Escarpment, are described as a new species of *Branchipolynoe, B. seepensis.* They show some differences from the previously described *B. symmytilida,* commensal with deep-sea mussels in the Galapagos hydrothermal vents.

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Among the abundant biological communities recently discovered in the abyssal eastern Gulf of Mexico near hypersaline seep-sites were large dense mats of mussels (Florida Escarpment Cruise Participants 1984, Paull et al. 1984, Turner and Lutz 1984, Denoux et al. 1985, Hecker 1985). They were collected in March 1984 during four dives of the submersible *Alvin* in 3266–3270 meters (26°02′N, 84°55′W). The mussels were found in dark iron-sulfide sediments at near-ambient temperatures in an area where dense hypersaline fluids seep out onto the sea floor. The communities were similar in many respects to the prolific communities found around the Galapagos hydrothermal vents and elsewhere in the Pacific.

Some polynoid polychaetes were found living commensally in the mantle cavities of these mussels. Six specimens were given to me for study by Dr. Barbara Hecker: five adults removed from the mussels by Dr. Ruth D. Turner, and a juvenile collected from washings of a clump of mussels.

It was of particular interest to compare these polynoids, commensal with the unnamed, non-hydrothermal, large, Gulf of Mexico mussels (to be described and named by Ruth Turner and Barry Wilson), with the polynoids commensal with the large mussels in the Galapagos hydrothermal vents, recently described under the name *Bathymodiolus thermophilus* by Kenk and Wilson (1985). The Galapagos polynoids were referred earlier to a new genus and species, *Branchipolynoe symmytilida,* in a new subfamily of the Polynoidae, Branchipolynoinae (Pettibone 1984). The Gulf of Mexico commensals are referred herein to a new species of *Branchipolynoe, B. seepensis.*

The types are deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

## Branchipolynoinae Pettibone, 1984

## *Branchipolynoe* Pettibone, 1984

*Type species.*—*Branchipolynoe symmytilida* Pettibone, 1984.

The generic diagnosis is emended to include *Branchipolynoe seepensis,* new species, commensal with deep-sea mussels in the Gulf of Mexico.

*Diagnosis, emended.*—Branchiae small to well developed, arborescent, on all parapodia from segment 2 or 3. Prostomium bilobed, with anterior lobes subtriangular or rounded, with or without minute frontal filaments; median antenna with ceratophore indistinct, style short; palps short to long. First or tentacular segment visible dorsally as short ring or fused to prostomium. Parapodia subbiramous or biramous; notopodia small, nodular or conical with projecting acicular process; notosetae few (0–3) or moderate in number (5–20). Neuropodia with or without truncate lobes enclosing conical acicular lobes; neurosetae very numerous, upper ones much stouter or only slightly stouter than lower ones. Commensal with deep-sea mussels at hydrothermal vents or hypersaline seep-sites.

### Key to the Species of *Branchipolynoe*

1. Elytra small, leaving greater part of dorsum uncovered (Pettibone 1984, figs. 1, 2A). Arborescent branchiae beginning on segment 2 (Pettibone 1984, figs. 2A, 3A). Anterior lobes of prostomium with minute frontal filaments (Pettibone 1984, fig. 2A). First or tentacular segment visible dorsally as small ring (Pettibone 1984, fig. 2A). Parapodia subbiramous, with notopodia small and 0 to few notosetae (Pettibone 1984, fig. 3F). Neuropodia with truncate lobes enclosing conical acicular lobes (Pettibone 1984, fig. 3F). Upper neurosetae much stouter than lower neurosetae (Pettibone 1984, fig. 3I, K). Ventral papillae on segments 11 and 12 short (Pettibone 1984, fig. 4C). Commensal with deep-sea mussels in Galapagos hydrothermal vents . ....... *B. symmytilida* Pettibone, 1984

– Elytra large, leaving middle third of body uncovered (Fig. 1A). Arborescent branchiae beginning on segment 3 (Fig. 2B). Anterior lobes of prostomium without frontal filaments (Fig. 1A). Tentacular segment fused to prostomium, not visible dorsally as separate ring (Fig. 1A). Parapodia biramous, with notopodia large, conical, with moderate number of notosetae (Fig. 2C, D). Neuropodia without truncate lobes enclosing conical acicular lobes (Fig. 2D). Upper neurosetae only slightly stouter than lower neurosetae (Fig. 2H, I). Ventral papillae on segments 11 and 12 long (Fig. 1D). Commensal with deep-sea mussels in hypersaline seeps in Gulf of Mexico .............. ............ *B. seepensis*, new species

### *Branchipolynoe seepensis*, new species
Figs. 1–4

*Material.*—Gulf of Mexico, from dives of *Alvin* in 1984, associated with mussels near hypersaline seeps at base of Florida Escarpment, in dark iron-sulfide sediment: Dive 1343, 9 Mar, 26°02′24″N, 84°54′48″W, 3266 m, from washings of clump of mussels, juvenile paratype (USNM 98782).—Dive 1344, 12 Mar, 26°02′N, 84°54′ 48″W, 3270 m, from mantle cavities of mussels, holotype (USNM 98779), 2 paratypes (USNM 98780).—Dive 1346, same data, 2 paratypes (USNM 98791).

*Measurements.*—Holotype (USNM 98779) 31 mm long, 13 mm wide, including setae, with 21 segments. Two adult paratypes (USNM 98780) 27–28 mm long, 11–13 mm wide, with 21 segments. Two smaller adult paratypes (USNM 98781) 12–16 mm long, 5–7 mm wide, with 21 segments. Juvenile paratype (USNM 98782) 8 mm long, 3.5 mm wide, with 18 segments, last 2 very small.

*Description.*—Body short, spindle-shaped, slightly tapered anteriorly and posteriorly, flattened ventrally and strongly arched dorsally. Fully-developed worms having 21 segments, first achaetous, with 10 pairs of elytra attached on large, low elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. Elytra (Figs. 1A, E–G, 3A, B, 4C, D) moderately large, oval, covering lateral thirds of body on larger adults and nearly covering body on juvenile. Elytra oval, opaque, smooth, soft, and attached near middle on first pair and eccentrically attached near their anterior borders on following elytra, sometimes showing branched "veins." Dorsal cirri on non-elytra-bearing

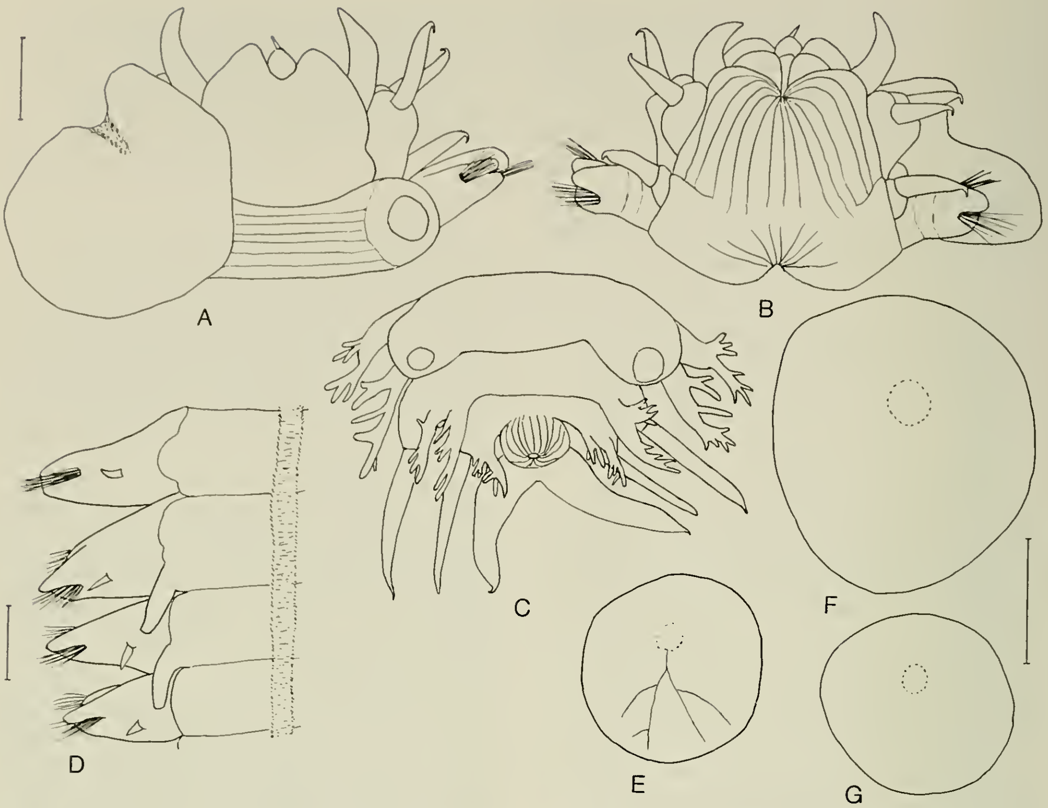

Fig. 1. *Branchipolynoe seepensis,* holotype (USNM 98779): A, Dorsal view of anterior end, right first elytron removed; B, Ventral view of anterior end; C, Dorsal view of posterior end showing segments 19 to 21 and pygidium, tenth elytra of segment 19 removed; D, Ventral view of right side of segments 10 to 13 showing elongate ventral papillae on segments 11 and 12; E, Right first elytron from segment 2, with "veins" indicated; F, Right fifth elytron from segment 9; G, Right tenth elytron from segment 19. Scales = 1.0 mm for A–C; 2.0 mm for D–G.

segments having short cylindrical cirrophores and short styles with slender tips, extending to about tips of neurosetae (Figs. 2B, E, 3D, 4E). Dorsal tubercles on cirrigerous segments indistinct. Branchiae well developed, arborescent, with rather short terminal filaments (Fig. 2B–F, J). Branchiae emerging from body in two short trunks, lower smaller group attached dorsal to bases of notopodia or cirrophores of dorsal cirri and upper larger one attached to lateral bases of elytrophores or dorsal tubercles.

→

Fig. 2. *Branchipolynoe seepensis,* holotype (USNM 98779): A, Right elytragerous parapodium from segment 2, anterior view, acicula dotted; B, Right cirrigerous parapodium from segment 3, posterior view, cirrophore of dorsal cirrus hidden from view; C, Right cirrigerous parapodium from segment 8, posterior view; D, Right elytragerous parapodium from segment 9, anterior view, acicula dotted, branchiae cut off; E, Lower branchia from same; F, Upper branchia from same; G, Three neurosetae from same, with detail of tips; H, Upper neuroseta from same, with detail of tips; I, Lower neuroseta from same, with detail of tips; J, Right elytragerous parapodium from segment 15, anterior view, acicula. Scales = 1.0 mm for A–F; 0.1 mm for G–I.


A
B
C
D
E
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G
H
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J

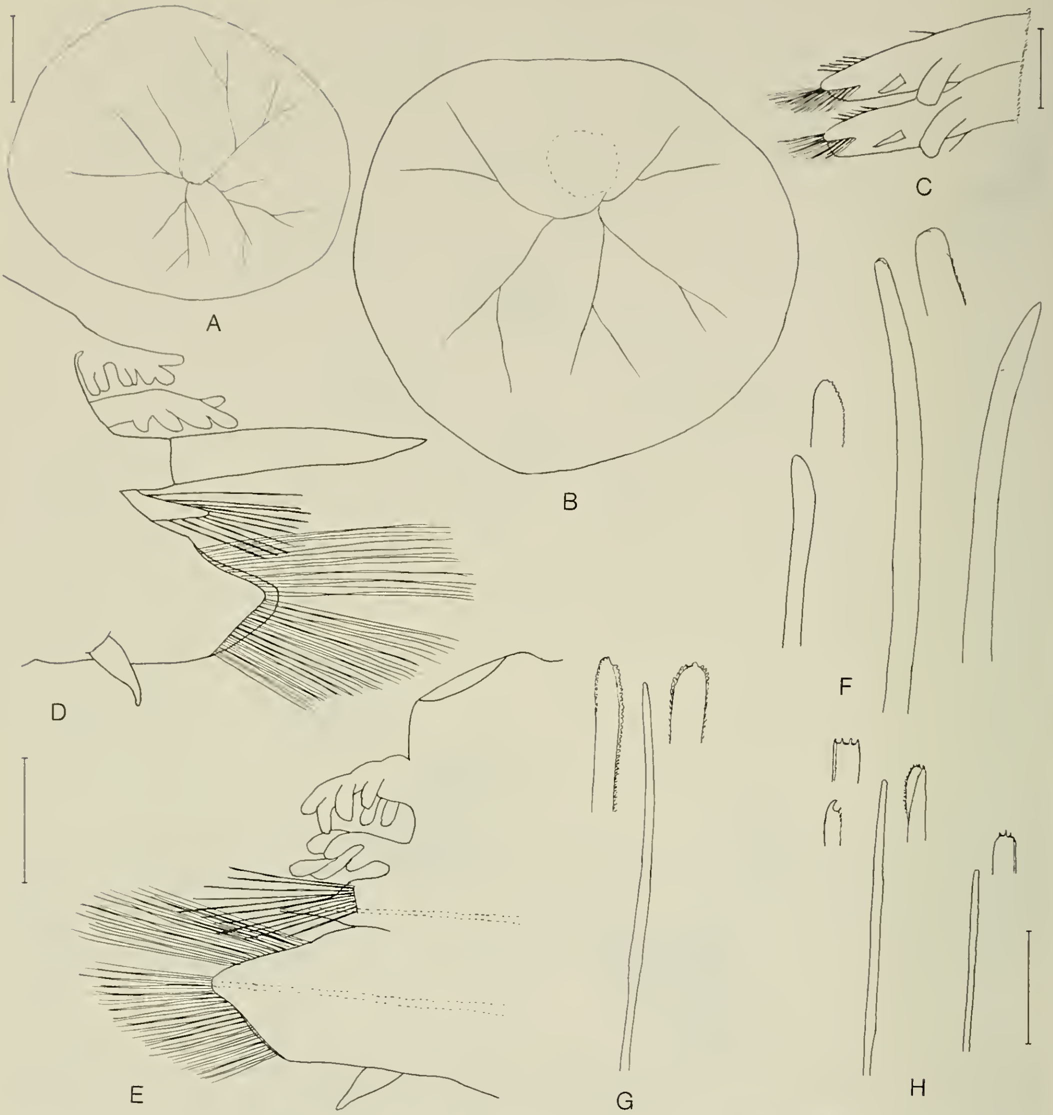

Fig. 3. *Branchipolynoe seepensis,* smaller adult paratype of 12 × 5 mm (USNM 98781): A, First elytron, with "veins" indicated; B, Middle elytron; C, Ventral view of right side of segments 11 and 12, showing elongate ventral papillae; D, Right middle cirrigerous parapodium, posterior view; E, Right middle elytragerous parapodium, anterior view, acicula dotted; F, Three notosetae from same, with detail of tips; G, Upper neuroseta from same, with detail of tips; H, Two lower neurosetae from same, with detail of tips. Scales = 0.5 mm for A, B; 1.0 mm for C; 0.5 mm for D, E; 0.1 for F–H.

Branches of branchiae somewhat flattened and spread anteriorly and posteriorly between parapodia. Branchiae beginning on segment 3 as 2 small groups (Fig. 2B), becoming larger with more numerous branches in middle region (Fig. 2C), and smaller posteriorly (Figs. 1C, 2J). Branchiae smaller on smaller adults (Fig. 3D, E), very small and incompletely developed on juvenile (Fig. 4E, F).

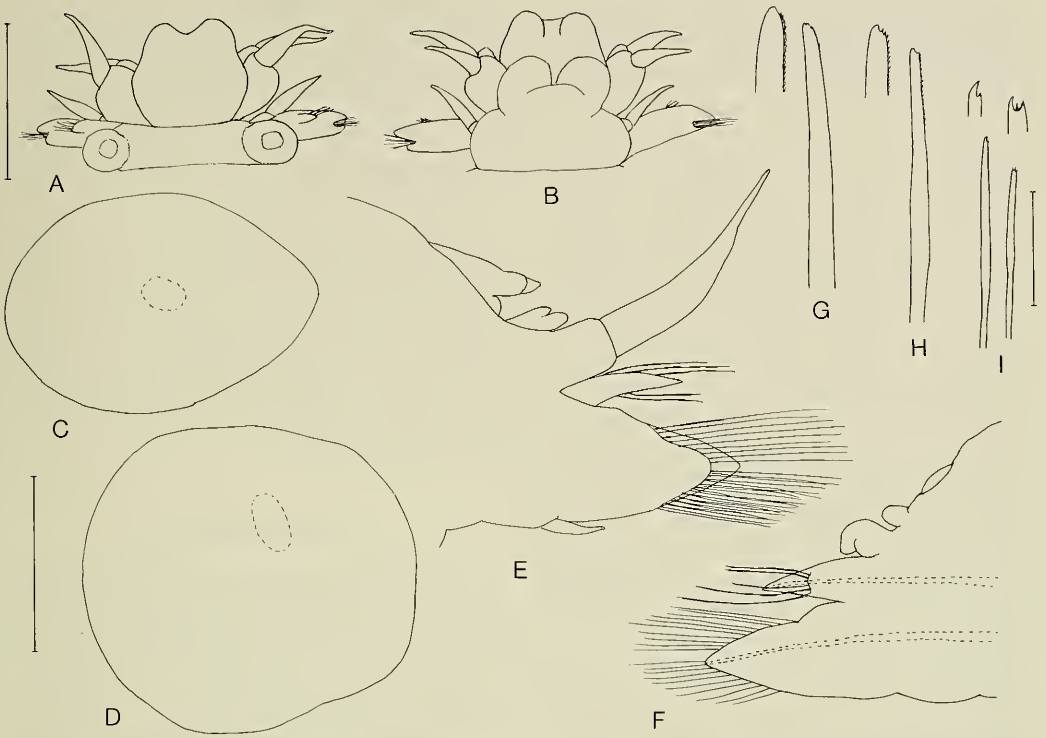

Fig. 4. *Branchipolynoe seepensis,* juvenile paratype, 8 × 3.5 mm, (USNM 98782): A, Dorsal view of anterior end, median antenna and palps missing; B, Ventral view of anterior end; C, Right first elytron; D, Right middle elytron; E, Right cirrigerous parapodium, posterior view; F, Right elytragerous parapodium, anterior view, acicula dotted; G, Notoseta from same, with detail of tip; H, Upper neuroseta from same, with detail of tip; I, Two lower neurosetae from same, with detail of tips. Scales = 1.0 mm for A, B; 0.5 mm for C–F; 0.1 mm for G–I.

Prostomium (Figs. 1A, B, 4A, B) oval, bilobed, with rounded anterior lobes lacking frontal filaments. Median antenna, lacking distinct ceratophore, inserted in anterior notch; short, conical, with slender tip; ventrolateral palps rather short, thick, smooth, and tapered, extending beyond prostomium; lateral antennae and eyes lacking. First or tentacular segment fused to prostomium and not distinct dorsally; tentaculophores, lateral to prostomium, achaetous, short and bulbous, each with pair of short cirriform tentacular cirri with slender tips, about as long as palps (Figs. 1A, B, 4A, B). Second or buccal segment bearing first pair of large elytrophores and elytra, biramous parapodia with smaller conical notopodia with up to 9 notosetae, and larger rounded neuropodia with numerous slender neurosetae and lower buccal cirri attached basally, similar to tentacular cirri (Figs. 1A, B, 2A, 4A, B). Mouth ventral with lateral and posterior lips, enclosed in tentacular and buccal segments (Figs. 1B, 4B). Thick muscular pharynx extended on one of paratypes (USNM 98780), with opening pulled tightly together; when cut open, 5 pairs of small, delicate, oval papillae around opening and 2 pairs of small jaws, lacking denticulated bases (similar to that figured for *B. symmytilida,* Pettibone 1984, fig. 2F, G), revealed.

Biramous parapodia having short conical

notopodia and long conical neuropodia (Figs. 2B–D, J, 3D, E, 4E, F). Notosetae moderate in number (up to 20 on adults, up to 5 on juvenile), short to long, extending nearly to tips of neuropodia; stouter than neurosetae, acicular, smooth or slightly roughened distally, with tips rounded (Figs. 2G, 3F, 4G). Presetal acicular lobes of neuropodia slightly longer than postsetal lobes. Neurosetae very numerous, long, slender, separated by slight gap into upper supra-acicular and lower subacicular groups. Upper neurosetae slightly stouter than lower ones, minutely serrated, with blunt tips (Figs. 2H, 3G, 4H), some with terminal bulb (Fig. 2H, upper right). Lower neurosetae more slender and having hooked tips with some longer denticles (Figs. 2I, 3H, 4I). Ventral cirri, attached to middle of neuropodia, short, tapered, and not reaching tips of neuropodia (Fig. 2C, D).

Pygidium rather large and bulbous, with terminal anus and pair of stout anal cirri basally fused; enclosed in parapodia of last two posterior segments (20, 21) and their long dorsal cirri (Fig. 1C). Distinct segmental or nephridial papillae not present, except for 2 pairs of long ventral papillae on segments 11 and 12, projecting posteriorly (Fig. 1D). Papillae shorter on smaller adult paratype (Fig. 3C), absent on juvenile.

*Etymology.*—Neo-Latin adjective *seepensis,* formed from seep, in reference to the distribution of the species in the hypersaline seeps in the Gulf of Mexico.

*Remarks.*—According to the preliminary report by Denoux et al. (1985), the chemosynthetic vent-type taxa found in hypersaline, cold water, hydrocarbon seeps in the Gulf of Mexico are associated with an abundance of non-chemosynthetic species and this enhanced community diversity suggests the possibility that the oil seep communities may be the progenitors of those at the deep-water vent sites and, thus, more primitive. There are some indications that the Gulf of Mexico commensal, *B. seepensis,* might very well be more primitive than the Galapagos commensal, *B. symmytilida.* In *B. seepensis,* the parapodia are biramous, with large notopodia and a moderate number of notosetae; the neuropodia have the form of conical acicular lobes, following the usual pattern in the Polynoidae. In *B. symmytilida,* the parapodia are subbiramous, with the notopodia small, nodular, and the notosetae few to none; the neuropodia have an extra truncate lobe enclosing the acicular lobe, thus, the development of a new structure. There is greater development of the arborescent branchiae in *B. symmytilida* than in *B. seepensis.*

## Acknowledgments

I wish to thank the Florida Escarpment Cruise Participants and especially Drs. Barbara Hecker and Ruth Turner for the material on which this study is based. The manuscript benefited from the reviews of Drs. Meredith L. Jones, Nancy J. Maciolek, and James A. Blake.

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# A NEOTYPE DESIGNATION FOR *PETROLISTHES TOMENTOSUS* (DANA), AND DESCRIPTION OF *PETROLISTHES HETEROCHROUS*, NEW SPECIES, FROM THE MARIANA ISLANDS (ANOMURA: PORCELLANIDAE)

Roy K. Kropp

*Abstract.*—*Petrolisthes tomentosus* (Dana) is determined to be a senior synonym of *P. penicillatus* (Heller) and a neotype of the former is designated. *Petrolisthes pubescens* Stimpson, a species previously confused with *P. tomentosus*, is redescribed and compared to the latter. The two can be distinguished primarily by the presence of elevated, setae-topped bosses on the carapace of *P. tomentosus* as compared to the flat carapace of *P. pubescens*. A new species, *P. heterochrous*, is also described.

For over 100 years carcinologists have confused several Indo-Pacific species of *Petrolisthes* characterized by having a very tomentose carapace and a pronounced fringe of plumose setae on the posterior margin of the manus. Lewinsohn (1969, 1979) has unraveled part of the problem. He (1969) recognized *P. pubescens* Stimpson as distinct from a group that includes *P. tomentosus* (Dana 1852), *P. penicillatus* (Heller 1862), and *P. villosus* (Richters 1880). Moreover, he (1979) summarized the confusion over possible synonymy of the latter three species. Briefly, Ortmann (1897) considered *P. villosus* to be a junior synonym of *P. penicillatus*. However, since then, the matter of synonymy between *P. tomentosus* and *P. penicillatus* has been unresolved. Lewinsohn (1979) examined a syntype of *P. penicillatus* and described it thoroughly. He (as well as Haig 1983) speculated that *P. penicillatus* might be a junior synonym of *P. tomentosus*, whose type has been lost. However, Lewinsohn declined to select a neotype for the latter because the type locality for *P. tomentosus* is the Tuamotu Archipelago, and he did not have specimens from French Polynesia.

Here I select and describe a neotype for *P. tomentosus* based on a specimen from Tahiti and compare it to *P. penicillatus* and *P. pubescens*. Also, I describe a new species of *Petrolisthes* from a collection of porcellanids from the Mariana Islands.

## Materials and Methods

Most of the material on which this report is based was collected by the author in 1979–1981 and 1984. Additional material was obtained from the collection of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Some specimens have been deposited in the Allan Hancock Foundation, Los Angeles, California, and the B. P. Bishop Museum, Honolulu, Hawaii.

Specimens were measured to the nearest 0.1 mm using an ocular micrometer on a Wild M-5 microscope. Measurements are given in the text as carapace length (along the midline) × carapace width (at the greatest dimension) for the type specimens and the largest male, the largest female, and the smallest ovigerous female. Other abbreviations used in the text are: OV = ovigerous females; juv. = juveniles; m = meters.

Setal terminology is based on Kunze and Anderson (1979). Setal measurements were made, but were extremely variable within and among individuals so are not included.

The figures were prepared with the aid of a drawing tube on a Wild M-5 or M-8 microscope.

## Systematic Account

### *Petrolisthes tomentosus* (Dana)

Fig. 1

*Porcellana tomentosa* Dana, 1852:420; 1855: pl. 26, fig. 10.

*Petrolisthes tomentosus.*—Stimpson, 1858: 227 (list); 1907:182 (list).—Kropp et al., 1981:40 (list).

*Porcellana penicillata* Heller, 1862:523; 1865:79.

*Porcellana villosa* Richters, 1880:160, pl. 17, figs. 11–12.

*Petrolisthes villosus.*—Ortmann, 1892:259 (key), 264; 1894:27 (key).—Ward, 1942: 63.

*Petrolisthes penicillatus.*—Ortmann, 1897: 287 (key), 288.—Lenz, 1910:566.—Miyake, 1942:347, text-figs. 11–12; 1943:55, 83, text-fig. 18.—Haig, 1964:368; 1966: 42; 1983:283.—Lewinsohn, 1979:45.—Yang, 1983:2, pl. 2.

*Petrolisthes villosus*?—Miers, 1884:559.

Not *Petrolisthes tomentosus.*—Ortmann, 1892:259 (key), 264; 1894:27 (key); 1897: 287 (key), 288.—Grant and McCulloch, 1906:39.—Miyake, 1943:55 (key), 85, text-figs. 19-21; 1956:310.—Haig, 1964: 364; 1966:47 (key).—Nakasone and Miyake, 1971:4. = *Petrolisthes pubescens* Stimpson.

*Type data.*—Much of the type material collected by Dana during the United States Exploring Expedition (1838–1842) was studied by Stimpson in Chicago. This material, along with Stimpson's North Pacific Exploring Expedition (1853–1856) was destroyed in the 1871 Chicago fire (Deiss and Manning 1981). Although some of Dana's types have since been rediscovered (Deiss and Manning 1981), I have been unable to locate the type of *Porcellana tomentosa.* I have searched the USNM, Yale Peabody Museum, and the Philadelphia Academy of Sciences without success. Dr. R. B. Manning has compiled an unpublished list of Dana material at the Museum of Comparative Zoology (Harvard) and the major European museums. A type of *P. tomentosa* is not among them. It is very probable that the type for this species has been destroyed. I located a disarticulated, but complete, specimen of Dana's species in the USNM. It is from Tahiti, close to the original type locality (Tuamotu) and is herein designated as the neotype.

*Neotype.*—TAHITI: Arue; under dead coral; 1963; Coll. H. A. Rehder; ♀ (OV); 5.3 × 4.8 mm; USNM 190776.

*Other material examined.*—OKINAWA: W of Onna, S of Manzamo Precipice; reef flat; 20 May 1984; Coll. R. B. Manning et al.; 1 ♀ (OV). MARIANA ISLANDS: PAGAN: Puntan Lagona; on dead coral; 1 m; 13 Mar 1981; 1 ♀. Bandeera Peninsula; intertidal; 11 Mar 1981; 1 ♀. Palapala Bay; subtidal under rock; 1.5 m; 14 Mar 1981; 1 ♂. Liyan; on base of *Pocillopora setchelli*; 1.5 m; 9 Mar 1981; 1 ♀ (OV). Apaan Santati; reef flat under rock; <1 m ; 10 Mar 1981; 1 ♂, 1 ♀. SAIPAN: Tanapag Barrier Reef; on dead coral; 6 m; 20 Nov 1980; 1 ♀. Agingan Pt.; reef margin on coralline algae; <1 m; 19 Nov 1980; 3 ♂ (1 with bopyrid isopod). GUAM: Tanguisson Pt.; reef front on dead branching coral; 11 m; 25 May 1984; 1 ♂. Piti Bay; outer reef flat S of Camel Rock; intertidal and subtidal on dead coral; 0–1.5 m; 13 Jun 1980; 5 ♂, 2 ♀ (OV). Luminao; reef flat on dead coral or under rocks; 1 m; 28 Mar 1980, 5 Apr 1980; 4 ♂, 6 ♀ (2 OV). Neye Is.; on *Pocillopora* sp.; 29 Jan 1981; Coll. R. H. Randall; 1 ♀. Toguan Bay; at reef margin on reef rock; <1 m; 14 Feb 1984; Coll. J. H. Dominguez; 1 ♂. Pago Bay; reef flat on coralline algae or intertidal under rock; 0–1 m; 18 May 1981, 16 Feb 1984; 2 ♂. FIJI: Nananu-i-Ra; intertidal pool; 3 Jun 1980; 1 ♀.

*Measurements.*—Largest male—5.4 ×

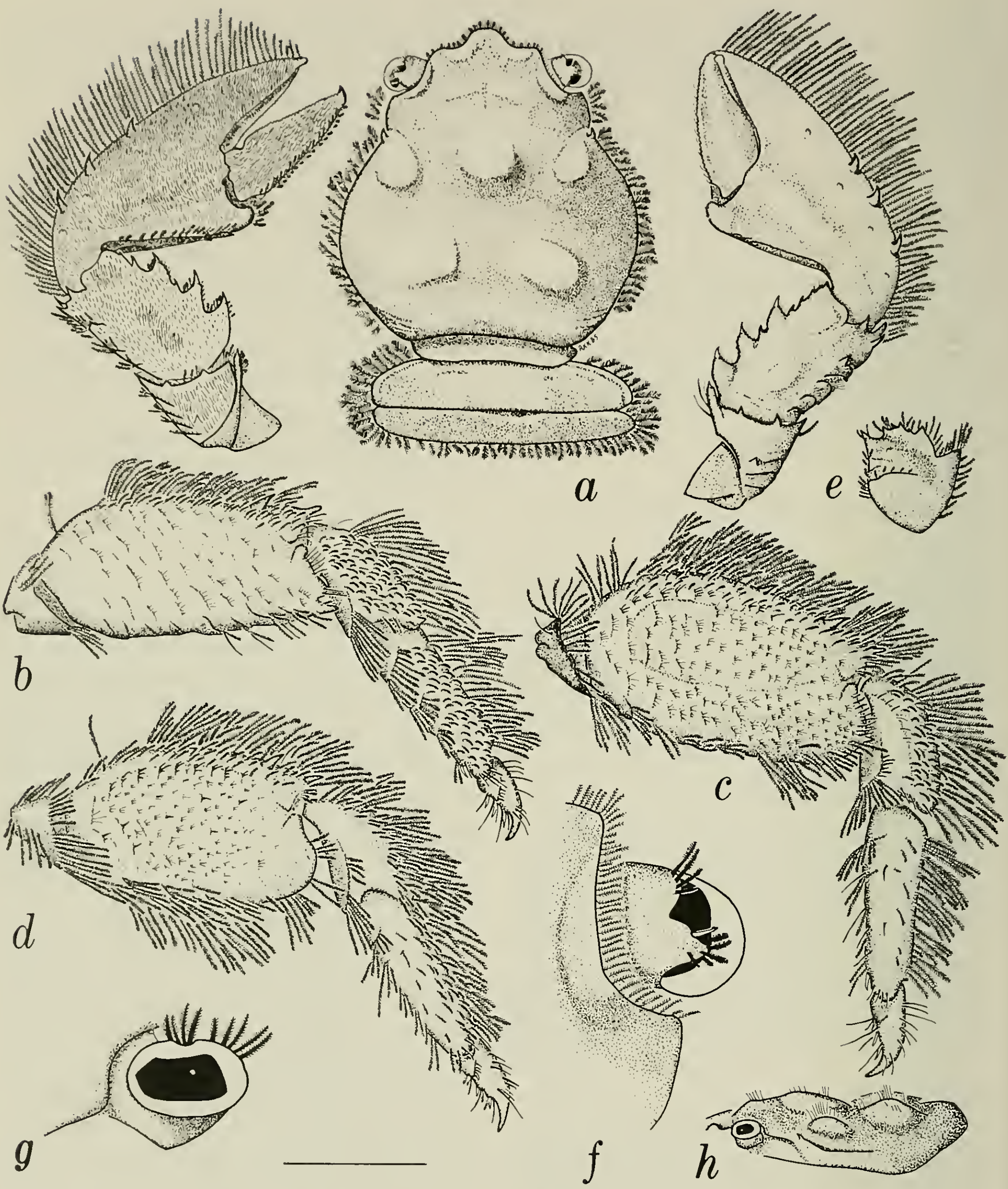

Fig. 1. *Petrolisthes tomentosus* (Dana), neotype ♀: a, Carapace and chelipeds; b, c, d, Right walking legs 1, 2, 3; e, Right antennule base; f, Right eye (dorsal view); g, Right eye (lateral view); h, Carapace (lateral view). Scale: 3 mm (a); 2 mm (b–e); 1 mm (f, g); 4 mm (h). [Surface setae on carapace and right cheliped not shown.]

5.2 mm; largest female—5.9 × 5.6 mm; smallest ovigerous female—4.1 × 3.9 mm.

*Neotype description.*—Carapace: Surface smooth; with 5 conspicuous rounded elevations, largest on gastric region, 1 on each medial epibranchial region, 2 flanking cardiac region; covered with distally-curved setae; elevations, frontal-gastric ridge with distally-pappose setae. Frontal-gastric ridge present, front indistinctly trilobate, median lobe most projecting; surface slightly concave; margin entire, fringed with plumose, simple setae; no supraocular spine. Lateral margin cristate at epibranchial region, 1 epibranchial spine; rounded posteriorly, no mesobranchial spines. Epimera with fringe of plumose setae.

Chelipeds: Subequal. Dorsal surface of all segments covered with distally-curved pappose setae. Merus with dorsal surface smooth; posterior margin rounded, with 1 subproximal spine; distal margin with 1 medial, 1 posterior spine; anterior margin with spine-tipped tooth; ventral surface smooth, distal margin with 2 spines anteriorly. Carpus with dorsal surface smooth, proximal median swelling, topped with distally-pappose setae; similar setae in clump distally near anterior margin; posterior margin with serrate squamae, 3 spines, distal spine single-pointed; anterior margin with 3 serrated, spine-tipped teeth (having plumose setae on distal margin), and 2–4 spines (other specimens with 3–5 teeth, 0–3 spines); distal margin entire, incised medially, with 1 spine posterior to incision. Manus with dorsal surface divided into upper and lower portions by rounded, longitudinal ridge, topped with distally-plumose setae; upper surface smooth, slightly concave; lower surface smooth, slightly concave, but with 5 biconical tubercles and 3 spines near posterior margin (other specimens with tubercles indistinct, 2–4 spines). Anterior margin of manus finely scalloped, no distal spine; posterior margin coarsely serrated, with fringe of plumose setae along entire length. Dactylus with dorsal rounded median longitudinal swelling; upper margin coarsely serrated, lined with stout, plumose setae; occlusal surfaces serrated; gape with scattered setae.

Walking legs: Merus with dorsal surface bearing fine transverse striae, covered with simple setae arising from striae; anterior margin fringed with plumose setae, of leg 1 with 2–3 spines, leg 2 with 3 spines, leg 3 with 1–2 spines; posterodistal spines 1, 2, 0 (other specimens 1–2, 1–2, 0). Carpus with plumose, scattered simple setae on anterior margin; leg 1 with, legs 2, 3 without anterodistal spine. Propodus with anterior and posterior margins bearing plumose, scattered simple setae; posterior surface with 2 movable spinules (1 medial, 1 subdistal), 2 laterally-placed movable spinules at distal margin. Dactylus with scattered simple setae; 3 movable spinules on posterior margin.

Ocular peduncle: Dorsal extension onto cornea triangular, with clump of pappose setae; cornea round in lateral view.

Antennules: Basal segment with few transverse striae on outer surface; anterior margin finely denticulate.

Third maxillipeds: Ischium smooth; upper portion with 3–4 lines of setae (absent in some specimens).

*Color alive.*—Based on material from the Mariana Islands. Overall color of carapace, chelipeds, walking legs off-white. Carapace with 6 or more pink areas. Chelipeds with more numerous pink areas of variable size, shape; similar blotches on walking legs. Body setae usually clear, sometimes yellow.

*Remarks.*—The pattern of elevations on the carapace and chelipeds, and the setation patterns on the carapace, chelipeds, and walking legs were consistent among all specimens examined. Setae on the elevated areas frequently may be worn away.

*Comparison.*—The neotype and other material examined fit Dana's description and illustration of *Porcellana tomentosa.*

Contrary to Lewinsohn (1979), I think Dana's figure is adequate to permit identification of this species.

Lewinsohn (1979) based his observations on the type of *P. penicillata* Heller. I compared the neotype of *P. tomentosus* and other material to his description and find that they agree very well. The number of spines near the posterior margin of the manus varies from 2–4 for my material, versus 4 for Heller's syntype. I found 2–3 anterior marginal spines on the meri of legs 1, 2 and 1–2 on leg 3, whereas Lewinsohn reported 2, 2, and 1 spines, respectively. There is no doubt in my mind that *Petrolisthes tomentosus* (Dana) is a senior synonym of *P. penicillatus* (Heller) and *P. villosus* (Richters).

*Petrolisthes tomentosus* was separated from *P. pubescens* by Lewinsohn (1969) and Haig (1979). The two species are most easily distinguished by the elevations on the carapace and the single-pointed distal spine on the posterior margin of the cheliped carpus in the former species, and the flat carapace and double-pointed distal spine on the posterior margin of the cheliped carpus in the latter.

*Habitat.*—Low intertidal under rocks; subtidal on dead coral, under rocks, or on the base of living corals to a depth of 11 m.

*Distribution.*—Widespread Indo-Pacific (summarized by Haig 1983:284).

### *Petrolisthes pubescens* Stimpson
Fig. 2

*Petrolisthes pubescens* Stimpson, 1858:228 (list), 241; 1907:183, pl. 22, fig. 3.—Lewinsohn, 1969:146.—Haig, 1979:126, figs. 8–9.—Kropp et al., 1981:39 (list).

*Petrolisthes tomentosus.*—Ortmann, 1892: 259 (key), 264; 1894:27 (key); 1897:287 (key), 288.—Grant and McCulloch, 1906: 39.—Miyake, 1943:55 (key), 85, text-figs. 19–21; 1956:310.—Haig, 1964:367; 1966: 47 (key).—Nakasone and Miyake, 1971: 4. Not *P. tomentosus* (Dana).

?*Petrolisthes tomentosus.*—Nobili, 1906:129 (key).—Bouvier, 1915:205.—Ramadan, 1936:3 (list).—Imanaka et al., 1984:54. These authors did not provide descriptions permitting confident assignment of their specimens to either nominal species. The first three records are placed here because the authors were probably following the thought of the period. The record of Imanaka et al. (1984) is probably following the thoughts of present Japanese authors, but additional evidence that they are referring to *P. pubescens* is the size of their specimen (9.3 mm carapace length) which is much larger than any specimen I have seen of *P. tomentosus* and which is near the range I have observed for *P. pubescens.*

Not *Petrolisthes pubescens.*—Balss, 1913:30, pl. 1, fig. 2. = *P. coccineus* (Owen). Misidentification. I agree with Laurie's (1926) supposition that the figure published by Balss (pl. 1, fig. 2) is of *P. coccineus.*

*Type data.*—It is very probable that Stimpson's type was destroyed by the 1871 Chicago fire (Deiss and Manning 1981). However, the identity of *P. pubescens* has been well-established (Lewinsohn 1969, Haig 1979) and a neotype designation is not warranted.

*Material examined.*—TAIWAN: Yeh Liu Pi; 28 Jun 1978; Coll. unknown; 1 ♀, USNM 210635. San Hsien Tai; under rock; 3 m: 25 Jul 1979; 1 ♂, USNM 210576. MARIANA ISLANDS: PAGAN: Bandeera Peninsula; intertidal; 11 Mar 1981; 1 ♂, 1 ♀ (OV), 2 juv. Palapala Bay; under rock; 1.5 m; 14 Mar 1981; 1 ♂, USNM 210572, 1 ♀. ANATAHAN: Observation spot; intertidal and subtidal under rocks; 0, 5–7 m; 19 Jul 1981; Coll. L. G. Eldredge, R. K. Kropp; 2 ♂, 4 ♀ (2 OV), USNM 210574 (in part). GUAM: Cabras Is.; intertidal at landward edge of bench; 18 Jun 1981; 1 ♂, 1 ♀ (OV). Luminao; reef front under rocks; 6 m; 8 Sep 1980; Coll. V. Tyndzik; 4 ♀ (2 OV), USNM 210573. MARQUESA ISLANDS: NUKU HIVA: Taiohae Bay; 1967; Coll. H. A.

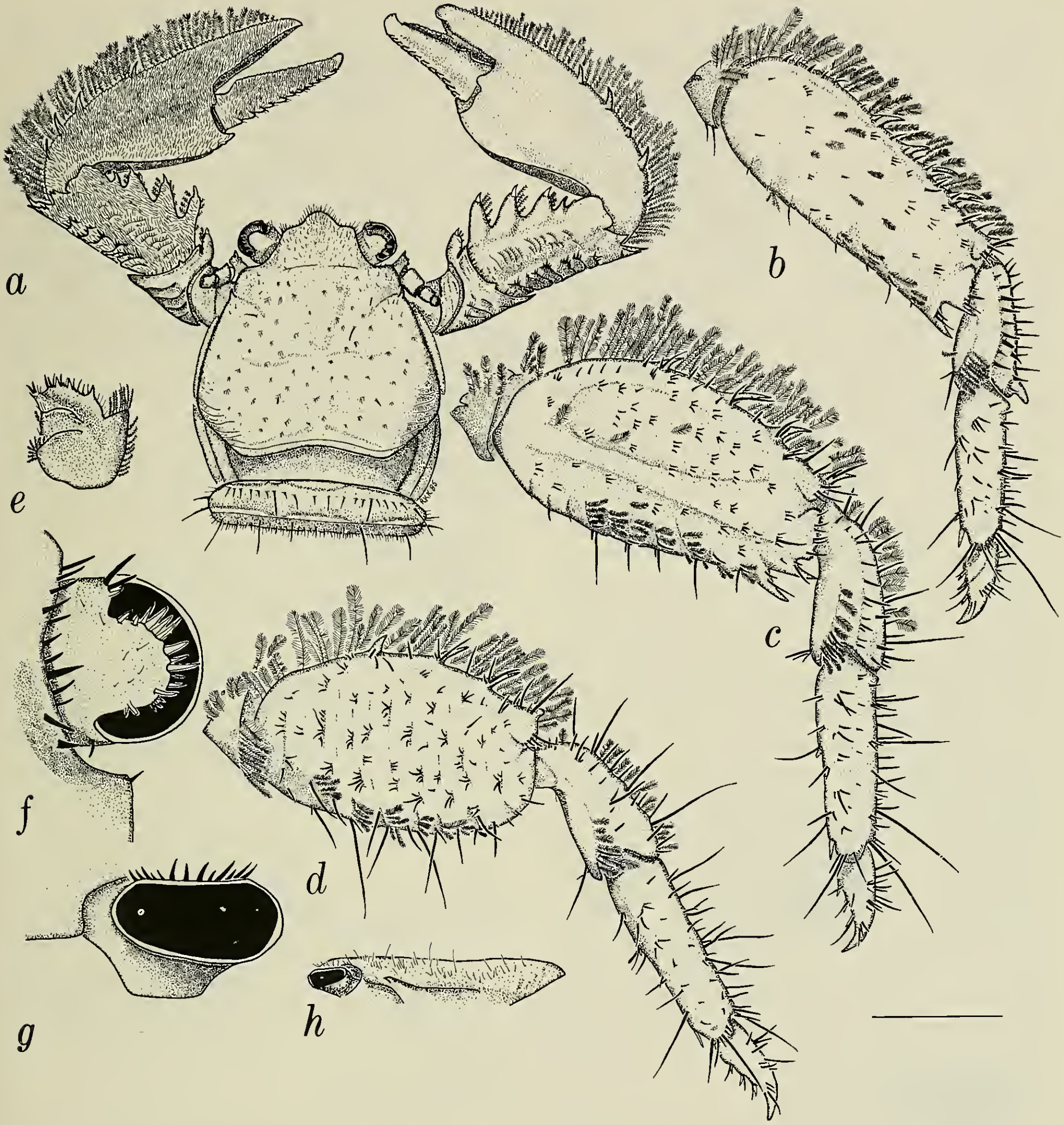

Fig. 2. *Petrolisthes pubescens* Stimpson, ♀ (USNM 210574): a, Carapace and chelipeds; b, c, d, Right walking legs 1, 2, 3; e, Right antennule base; f, Right eye (dorsal view); g, Right eye (lateral view); h, Carapace (lateral view). Scale: 4 mm (a, h); 2 mm (b–e); 1 mm (f, g). [Surface setae on carapace and right cheliped not shown.]

Rehder; 2 ♂, USNM 190769. Taiohae Bay; beach near wharf; 4 Oct 1967; Coll. B. R. Wilson; 1 ♀ (OV). Anse Haka Paa Baie du Controleur; shore of Smerres; 17 Sep 1967; Coll. B. R. Wilson; 1 ♀ (OV, with bopyrid isopod), USNM 210978.

*Measurements.*—Largest male—7.9 × 7.9 mm; largest female—8.5 × 8.5 mm; smallest ovigerous female—4.2 × 4.1 mm.

*Description.*—Based on all material examined. Carapace: Surface smooth, flat, sparsely to thickly covered with simple setae. Frontal-gastric ridge indistinct; front indistinctly trilobate, median lobe most projecting; with slight median longitudinal concavity; margin entire, with some setae; no supraocular spine. Lateral margin cristate anteriorly, 1 epibranchial spine; rounded posteriorly, no mesobranchial spines. Epimera with scattered plumose setae.

Chelipeds: Subequal. Dorsal surface of all segments covered with pappose setae. Merus with few transverse striae on dorsal surface; posterior margin rounded, with scalloped squamae, no spine; distal margin with 1 medial, 2 posterior spines; anterior margin with spine-tipped tooth; ventral surface smooth, distal margin with 1 spine anteriorly. Carpus with dorsal surface smooth, longitudinal swelling of transverse striae; posterior margin with raised squamae, 2–3 spines, distal spine double-pointed; anterior margin with 3–4 serrated or entire, spine-tipped teeth, (having plumose setae on distal margin), and 0–2 spines; distal margin entire, incised medially, with 1 spine posterior to incision. Manus with dorsal surface divided into upper and lower portions by indistinct, longitudinal swelling; upper and lower surfaces smooth, slightly concave; lower surface with few biconical tubercles proximally, with 4–8 spines near posterior margin. Anterior margin cristate, with squamae distally; posterior margin serrated, with fringe of plumose setae along entire length. Dactylus with prominent medial swelling on dorsal surface; upper margin with raised squamae; occlusal surfaces finely serrated; gape with cover of setae.

Walking legs: Merus with dorsal surface smooth, simple setae posteriorly; anterior margin with fringe of plumose setae, margin of leg 1 with 4–5 spines, leg 2 with 3–5 spines, leg 3 with 3–4 spines; posterodistal spines 1–2, 1–2, 0. Carpus with scattered simple setae, leg 1 with, legs 2, 3 without anterodistal spine. Propodus with scattered simple setae; posterior surface with 2 movable spinules (1 medial, 1 subdistal), distal margin with 2 laterally-placed movable spinules. Dactylus with scattered simple setae; posterior margin with 3 movable spinules.

Ocular peduncle: Dorsal extension onto cornea oval, lined with stout simple setae; cornea slightly flattened in lateral view.

Antennules: Basal segment with few transverse striae on outer surface; anterior margin irregularly spinose.

Third maxillipeds: Ischium with transverse striae; without rows of setae.

*Remarks.*—The specimens from Taiwan agree well with Stimpson's (1858, 1907) description and figure except that they have fewer spines on the posterior margin of the manus. The Marianas and Marquesas specimens differ from the Taiwan material by having three more regularly-shaped teeth and only one spine on the anterior margin of the cheliped carpus.

*Comparison.*—For comparison see this section under *P. tomentosus.*

*Habitat.*—Low intertidal or subtidal under rocks.

*Distribution.*—Previously known from the Indian Ocean and the extreme western Pacific (Haig 1979), now known as far east as the Marquesa Islands.

### *Petrolisthes heterochrous,* new species

Fig. 3

*Petrolisthes* n. sp. 3.—Kropp et al., 1981:39 (list).

*Holotype.*—GUAM: Agana Bay; reef front on dead coral; 10 m; 11 Sep 1984; Coll. J. H. Dominguez; ♂ (3.1 mm × 2.9 mm) USNM 222529.

*Paratypes.*—GUAM: same collection as holotype; 1 ♂ (2.6 mm × 2.4 mm), 1 ♀ (OV) (3.3 mm × 3.2 mm); USNM 222530. Tanguisson Pt., reef front on dead coral; 11–12 m; 25 May 1984; 1 ♂ (3.0 mm × 2.9 mm), 1 ♀ (OV) (3.6 mm × 3.6 mm); AHF 841; 1 ♂ (2.9 mm × 2.6 mm), 1 ♀ (OV) (3.2 mm × 3.2 mm); BPBM S10460. Tanguisson Pt.; reef front on dead branching coral; 18 m; 7 Feb 1984; 1 ♂ (3.0 mm × 2.7 mm), 1 ♀ (2.8 mm × 2.6 mm); USNM 222552.

*Other material examined.*—GUGUAN: "Western Bay"; reef front on base of *Po-*

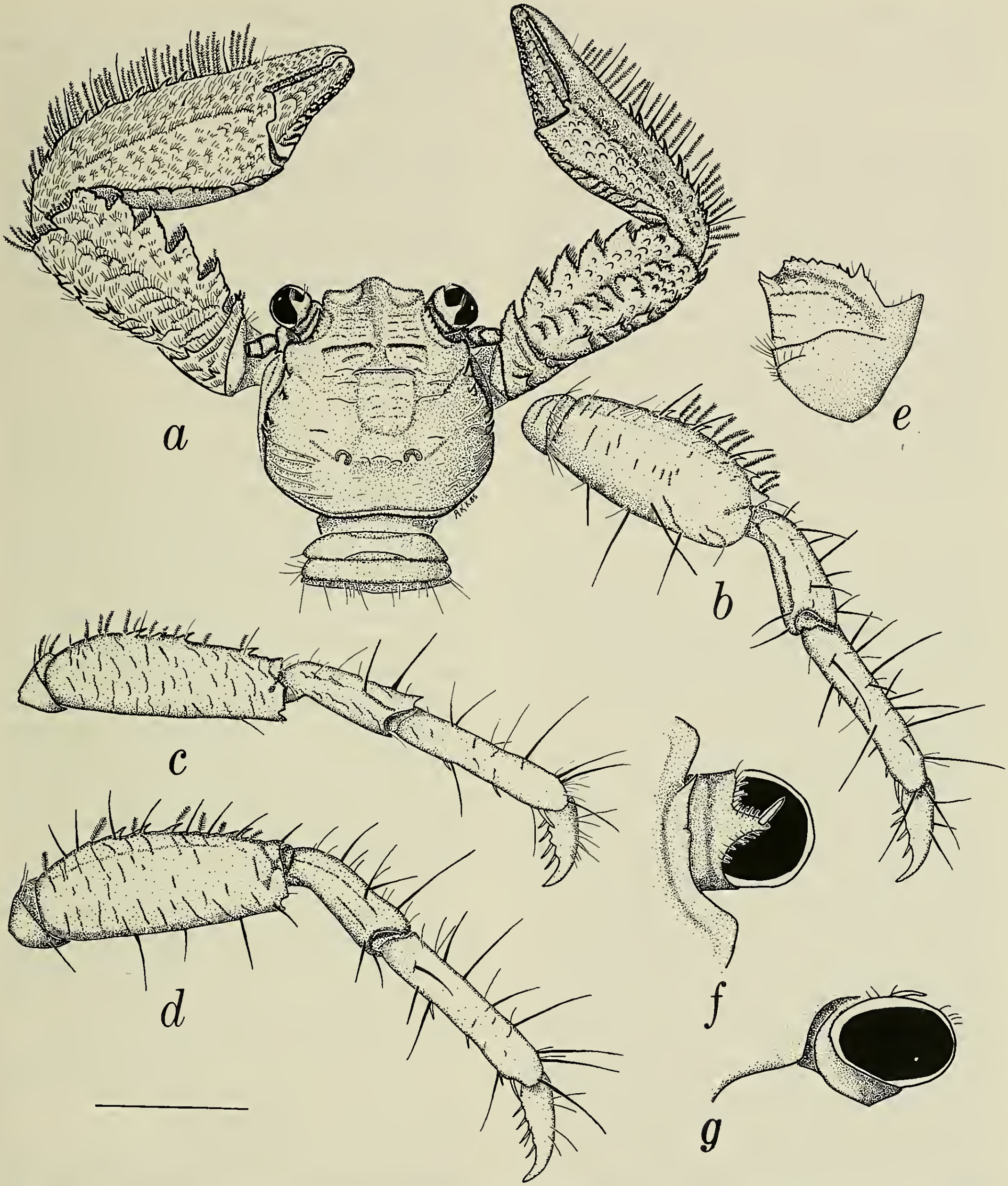

Fig. 3. *Petrolisthes heterochrous,* new species, holotype ♂ (a, f, g), ♂ paratype, USNM 222530 (b–e): a, Carapace and chelipeds; b, c, d, Right walking legs 1, 2, 3; e, Right antennule base; f, Right eye (dorsal view), g, Right eye (lateral view). Scale: 2 mm (a); 1.2 mm (b–d); 1 mm (e–g). [Surface setae on carapace and right cheliped not shown.]

*cillopora* sp.; 10 m; 2 Jan 1975; Coll. unknown; 1 ♂, 2 ♀ (OV). SAIPAN: Tanapag Barrier Reef; reef front on dead coral; 6 m; 20 Nov 1980; 4 ♂, 5 ♀ (3 OV). Tanapag Lagoon; from base of *Stylophora mordax*; 3 m; 19 Nov 1980; 1 ♀ (OV). GUAM: Adelup Pt.; reef front on articulated coralline algae; 11 m; 22 Nov 1979; 1 ♂, 1 ♀. Calalan Bank; reef front on dead branching coral; 10 m; 16 Oct 1984; 1 ♀ (OV), 2 juv. Pago Bay; reef front on dead coral; 20, 23 m; 17 Sep 1980, 28 Feb 1984; 3 ♂, 2 ♀. All collected by the author unless stated otherwise.

*Holotype description.*—Carapace: Surface with fine, beaded transverse rugae; relatively flat; rugae lined with setae, most evident on posterolateral and gastric regions. Frontal-gastric ridge distinct, front trilobate, median lobe most projecting; surface concave; margin finely denticulate, no setae; supraocular spine present. Lateral margin cristate anteriorly, 2 epibranchial spines present; rounded posteriorly, 2 mesobranchial spines. Epimera with few scattered, plumose setae.

Chelipeds: Slightly unequal. Merus with dorsal surface transversely striated; posterior margin rounded, with 1 subproximal, distal margin with 0–1 medial, 1 posterior spine; anterior margin with spine-tipped tooth. Merus with ventral surface transversely striated; distal margin with 2–3 spines anteriorly. Carpus with dorsal surface bearing distinct longitudinal ridge of raised, scalloped squamae along midline, without obvious setation; posterior, anterior surfaces with smaller, scalloped squamae; posterior margin with raised squamae, and 4 spines (paratypes with 4–7 spines), distal spine double-pointed; anterior margin with 4 serrate, spine-tipped teeth having plumose setae on distal margin; distal margin roundly serrated, incised medially, without posterior spine. Manus with dorsal surface divided into upper and lower portions by longitudinal row of scalloped squamae placed end-to-end; upper surface with raised, scalloped tubercles, slightly convex; lower surface with irregularly-placed conical tubercles of varying size, slightly convex, row of 7–9 spines near posterior margin (paratypes with 7–10 spines). Anterior margin of manus with row of raised scalloped squamae, and distal spine; posterior margin serrated, with fringe of plumose, scattered simple setae extending from carpal joint to beginning or middle of immovable finger. Dactylus with dorsal raised, serrated squamae; upper margin with row of overlapping, scalloped squamae; occlusal surfaces finely serrated; gape without setae.

Walking legs: Merus with few transverse striae on dorsal surface, and scattered simple setae; anterior margin with few scattered plumose, simple setae; margin of legs 1, 2 with 5 spines (paratypes, leg 1 with 3–6, leg 2 with 3–5 spines), leg 3 with 4 spines (paratypes with 3–4 spines); posterodistal spines 1-1-0. Carpus with few scattered simple setae; carpus of leg 1 only with anterodistal spine. Propodus with scattered simple setae; posterior surface of legs 1, 2 with 3 movable spinules, leg 3 with 2 movable spinules; distal margins of all legs with 1 laterally-placed movable spinule. Dactylus with scattered simple setae; posterior margin with 4 movable spinules.

Ocular peduncle: Dorsal extension onto cornea triangular, with 1 simple seta distally; cornea round in lateral view.

Antennules: Basal segment with few transverse striae on outer surface; anterior margin irregularly denticulate.

Third maxillipeds: Ischium with transverse beaded rugae, each lined with stout simple setae on free margin.

*Variations.*—Among the non–paratype material examined, I have observed the following variations from the holotype. There may be three spines on the mesobranchial region of the carapace. The anterior margin of the cheliped carpus may have five teeth and the posterior margin four spines. The outer margin of the manus may have as few as six spines.

*Color alive.*—Color extremely variable.

One extreme, carapace almost uniform red-purple with 2 white spots at mesobranchial spines; sometimes reddish with scattered orange patches, with transverse white, orange band on rostrum. Other extreme, carapace light tan with mottled pattern of blue-green, tan-orange. Penultimate segment of third maxilliped palp of all specimens with series of longitudinal red-purple lines. Both extremes, as well as many intermediate patterns, occur within the same collection.

*Comparison.*—Among Indo-Pacific species of *Petrolisthes, P. heterochrous* is most similar to *P. militaris* (Heller) and *P. scabriculus* (Dana). All have a transversely rugose carapace, two epibranchial spines, and marginal mesobranchial spines. The new species can be distinguished from the other two by its trilobate front and distinct longitudinal ridge of raised squamae on the cheliped carpus. *Petrolisthes militaris* and *P. scabriculus* each have a triangular front and no ridge on the cheliped carpus. Neither of the latter species occurs in the Mariana Islands.

*Etymology.*—From the Greek "heterochrous," meaning "of different colors," a noun in apposition, referring to the variety of color patterns among the specimens of this species.

*Habitat.*—Subtidal to a depth of 23 m, occurring in crevices in dead coral rubble, dead branching coral, and on the base of living coral.

*Distribution.*—Known only from the Mariana Islands.

## Discussion

During this study I observed and used characters not previously used in systematic studies of porcellanids. These characters were the shape of the dorsal extension of the ocular peduncle onto the cornea, the setae found on this extension, and the shape of the cornea in lateral view. The three species discussed here can be distinguished by these three characters, in combination with others. These characters may also be useful in distinguishing among other species of porcelain crabs.

## Acknowledgments

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# THREE NEW SPECIES OF PILARGIDAE (ANNELIDA: POLYCHAETA) FROM THE EAST COAST OF FLORIDA, PUERTO RICO, AND THE GULF OF MEXICO

Paul S. Wolf

*Abstract.*—A new species of *Litocorsa* Pearson, 1970, and two new species of *Synelmis* Chamberlin, 1919, are described from Puerto Rico, the east and west coasts of Florida, and Texas.

The genus *Litocorsa* Pearson, 1970, was erected for a single species, *L. stremma* Pearson, found off the west coast of Scotland (Pearson 1970) and from the Mediterranean Sea (Katzmann et al. 1974). Wolf (1984:29–41) identified another species, *Litocorsa* sp. A, in material collected in the Gulf of Mexico. This species is here described, and the generic diagnosis is emended.

The genus *Synelmis* Chamberlin, 1919, was recorded from Florida and the Caribbean as *Synelmis albini* (Langerhans 1881) by Pettibone (1966:191, with synonymies); however, judging by her figures of specimens from different localities, it appears she was actually dealing with two or perhaps as many as four species. Wolf (1984) identified three apparently undescribed species of *Synelmis* from the Gulf of Mexico. Two of them are here newly described.

The bulk of the material examined for this study was collected as part of a U.S. Bureau of Land Management (now Minerals Management Service) Outer Continental Shelf baseline study conducted during 1975–1981. MAFLA stations were those designated within the Mississippi-Alabama-Florida portion of the program; SOFLA stations were those located off southwest Florida; STOCS stations were located off the Texas coast (see Uebelacker and Johnson 1984). IXTOC stations were collected as part of the IXTOC Oil Spill Assessment Study off the southern coast of Texas and were also included in Uebelacker and Johnson (1984). The remaining material was collected under the auspices of the Environmental Protection Agency (EPA) during contracts issues to Battelle, Columbus Laboratories (EPA/Bat stations), Interstate Electronics Corp. (IEC stations) and Science Applications International Corp. (SAI stations) for studies located off Puerto Rico, east and west coasts of Florida, and Texas (see Acknowledgments).

The type material and some additional specimens are deposited in the U.S. National Museum of Natural History, Smithsonian Institution (USNM). Other specimens are in the laboratory museum of Barry A. Vittor & Associates, Inc., Mobile, Alabama.

## Figure Abbreviations

| | |
|---|---|
| a | alimentary canal |
| anC | anal cirrus |
| b | brain |
| cM | circular muscle |
| dbVe | dorsal blood vessel |
| dC | dorsal cirrus |
| dlM | dorsal longitudinal muscle |
| dlVe | dorsal lateral vessel |
| dtC | dorsal tentacular cirrus |
| e | epidermis |
| lAn | lateral antenna |
| m | mouth |
| mAn | median antenna |
| mvC | midventral cirrus |
| nC | nerve cord |

| | |
|---|---|
| neAc | neuropodial aciculum |
| neSp | neuropodial spine |
| noAc | notopodial aciculum |
| noSp | notopodial spine |
| oM | oblique muscle |
| pa | palp |
| paSt | palpostyle |
| t | testis |
| vbVe | ventral blood vessel |
| vC | ventral cirrus |
| vlM | ventral longitudinal muscle |
| vlVe | ventral lateral vessel |
| vTc | ventral tentacular cirrus |

### *Litocorsa* Pearson, 1970

*Type species.*—*Litocorsa stremma* Pearson, 1970:69.

*Diagnosis (emended).*—Palps fused dorsally, with or without ventrolateral palpostyles. Antennae present or absent. Two pairs of small tentacular cirri present. Notopodia each with single acicular spine. Neuropodia with 1–2 stout emergent spines, and slender serrate setae having fine tips. Pygidium smooth, with pair of smooth, slender anal cirri. Body with smooth integument.

*Remarks.*—The above diagnosis is modified from Pearson (1970:69) to include the new species described herein. The pointed prostomium described by Pearson (1970: 70) and Katzmann et al. (1974:14) for *Litocorsa stremma* is here interpreted as palps that are fused dorsally.

### *Litocorsa antennata,* new species
Fig. 1a–j

*Litocorsa stremma.*—Flint and Rabalais, 1980:195, 197–201 [not Pearson, 1970].
*Litocorsa* sp. A.—Wolf, 1984:29–41, figs. 29–39, 29–40a–j.

*Material examined.*—PUERTO RICO: SAI Sta A1-1, Mar 1984, 18°29.7′N, 66°43.4′W, muddy silt, 145 m, 1 specimen. FLORIDA: SOFLA Sta 4B, D, Aug 1981, 26°45.81′N, 83°32.12′W, medium sand, 56 m, 4 specimens (USNM 86944-5).—Sta 25, Nov 1980, 24°47.95′N, 82°13.26′W, silt/clay, 24 m, 1 specimen (USNM 86946); MAFLA Sta 2208G, Jun 1976, 27°45′00″N, 83°27′30″W, clayey sandy silt, 30 m, 2 specimens (USNM 86941).—Sta 2209H, Aug 1977, 27°52′30″N, 83°33′59″W, clayey sandy silt, 34 m, 1 specimen (USNM 86943).—Sta 2422C, Jun 1976, 29°30′N, 14°27′W, medium fine sand, 24 m, 26 specimens.—Sta 2423B, C, Jul 1976, 29°37′00.8″N, 84°17′00.2″W, silty fine sand, 19 m, 146 specimens including HOLOTYPE (USNM 98772) and 59 Paratypes (USNM 98773).—Sta 2424C, Jul 1976, 29°13′00.7″N, 85°00′01.4″W, medium sand, 27 m, 1 specimen. TEXAS: IEC Sta 003-006, 28 Sep 1979, 29°32.2′N, 93°47.1′W, sandy clay, 12 m, 1 specimen; Sta 011-009, 28 Sep 1979, 29°26.8′N, 93°42.2′W, sand, 12 m, 3 specimens.—STOCS Sta II/6-3, Aug 1976, 27°24′N, 96°29′W, silty clay, 98 m, 1 specimen (USNM 86948).—Sta III/2-5, Spring 1976, 26°58′N, 96°48′W, silty clay, 65 m, 2 specimens (USNM 86949).—Sta III/4-5, Fall 1976, 26°58′N, 97°20′W, sand, 15 m, 13 specimens (USNM 86951).—Sta III/4-4, same location, Winter 1977, 1 specimen (USNM 86950).—Sta IV/1-6, Winter 1976, 26°10′N, 97°01′W, clayey sand, 27 m, 2 specimens (USNM 86952).—IXTOC Sta S52-6, Nov 1979, 26°10′00″N, 97°01′00″W, silty sand to clayey sand, 27 m, 1 specimen (USNM 86947).

*Description.*—Length to 25 mm, width to 0.2 mm. Largest specimen complete with 107 setigers. Prostomium with minute median and lateral antennae (Fig. 1a). Eyes absent. Palps fused dorsally, with pair of minute ventrolateral palpostyles (Fig. 1b). Dorsal and ventral tentacular cirri short, digitiform, similar in size and shape to dorsal cirri (Fig. 1a–c). Ventral cirri, beginning on setiger 2, slightly smaller than dorsal cirri. Parapodia poorly developed, not set off from body wall (Fig. 1d).

Stout notopodial acicular spines beginning on setigers 6–8, accompanied by slender internal aciculum (Fig. 1d). Slender, serrate neurosetae (Fig. 1e) present throughout,

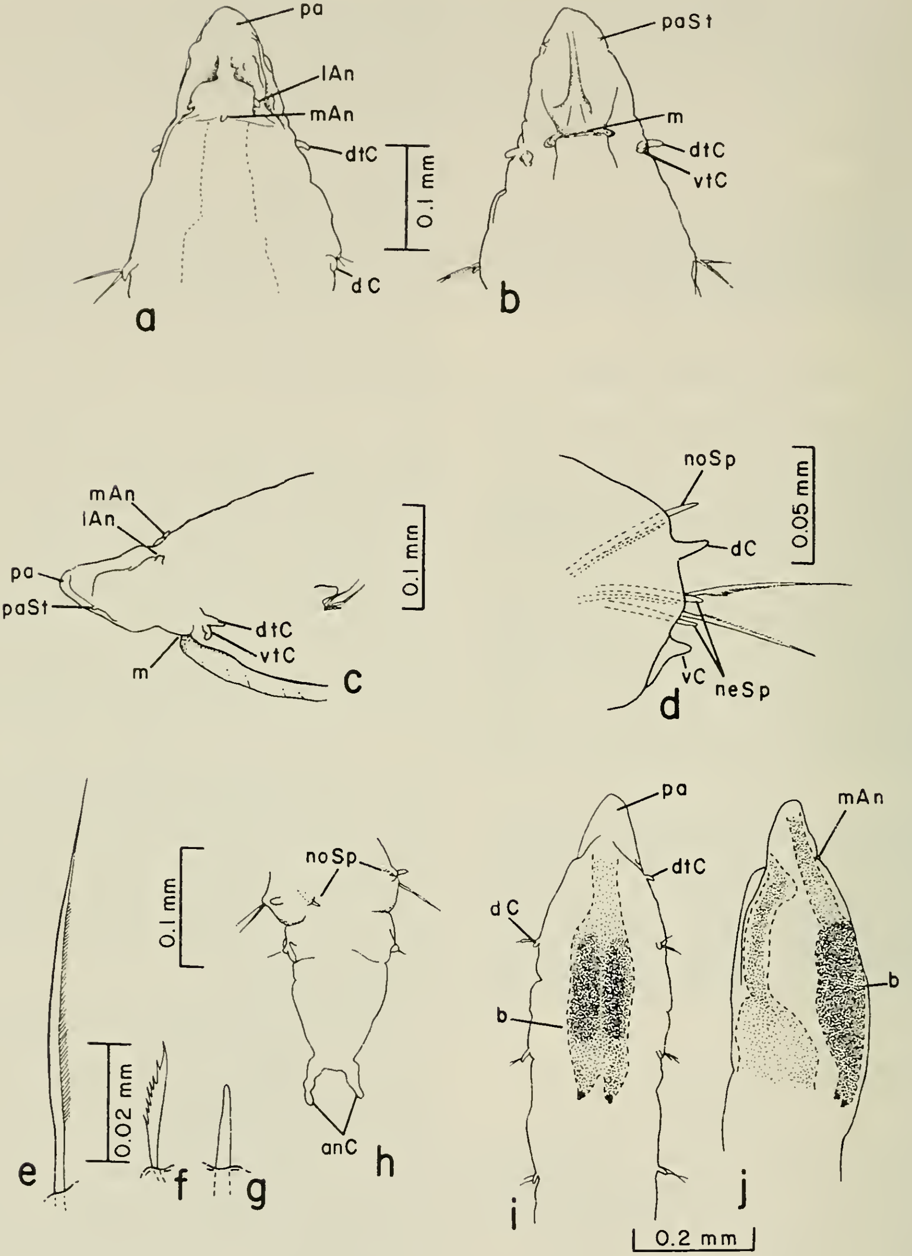

Fig. 1. *Litocorsa antennata*: a, Anterior end, dorssal view; b, Same, ventral view; c, Same, lateral view; d, Middle parapodium, anterior view; e, Upper neuroseta; f, Neuropodial spine from setiger 3; g, Same, from middle setiger; h, Posterior end, dorsal view; i, Anterior end showing brain; j, Same, lateral view. (All figures from Wolf 1984, figs. 29–40a–j.)

accompanied by 1–2 acicular spines. Neuropodial spines serrate on first 1–3 or 4 setigers (FIg. 1f), gradually becoming smooth thereafter (Fig. 1g).

Pygidium with pair of smooth, filiform anal cirri (Fig. 1h).

Brain visible through integument, posteriorly bilobed extending into setiger 3, with lobes divergent, more darkly pigmented at tips (Fig. 1i, j).

*Remarks.*—*Litocorsa antennata* differs from *Litocorsa stremma,* the only other described species in the genus, in having antennae and palpostyles instead of lacking them. Examination of specimens of *L. stremma,* loaned by Dr. Pearson, confirms the absence of any head appendages on his specimens. The setal morphology of both species is identical, including the serrate neuropodial spines of the anterior few setigers.

Pearson (1970:72) and Wolf (1984:29–41) described an internal, dorsal, glandular organ for *L. stremma* and *L.* sp. A, respectively. This "organ" is obviously the brain similar to that already described for some syllids, for example (Perkins 1980:1114).

*Etymology.*—The specific epithet refers to the presence of antennae.

*Distribution.*—Gulf of Mexico, Florida to Texas; Puerto Rico, 12–145 m.

## *Synelmis* Chamberlin, 1919

*Type species.*—*Synelmis simplex* Chamberlin, 1919.

*Diagnosis.*—Palps not fused; palpostyles present. Three antennae present, usually quite small. Two pairs of tentacular cirri present. Acicular notosetae straight or slightly curved. Neurosetae including smooth, straight acicular spines or spines with teeth or serrations; furcate setae; and serrate setae tapering to entire or minutely bifid tips. Pygidium smooth, with a pair of long, slender, smooth, anal cirri. Body with smooth, iridescent integument.

## *Synelmis acuminata,* new species

Fig. 2a–k

*Synelmis* sp. C.—Wolf, 1984:29–39, figs. 29–37, 29–38a–k.

*Material examined.*—PUERTO RICO: IEC Sta 003–006, Jan 1980, 18°30.12′N, 66°09.00′W, silty clay, 220 m, HOLOTYPE (USNM 98766).—Sta 003–005, Jun 1980, same location, 1 Paratype (USNM 98767). FLORIDA: EPA/Bat Port Everglades Sta PE4-1, Feb 1984, 26°06.00′N, 80°04.24′W, sand and coral rubble, 56 m, 2 Paratypes (USNM 98768).—SOFLA Sta 4D, Aug 1981, 26°45.81′N, 83°32.12′W, medium sand, 56 m, 1 specimen (USNM 86991).—MAFLA Sta 2313E, Nov 1977, 28°23′59.3″N, 85°15′03.0″W, clayey sandy silt, 177 m, 1 specimen (USNM 86990).—Sta 2422C, Jun 1976, 29°30′N, 84°27′W, medium fine sand, 24 m, 1 specimen.—Sta 2957G, Nov 1977, 25°40′N, 84°15′W, silty very fine sand, 180 m, 1 specimen. TEXAS: STOCS Sta HR1-5, Fall 1976, 27°32′05″N, 96°28′19″W, 75 m, 1 specimen (USNM 86992).

*Description.*—Length to 13 mm, width to 0.3 mm. Largest specimen complete with 50 setigers. Prostomium (Fig. 2a) with 3 small digitiform antennae, equal in length. Eyes located dorsolaterally near posterior margin of prostomium. Palps with small ventral palpostyles (Fig. 2b, c). Dorsal and ventral pairs of tentacular cirri equal in length, about 1.5 times longer than antennae (Fig. 2b). Dorsal cirri all similar in length, extending just beyond neuropodia (Fig. 2d). Ventral cirri present throughout, smaller than dorsal cirri (Fig. 2d).

Notopodia each with single acicular spine (Fig. 2e) beginning on setiger 5, accompanied by slender internal aciculum (Fig. 2d). Neuropodia of anterior 14–17 setigers with about 9 serrate setae tapering to fine tips (Fig. 2f); thereafter, teeth of middle and lower neurosetae gradually becoming rounded and arranged in 2 rows on convex

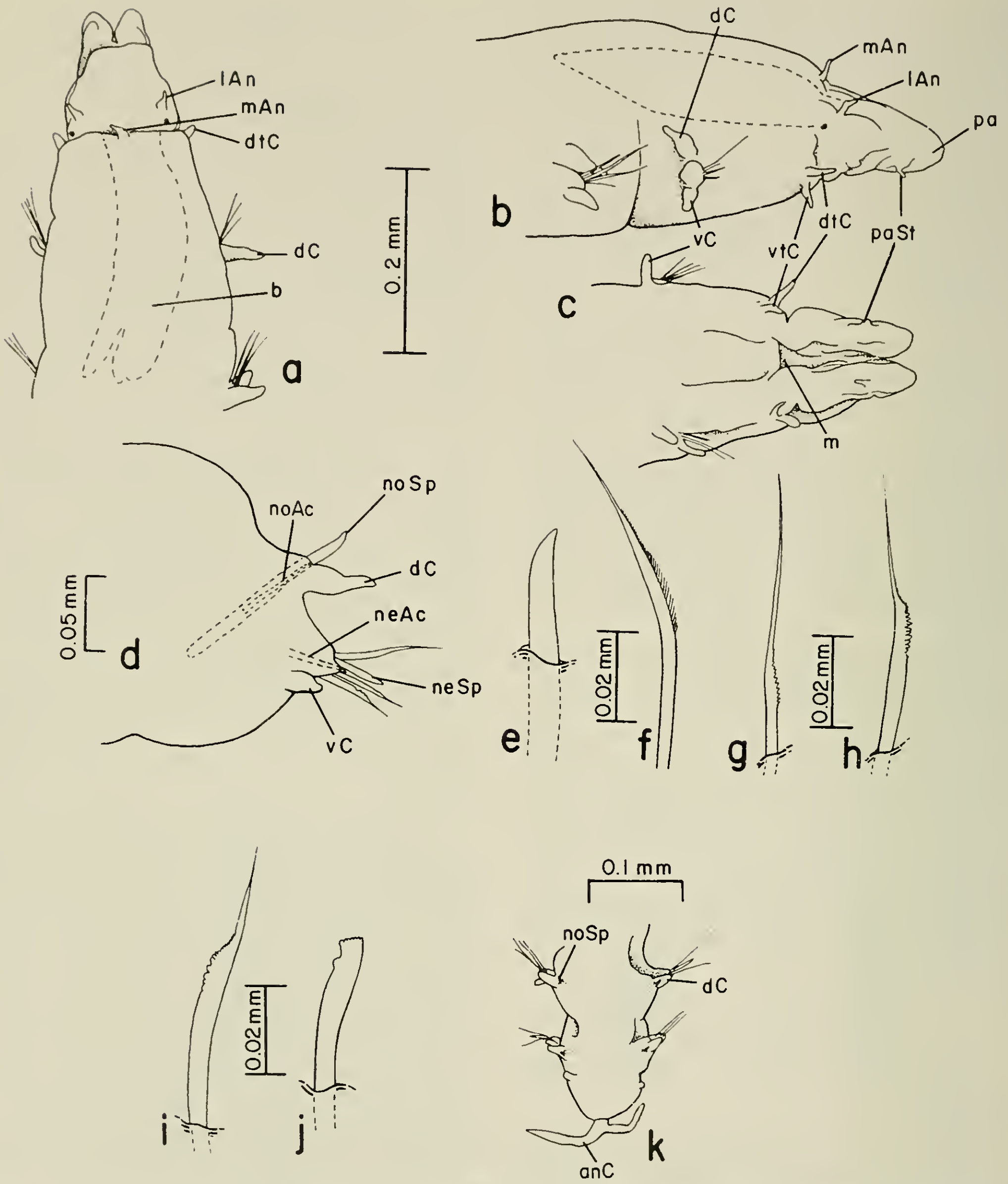

Fig. 2. *Synelmis acuminata*: a, Anterior end, dorsal view; b, Same, lateral view; c, Same, ventral view; d, Middle parapodium, anterior view; e, Notopodial spine; f, Upper neuroseta from setiger 4; g, Middle neuroseta from setiger 15; h, Same, from setiger 20; i, Same, from setiger 30; j, Same, from setiger 38; k, Posterior end, dorsal view. (All figures from Wolf 1984, figs. 29–38a–k.)

margin below an acuminate tip (Fig. 2g, h). Acuminate neurosetae becoming stouter posteriorly and variously shaped (Fig. 29i, j). Larger specimens with supraacicular, smooth, emergent neuropodial spine beginning about setigers 18–25 (Fig. 2d); smaller specimens lacking spines.

Pygidium smooth, with pair of anal cirri (Fig. 2k).

Brain visible through integument, bilobed posteriorly and extending into setiger 2, not pigmented (Fig. 2a, b).

*Remarks.*—*Synelmis acuminata* differs from all other described species of the genus in having acuminate neurosetae with one or two rows of teeth.

*Etymology.*—The species name refers to the peculiar acuminate neurosetae.

*Distribution.*—Puerto Rico; east and west coast of Florida to Texas, 24–220 m.

### *Synelmis ewingi*, new species

Fig. 3a–h

*Synelmis albini.*—Pettibone, 1966:191 [in part], fig. 21a–d.

*Synelmis* sp. B.—Wolf, 1984:29–37, figs. 29–35, 29–36a–f.

*Material examined.*—FLORIDA, off Port Everglades: EPA/Bat Sta PE9-2, Feb 1984, 26°06.05′N, 80°05.00′W, sand, 21 m, 1 specimen.—Off Tampa Bay: EPA/Bat Sta 1135-IV-C1-1, 27°25.36′N, 83°03.12′W, sand, 22 m, Mar 1985, 4 Paratypes (USNM 98770).—Sta 1135-IV-C1-2, same data, HOLOTYPE (USNM 98769) and 5 Paratypes (USNM 98771).—MAFLA Sta 2422C, D, Jun 1976, 29°30′N, 84°27′W, medium fine sand, 24 m, 2 specimens (USNM 86988-9).

*Description.*—Length 28+ mm, width to 0.6 mm. Largest specimen incomplete with 60 setigers. Prostomium (Fig. 3a, b) with 3 small digitiform antennae, equal in length. Eyes minute, located laterally below and anterior to bases of lateral antennae (Fig. 3b). Palps with small ventrolateral palpostyles (Fig. 3b). Dorsal and ventral tentacular cirri equal in length, about twice as long as antennae. Dorsal cirri of anterior setigers broad basally (Fig. 3c), becoming longer and more filiform on posterior setigers (Fig. 3d). Ventral cirri present throughout, similar in length to dorsal cirri anteriorly (Fig. 3c), becoming relatively shorter posteriorly (Fig. 3d).

Notopodia each with single acicular spine becoming emergent by about setiger 17–18, each spine accompanied by slender internal aciculum (Fig. 3d). Anterior neuropodia with slender serrate setae (Fig. 3e) and 1–2 small emergent spines. Posteriorly, neuropodial spines becoming larger, more prominent, numbering 2 per parapodium (Fig. 3d).

Pygidium smooth, with pair of slender anal cirri (Fig. 3f).

Brain visible through integument, extending into setiger 2, bilobed and pigmented posteriorly (Fig. 3a, b). Subdermal glands present laterally between parapodia, some distinctly pigmented in freshly preserved material (Fig. 3g).

*Remarks.*—A complete juvenile specimen with 34 setigers differs from the adult in having the notopodial spines becoming emergent by setiger 8 instead of 17 or 18.

A cross section of a large, mature male was taken at the parapodia at setiger 15 (Fig. 3h). It shows the body to be made up of three lobes with the dorsal lobe, i.e., the dorsum of the worm, to be the largest. This dorsal lobe contains the alimentary canal suspended in place by about three or four dorsal and ventral mesentery bands. The ventral blood vessel is just ventral to the alimentary canal. The dorsal blood vessel is adhering to the dorsal longitudinal muscle band. A pair of dorsal lateral vessels is located on either side of the alimentary canal. A pair of very wide oblique muscle bands separates the large dorsal lobe from the two ventral lobes. Each ventral lobe contains well-developed ventral longitudinal muscles, a ventral lateral blood vessel, and a testis, covered with a small amount of sperm. In far posterior setigers a larger amount of sperm nearly fills the ventral cavities.

A cross-section suitable for drawing could not be obtained from either *Synelmis acuminata* or *Litocorsa antennata*; however, cursory observations reveal that in both, the body shape is quite similar. One possible difference is that the oblique muscle bands of *S. acuminata* and *L. antennata* are much more narrow than those of *S. ewingi*; how-

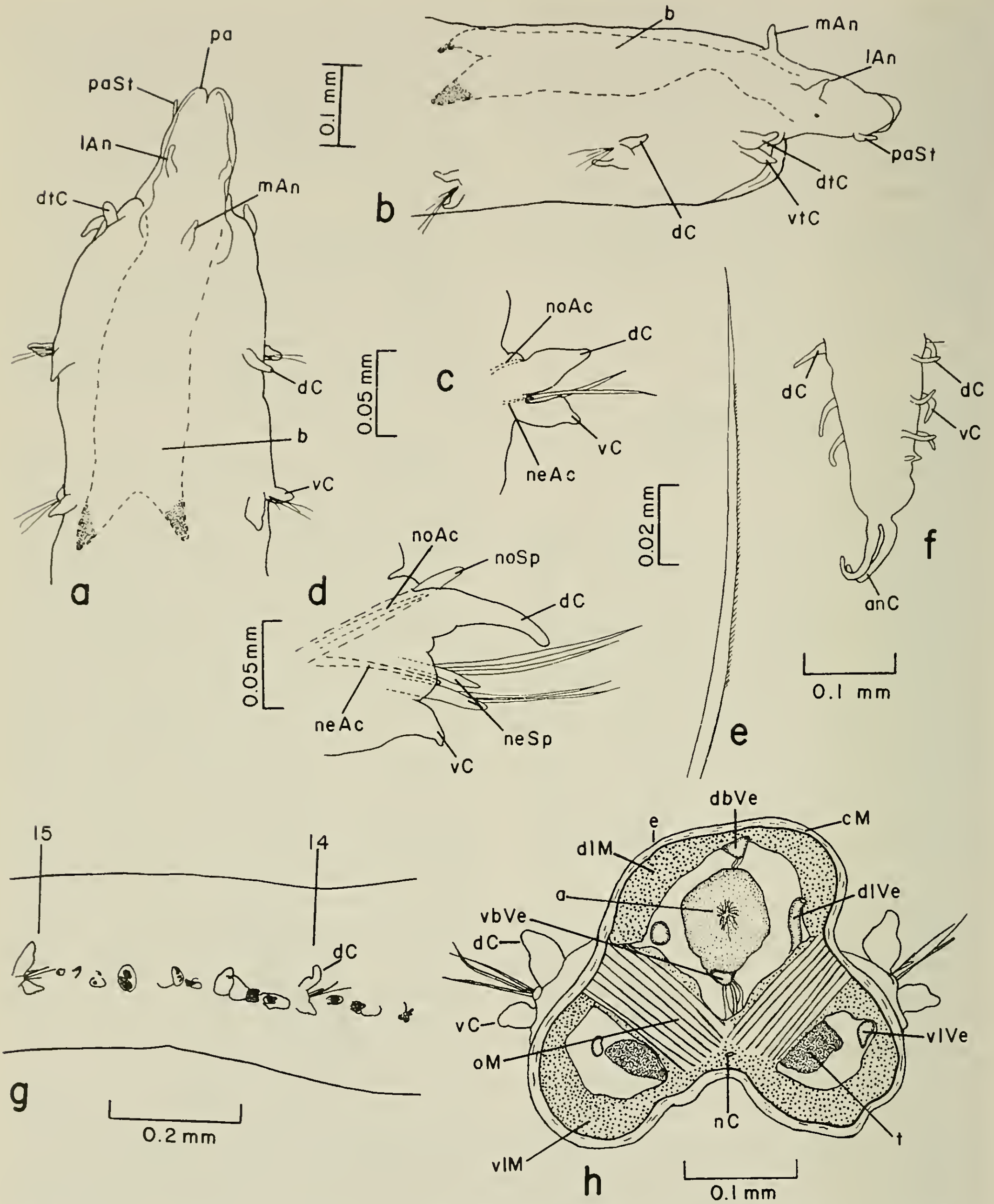

Fig. 3. *Synelmis ewingi*: a, Anterior end, dorsal view; b, Same, lateral view; c, Anterior parapodium, anterior view; d, Posterior parapodium, anterior view; e, Upper neuroseta; f, Posterior end, dorsal view; g, Setigers 14 and 15, lateral view; h, Cross-section of setiger 15, anterior view. (Figures a–f from Wolf 1984, figs 29–36a–f.)

ever, this observation must, for now, stand unconfirmed.

*Synelmis ewingi* includes specimens from Old Tampa Bay, Florida, considered by Pettibone (1966:191, fig. 21a–d) to be a form of *S. albini* (Langerhans 1881). *Synelmis ewingi* is similar to *S. albini*; but differs in having two stout emergent spines in the neuropodia instead of lacking them. *Synelmis ewingi* differs from all other described species of the genus in having two stout neuropodial spines in middle and posterior parapodia.

*Etymology.*—This species is named in honor of Mr. R. Michael Ewing, Old Dominion University, a friend, colleague, and talented polychaetologist.

*Distribution.*—East and west coast of Florida, 19–24 m.

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# EPIZOIC BARNACLES ON PLEURODIRAN TURTLES: IS THE RELATIONSHIP RARE?

J. G. Frazier

*Abstract.*—The occurrence of epizoic *Balanus improvisus* on a side-necked turtle in Argentina illustrates the southern extent of this barnacle's wide geographic range, and the diversity of habitats and substrates used. Preferred settling sites for epizoa are similar on all non-marine turtles described as hosts; barnacles concentrate on the posterior of the carapace. The present account of epizoa on a pleurodiran turtle raises questions as to whether the lack of records reflects a true lack of epizoic barnacle-Pleurodira relationships, or a lack of observations. Because the symbiotic relationship is dependent on the turtles' occurrence in estuarine habitats, a better understanding of pleurodiran distributions is needed. The little data there are suggest that recent Pleurodire turtles are generally restricted to fresh water, but a few species may inhabit saline waters and they are therefore likely to host epizoic barnacles.

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Epizoic barnacles have been reported on few species of Testudines. There is an obligate relationship between several barnacles of the Chelonibiinae and half a dozen marine species in the families Cheloniidae and Dermochelyidae (Ross 1963a, b; Zullo and Bleakney 1966; Ross and Newman 1967; Ernst and Barbour 1972; Zullo 1979). In some populations of marine turtles chelonibiine infestations are common (Frazier, unpublished data).

At least five species of "freshwater" turtles (Chelydridae and Emydidae) have been reported to carry epizoic barnacles, but such reports are rare, for they evidently represent an opportunistic relationship. An adult male alligator snapping turtle, *Macroclemys temminckii* (Troost), near Mobile Bay, Alabama, had 43 *Balanus improvisus* Darwin, mostly on its posterior carapace (Jackson and Ross 1971b). The carapace of an adult male Alabama red-belly turtle, *Chrysemys* (=*Pseudemys*) *alabamensis* (Baur), also from Mobile Bay, Alabama, carried more than 600 *Balanus improvisus* (Jackson and Ross 1972), as well as Bryozoa (Jackson and Ross 1975). Carr (1940) mentioned barnacles being on several discarded shells of *Chrysemys concinna suwanniensis* (Carr) at Cedar Key, Florida. An adult female red-belly turtle, *Chrysemys r. rubriventris* (Le Conte), near the mouth of the Delaware River had 12 *Balanus improvisus* on the posterior of its carapace (Arndt 1975).

There are numerous records of epizoic barnacles on diamondback terrapins, *Malaclemys terrapin* (Schoepff), from eastern and western Florida. Ross and Jackson (1972) reported two *Balanus improvisus* attached to epizoic oysters (Jackson and Ross 1971a) that were on the posterior of the carapace, and two *Chelonibia patula* (Ranzani) that were on a posterior ventral marginal surface, of an adult female. Jackson et al. (1973) found a vacant *Balanus eburneus* Gould, occupied by a bivalve mollusk, on the posterior carapace of an adult female terrapin. Seigel (1983) has done the only detailed study on levels of infestation, reporting three species of epizoic barnacles on two populations of diamondback terrapins: *Chelonibia manati* Gruvel infested 47.9% of the total; *Balanus eburneus,* 42.4%; and *Chelonibia testudinaria* (L.), 9.5%.

Fig. 1. Oblique posterior view of *Hydromedusa tectifera* (JGF 4007) showing *Balanus* aff. *improvisus* (USNM 211283) and several white basal disks where barnacles were once affixed (tape in cm).

All of the above-mentioned turtles are members of the Cryptodira that either live in, or occasionally have contact with, marine environments. The only turtle of the suborder Pleurodira that has been previously recorded to host epizoic barnacles, is a matamata, *Chelus fimbriatus* (Schneider), that washed up on Trinidad (Boos in Pritchard and Trebbau 1984:97, 107, pl 31 F). The present note reports the occurrence of a wide ranging barnacle on the South American pleurodire *Hydromedusa tectifera,* and discusses the general phenomena of epizoic barnacles on pleurodires.

## Materials and Methods

In August or September of 1982 a female side-necked turtle, *Hydromedusa tectifera* Cope (Pleurodira: Chelidae), was collected during the day while crossing route No. 11 (or No. 2) several kilometers west of the Bay of Samborombon, Province of Buenos Aires, Argentina (36°S, 57°W). On its carapace were about a dozen live barnacles. It was isolated from conspecifics in a freshwater tank in Villa Gessel, where the barnacles died shortly thereafter (R. Gessel, pers. comm.). On 11 March 1983 I measured and photographed the specimen (JGF 4007; Fig. 1). Collections of *H. tectifera* in Argentine museums in Buenos Aires and La Plata were examined for additional occurrences of epizoic barnacles.

## Results and Discussion

The turtle's curved medial carapace length was 27 cm. It was evidently an adult in good health, for in January 1983, four to five months after capture, it laid seven or eight eggs. On the posterior half of the carapace were two barnacle shells (external plates without any soft parts inside) and ten white basal disks where barnacles had once been affixed.

The barnacles were identified as *Balanus* sp. aff. *B. improvisus* Darwin. The larger specimen (USNM 211283) measured 5.0 mm in height and 12.0 mm in rostro-carinal diameter. Barnacles of the same species are common in the sublittoral of the southwestern Atlantic—notably in the Bay of Samborombon and in waters of low salinity several km from the Bay, where they often form dense encrustations on shallow water crabs (Bastida, pers. comm.; Botto, pers. comm.; pers. obs.).

*Balanus improvisus* is remarkable for occurring in waters of many subtropical and temperate seas (having been introduced into several regions by human activities) in depths from low tide to nearly 40 m (Darwin 1854, Pilsbry 1916, Bousfield 1954, Utinomi 1966, Carlton and Zullo 1969, Newman and Ross 1976). It has wide thermal and salinity tolerances, surviving extended periods in a variety of estuarine and marine conditions; substrates are known to include various inanimate objects and hard-shelled sessile and sedentary invertebrates (Bousfield 1955, Newman 1967, Gordon 1969, Gosner 1971, Carlton and Zullo 1969). *Balanus improvisus* has been recorded on more species of "freshwater" turtles than has any other barnacle (Jackson and Ross 1971b, 1972; Ross and Jackson 1972; Arndt 1975). Hence its occurrence on a side-necked turtle from an estuary in Argentina is consistent with the barnacle's known habits.

Several authors have estimated the ages of epizoic *Balanus improvisus* on the basis of growth data presented by Costlow and Bookhout (1957). The estimated relationships between size (rostro-carinal diameter) and age were: 4.6 to 10.4 mm—three to ten weeks old (Jackson and Ross 1971b); 1.0 to 10.2 mm—two days to ten weeks and older (Jackson and Ross 1972); and 4.3 to 9.9 mm—three to four months old. In this light, the 12 mm specimen from Samborombon may have lived for about three months on the *Hydromedusa tectifera.* The basal disks left by several other barnacles on this turtle were of comparable diameters, and probably of a similar age; some were smaller and probably younger.

Although the orientation of the barnacles on the *H. tectifera* was not determined, their concentration at the posterior of the carapace is consistent with reports of epizoic barnacles on other turtles, where water currents and food availability were thought to influence the site and orientation of attachment (Jackson and Ross 1972, Ross and Jackson 1972, Jackson et al. 1973, Arndt 1975, Seigel 1983). The posterior of the carapace apparently has the best conditions of water flow, while being a relatively protected site for the barnacles.

Affixing to a turtle is evidence for highly opportunistic settling behavior, which is well supported by the variety of substrates on which *Balanus improvisus* has been recorded. Since *B. improvisus* can withstand only about 24 hours of desiccation (Newman 1967), the survival of epizoan individuals is dependent on the behavior of the host. In the case of *H. tectifera,* there is probably little risk of extended terrestrial forays.

Pleurodiran turtles are generally regarded as restricted to freshwater habitats (Freiberg 1979, Pritchard 1979), but little is known of their salinity tolerances. Pritchard and Trebbau (1984) argued that the inability to cross, or survive, salt-water has been a major factor in shaping the distributions and evolution of pleurodiran turtles. Pritchard (1984) argued this point further, especially for the Chelidae, thus challenging the detailed phylogenetic studies of Gaffney (1977).

There are, however, several records of Pleurodires (including chelids) in salt-water. Broadley (in litt., 16 Nov 1984) has found "*Pelomedusa subrufa* in brackish water on the periphery of the Makgadigadi Pans, Botswana," and *Pelusios castaneus castanoides* within a few meters of the mangrove swamp on Inhaca Island, Mozambique. Bour (in litt., 22 Mar 1985) found *Pelusios subniger* in estuaries in Seychelles and Madagascar. Rhodin and Mittermeier (1976) reported *Chelodina siebenrocki* in "tidally-influenced coastal swamps" along southern New Guinea and on offshore islands. Cogger (in litt., 7 Jan 1985) reported "a number of records" of *Chelodina longicollis* from estuarine conditions in Australia. In addition, there is strong evidence that several fossil pleurodires (all of them pelomedusids) were marine, including *Stupendemys geographicus* (Wood), the world's largest turtle (Wood 1976:15).

*Hydromedusa tectifera,* common in freshwater systems where filamentous algae commonly cover the carapace, is previously unrecorded from saline waters, but E. Gudynas (pers. comm.) has records of this species swimming in Rio de la Plata as far seaward as Punta del Este, Uruguay, where conditions are nearly marine. The size of the epizoic barnacles reported herein illustrate that *H. tectifera* can survive estuarine conditions with no ill effects for at least several days—the time necessary for *B. improvisus* to settle, metamorphose and begin sessile growth (see Zullo et al. 1972). The record also represents a range extension for *Hydromedusa tectifera* at least as far south as the Bay of Samborombon; the next nearest southern record is La Plata, 150 km to the northwest (Frazier, in prep.).

No museum specimens with evidence of epizoic barnacles were found among the 30 specimens examined. However, epizoa are frequently removed to show better the morphological features of the host, and the rate of occurrence of epizoa on museum specimens probably does not reflect the natural situation.

The paucity of reports of epizoic relationships between pleurodiran turtles and barnacles could reflect a lack of observations. Although some cryptodiran populations are heavily infested (Seigel 1983), and several species serve as hosts, the epizoan phenomenon is poorly documented in this suborder also. There is no a priori reason why side-necked turtles in estuarine conditions in South America, Africa, and Australia should not carry epizoa. The question is: how many pleurodiran populations venture into estuarine conditions? Distributional data suggest that few pleurodiran turtles (except *Chelodina siebenrocki* and possibly also *Hydromedusa tectifera*) commonly occur outside of fresh water (e.g., Broadley 1981, in litt., 16 Nov 1984; Bour 1983; Pritchard and Trebbau 1984), but more detailed data are needed.

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# *PSOLUS PAWSONI* (ECHINODERMATA: HOLOTHUROIDEA), A NEW BATHYAL SEA CUCUMBER FROM THE FLORIDA EAST COAST

John E. Miller and Richard L. Turner

*Abstract.*—*Psolus pawsoni,* new species, is described and illustrated from material collected off northeast Florida at a depth of 322 m. A key to the 11 species of *Psolus* known to occur in the western Atlantic is given.

The holothurian genus *Psolus* Oken, 1815, comprises approximately 30 species distributed from the tropics to the polar regions (Deichmann 1941). Within the past two decades, three new psolids (*Lissothuria antillensis* Pawson, 1967; *Psolus megaloplax* Pawson, 1968; *Psolidium prostratum* Pawson and Valentine, 1981) have been described from the western Atlantic. Like many members of the family Psolidae, these three diminutive species lead a sedentary, cryptic existence firmly attached to hard substrata by large podia arising from a flattened ventral sole. Psolids are frequently overlooked because of their small size and their ability to contort their bodies to conform to irregularities of the substratum. Accordingly it was not surprising to discover yet another new psolid affixed to a single rock dredged from a depth of 322 m off Jacksonville, Florida. This new species, *Psolus pawsoni,* shares its closest affinities with two western Atlantic congeners, *P. megaloplax* Pawson, 1968, and *P. valvatus* Östergren, 1904. The type material described here was collected during the SEAMAP program of the Atlantic States Marine Fisheries Commission and has been deposited at the National Museum of Natural History (USNM), the Harbor Branch Foundation, Inc. (IRCZM), and the Florida Department of Natural Resources (FSBC).

Order Dendrochirotida Grube, 1840
Family Psolidae Perrier, 1902
*Psolus pawsoni,* new species
Figs. 1–3

*Diagnosis.*—Dorsal plates lacking layer of granules; mouth and anus separated by 3–4 plates; several dorsal plates 2–3 times larger than oral valves; oral radial "teeth" absent; ossicles of sole exclusively knobbed plates with 4–12 perforations; margin of sole with single row of podia; tentacles with perforated plates.

*Material examined.*—HOLOTYPE: UNSM E33327, 9.9 mm total length (TL), R/V *Chapman,* Cr 85-03, Sta 11, 5 Jun 1985, 30°31.4′N, 79°59.5′W to 30°30.2′N, 79°59.9′W, 322 m, 55′ shrimp trawl, clinging to large phosphorite nodule.—PARATYPES: (same locality data as holotype); USNM E33328, 7 specimens, 4.5–10.8 mm TL; IRCZM 71:305, 1 specimen, 9.2 mm TL; FSBC I 31952, 1 specimen, 9.0 mm TL.

*Description of holotype.*—Small, elliptical, flattened specimen (9.9 mm TL × 6.9 mm W × 1.3 mm H) with dorsal surface slightly convex (Fig. 1A); greatest height determined by distal tips of oral valves. Excepting lateral fringe of 1–2 rows of small plates, dorsal plates large (largest plate 3.6 mm long), scarcely imbricate, with granular

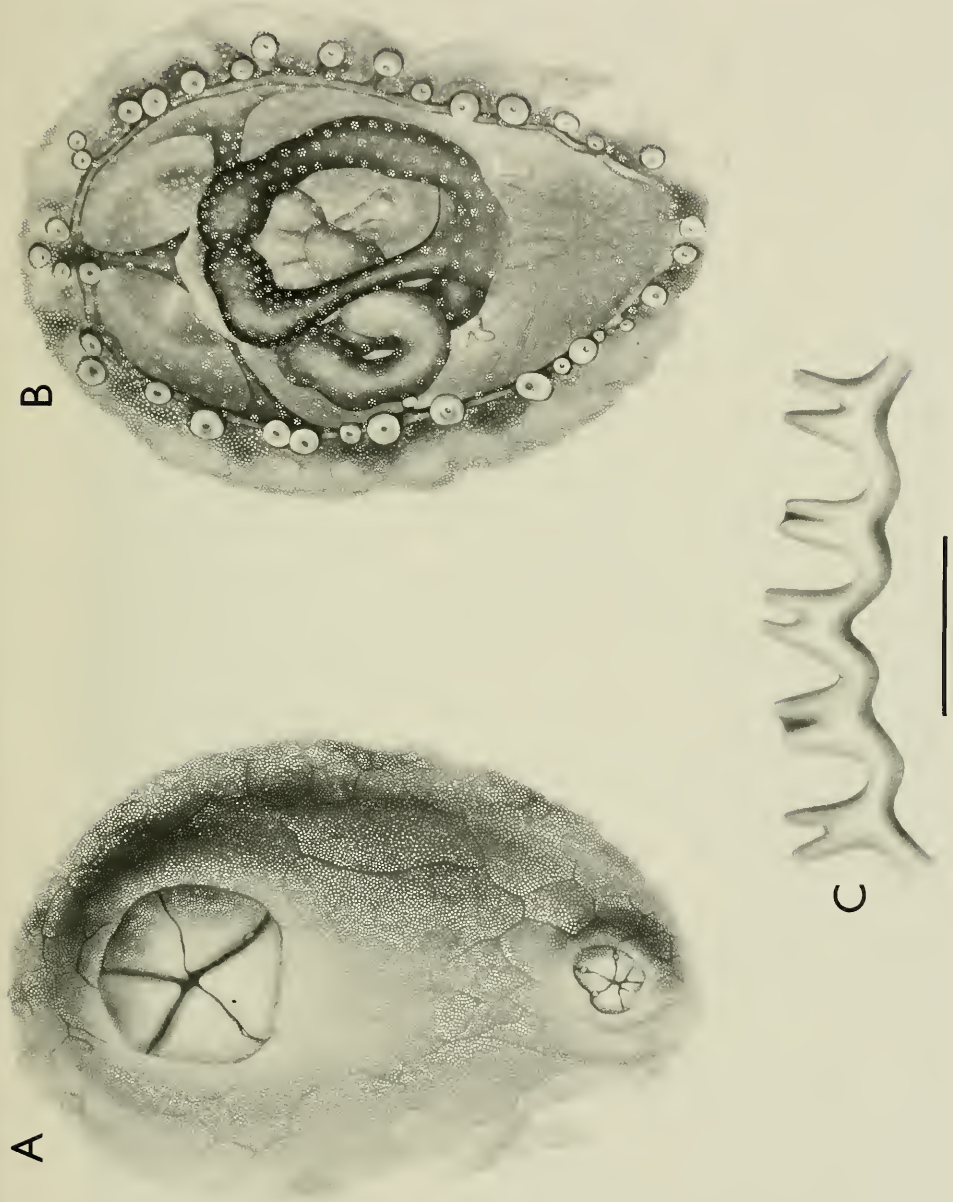

Fig. 1. *Psolus pawsoni*, Holotype, USNM E33327, 9.9 mm TL: A, Dorsal aspect; B, Ventral aspect; C, Three radial and two interradial segments of calcareous ring from paratype, USNM E33328, 10.8 mm TL. Scale bar = 1.0 mm (C only).

appearance but lacking layer of distinct granules. Several dorsal plates 2–3 times larger than oral valves. Mouth and anus separated by 3 plates. Introvert and all but one tentacle retracted, concealed by 5 large triangular oral valves placed interradially; radial oral "teeth" absent. A small papilla is found at the base of two adjacent oral valves; another is visible deeper in the aperture. Anus surrounded by 5 triangular valves, 2 of which appear to be subdivided. A single small papilla is situated between 4 of the 5 anal valves near the base of the plates.

Ventral surface flattened, covered by thin, fragile, transparent sole, through which internal anatomy visible (Fig. 1B). Margin of sole defined by single row of 36 nearly evenly spaced podia. Midventral radius naked, excepting single podium at anterior end.

*Variation in type series.*—Smallest specimens (4.5–8.8 mm TL) scale-like, subcircular in outline. On each of two specimens (6.5–8.8 mm TL), 2 podia found on midventral radius near posterior end; another specimen (9.2 mm TL) with 3 podia on posterior end and 1 podium on anterior end of midventral radius. Number of plates between mouth and anus 3 or 4.

*Description of internal anatomy.*—(Dissection of paratype, 10.7 mm TL): Calcareous ring simple with undulating posterior margin (Fig. 1C). Radial pieces with deep anterior notch for insertion of retractor muscle; interradial pieces shorter, with shallow anterior groove. Tentacles short (1.3–1.6 mm long), equal, weakly branched. Polian vesicle single, bulbous, arising from water ring in left ventral interradius. Stone canal short (300–400 μm), embedded in dorsal mesentery and terminating with small, spherical madreporite composed of numerous curved ossicles. Mouth connected to intestine by distinct esophagus. Intestine emptying into large cloaca, supported by complex system of cloacal suspensors occupying posterior third of body cavity. Respiratory trees poorly developed, extending from cloaca to posteriormost loop of intestinal tract. No gonadal tubules found.

*Description of skeletal ossicles.*—(Refer to Table 1 for measurements.)

Ventral sole: Ossicles exclusively a single layer of well-spaced, perforated plates with 4–12 perforations. Margin and central network of plates with smooth, rounded knobs on outer surface (Fig. 2A, D–F); knobs few or absent on inner surface of plates (Fig. 2E, G). Incomplete perforations and knobs on margin give plates a spinous appearance. Plates more crowded at anterior and posterior ends of sole.

Tube feet: Straight to curved perforated plates similar to those found in the sole (Fig. 3A–D). Plates in distal portion of podia with fewer knobs. Well-developed end plates 250–300 μm in diameter (Fig. 3E, F). Largest end plates with secondary network. Diameter of end-plate perforations increasing from center to margin of plate.

Tentacles: Straight to curved, smooth, irregular, perforated plates with undulating margin (Fig. 3G–I); rods absent.

Internal organs: No deposits were found in the intestine, respiratory trees, polian vesicle or cloaca of the dissected paratype.

*Coloration and habit.*—Color in life very pale, nearly white; alcoholic specimens white. Easily mistaken by the casual observer as juvenile slipper limpets (Crepidulidae), jingle shells (Anomiidae), oysters (Ostreidae), or bleached chitons (Polyplacophora).

*Examination of gut contents.*—Gut contents were removed from the dissected paratype and examined at 400 ×. Although most material found in the intestine was unidentifiable, recognizable food items consisted of diatoms, remains of filamentous algae, and a few foraminiferans and sponge spicules.

*Remarks.*—In its small size and the shape of skeletal ossicles found in the ventral sole, *P. pawsoni* appears to be most closely related to *P. megaloplax* Pawson, 1968, from

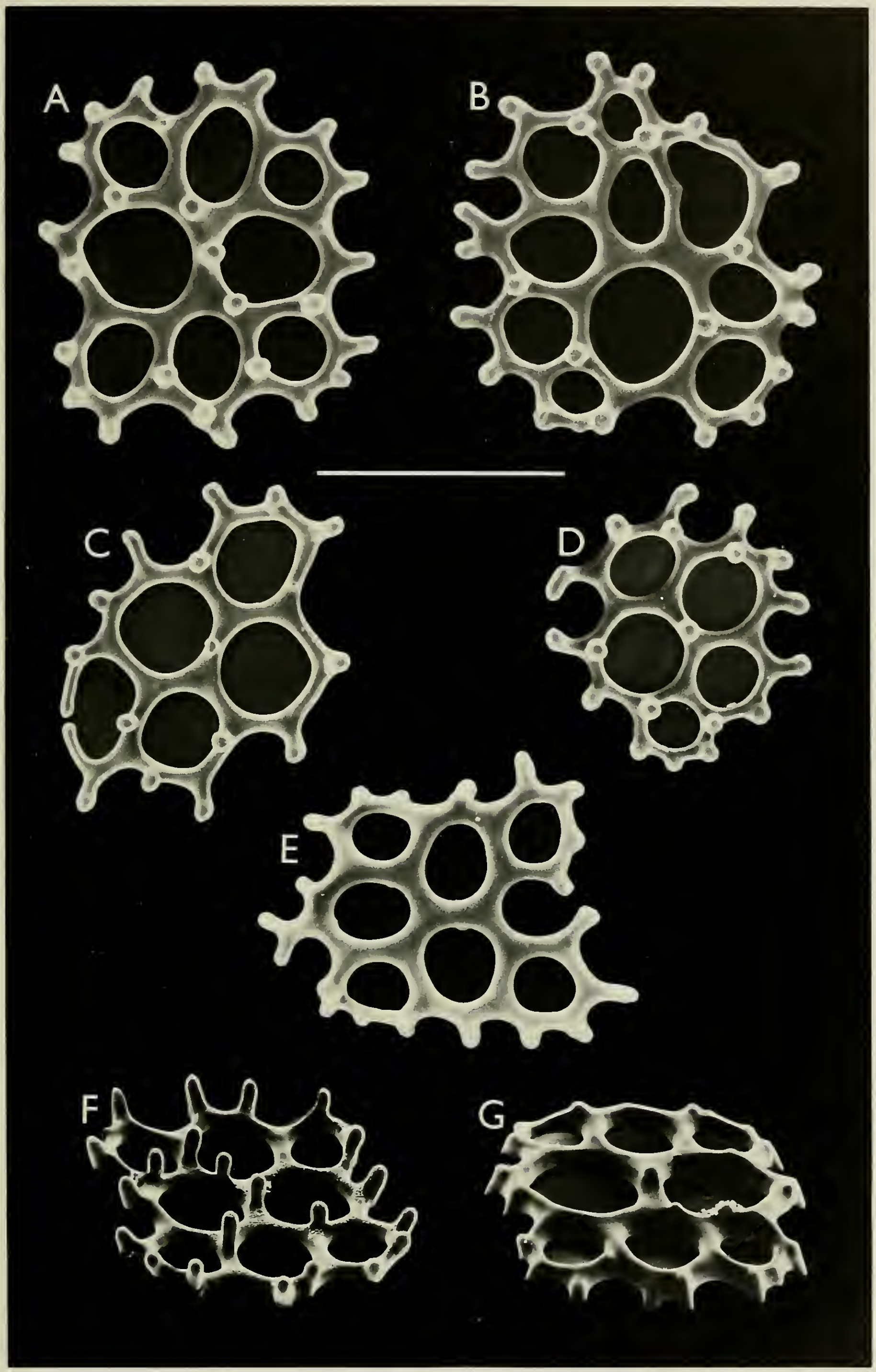

Fig. 2. Scanning electron micrographs of skeletal ossicles from *Psolus pawsoni*: A–G, Plates from sole, showing outer [A–D, F (oblique view)] and inner [E, G (oblique view)] surface of plates. Scale bar = 100 μm.

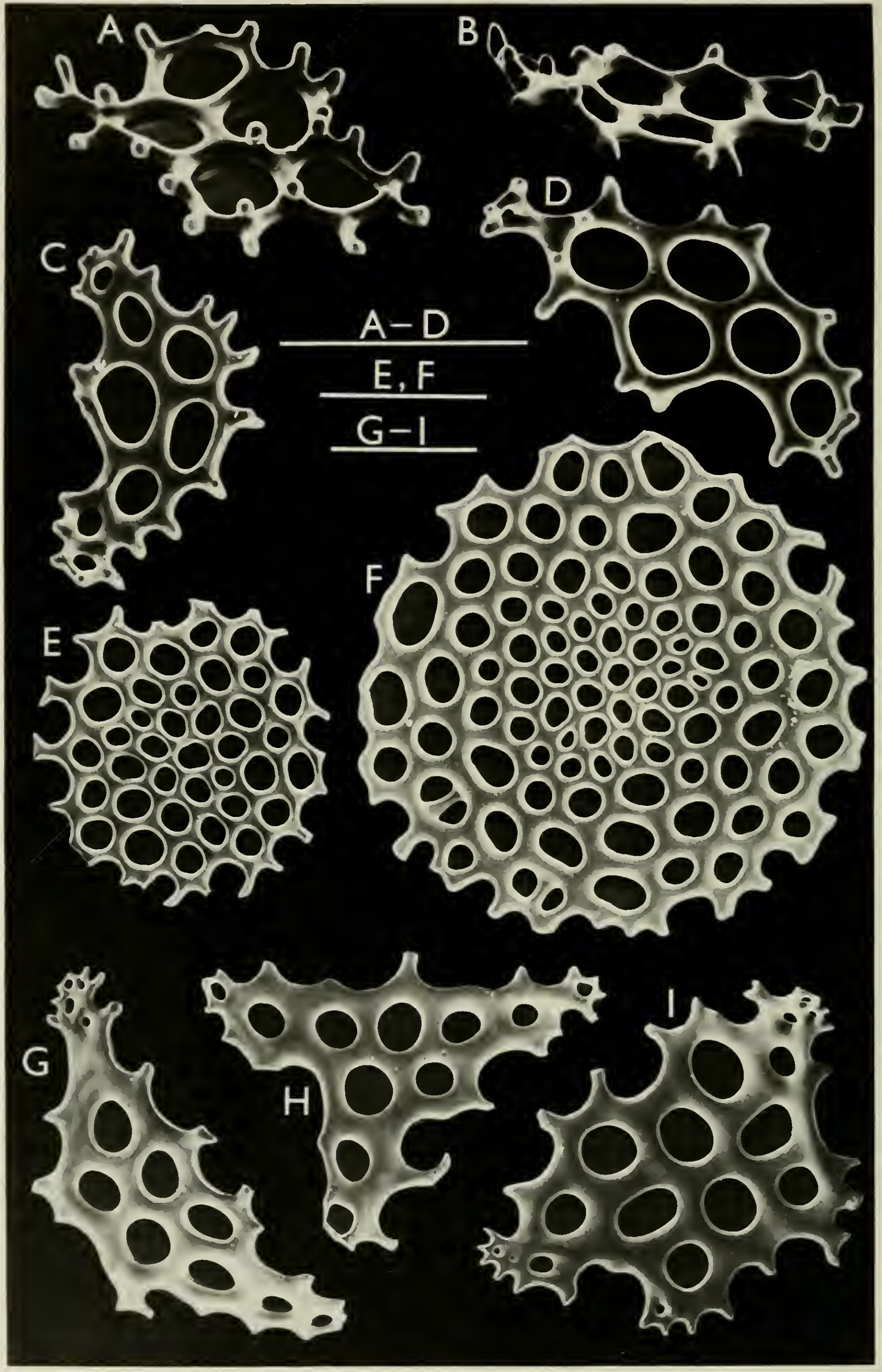

Fig. 3. Scanning electron micrographs of skeletal ossicles from *Psolus pawsoni*: A–D, Plates from podia; E, F, End plates from podia; G–I, Plates from tentacles. Scale bars = 100 μm.

Table 1.—Dimensions and number of perforations of body wall ossicles in *Psolus pawsoni*. n, number of ossicles (or knobs) examined; $\bar{x}$, mean; SD, standard deviation; ossicles taken from specimens 8.5–10.8 mm TL.

| | n | $\bar{x}$ | SD | Range |
|---|---|---|---|---|
| Plates of sole: | | | | |
| Length (μm) | 60 | 124 | 13 | 93–159 |
| Width (μm) | 60 | 105 | 15 | 49–150 |
| Height of knobs (μm) | 19 | 9.3 | 1.4 | 7.6–12.6 |
| Width of knobs (μm) | 19 | 5.8 | 0.5 | 5.1–6.8 |
| No. of perforations | 60 | 7.5 | 1.8 | 4–12 |
| Plates of tube feet: | | | | |
| Length (μm) | 30 | 139 | 21 | 102–203 |
| Width (μm) | 30 | 85 | 19 | 59–132 |
| No. of perforations | 30 | 8.1 | 2.5 | 4–12 |
| Plates of tentacles: | | | | |
| Length (μm) | 30 | 179 | 57 | 93–282 |
| Width (μm) | 30 | 120 | 28 | 75–190 |
| No. of perforations | 30 | 11.8 | 2.9 | 7–20 |

St. Croix, Virgin Islands, and *P. valvatus* Östergren, 1904, occurring off Norway, Ireland, Iceland, Greenland, and New England. None of these species is known to exceed 21 mm TL, and all have similarly shaped knobbed plates in the sole, although the number of perforations differs. Table 2 compares these three congeners.

It is notable that a juvenile specimen of *Psolus tuberculosus tuberculosus* Deichmann, 1930 (IRCZM 71:306) was removed from the same rock on which the type series of *P. pawsoni* was found. The single specimen measures 7 mm TL and is quite distinguishable from *P. pawsoni,* even at this small size, by four features: presence of radial oral "teeth"; tuberculation on dorsal plates; radially arranged accessory plates externally at base of oral valves; outer row of reduced podia perforating marginal plates.

*Etymology.*—The species is named for David L. Pawson, Smithsonian Institution, in recognition of his contributions to holothurian systematics.

*Distribution.*—Currently known only from the type locality.

Table 2.—Comparison of *Psolus pawsoni*, n. sp., *P. megaloplax* Pawson, and *P. valvatus* Östergren. Comparisons based on examination of following specimens and publications: *P. pawsoni* [type series]; *P. megaloplax* [type series, Universitetets Zoologiske Museum, Copenhagen; original description, Pawson (1968)]; *P. valvatus* [Museum of Comparative Zoology MCZ 1452, 1 specimen, 12 mm TL; Mortensen (1927); Deichmann (1930)]; +, present; −, absent.

| | *P. pawsoni* | *P. megaloplax* | *P. valvatus* |
|---|---|---|---|
| Number of plates separating mouth and anus | 3–4 | 2 | 5–10* |
| Several dorsal plates 2–3 times larger than oral valves | + | + | − |
| Layer of granules covering dorsal plates | − | + | − |
| Marginal fringe of small plates | + | − | + |
| Average number of perforations in ossicles of sole | 7–8 | 4 | 4 |
| A cycle of radial "teeth" present below oral interradial valves | − | + | − |
| Outer row of reduced marginal podia | − | + | + |

* Mortensen (1927) and Deichmann (1930) state that *P. valvatus* has about 5 dorsal plates between the mouth and anus. Our examination of MCZ 1452 (identified by Deichmann) revealed that there are 10 plates separating the mouth and anus in this specimen.

## Key to Species of the Genus *Psolus* from the Western Atlantic Ocean

1. Oral aperture surrounded by 5 large interradial valves .............. 2
– Oral aperture surrounded by many small plates, although the plates in some species may occur in cycles of about 5 plates each .......... 10
2. Baskets embedded in sole ...... 3
– No baskets in sole ............. 4
3. Dorsal plates with numerous spiniform granules; 2 dorsal plates between oral and anal valves [Brazil, 50–100 m] ....................
......... *P. vitoriae* Tommasi, 1971

– Dorsal plates naked; 4 dorsal plates between oral and anal valves [Brazil, 95 m] ..................... ......... *P. marcusi* Tommasi, 1971

4. Oral aperture with 5 narrow radial "teeth" within interradial oral valves ........................ 5

– Radial oral "teeth" absent ...... 9

5. Dorsal integument with baskets [Barbados, 250 m] ............. ....*P. complicatus* Deichmann, 1930

– Dorsal integument without baskets ........................... 6

6. Dorsal plates tuberculated; plates in sole with dozens of perforations ............................. 7

– Dorsal plates not tuberculated; plates in sole with about 4 perforations ........................ 8

7. Oral aperture with 5 radial accessory plates externally at base of oral valves [Gulf of Mexico to South Carolina, 73–185 m] ........... *P. tuberculosus tuberculosus* Théel, 1886

– Radial accessory oral plates absent [Barbados, Dominica, 133–229 m] *P. tuberculosus destituta* Deichmann, 1930[1]

8. Oral aperture with 5–12 radial accessory oral plates externally at base of oral valves; anal valves absent; dorsal plates imbricate, 3–10 between oral valves and anal aperture [Sand Key and Key West (Florida), Barbados, 147–250 m] ..... *P. operculatus* (Pourtalès, 1868)

– Radial accessory oral plates absent; anal valves present; dorsal plates tessellated, 2–3 between oral and anal valves [St. Croix, 90–360 m] .... *P. megaloplax* Pawson, 1968

9. About 5 dorsal plates between oral and anal valves; plates in sole with 4–5 perforations; two rows of podia on margin of sole, outer podia reduced [Norway to New England, 20–500 m] ..................... ......... *P. valvatus* Östergren, 1904

– Three to 4 dorsal plates between oral and anal valves; plates in sole with 5–12 perforations; single row of podia along margin of sole [Atlantic coast of Florida, 322 m] .. .................. *P. pawsoni*, n. sp.

10. Dorsal plates lacking granules; ossicles of sole smooth plates with 4 perforations or cruciform bodies [Scotland to Gulf of Maine, 1096–2091 m] ... *P. pourtalesi* Théel, 1886

– Dorsal plates covered with granules; ossicles of sole consisting of baskets or complex oval/spherical bodies ........................ 11

11. Posterior end tail-like; anal aperture surrounded by many cycles of plates; sole comparatively small, rectangular; midventral ambulacrum complete [Norway to New England, 0–400 m] ............ ...*P. phantapus* (Strussenfeldt, 1765)

– Tail absent; few periproctal cycles of plates; sole large, oval; midventral ambulacrum incomplete [Norway to New England, 0–1800+ m] .. *P. fabricii* (Düben and Koren, 1846)

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[1] We have examined the type material (MCZ 338) of *Psolus tuberculosus* var. *destituta* Deichmann, 1930. Based on available morphological and geographic information, we believe the material represents a valid subspecies. There is no reason to suspect that Deichmann used "variety" as an infrasubspecific rank in this case, and thus we regard the name to be available [ICZN Art. 12a, 16, 45f and g(ii)]. We assume [Art. 31b(i)] that Deichmann wrote *destituta* as a noun in apposition, derived from the Latin *destituere*, to abandon, in reference to the lack of accessory oral plates.

ment of Natural Resources, who served as chief scientist on the Florida leg (Florida East Coast Benthic Mapping Study). We thank Haydee Hernandez, Florida Institute of Technology, and Stephen E. Stancyk, University of South Carolina, for translating parts of Tommasi (1971). Patricia Linley, Harbor Branch Foundation, Inc. (HBF), assisted with SEM photography. The holotype was illustrated by Charissa Lounibus. Loan of type material from the MCZ was made possible by Robert M. Woollacott. This paper is HBF Contribution no. 530.

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(JEM) Indian River Coastal Zone Museum, Harbor Branch Foundation, Inc., RR 1, Box 196, Ft. Pierce, Florida 33450. (RLT) Department of Biological Sciences, Florida Institute of Technology, 150 W. University Blvd., Melbourne, Florida 32901.

Note added in proof:

We thank Patricia A. Lindsay and John B. Wise, South Carolina Department of Wildlife and Marine Resources, for bringing to our attention 4 more specimens of *Psolus pawsoni*: IRCZM 71:341, 7–11 mm TL, R/V LADY LISA, Golden Crab Project, Year II, 19 May 1986, vicinity of 31°21′N, 79°34′W (east of Brunswick, Georgia), ≈450 m, rocket grab, clinging to rock. A specimen of *P. operculatus* (IRCZM 71:342) from the same rock represents a considerable range extention for this species.

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# ON THE ELEVATION OF THE *STEPHANOPHYLLIA* SUBGENUS *LETEPSAMMIA* TO GENERIC RANK (COELENTERATA: SCLERACTINIA: MICRABACIIDAE)

Joan Murrell Owens

*Abstract.*—The differentiating macrostructural and microstructural characteristics of the subgenus *Letepsammia* Yabe and Eguchi are described, and the subgenus is officially elevated to the taxonomic rank of genus. *Letepsammia* differs most significantly from *Stephanophyllia* and other genera of the Micrabaciidae in its numerous coarse perforations in all septa, and its slender, wavy, and irregularly spaced trabeculae. Fossil specimens of *Letepsammia* are found in the Plio-Pleistocene of Japan, while living specimens have been retrieved from depths of less than 100 meters to nearly 1000 meters over a wide area of the Pacific and Indian Oceans.

*Letepsammia* was described as a subgenus by Yabe and Eguchi in 1932, primarily on the basis of the well-developed, spongy columella in *S. formosissima* Moseley, the type species. Although they acknowledged differences in septal perforations between *Letepsammia* and the other subgenera of *Stephanophyllia,* they evidently did not consider these septal differences to be of generic significance. Similarly, Vaughan and Wells (1943) and Wells (1956) considered *Letepsammia* to be synonymous with *Stephanophyllia.* More recent authors, most notably Squires (1965, 1967), Keller (1977), Cairns (1982), and Owens (1984a, b, 1986), have tacitly accepted the septal and columellar differences as worthy of generic separation, and have informally recognized the subgenus as *Letepsammia.* A review of the literature, however, reveals that *Letepsammia* has never been officially elevated to generic status. This paper, therefore, is intended to do so.

Order SCLERACTINIA Bourne, 1900
Suborder FUNGIIDA Duncan, 1881
Superfamily FUNGIOIDEA Vaughan and Wells, 1943
Family MICRABACIIDAE Vaughan, 1905
Genus *LETEPSAMMIA* Yabe and Eguchi, 1932

*Stephanophyllia* (*Letepsammia*) Yabe and Eguchi, 1932:58.—Wells, 1933:51.—Yabe and Eguchi, 1934:280–281, figs. 1–3.
*Letepsammia* Vaughan and Wells, 1943: 145.—Wells, 1956:F390.—Squires, 1965: 878; 1967:505–508.—Keller, 1977:41–43.—Cairns, 1982:9.—Owens, 1984a: 519–521, fig. 4; 1984b:88, fig. 4; 1986: 248–255.

*Diagnosis.*—Corallum large, loosely built, with highly perforated septa and wall, well-developed deltas, and prominent marginal shelf. Wall horizontal or nearly so, very thin, with septa alternating in position with costae. Septa slender, with varied, complex dentation; interspaces wider than septa. Vepreculae inconspicuous or absent. Costae slender, serrated on outer edge, and separated by broad intercostal loculi interrupted by closely spaced, concentric rows of synapticulae. Columella broad, spongy, and elongate. Trabeculae thin, wavy, poorly organized, ramified in some species along unperforated growing edge; 10–20 in number.

Low height : diameter ratio. Generally 120 septa.

*Occurrence.*—Plio-Pleistocene, Ryukyu Islands; Recent, Japan Sea, Celebes Sea, Banda Sea, Coral Sea, Philippine Islands, Hawaiian Islands, Australia, New Zealand, East African Coast. 50–960 meters.

*Type species.*—*Stephanophyllia formosissima* Moseley, 1881, by monotypy, by Yabe and Eguchi, 1932. Deposited in the British Museum (Natural History).

*Taxa included.*—*Letepsammia formosissima* Moseley, 1881, and *Letepsammia superstes* Ortmann, 1888.

*Discussion.*—When Yabe and Eguchi (1932:58) established *Letepsammia,* they based it solely on their type of the subgenus, *S.* (*L.*) *formosissima,* and described the subgenus as follows:

> "Skeletal elements very delicate. Columellar fossa distinct, deep; columella spongy, well developed. Septa usually and horizontal wall always coarsely perforated, being a network of slender trabeculae. Pores of the horizontal wall circular, coarser, and are easily distinguished from the smaller, elongate or oval perforations in the other subgenera . . ."

Later, Yabe and Eguchi (1934:280–281) included in this subgenus a fossil form from Japan, *S.* (*L.*) *japonica* nov. Although this form was subsequently determined to be a fossil representative of the living species *S. superstes,* it nonetheless proved the validity of perforated septa and spongy columella as identifying characters of their subgenus. Recently I acquired from the National Museum of Natural History a new, undescribed species that also has these characters. Nowhere else among the genera and subgenera of the Micrabaciidae are septa of both lower and higher cycles so highly and conspicuously perforate. On this basis, if on no other, recent authors of studies on the Micrabaciidae have informally recognized *Letepsammia* as a genus.

The diagnosis given earlier in this paper is intended to expand and emend Yabe and Eguchi's original description of their subgenus so as to incorporate other common characters of the species of that group that seem to be of generic significance.

*Letepsammia,* at present, contains two described species:

*L. formosissima* Moseley, 1881. Recent, Celebes, Banda, and Coral Seas, Philippine and Hawaiian Islands.
*L. superstes* Ortmann, 1888. Plio-Pleistocene, Ryukyu Islands; Recent, Japan Sea.

Squires (1967:505) alluded to six species of letepsammid corals found in the Pacific and Indian Oceans. Undoubtedly, this number included the two described species, and probably also the new, undescribed species from the National Museum of Natural History; the remaining species to which he refers have not, to date, been either described or verified.

Although *Letepsammia* was originally assigned as a subgenus of *Stephanophyllia,* it bears only a superficial resemblance to that genus. The corallum in *Letepsammia* is relatively large and loosely built, with all septa highly perforated and adorned with prominent, complex dentation. In *Stephanophyllia,* the corallum is small-to-medium and generally quite compact; perforations are present, but they are restricted to the lower portions of higher cycle septa and are often sparsely and irregularly distributed. Septal edges are noticeably dentate, but the dentation is of the simple acute or lacerate type. The basal wall in *Letepsammia* is thin and generally projects as a prominent shelf, whereas it forms a rather tight rim in *Stephanophyllia* with little or no marginal shelf. In each case, the columella is elongate, but it is very porous in *Letepsammia,* lamellar in *Stephanophyllia.*

Septal microstructure also differs in the two genera. Trabeculae in *Stephanophyllia* are regularly spaced in a well-organized fan system, with ends of the sclerodermites projecting laterally to form vepreculae along the flanks of each septum. In *Letepsammia*, the trabeculae are thin, wavy, irregularly spaced in a very loose fan, and are reduced in number. The sclerodermites rarely project beyond the plane of the septum, but when they do, they form only rudimentary vepreculae.

Superficially, *Letepsammia* does resemble *Stephanophyllia* in that both possess true deltas, dentate septa, and septal perforations to some degree. However, the differences between them far outweigh their similarities. These differences, moreover, are fundamental enough to warrant official elevation of *Letepsammia* to the rank of genus.

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# THE TAXONOMIC STATUS OF *GLOSSOPHAGA MORENOI* MARTINEZ AND VILLA, 1938 (MAMMALIA: CHIROPTERA: PHYLLOSTOMIDAE)

Alfred L. Gardner

*Abstract.*—A review of the nomenclatural history of Mexican *Glossophaga,* the identity of the neotype of *G. morenoi,* and the content of the species described as *G. mexicana* leads to the conclusion that *G. morenoi* is the correct name for the species currently known as *G. mexicana.*

The taxonomy and nomenclature of Mexican species of the genus *Glossophaga* have a complex history. Confusion has resulted from the misallocation of *Monophyllus leachii* Gray, 1844; the apparent loss of the type and paratypes of *Glossophaga morenoi* Martinez and Villa, 1938; and the recently confirmed presence of four species of *Glossophaga* in Mexico (Webster and Jones 1980) instead of only one, the ubiquitous *G. soricina* (Pallas, 1766).

Based on Miller's (1913) revision of *Glossophaga, G. soricina leachii* (Gray, 1844) was the name applied to all North American mainland populations and *G. soricina mutica* Merriam, 1898, to the Tres Marias Islands populations. In 1938, Martinez and Villa described *G. morenoi* based on material from Xiutepec, Morelos. Davis (1944) described *G. soricina alticola* from 13 km northeast of Tlaxcala, Tlaxcala, but did not mention *G. morenoi.*

Villa (1953) considered *G. soricina alticola* to be a synonym of *G. soricina morenoi.* In contrast, Davis and Russell (1954) continued to recognize *G. soricina alticola,* treating *G. morenoi* as a synonym of *G. soricina leachii,* the name by which all other Mexican mainland populations of *Glossophaga* were known. Hall and Kelson (1959:114) followed Davis and Russell (1954) but commented on their doubt concerning "the correct taxonomic arrangement of the central Mexican material."

Gardner (1962) described *G. commissarisi* (type locality 10 km SE of Tonalá, Chiapas) based on material from Nayarit, Colima, and Chiapas, Mexico. This prompted Villa (1964) to review the names that had been applied to Mexican *Glossophaga.* He concluded that *G. soricina alticola* and *G. commissarisi* were junior synonyms of *G. morenoi,* which he again recognized as a species distinct from *G. soricina.* In addition, Villa (1964:387) designated a neotype for *G. morenoi* because the original material had disappeared.

Alvarez (1966) reported on the discovery of specimens of small mammals in the Museo Nacional de Historia Natural that included some long missing types of bats and four specimens of *Glossophaga,* which he identified as *G. soricina.* Although admitting that there was no proof, Alvarez believed the four *Glossophaga* were used by Martinez and Villa (1938) when they described *G. morenoi.* Alvarez stated that Villa's (1964) designation of a neotype of *G. morenoi* was invalid, because Villa's action did not conform with Article 75 of the International Code of Zoological Nomenclature (Code). Alvarez (1966) did not consider Villa's work a revision of a genus because the description of the neotype did not permit its recognition and its characterization was not consistent with the original description. Thus Alvarez concluded that *G. morenoi* was best considered a "*nomen dubius.*"

Baker (1967) did not use the name *G. morenoi.* Instead he used the names *G. alticola* and *G. commissarisi,* in addition to *G. soricina,* based on identifications by J. Knox Jones, Jr., for Mexican species.

In their review of North American *Glossophaga,* Webster and Jones (1980) clarified relationships among the Middle American and Mexican species. They recognized four sympatric species in Mexico: *G. soricina, G. leachii, G. commissarisi,* and *G. mexicana.* The latter they described as new. They assigned *G. soricina alticola* and *G. morenoi* to *G. leachii,* citing Villa's (1953, 1964, 1967) argument that *G. morenoi* was an earlier name for *G. soricina alticola.* Therefore, this made *G. morenoi* a junior synonym of *G. leachii.* Webster and Jones (1980:5) also described *G. soricina handleyi* to provide a name for the subspecies that had been known for so many years as *G. soricina leachii.*

*Glossophaga soricina leachii* (with *G. mutica* and *G. morenoi* as synonyms), *G. alticola,* and *G. commissarisi* were the three taxa recognized by Hall (1981) as occurring in Mexico. In 1982, Webster and Jones named and described the northwestern Mexican population of *G. commissarisi* as *G. c. hespera.*

Urbano and Sanchez (1983) agreed with Webster and Jones' (1980) decision to place *G. morenoi* in the synonymy of *G. leachii.* They incorrectly identified the neotype of *G. morenoi* as an example of *G. soricina* and reiterated Alvarez's (1966) opinion that Villa (1964) had not conformed to the requirements of Article 75 (sections a and c) of the Code when designating a neotype for *G. morenoi.*

Webster and Jones (1984a) proposed the name *G. mexicana brevirostris* for the northern population of *G. mexicana.* They also commented (p. 4), "It is of passing note that the specimen (UNAM 7383) designated as the 'neotype' of *Glossophaga morenoi* by Villa-R. (1964) actually represents *G. m. brevirostris* . . . ." In the mammalian species account on *G. leachii,* Webster and Jones (1984b) provided a key to the species, remarked on the taxonomic history of *G. leachii,* and included *G. morenoi* in the synonymy of *G. leachii.*

The latest published report concerning the systematics and natural history of Mexican *Glossophaga* is the mammalian species account on *G. mexicana* by Webster and Jones (1985). This account contained no mention of *G. morenoi.*

The argument advanced by Alvarez (1966) and Urbano and Sanchez (1983) that Villa's (1964) designation of the neotype of *G. morenoi* was invalid because he did not conform with the requirements of Article 75 of the Code (Stoll et al. 1964) is not supported by the evidence. Villa's review of the taxonomy of the Mexican species of *Glossophaga* known to him, although not a revision of a genus, is clearly "revisory" in the sense of Article 75(a) of the Code. Furthermore, Villa's designation conforms with the requirements of Article 75(c) of the Code. In other words, although Villa's (1964) taxonomic conclusions were wrong, his actions were nomenclaturally correct. Therefore, the name *G. morenoi* has standing based on the neotype.

The conspecificity of the neotype of *G. morenoi* and specimens identified by W. David Webster as *G. mexicana* has been independently confirmed by Oscar Sanchez and Rodrigo Medellín (pers. comm.). In the original description, *G. morenoi* was characterized as similar to *G. soricina* in dental formula and morphology of the upper and lower incisors. However, differences included larger size, absence of a tail, and undefined differences in the ear and nose leaf. The upper incisors of *G. mexicana* are more similar to those of *G. soricina* in size and procumbency than are those of either *G. leachii* or *G. commissarisi,* but the lower incisors of *G. mexicana* are distinctly more similar to those of *G. leachii* and *G. commissarisi.* In Mexico, *Glossophaga leachii* (with *G. alticola* a synonym) averages larger than *G. soricina* in external measurements and in breadth of braincase whereas *G. commissarisi* averages smaller than *G. soricina* in all dimensions; however, *G. mexicana brevirostris* is approximately the same size or slightly larger than *G. soricina* and *G. mexicana mexicana* is even larger (Webster 1983). The purported absence of a tail cannot be evaluated at this time and may represent an oversight on the part of Martinez and Villa (1938).

A factor that undoubtedly influenced opinions concerning the taxonomy of Mexican *Glossophaga* was the number of species believed to be present in the country. The prevailing opinion up to the time Gardner (1962) described *G. commissarisi* was that there was one species (*G. soricina*) with one, two, or possibly three subspecies. When describing *G. commissarisi,* Gardner (1962:4) recognized the presence of two additional species besides *G. soricina.* One represents *G. leachii* as understood today; the other was later described as *G. mexicana* (see Webster and Jones 1980:6). Nevertheless, Villa (1964, 1967) apparently believed that only two (*G. soricina* and *G. morenoi*) were present. It remained for Webster and Jones (1980) to sort out the taxa and to confirm the presence of four species in Mexico.

Clearly, the neotype of *G. morenoi* represents the same species described by Webster and Jones (1980) as *G. mexicana.* Villa's (1964) designation of the neotype of *G. morenoi* conforms to the requisites of Article 75 of the International Code of Zoological Nomenclature. Therefore, *G. mexicana* is a junior synonym of *G. morenoi,* whose synonymy is described as follows:

### *Glossophaga morenoi* Martinez and Villa, 1938
### Moreno's long-tongued bat

*Glossophaga morenoi* Martinez and Villa, 1938:347; type locality "Xiutepec," Morelos, Mexico. Type and paratypes lost (Villa 1953, 1964, 1967). Neotype designated by Villa (1964:387); type locality "Cueva del Idolo, 1 Km. S. tequesquitengo 970 m., Estado de Morelos," Mexico.

*Glossophaga mexicana* Webster and Jones, 1980; type locality "Río Guamól, 34 mi. S (by Hwy. 190) La Ventosa Jct., Oaxaca, México."

*Glossophaga mexicana brevirostris* Webster and Jones, 1984a:2; type locality "6 mi. W Yautepec, 4500 ft., Morelos, México."

The northern subspecies distinguished by Webster and Jones (1984a) as *G. mexicana brevirostris* should be known as *G. morenoi morenoi* Martinez and Villa, 1938, and the southern populations as *G. morenoi mexicana* Webster and Jones, 1980.

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# TRINERVATE LEAVES, YELLOW FLOWERS, TAILED ANTHERS, AND POLLEN VARIATION IN *DISTEPHANUS* CASSINI (VERNONIEAE: ASTERACEAE)

Harold Robinson and Brian Kahn

*Abstract.*—The genus *Distephanus* Cassini is resurrected for a series of mostly western Indian Ocean and eastern African species of Vernonieae including the only members of the tribe having trinervate leaves and yellow flowers. The genus is characterized by distinct basal stylar nodes, sclerified basal appendages on the anther thecae, and a unique form of pollen. Twenty-six species are recognized in the genus, 24 being newly transferred, and additional possible members are listed.

The broad concept of *Vernonia* suffers from most of the ills of a core genus, being excessively paraphyletic, distracting from more appropriate phyletic comparisons between its parts and other genera of the tribe, and being defined primarily by what it is not rather than by what it is. Such concepts ultimately encourage shoddy taxonomy, and *Vernonia* is no exception, having come to include elements that do not even fit the broadest definition of the genus when examined critically.

It is by virtue of such lapses of careful study that the Paleotropical genus *Distephanus* has fallen into the synonymy of *Vernonia. Distephanus* is a genus with predominantly yellow flowers in a tribe that otherwise lacks them, and the genus includes the only members of the tribe with trinervate leaves. Furthermore, the anther thecae of the genus are almost as prominently appendaged at their bases as those of the American genus *Piptocarpha* which is distinguished by that character.

*Distephanus* was first described by Cassini (1817) on the basis of a single species, *Conyza populifolia* Lam., from Mauritius. Cassini (1819) distinguished the genus by its pappus, described as 10 short outer squamellate scales alternating with 10 longer inner linear–squamellate scales. His description mentioned the yellow-flowered heads, and a microfiche of the specimen in the Jussieu herbarium shows that the poplar-like leaves are trinervate. The claimed pappus distinction seems to have been ignored in subsequent literature as *Distephanus* has fallen into the synonymy of *Vernonia,* and the pappus was not mentioned by Humbert (1960) who related the yellow-flowered *Vernoniae* of Madagascar to the genus. The genus name has been transferred to sectional status by Bentham and Hooker (1873) for the single species, and to subsectional status by Jones (1981) for mostly unrelated species of Malayasia. With these latter exceptions, the name *Distephanus* has been ignored in recent literature.

It is the African members of the same group that were later segregated from *Vernonia* as the genus *Gongrothamnus* Steetz, a genus that was transferred to the Senecioneae by Bentham and Hooker (1873) on the basis of its yellow flowers and trinervate leaves. *Gongrothamnus* was reduced to synonymy under *Vernonia* by Hoffmann (1890–1894) at the same time that he named a new genus *Newtonia* in the same Senecioneae on the basis of still another species of the group from Angola. The name *Newtonia* was a later homonym and a new name, *Antunesia* was provided by Hoffmann in 1893. Hoffmann (1902) ultimately corrected his error, recognizing *Gongrothamnus* at generic level and placing *Antunesia* in its synonymy. Brown (1909) briefly summarized some of the work in *Gongrothamnus,* but reduced it again to synonymy under *Vernonia,* being unaware of the importance of the trinervate leaves, and knowing no other character except the yellow flowers.

Almost all recent students of the Vernonieae have treated the yellow-flowered species as part of *Vernonia.* Wild (1978) placed the yellow-flowered species of the Zambezica area in *Vernonia* along with some trinervate species with reddish to purplish flowers. Humbert (1960) placed the yellow-flowered species of Madagascar in two groups with the note that the name *Distephanus* would apply to his Group V. Jones (1981) recognized the yellow-flowered species as a subsection of *Vernonia* in his classification of the Paleotropical members of the genus, but as mentioned above, treated *Distephanus* as a distinct indirectly related subsection.

The retention of the name *Gongrothamnus* at the generic level by Robinson et al. (1980) was based on the difference in flower color along with the realization that subdivision of *Vernonia* seemed inevitable. A firm basis for the distinction of the yellow-flowered species has arisen from the present study initiated as a review of stylar nodes in the tribe. The nodes as well as the leaf trinervation, flower color, anther tails, endothecial cells, and pollen variation all indicate a distinctive element of small shrubby or scandent Vernonieae distributed primarily in the western Indian Ocean. The characters involved warrant the following individual analyses.

*Trinervate leaves.*—Early observations of *Gongrothamnus* by the senior author, and studies by most other authors (Humbert 1960, Wild 1978) were without recognition of the importance of the trinervate character in the tribe. Only Bentham and Hooker (1873) seem to have appreciated how unusual the character is in the tribe when giving their reasons for transferring *Gongrothamnus* to the Senecioneae. Trinervation versus pinnate venation is certainly highly variable in most other tribes in the family, commonly varying within genera. It was only with more detailed studies of Neotropical Vernonieae that the senior author noted the fundamentally pinnate nature of leaf venation in the Vernonieae (Robinson et al. 1980) and commented upon the lack of trinervation in the tribe in comparisons with the Liabeae (Robinson 1983, Robinson et al. 1985). The species of *Distephanus* can now be seen as an exception in the Vernonieae, an exception in which most of the species are trinervate or have leaves reduced to an ill-defined venation pattern. Trinervation has been seen in no other Vernonieae and is regarded as uniquely derived in this Indian Ocean element of the tribe.

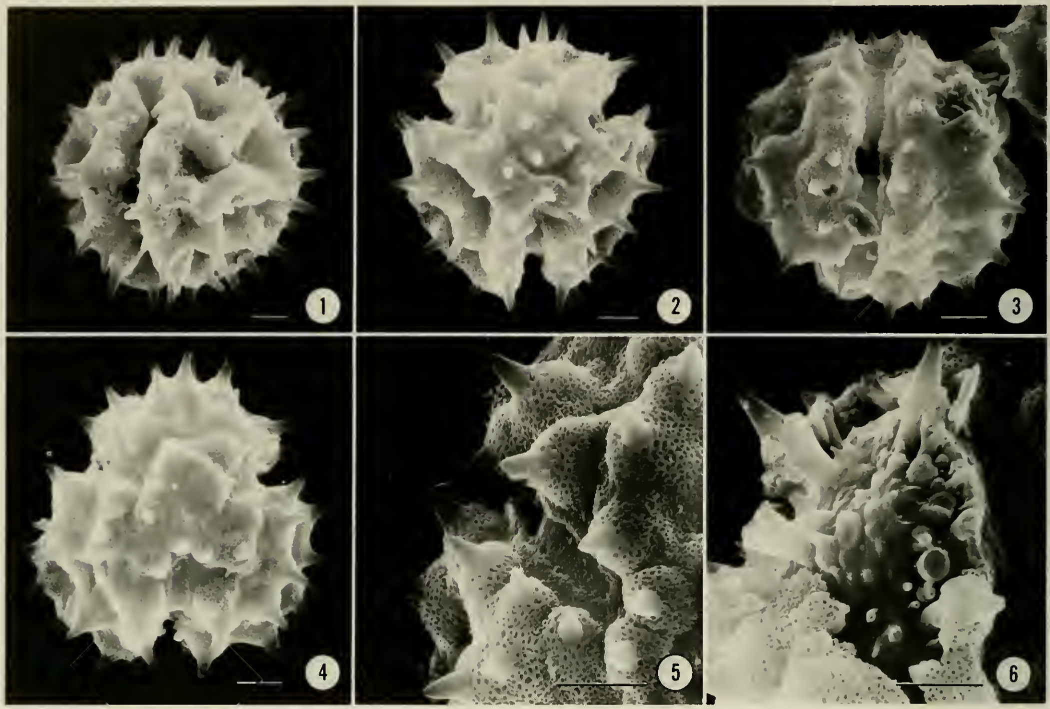
*Yellow flowers.*—Closely correlating with the trinervate leaves in the Vernonieae are the yellow flowers. The latter character is sufficiently exceptional in the tribe to have caused both Bentham and Hooker (1873) and Hoffmann (1890—1894) to place members of the genus in the tribe Senecioneae. A few species on the African mainland were noted by Wild (1978) as having trinervate leaves but not having yellow flowers. These are scandent like the yellow-flowered species of *Distephanus* on the mainland and have stylar nodes, basal appendages on the anther thecae, and mostly unstriated endothecial sclerified shields as in that genus. These reddish species appear to be members of *Distephanus,* but occur outside of the apparent center of distribution of the genus, where they seem to be a derived element. Since hybridization is common in the Asteraceae, such convergences in the Vernonieae may well represent borrowing of traits from the associated reddish-flowered Vernonieae on the continent. In any case, the character failure is regarded as a de-differentiation between two well-defined elements of the tribe and not a relict of any ancestral type.

*Basal appendages of the anther.*—The Vernonieae, like almost all Cichorioideae, have spurred bases on the anthers, but in addition to the fertile extensions, most thecae have at least a fringe of sterile tissue at the lower end. In typical *Vernonia* and most species that have been placed in the genus, the sterile tissue is usually unsclerified and easily overlooked, but some species in basically unappendaged groups, such as *V. megaphylla* Hieron. have a small sclerified basal appendage. In Neotropical Vernonieae, prominent narrow sclerified basal appendages are the character by which *Piptocarpha* has traditionally been distinguished from *Vernonia.* In Paleotropical members of the tribe such as *Distephanus,* basal anther appendages have not been noted, probably because they usually are broad and do not have the form of a narrow tail. One African segregate of *Vernonia, Baccharioides* (*Vernonia* subgenus *Stengelia*), has no sclerified appendage, but all of *Distephanus,* typical *Gymnanthemum,* and some species of Humbert's (1960) Group IV from Madagascar show distinct basal appendages. A narrow basal appendage in the form of a broad tail does occur in *Distephanus glandulicincta.* The character technically places these elements outside of the traditional definition of *Vernonia,* even though the less obvious appendages of these African Vernonieae have traditionally been ignored. The appendages in *Gymnanthemum* and Group IV may indicate relationship of these groups to *Distephanus,* but other characters such as the trinervate leaves and flower color are different. Of these, only some species of Group IV have a distinct stylar node, but they differ by having deciduous inner bracts in the involucre.

*Endothecial cells.*—All members of *Distephanus* examined have median endothecial cells with a single unlined sclerified shield on the outer surface. These superficially appear like a series of non-contiguous cells in the endothecium. This contrasts with the more annulated appearance of other Vernonieae that have been seen. A tendency toward an intermediate condition occurs in *D. angulifolius,* a species of continental Africa noted above for possible introgression with other Vernonieae in flower color. *Gymnanthemum* and Humbert's Group IV both can have sclerified shields approaching those of *Distephanus* in form but with multifid ends. Those of typical *Gymnanthemum* differ further in their frequently oblique or nearly transverse direction.

*Apical anther appendages.*—Glands occur on the apical anther appendages of typical *Vernonia* and on many other Neotropical species placed in the genus. Such glands are lacking in some of the American species which seem to have generally lost the ability to produce glands anywhere on the plant. The African groups seen in the present study show no glands on the appendages in any species, even when glands occur on other parts.

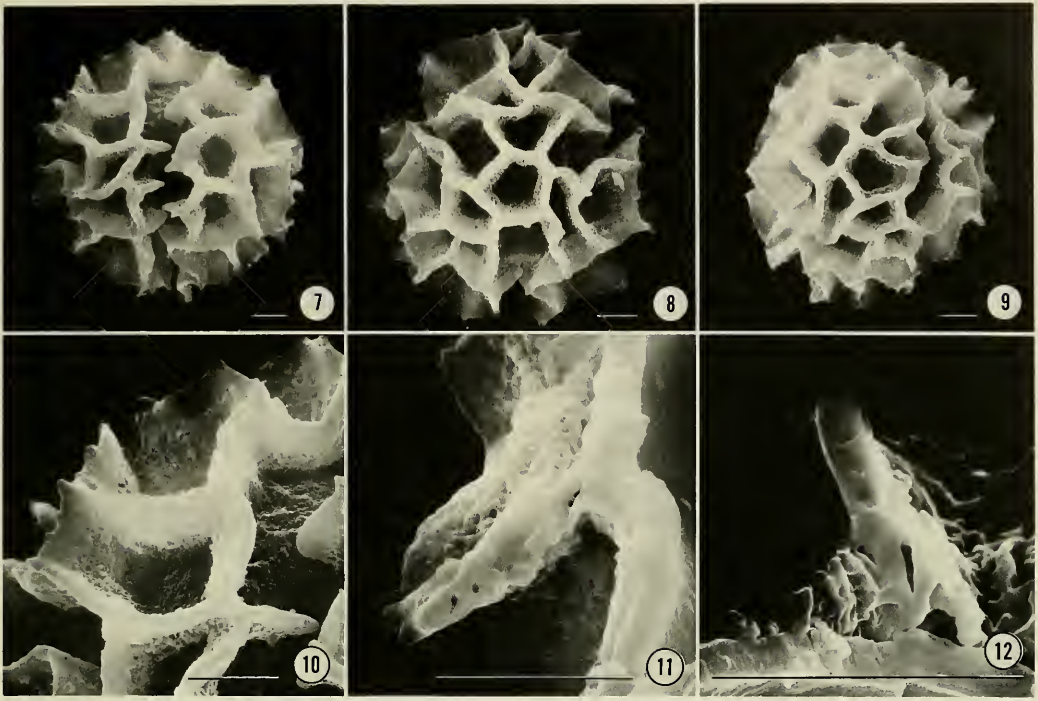
*Stylar node.*—An expanded node with sclerified cells at the base of the style occurs commonly in the Vernonieae, and the character may be basic to the tribe. The character is most common, however, in Neotropical members of the tribe; it has a comparatively restricted distribution among Paleotropical species. A few African entities such as *V. bainesii* Oliv. & Hiern, have slight nodal development, but distinct nodes as large as any in the tribe seem almost totally restricted to and characteristic of *Distephanus* among the Paleotropical Vernonieae. The mature node of *Distephanus* is puck-like, narrowing abruptly above into the stalk partly as a result of shrinkage of unsclerified stalk tissue. A few species from Madagascar placed by Humbert (1960) in his Group IV, such as *V. andrangovalensis* Humb. and *V. appendiculata* Less., have nodes as large, but the latter group differs by being larger shrubs and trees, having reddish flowers normal for the tribe, and having deciduous inner bracts of the involucre.



Figs. 1–6. Pollen of *Gymnanthemum* and *Distephanus,* lines = 5 μm. 1–2, *G. coloratum* (Willd.) R. & K., Equatorial and polar views showing sublophate intercolpar surface; 3–6, *D. divaricatus* (Steetz) R. & K., Colpar view; 4, Polar view, showing lack of regular sublophate intercolpar surface; 5, End of colpus; 6, Area of broken tectum showing basal columellae.

*Pollen.*—The so-called Lychnophora-type pollen (Stix 1960) or Type A pollen (Keeley and Jones 1979), the most widely distributed pollen type in the Vernonieae, is found in most species of *Distephanus* and in *Gymnanthemum* and Humbert's Group IV. The grains seen in *Distephanus* and Group IV are ca. 38–40 μm in diameter while those of typical *Gymnanthemum* ca. 45–47 μm in diameter. In *Distephanus* the Type A pollen occurs in all non-Madagascar species (Figs. 3–4) and six species seen from Madagascar, *D. antandroy, D. glandulicinctus, D. malacophytus, D. nummulariaefolius, D. rochonioides* and *D. subluteus.* The Type A pollen grains of *Distephanus* seem unusual in the irregularity of the surface pattern, an irregularity not seen in *Gymnanthemum* (Figs. 1–2) and believed here to be related to the irregularity seen in the surface pattern of the non-Type A grains found in other species of *Distephanus.* Another aspect of these Type A grains that might be unusual shows in broken areas of *D. divaricatus* pollen, where separate smaller basal columellae occur in the spaces between the primarily basal columellae under the spines (Fig. 6).

Seven other species of *Distephanus* from Madagascar, *D. cloiselii, D. eriophyllus, D. mahafaly, D. mangokensis, D. ochroleucus, D. swinglei,* and *D. trinervis,* have a distinctive type of pollen not seen elsewhere in the tribe (Figs. 7–12). It is lophate with areolae distinct but lacking any definite order. The ridges are not pitted or perforated on the edges, but a weakly perforated tectum lines the lower sides and bottoms of the areolae (Fig. 10). The direct attachment of the crests to the foot layer seems intermittent within the area covered by perforated



Figs. 7–12. Pollen of *Distephanus ochroleucus* (Baker) R. & K., lines = 5 μm. 7, Colpar view; 8, Polar view; 9, Oblique view of intercolpar area showing irregular lophate pattern; 10, Areolae showing non-perforate edges of tectum ridges and perforate basal parts; 11–12, Broken sections of ridges showing parts with and without direct median attachment of the foot layer.

tectum. The pores are located in long colpi into which walls partially intrude in an alternating pattern (Fig. 7). The alternating pattern of the intruding walls seems characteristic and is apparently directly linked to the characteristic irregularity of the tectum areolation. The ridges of these species of *Distephanus* (Figs. 11–12) are reminiscent of those in the pollen of *Cyanthillium* Blume, *Phyllocephalum* Blume, *Stokesia* L'Her., or the Elephantopinae, but the latter have more regular reticulations, have more truncated colpi or complete cross-walls above and below the pores which interrupt any colpi, and have the ridges raised on a series of small columellae or a fenestrated curtain above the surface of the foot layer. None have the partial perforated tectum seen in *Distephanus.*

The presence of variation of pollen type within the well defined related group *Distephanus* is not the first example of such variation in the Vernonieae. As in other examples, the variation involves the Type A pollen and is not a variation between two of the lophate types. This type of anomalous occurrence along with the general pattern of distribution of Type A in the tribe suggests that the Type A is often the product of reversion and not necessarily the primitive form. In this particular case, one can theorize that it is only necessary developmentally to limit the type of structure seen on the ridge margins to the isolated spine tips and allow the perforated tectum to become the continuous structure of the surface instead. In any case, the presence of Type A pollen is not regarded here as evidence of either primitiveness or direct relationship between the species in which it occurs. Considering the specialized lophate pollen of *Distephanus* alone seems to present a more realistic picture of relationship, with the type being restricted to the distinctive genus centered geographically in Madagascar.

*Distephanus* is a genus differing in two obvious characters from all other Vernonieae. All the species have either the yellow flowers or the trinervate leaves, neither feature occurring elsewhere in the tribe. The naturalness of the group is supported by other less obvious but nearly as unique features such as the puck-like stylar node, and the simple broad sclerified shields of the endothecial cells. The basal appendages of the anther thecae place *Distephanus* with *Gymnanthemum* and parts of Humbert's Group IV technically outside of the traditional definition of *Vernonia* to whose North American type they have only an extremely paraphyletic relationship. Species of *Distephanus* showing flower color or endothecial cells approaching the type seen in "*Vernonia*" are seen as recent introgressions. The genus *Distephanus* is resurrected and defined as follows.

### **Distephanus** Cassini

*Distephanus* Cassini, Bull. Soc. Philom. 1817:151. 1817. Type *Conyza populifolia* Lam.

*Vernonia* sect. *Distephanus* (Cassini) Bentham & Hooker f., Gen. Pl. 2:228. 1873.

*Vernonia* subsect. *Distephanus* (Cassini) Jones, Rhodora 83:68. 1981.

*Gongrothamnus* Steetz ex Peters, Reise Mossamb. Bot. 336. 1862. Type *Gongrothamnus divaricatus* Steetz.

*Vernonia* subsect. *Gongrothamnus* (Steetz) Jones, Rhodora 83:65. 1981.

*Newtonia* O. Hoffmann, Engler & Prantl., Natürl. Pflanzenfam. 4(4):285. 1892. Type *Newtonia angolensis* O. Hoffmann. Not *Newtonia* Baill. 1888.

*Antunesia* O. Hoffmann, nom. nov., Bolet. Soc. Brot. 10:178. 1893. Type *Newtonia angolensis* O. Hoffmann.

Small shrubs or vines. Leaves alternate, blades usually trinervate, often with truncate or subcordate bases, less often narrow with cuneate bases and irregularly pinnate venation. Inflorescences terminal on branches, of corymbose cymes, with minute bracts, peduncles short but distinct. Heads campanulate; involucral bracts mostly 21–24, ca. 75 in *D. forrestii,* persistent, multiseriate, graduated, unappendaged apically; receptacle epaleaceous. Flowers mostly 10–16 in a head, ca. 75 in *D. forrestii.* Corollas usually yellow, purplish in a few continental African species; thecae of anthers with distinct broad sclerified basal appendages; endothecial cells with simple, broad, non-contiguous, sclerified shields; apical appendages of anthers without glands; style base with large abruptly broadened node. Achenes cylindrical to prismatic, sometimes subtriquetrous or quadrangular, with 5–12 ribs, usually 10, setulae or glands present or absent; carpopodium turbinate; pappus of 10 or more shorter outer squamellae alternating with 10 or more longer capillary or linear inner bristles or squamellae. Pollen in many species Type A with continuous intercolpar perforated tectum and subreticulately arranged spines, in some Madagascar species irregularly lophate with perforated tectum restricted to lower sides and bases of crests, with distinct colpi intruded upon by short alternating spurs of reticulate tectum.

The species recognized in the genus in this study are as follows:

### **Distephanus angolensis** (O. Hoffmann) H. Robinson & B. Kahn, comb. nov.

*Newtonia angolensis* O. Hoffm., Natürl. Pflanzenfam. 4(5):285. 1892. *Antunesia angolensis* (O. Hoffm.) O. Hoffm., Bolet. Soc. Brot. 10:178. 1893. *Gongrothamnus angolensis* (O. Hoffm.) Hiern, Cat. Welw. Afr. Pl. 1:592. 1898. *Vernonia angolensis* (O. Hoffm.) N. E. Brown, Kew Bull. 1909: 116. 1909. SW Africa.

**Distephanus anisochaetoides** (Sond) H. Robinson & B. Kahn, comb. nov.

*Vernonia anisochaetoides* Sond, Linnaea 23: 61. 1850. SE Africa.

**Distephanus angulifolius** (DC.) H. Robinson & B. Kahn, comb. nov.

*Vernonia angulifolia* DC., Prodr. 5:29. 1836. SE Africa.

**Distephanus antandroy** (H. Humbert) H. Robinson & B. Kahn, comb. nov.

*Vernonia antandroy* H. Humb., Not. Syst. Paris 8(1):7. 1939. Madagascar.

**Distephanus cloiselii** (Moore) H. Robinson & B. Kahn, comb. nov.

*Vernonia cloiselii* Sp. Moore, Journ. Bot. 44:145. 1906. Madagascar.

**Distephanus divaricatus** (Steetz) H. Robinson & B. Kahn, comb. nov.

*Gongrothamnus divaricatus* Steetz in Peters, Reise Mossamb. Bot. 2:342. 1864. Not *V. divaricatus* Swartz, 1806. *Gongrothamnus aurantiacus* O. Hoffm., Bot. Jahrb. 30:433. 1901. *Vernonia aurantiaca* (O. Hoffm.) N. E. Brown, Kew Bull. 1909:116. 1909. *Vernonia vitellina* N. E. Brown, Kew Bull. 1909:117. 1909. East Africa.

**Distephanus eriophyllus** (Drake) H. Robinson & B. Kahn, comb. nov.

*Vernonia eriophylla* Drake, Bull. Soc. Bot. Fr. 46:230. 1889. Madagascar.

**Distephanus forrestii** (Anthony) H. Robinson & B. Kahn, comb. nov.

*Vernonia forrestii* Anthony, Notes Bot. Gard. Edinb. 18:35. 1933. Yunnan.

**Distephanus garnieriana** (Klatt) H. Robinson & B. Kahn, comb. nov.

*Vernonia garnieriana* Klatt, Linnaea 37:508. 1872. *Vernonia parviflora* (error for *parvifolia*) Klatt, Ann. Sc. Nat. 5$^{e}$ sér. Bot. 362. 1873. *Vernonia lyallii* Baker, J. Linn. Soc. 20:174. 1883. *Vernonia moquinioides* Baker, J. Linn. Soc. 20:177. 1883. *Vernonia alboviridis* Baker, J. Linn. Soc. 25:325. 1890. Madagascar.

**Distephanus glandulicinctus** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia glandulicincta* H. Humb., Not. Syst. Paris 8(4):306. 1948. Madagascar.

**Distephanus glutinosus** (DC.) H. Robinson & B. Kahn, comb. nov.

*Vernonia glutinosa* DC., Prodr. 5:18. 1836. *Vernonia scariosa* Baker, Journ. Bot. 20: 169. 1882, hom. illeg. *Vernonia lepidophylla* Drake, Bull. Soc. Bot. Fr. 46:229. 1889. Madagascar.

**Distephanus lastellei** (Drake) H. Robinson & B. Kahn, comb. nov.

*Vernonia lastellei* Drake, Bull. Soc. Bot. Fr. 46:232. 1899. *Vernonia goudotii* Drake, Bull. Soc. Bot. Fr. 46:239. 1899. Madagascar.

**Distephanus mahafaly** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia mahafaly* H. Humb., Not. Syst. Paris 8(1):10. 1939. Madagascar.

**Distephanus majungensis** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia majungensis* H. Humb., Not. Syst. Paris 13:308. 1948. Madagascar. Lectotype designated here, *Humbert & Perrier 2117* (P).

**Distephanus malacophytus** (Baker) H. Robinson & B. Kahn, comb. nov.

*Vernonia malacophyta* Baker, Journ. Linn. Soc. 25:323. 1890. *Vernonia rampans*

Baker, Journ. Linn. Soc. 25:323. 1890. *Vernonia grandidieri* Drake, Bull. Soc. Bot. Fr. 46:240. 1899. Madagascar.

**Distephanus manambolensis** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia manambolensis* H. Humb., Not. Syst. Paris 13:306. 1948. Madagascar.

**Distephanus mangokensis** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia mangokensis* H. Humb., Bull. Soc. Bot. Fr. 87:347. 1940. Madagascar.

**Distephanus nummulariaefolius** (Klatt) H. Robinson & B. Khan, comb. nov.

*Decaneurum* (*Gymnanthemum*) *nummulariaefolium* Klatt, Ann. Sc. Nat. 5$^{e}$ sér. Bot. 18:363. 1873. *Gongrothamnus multiflorus* Klatt, Flora 68:205. 1885. *Vernonia leucolepis* Baker, Journ. Bot. 25: 322. 1890. Madagascar.

**Distephanus ochroleucus** (Baker) H. Robinson & B. Kahn, comb. nov.

*Vernonia ochroleuca* Baker, Journ. Linn. Soc. 20:179. 1885. *Vernonia trichantha* Baker, Journ. Linn. Soc. 21:416. 1884. Madagascar.

**Distephanus polygalaefolia** (Less.) H. Robinson & B. Kahn, comb. nov.

*Vernonia polygalaefolia* Less, Linnaea 6: 628. 1831. *Vernonia arbutifolia* Baker, J. Bot. 20:169. 1882. *Vernonia perrieri* Drake, Bull. Soc. Bot. Fr. 46:229. 1899. Madagascar.

*Distephanus populifolius* (Lamarck) Cassini

*Conyza populifolia* Lamarck, Encyc. 2:87. 1786. *Distephanus populifolius* (Lamarck) Cassini, Bull. Soc. Philom. 1817: 151. 1817. *Vernonia populifolia* (Lamarck) Spreng., Syst. 3:434. 1826. Mauritius.

**Distephanus rochonioides** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia rochonioides* H. Humb., Bull. Soc. Bot. Fr. 87:346. 1940. Madagascar.

**Distephanus streptocladus** (Baker) H. Robinson & B. Kahn, comb. nov.

*Vernonia streptoclada* Baker, Journ. Linn. Soc. 21:416. 1885. Madagascar.

**Distephanus subluteus** (S. Elliot) H. Robinson & B. Kahn, comb. nov.

*Vernonia sublutea* S. Elliot, Journ. Linn. Soc. 29:26. 1891. Madagascar.

**Distephanus swinglei** (H. Humb.) H. Robinson & B. Kahn, comb. nov.

*Vernonia swinglei* H. Humb., Not. Syst. Paris 8(1):8. 1939. Madagascar.

*Distephanus trinervis* Boj. ex DC.

*Distephanus trinervis* Boj. ex DC., Prodr. 5: 75. 1836. *Distephanus capitatus* Boj. ex DC., Prodr. 5:74. 1836. *Vernonia capitata* (Boj. ex DC.) Drake in Grandidier, Hist. Madag. Pl. VI, Atlas, pl. 464. 1897. *Vernonia trinervis* (Boj. ex DC.) Drake, Bull. Soc. Bot. Fr. 46:228. 1899. *Vernonia rusillonii* Hochr., Ann. Cons. Genève, 11–12:117. 1908. Madagascar.

Additional species having the characters of the genus according to Humbert (1960) but not seen in this study are as follows: *Vernonia ambongensis* H. Humb., *V. bara* H. Humb., *V. bakeri* Vatke, *V. capuronii* H. Humb., *V. Grevei* Drake, *V. ibityensis* H. Humb., *V. madagascariensis* Less., *V. poissonii* H. Humb., *V. polytricholepis* Baker, *V. quartziticola* H. Humb., *V. rhodopappa* Baker, *V. spiciforma* Klatt.

In the course of the present study it has seemed best to recognize *Gymnanthemum* at the generic level also, since it also falls outside of the definition of traditional *Vernonia,* and the status is inevitable in any final revision of the tribe. This would not be so important at the present time except for the fact that the oldest name for the type species *G. cupulare* Cass. has never been transferred to the genus. There seems to be no reason for the precedence usually given to the Persson name *Baccharis senegalensis* since the Willdenow name antidates it by four years, unencumbered by inadequate description or homonymy.

**Gymnanthemum coloratum** (Willd.) H. Robinson & B. Kahn, comb. nov.

*Eupatorium coloratum* Willd., Sp. Pl. 3: 1768. 1803.

## Acknowledgments

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# A NEW VULTURE (VULTURIDAE: *PLIOGYPS*) FROM THE LATE MIOCENE OF FLORIDA

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*Abstract.*—A new vulture, *Pliogyps charon* n. sp., from the late Miocene (latest Clarendonian) Love Bone Bed locality, Alachua Co., Florida, is described from a complete tarsometatarsus and referred distal ends of the tibiotarsus and humerus. *Pliogyps charon* is distinguished from *Pliogyps fisheri* Tordoff (1959) by smaller size, and by proportions and qualitative characters of the tarsometatarsus.

Pre-Quaternary vultures are poorly known. Recently, Olson (1985) reviewed the fossil history of this family. The earliest record of the family Vulturidae is from the late Eocene and early Oligocene deposits of the Phosphorites du Quercy, France, and in the early Oligocene of Mongolia. In South America, the oldest vulture is *Dryornis pampeanus* Moreno and Mercerat, from the Monte Hermoso Formation in Argentina, which is probably close to the living genus *Vultur* (Tonni 1980). The oldest records of vultures in North America are *Sarcoramphus kernensis* from the late Miocene (mid-Hemphillian) of Kern River, California, and a specimen under study from the mid-Barstovian Sharkstooth Hill local fauna (Emslie, pers. comm.). While there are several described genera and species of vultures from the Pliocene and Pleistocene (Brodkorb 1964, Olson 1985), the true number of valid taxa among them remains to be determined.

This paper describes a new species of New World vulture (Family Vulturidae), discusses functional aspects of the genus *Pliogyps,* and comments on the generic status of living and fossil members of this group.

## Material and Methods

Recent specimens examined are in the Florida State Museum, the collection of Pierce Brodkorb, and the National Museum of Natural History. Recent skeletons of Vulturidae examined: *Gymnogyps californianus,* 7; *Vultur gryphus,* 9; *Sarcoramphus papa,* 9; *Coragyps atratus,* 16; *Cathartes aura,* 4. Fossil specimens are in the vertebrate paleontology collections of the Florida State Museum (UF) and the Museum of Paleontology, University of Michigan. Anatomical terminology follows Baumel et al. (1979). Measurements, defined in Table 1 and Figs. 2 and 3, were taken with dial calipers accurate to 0.05 mm, and rounded to the nearest 0.1 mm.

## Systematics

### Order Accipitriformes (Vieillott, 1816)
### Family Vulturidae (Illiger, 1811)
### *Pliogyps* Tordoff, 1959

*Emended generic diagnosis.*—Tarsometatarsus of *Pliogyps* differing from that of other living and fossil genera of vultures in having a proportionately large trochlea for digit III, proximal articular surface wide and deep in comparison to length of bone, a generally columnar form, with symmetrical lateral and medial flaring, both proximally and distally; shaft wide in comparison to length of bone; hypotarsus merging distally with shaft by means of broad, rounded ridge (as in *Vultur, Breagyps, Gymnogyps,* and *Geranogyps*; more narrow in *Coragyps, Cathartes,* and *Sarcoramphus*). This last character may be strictly size dependent and if so, not of value as a generic character.

*Remarks.*—Two characters (shaft less deeply and extensively excavated anteriorly; groove of trochlea for digit III ending anteroproximally in a shallow, but distinct pit) used by Tordoff (1959) to define this genus are variable within a given species, and therefore should not be used as generic characters.

### *Pliogyps charon,* new species
Fig. 1

*Holotype.*—UF 25952, complete right tarsometatarsus, missing a small portion of hypotarsus.

*Paratype.*—UF 25886, distal end left tibiotarsus.

*Referred material.*—UF 25719, fragment of shaft of left humerus, tentatively referred.

*Type locality.*—Love Bone Bed local fauna, along State Road 241, near Archer, Alachua County, Florida (NW ¼, SW ¼, NW ¼, Sec. 9, T. 11 S., R. 18 E., Archer Quadrangle, U.S. Geologic Survey 7.5 minute series topographical map, 1969). Fossil vertebrates occurring in the Alachua Formation (Williams et al. 1977) are considered latest Clarendonian in age (Webb et al. 1981), about 9 million years before present. The known avifauna of the Love Bone Bed is primarily aquatic, with a few terrestrial species being present (Becker 1985a, b).

*Diagnosis.*—Tarsometatarsus distinguished from that of *Pliogyps fisheri* Tordoff (1959) in smaller size, in having a narrow ridge extending from hypotarsus farther down shaft (caudal view), in having sulcus extensorius more excavated and extending farther down shaft (cranial view), and in having shaft and trochlea III proportionately less deep.

*Etymology.*—The specific name *charon,* Greek, masculine, is a noun in apposition. In Greek mythology Charon, portrayed as a robust old man, ferries the souls of the dead across the River Styx (considered by some authorities to be the River Acheron) into the lower world. This name also reflects the proximity of a modern River Styx, located 18 miles due east of the Love Bone Bed locality on the northern edge of Orange Lake, Alachua County, Florida.

*Description.*—In cranial view, the proximal vascular foramina are large and are approximately equal in size. The papilla for

Table 1.—Measurements of the tibiotarsi and tarsometatarsi of the vultures *Coragyps atratus atratus* (n = 16, 8 males, 8 females), *Pliogyps fisheri,* and *Pliogyps charon,* new species. Data are mean ± standard deviation and range. Measurements of tibiotarsus are W-DIST-CR, Transverse width of distal end, measured across cranial portion of condyles; D-MCON, Greatest depth of medial condyle. Measurements of tarsometatarsus: LENGTH, Greatest length from intercondylar eminence (Eminentia intercondylaris) through trochlea for digit III (Trochlea metatarsi III). W-PROX, Greatest transverse width proximal articular surface, measured across dorsal surface. D-PROX, Depth of proximal end, measured from dorsal edge of the proximal articular surface through the lateral hypotarsal crest (Crista lateralis hypotarsi). W-DIST, Greatest transverse width of distal end. W-TRIII, Greatest transverse width of trochlea III. D-TRIII, Greatest depth of trochlea III. Measurements of *Coragyps* are included to show amount of variation present in a living population of vultures.

| Measurements | *C. a. atratus* | *P. fisheri* | *P. charon* |
|---|---|---|---|
| Tibiotarsus | | | |
| W-DIST-CR | 12.79 ± 0.41<br>12.1–13.6 | – | 19.5 |
| D-MCON | 13.67 ± 0.41<br>13.2–14.6 | – | [18.1] |
| Tarsometatarsus | | | |
| LENGTH | 84.43 ± 1.54<br>80.4–87.1 | 94.0 | 86.6 |
| W-PROX | 15.11 ± 0.53<br>14.1–16.2 | 21.9 | 21.1 |
| D-PROX | 11.71 ± 0.42<br>11.1–12.4 | – | – |
| W-DIST | 16.59 ± 0.57<br>15.6–17.6 | 33.0 | – |
| W-TRIII | 6.43 ± 0.21<br>6.0–6.7 | 9.6 | 9.2 |
| D-TRIII | 9.99 ± 0.32<br>9.4–10.6 | 15.2 | 13.5 |

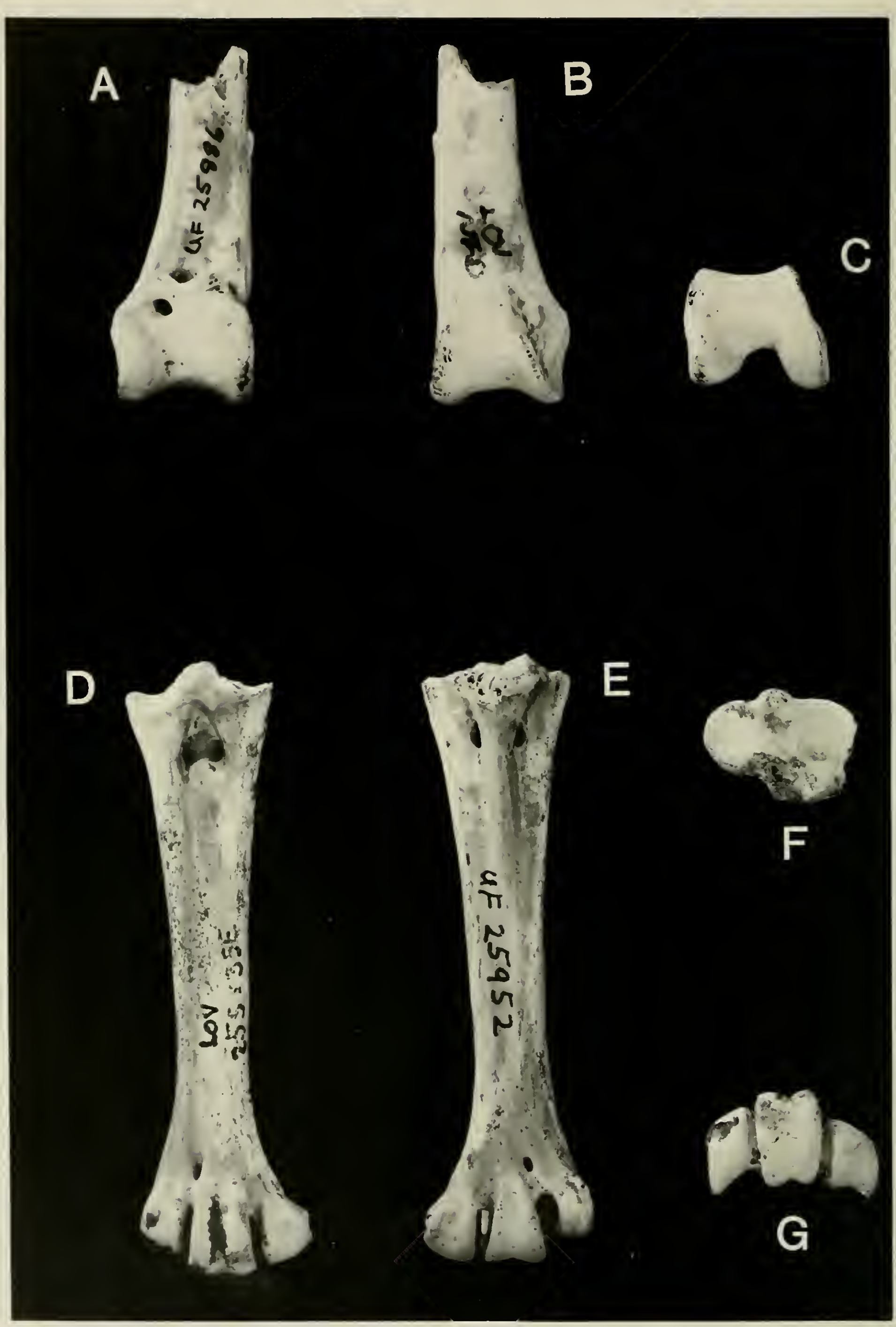

Fig. 1. Photographs of holotype and paratype of *Pliogyps charon,* new species. A–C, UF 25886, distal end of left tibiotarsus, paratype. D–G, UF 25952, right tarsometatarsus, holotype. A, D, Cranial (dorsal) view; B, E, Caudal (plantar) view; C, G, Distal end view; F, Proximal end view.

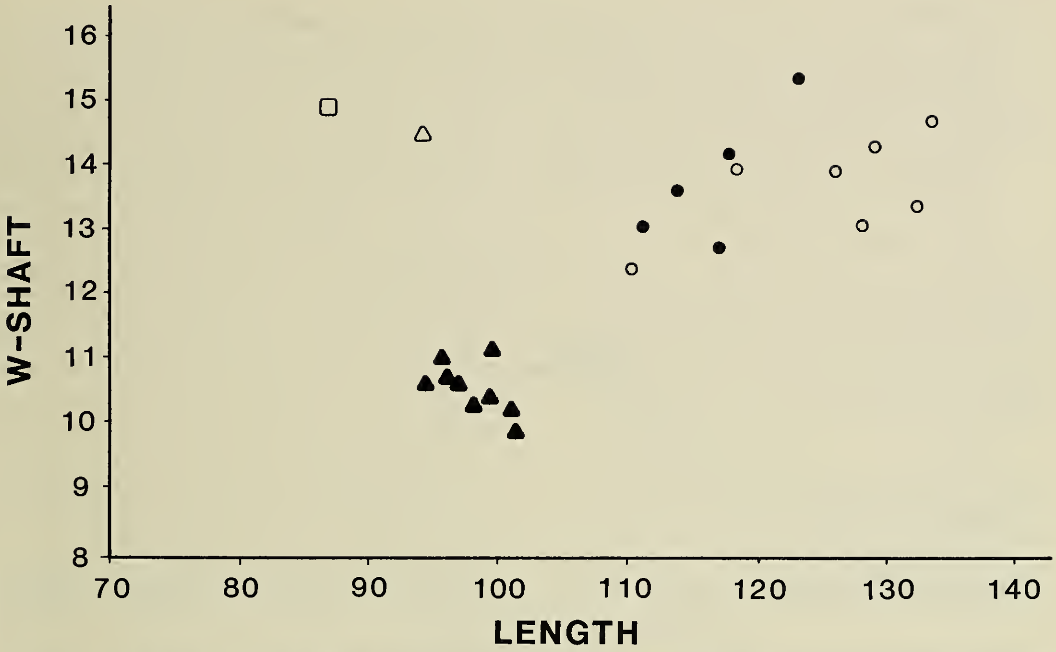

Fig. 2. Bivariate plot of greatest length from intercondylar eminence (Eminentia intercondylaris) through trochlea for digit III (Trochlea metatarsi III) (LENGTH) versus transverse width of shaft (W-SHAFT) of the tarsometatarsi of the following species of vultures: open square—*Pliogyps charon,* new species, open triangle—*Pliogyps fisheri,* solid triangles—*Sarcoramphus papa,* open circles—*Vultur gryphus,* solid circles—*Gymnogyps californianus.*

the attachment of M. tibialis cranialis is rounded and is in two parts. The sulcus extensoris, with a sharp lateral border, extends down the shaft to the distal foramen. A distinct intermuscular line extends obliquely through this sulcus (separating attachments for the extensor digitorum brevis pars hallucis and extensor digitorum brevis pars adductor-extensor digiti IV; Jollie 1977:43). In caudal view, the tarsometatarsus has a long ridge extending down the shaft from the hypotarsus. This ridge terminates in an intermuscular line that extends to the level of the articular facet of metatarsal I.

The distal end of tibiotarsus has a broad extensor sulcus. There is a slight projection of bone on the lateral surface of the distal end (approximately 4 cm from distal end) for attachment of the fibula. The intercondylar sulcus is broad, and the external condyle merges evenly into it. In distal end view, the intercondylar sulcus is asymmetrical, with the lateral border sloping gradually, and the medial border sloping abruptly, up from the base of the intercondylar sulcus (symmetrical or U-shaped in *Coragyps, Sarcoramphus, Breagyps, Gymnogyps*; asymmetrical in *Cathartes*). Measurements are given in Table 1. Humerus fragment tentatively referred.

*Discussion.*—There is a strong correlation between the cross-sectional area of the tibiotarsus of a given avian species and its live weight (Campbell and Tonni 1983, Prange et al. 1979). The following empirically derived regression equation,

$$\log Y = 2.54 \log X - 0.19906$$

where Y is the live body weight (gms) and X is the least shaft circumference of the tibiotarsus (mm), has a correlation coefficient of 0.986, showing that the predictions of the

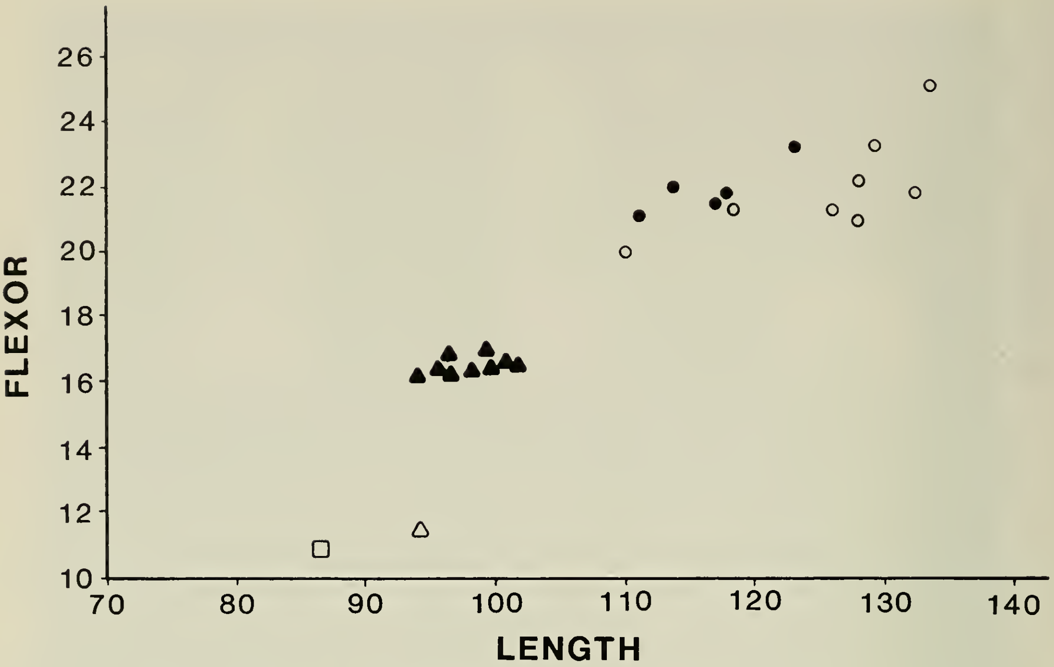

Fig. 3. Bivariate plot of greatest length (LENGTH) versus length from intercondylar eminence to middle of tubercle for tibialis anterior (Tuberositas m. tibialis cranialis) (FLEXOR) of tarsometatarsi of the following species of vulture: open square—*Pliogyps charon,* new species, open triangle—*Pliogyps fisheri,* solid triangles—*Sarcoramphus papa,* open circles—*Vultur gryphus,* solid circles—*Gymnogyps californianus.*

live weight should be very accurate. The least shaft circumference of the paratype of *Pliogyps charon* (UF 25886) measures 32 mm, yielding a predicted weight of 5.2 kg. *Sarcoramphus papa,* which has a similar tarsometatarsal length, weighs between 3.0 and 3.75 kg (5 individuals, Brown and Amadon 1968). This supports Tordoff's (1959:341ff) contention that *Pliogyps* is relatively a heavy-bodied, short-legged vulture.

Figures 2 and 3 show the length of the tarsometatarsus plotted against the width of the shaft and the flexor length. Species of *Pliogyps* have an average flexor length, but a very broad tarsometatarsus in comparison to its length. When considered in conjunction with the well-developed muscle attachments discussed above, a powerful pelvic limb is suggested. It is possible that *P. charon* was more rapacious than other living or fossil vultures, or that this powerful pelvic limb is merely a reflection of a heavy body. As additional fossil material of this species becomes available, these tentative suggestions should be examined further.

The intergeneric relationships of living and fossil vultures are difficult to determine, owing to a paucity of pre-Pleistocene fossil specimens and the conservative nature of the tarsometatarsus (the holotypical element in most fossil species). *Pliogyps* shares some tarsometatarsal characters with *Sarcoramphus* (anterior fossa continuing down shaft to the distal foramen, a similar size of the distal foramen and a similar shape of the hypotarsal ridge), but differs from *Sarcoramphus* in the degree of elevation of trochlea III (proximal border merging smoothly with shaft [plantar surface] in all modern skeletons of *Sarcoramphus* examined), and the amount of excavation of the lateral parahypotarsal sulcus. *Pliogyps* also shares the following characters with *Vultur* and *Gymnogyps*: the lateral side of the area proximal to trochlea IV is inclined and the excavation of the anterior fossa extends to the distal foramen (although to a lesser degree than in *Sarcoramphus*).

Mayr and Short (1970) proposed that *Pliogyps, Vultur,* and *Gymnogyps* should be viewed as congeneric. The proportions of the tarsometatarsus of both species of *Pliogyps* are quite distinct from all species of *Gymnogyps* and *Vultur.* Considering the conservative nature of the tarsometatarsus in this family, I would maintain *Pliogyps* as separate from all other large vultures.

It does appear possible though, that the large condors (species of *Vultur* and *Gymnogyps* and probably *Geranogyps* and *Breagyps*) are all part of one radiation that differ primarily in the degree of cranial specialization (*Vultur* being primitive; *Gymnogyps* and *Breagyps* more specialized, Jollie 1977: 110; *Geranogyps* unknown). Fisher (1944, 1946) discusses a number of characters of the skull and locomotor apparatus that unites the condors as a group separate from the more primitive genera *Cathartes* and *Coragyps.*

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# THREE NEW SPECIES OF WATER SCAVENGER BEETLES OF THE GENUS *CHAETARTHRIA* FROM SOUTH AMERICA (COLEOPTERA: HYDROPHILIDAE)

Paul J. Spangler

*Abstract.*—Three new species of water beetles, *Chaetarthria porknockeri* from Guyana, and *Chaetarthria ayacuchana* and *Chaetarthria gavilana* from Venezuela are described. Distinguishing characters for the three species are illustrated with pen and ink line drawings and their habitats are described. A key is provided to separate the new species from two previously described species.

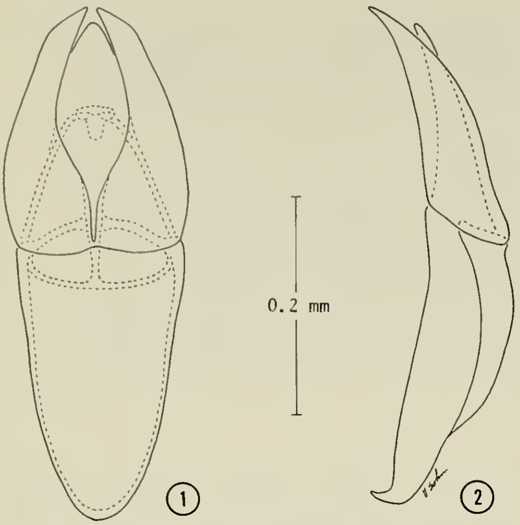
The species of *Chaetarthria* from the Western Hemisphere were revised by Miller in 1974; at that time 32 species and subspecies were known. Since Miller's revision was published three new species from Ecuador were described by Spangler (1977). During the past several years three additional new species have been collected from South America. One species was collected in December 1983 during an Earthwatch expedition to the Takutu Mountains of Guyana. A second species was collected at Puerto Ayacucho, Venezuela, in January 1985 while I participated in an expedition to the tepui Cerro de la Neblina, in southern Venezuela and the third species was collected near Puerto Ayacucho, Venezuela, in February 1986. With the description of these new taxa, 38 species are now known from the Western Hemisphere for the genus *Chaetarthria*. The three new species described below key to couplet 41 in Miller's key where *C. granulata* Miller and *C. brasilia* Miller are separated. The five species now keying to couplet 41 may be identified by using the key following the description of *C. gavilana*, new species.

### *Chaetarthria porknockeri*, new species
Figs. 1, 2

*Holotype male.*—Body form: Very convex, hemispherical. Length, 1.34 mm; greatest width, 1.1 mm, at about midlength.

*Color.*—Black dorsally except reddish brown around margins of pronotum and lateral margins of elytra. Ventral surface reddish brown with antennae and palpi light yellowish brown.

*Head.*—Punctures indistinct, extremely fine and sparse; punctures between eyes separated by 6 to 8 times their diameter; punctures slightly more dense along anterior margin of clypeus. Clypeus with lateral margins moderately arcuate and rimmed; anterior margin shallowly, broadly emarginate. Labrum more distinctly punctate than head, strongly rounded anteriorly. Eyes almost round viewed dorsally but oblong viewed ventrally; shallowly emarginate where clypeus extends into anterior margin of eye. Ventral surface of head microalutaceous behind eyes. Mentum smooth and shiny, strongly rounded apically. Submentum between maxillae microalutaceous. Antenna, 8 segmented; basal segment long, sinuous; second segment almost globular; third, fourth, and fifth segments slender, platelike; sixth, seventh, and eighth segments increasingly larger; sixth segment with few setae apically; seventh and eighth segments with long, rather dense setae; eighth segment ending in narrow apical projection. Maxillary palpus, 4 segmented; basal segment tiny; second (pseudobasal) segment almost as long as apical segment; third segment one-third as long as second segment;



Figs. 1 and 2. *Chaetarthria porknockeri,* n. sp.; male genitalia. 1, Dorsal view. 2, Lateral view.

apical segment longest; pseudobasal segment when lying along stipes not attaining base of stipes. Labial palpus, 3 segmented; basal segment very small; second segment longest and bearing 2 long, golden setae near apex; apical segment about one-fourth shorter than second segment and bearing 2 long, golden, hairlike setae dorsally just before apex.

*Thorax.*—Pronotum strongly convex; sides, posterolateral angles, and anterolateral angles moderately rounded; lateral margins finely rimmed; anterior margin arcuate medially and slightly angulate behind eyes; disc essentially impunctate, punctures indistinct, very fine and sparse. Scutellum an equilateral triangle. Elytron 1.0 mm long; strongly convex; widest near midlength; distinctly rimmed along base laterally; lateral margins finely rimmed, sinuate in lateral view; punctures on disc fine, indistinct, and sparse like those on pronotum, separated by 4 to 8 times their diameter; sutural stria extending and widening from slightly before midlength to apex; sides strongly declivous, without obvious epipleura. Metathoracic wings present. Prosternum, mesosternum, and metasternum glabrous and shiny except middle of metasternum with fine, sparse, seta-bearing punctures. Prosternum narrow in front of procoxae. Mesosternum with a small, transverse, carinate process between and slightly in front of mesocoxae. Metasternum with slightly raised discal area; sides shallowly depressed. Profemur and mesofemur with dense, hydrofuge pubescence on basal two-thirds; apices glabrous. Metafemur finely, sparsely punctate; without dense pubescence except marginally along anterior third. Protarsus, mesotarsus, and metatarsus with basal segment shortest; second segment of mesotarsus and metatarsus slightly longer than third and fourth segments combined; fifth segment slightly shorter than second segment. Metatrochanter moderately elongate and pubescent.

*Abdomen.*—First and second abdominal sterna with a common, deep concavity. First sternum shiny; with numerous, very long, golden, hairlike setae along anterior margin and extending posteriorly as far as third sternum and holding a hyaline mass in concavity. Midline feebly raised longitudinally on first and second sterna. Sterna 3, 4, and 5 covered with short, dense, golden setae; fifth sternum rounded, not emarginate apicomedially.

*Male genitalia.*—As illustrated (Figs. 1, 2).

*Female.*—Unknown.

*Type data.*—Holotype male: GUYANA: Mazaruni-Potaro District: Takutu Mountains, 6°15′N, 59°05′W, 18 Dec 1983, P. J. Spangler, M. Levine, E. Vystricil; deposited in the National Museum of Natural History, Smithsonian Institution. Paratype: Same data as holotype, 1 male.

*Etymology.*—On weekends, when guyanese gold miners would arrive in town late in the evening after stores were closed, the hungry miners would knock on the doors and demand to buy pork and other food. Sometimes, with their new-found wealth, they would buy the entire contents of the store. Consequently, those miners earned the name "pork-knockers." This new species is named for the friendly gold miners who were panning gold in the lower reaches of the stream from which we "mined" this and other new species of aquatic beetles.

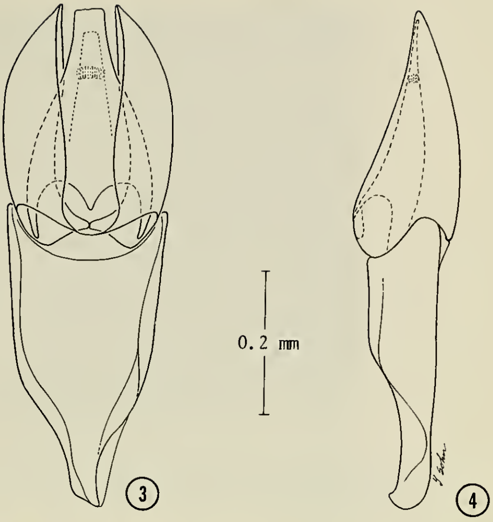
*Habitat.*—The specimens were obtained by placing leaves in berlese funnels and recovering the specimens from the berleseate. The wet, rotting leaves were collected from the margin of a small brook heavily shaded by the rainforest.

### *Chaetarthria ayacuchana,* new species
Figs. 3–5

*Holotype male.*—Body form: Very convex, hemispherical. Length, 1.24 mm; greatest width, 1.0 mm, at about midlength.

*Color.*—Black dorsally except reddish brown around margins of pronotum and lateral margins of elytra. Ventral surface of head dark reddish brown except antennae and palpi light yellowish brown; remainder of venter light reddish brown.

*Head.*—With moderately coarse, sparse punctures; punctures between eyes separated by 2 to 4 times their diameter; punctures slightly more dense along inner margin of each eye. Clypeus with lateral margins moderately arcuate and rimmed; anterior margin shallowly, broadly emarginate. Labrum more distinctly punctate than head and almost truncate anteriorly. Eyes almost round viewed dorsally but oblong viewed laterally; shallowly emarginate where clypeus extends into anterior margin of eye. Ventral surface of head microalutaceous behind eyes. Mentum smooth and shiny, strongly rounded apically. Submentum finely, sparsely punctate between maxillae. Antenna, 8 segmented; basal segment long, sinuous; second segment almost globular; third, fourth, and fifth segments slender, platelike; sixth, seventh, and eighth segments increasingly larger; sixth segment with few setae apically; seventh and eighth segments with long, rather dense setae; eighth segment ending in slender apical projection about one-sixth as long as swollen basal part. Maxillary palpus, 4 segmented; basal segment tiny; second (pseudobasal) segment swollen and almost as long as apical segment; third segment one-third as long as second segment; apical segment longest; pseudobasal segment when lying along stipes not attaining base of stipes. Labial palpus, 3 segmented; basal segment very small; second segment longest and bearing numerous, long, golden setae medially and 1 near apex laterally; apical segment about one-fourth shorter than second segment and bearing numerous, long, golden setae medially and 3 long, golden, hair-like setae dorsally just before apex.



Figs. 3 and 4. *Chaetarthria ayacuchana,* n. sp.; male genitalia. 3, Dorsal view. 4, Lateral view.

*Thorax.*—Pronotum strongly convex; sides, posterolateral angles, and anterolateral angles moderately rounded; lateral margins finely rimmed; anterior margin arcuate medially and slightly angulate behind eyes; punctures on disc moderately coarse, sparse, separated by 4 to 8 times their diameter. Scutellum an equilateral triangle. Elytron 0.97 mm long; strongly convex; widest near midlength; distinctly rimmed along base laterally; lateral margins finely

Fig. 5. *Chaetarthria ayacuchana,* n. sp.; biotope. "Tobogán" area, 40 km south of Puerto Ayacucho, T.F. Amazonas, Venezuela.

rimmed, slightly sinuate in lateral view; seta-bearing punctures on disc coarse, distinct, and rather dense and much more coarse and dense than those on pronotum, separated by 3 to 4 times their diameter; sutural stria deep, extending and widening from slightly before midlength to apex; sides strongly declivous, without obvious epipleura. Metathoracic wings present. Prosternum, mesosternum, and metasternum glabrous and shiny. Prosternum narrow in front of procoxae. Mesosternum with small, transverse, carinate process between and slightly in front of mesocoxae. Metasternum with slightly raised discal area; sides shallowly depressed. Procoxa with 5 very stout spines apicoventrally. Profemur with dense, hydrofuge pubescence on basal two-thirds; apices glabrous. Mesofemur with fine, sparse, seta-bearing punctures; punctures denser along anterior third. Metafemur with fine, sparse, seta-bearing punctures marginally along anterior third. Protarsus, mesotarsus, and metatarsus with basal segment shortest; second segment of mesotarsus and metatarsus slightly longer than third and fourth segments combined; fifth segment slightly shorter than second segment. Metatrochanter moderately elongate and sparsely pubescent.

*Abdomen.*—First and second abdominal sterna with a common, deep concavity. First sternum shiny; with numerous, very long, golden, hairlike setae along anterior margin and extending posteriorly as far as third sternum and holding a hyaline mass in concavity. Midline feebly raised longitudinally on first and second sterna. Sterna 3, 4, and 5 covered with short, sparse, golden setae; fifth sternum rounded, not emarginate apicomedially.

*Male genitalia.*—As illustrated (Figs. 3, 4).

*Female.*—Similar to male except length of female is greater.

*Type data.*—Holotype: VENEZUELA: Territorio Federal Amazonas: Puerto Ayacucho (40 km S) at "Tobogán," 22 Jan 1985, P. J. and P. M. Spangler, R. A. Faitoute, W. E. Steiner; deposited in the National Museum of Natural History, Smithsonian Institution. Allotype: Same data as holotype. Paratypes: Same data as holotype, 3 males, 4 females; same locality, 25 Feb 1986, P. J.

Spangler, 1 male; same locality, 27 Feb 1986, P. J. Spangler, 1 male. Paratypes deposited in the Instituto de Zoologia Agricola, Facultad de Agronomia, Maracay, Venezuela, and the British Museum (Natural History), London.

*Etymology.*—The trivial epithet *ayacuchana* (adjective) is named for the town near which this new species was collected.

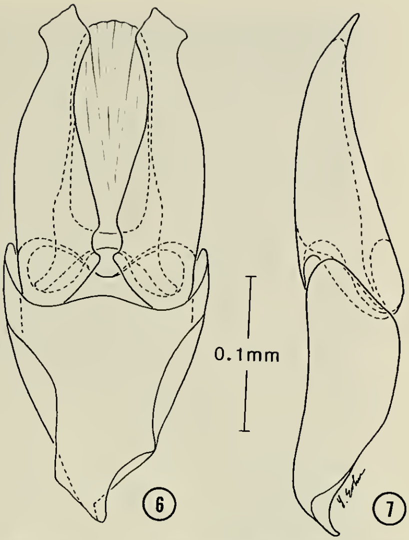
*Habitat.*—Enroute to Cerro de la Neblina, the participants in the expedition had to layover in Puerto Ayacucho for two days awaiting air transportation. During that time we visited an interesting area about 40 km south of Puerto Ayacucho known locally as the "Tobogán"; so named because water running over an extensive area of bedrock had polished the rock and formed a slide-like channel on one side of the outcropping. The water dropped into a pool at the base of the slide area and drained away in a shallow stream with a sandy substratum. Collections of aquatic insects were made from the stream and its sandy margins. The type specimens of *C. ayacuchana* were collected from the sandy margins in the sunny part of the stream before it entered the shade of the forest (Fig. 5). Colorimetric water chemistry tests provided the following data: Oxygen, 15 ppm; pH, 6; hardness, 0. The water temperature was 28°C and the air temperature was 37°C at the time the data were collected.

### *Chaetarthria gavilana*, new species
Figs. 6–8

*Holotype male.*—Body form: Very convex, hemispherical. Length, 1.54 mm; greatest width, 1.04 mm, at about midlength.

*Color.*—Black dorsally except reddish brown around margins of pronotum. Ventral surface of head, thorax, abdomen and appendages reddish brown.

*Head.*—With moderately coarse, sparse punctures; punctures between eyes separated by 4 to 6 times their diameter; slightly alutaceous along inner margin of each eye. Clypeus with lateral margins moderately arcuate and rimmed; anterior margin shallowly, broadly emarginate. Labrum more distinctly punctate than head; almost truncate; with short, dense fringe of setae anteromedially. Eyes almost round viewed dorsally but oblong viewed laterally; shallowly emarginate where clypeus extends into anterior margin of eye. Ventral surface of head microalutaceous behind eyes. Mentum and submentum finely, sparsely punctate between maxillae. Antenna, 8 segmented; basal segment long, sinuous; second segment almost globular; third, fourth, and fifth segments slender, platelike; sixth, seventh, and eighth segments increasingly larger; sixth segment with few setae apicolaterally; seventh and eighth segments with long, rather dense setae; eighth segment ending in narrow elongate apical projection longer than swollen basal part. Maxillary palpus, 4 segmented; basal segment tiny; second (pseudobasal) segment swollen apically and almost as long as apical segment; third segment slightly more than half as long as second segment; apical segment about a sixth long-



Figs. 6 and 7. *Chaetarthria gavilana*, n. sp.; male genitalia. 6, Dorsal view. 7, Lateral view.

Fig. 8. *Chaetarthria gavilana,* n. sp.; biotope. Caño near the village of Gavilán, 35 km southeast of Puerto Ayacucho, T.F. Amazonas, Venezuela.

er than second segment; pseudobasal segment when lying along stipes not attaining base of stipes. Labial palpus, 3 segmented; basal segment very small; second segment longest; both basal and second segments bearing numerous, long, golden setae especially on medial and lateral surfaces; apical segment about one-fourth shorter than second segment and bearing several, long, golden setae subapically and 3 long, golden, hairlike setae dorsally on apex.

*Thorax.*—Pronotum strongly convex; sides, posterolateral angles, and anterolateral angles moderately rounded; lateral margins finely rimmed; anterior margin arcuate medially and angulate behind eyes; punctures on disc moderately coarse, sparse, separated by 4 to 8 times their diameter. Scutellum an equilateral triangle; very finely and sparsely punctate. Elytron 1.15 mm long; strongly convex; widest near midlength; distinctly rimmed along base laterally; lateral margins finely rimmed, slightly sinuate in lateral view; seta-bearing punctures on disc coarse, distinct, and rather dense and much more coarse and dense than those on pronotum, separated by 3 to 4 times their diameter; punctures on sides of elytra very coarse; sutural stria deep, extending and widening from slightly before midlength to apex; sides strongly declivous, without obvious epipleura. Metathoracic wings present. Prosternum, mesosternum, and metasternum mostly glabrous and shiny; metasternal disc with sparse, fine punctures. Prosternum narrow in front of procoxae. Mesosternum with small, transverse, carinate process between and slightly in front of mesocoxae. Metasternum with slightly raised discal area; sides shallowly depressed. Procoxa with 3 very stout spines apicoventrally. Profemur and mesofemur with dense, hydrofuge pubescence on basal two-thirds; apices glabrous. Metafemur with fine, sparse, seta-bearing punctures marginally along anterior third. Protarsus, mesotarsus, and metatarsus with basal segment shortest; second segment of mesotarsus and metatarsus slightly longer than third and fourth segments combined; fifth segment slightly shorter than second segment. Metatrochanter moderately elongate and sparsely pubescent.

*Abdomen.*—First and second abdominal sterna with a common, deep concavity. First sternum shiny; with numerous, very long, golden, hairlike setae along anterior margin and extending posteriorly as far as third sternum and holding a hyaline mass in concavity. Midline feebly raised longitudinally on first and second sterna. Sterna 3, 4, and 5 covered with short, sparse, golden setae; fifth sternum rounded, not emarginate apicomedially.

*Male genitalia.*—As illustrated (Figs. 6, 7).

*Female.*—Unknown.

*Type data.*—Holotype: VENEZUELA: Territorio Federal Amazonas: Puerto Ayacucho (35 km SE), Gavilán area, 20 Feb 1986, P. J. Spangler and W. Sanchez; deposited in the National Museum of Natural History, Smithsonian Institution.

*Etymology.*—The trivial epithet *gavilana* (adjective) is named for the Indian village and river of the same name near which this new species was collected.

*Habitat.*—The specimen described above was collected from the sandy margins of an unnamed caño 2 km west of the village of Gavilán (35 km southeast of Puerto Ayacucho). The caño (Fig. 8) was about 0.5 m deep and 1 m wide. Colorimetric water chemistry tests provided the following data: Oxygen, 12 ppm; pH, 6; hardness, 0. The water temperature was 27°C and the air temperature was 37°C at the time the data were collected.

The following key should serve to distinguish the five species which key to couplet 41 in Miller's (1974) key.

1. Head, pronotum, and elytra shiny; punctures indistinct, extremely fine and sparse. Male genitalia as illustrated (Figs. 1, 2). Guyana ....... ............ *porknockeri,* new species
– Head, pronotum, and elytra distinctly punctate .................. 2
2. Elytra with moderately coarse, moderately sparse, seta-bearing punctures on discal area; lateral punctures very coarse and dense, especially at midlength; setae arranged in widely separated rows. Male genitalia as illustrated (Figs. 6, 7). Venezuela .. *gavilana,* new species
– Elytra with fine or moderately coarse and moderately sparse, seta-bearing punctures on discal area; lateral punctures moderately coarse at midlength; setae in narrowly separated rows or scattered over surface ............................... 3
3. Elytra with rows of moderately coarse, dense, seta-bearing punctures over entire surface; setae very dense; rows of punctures becoming substriate toward apex. Brazil .... .................... *granulata* Miller
– Elytra with fine or moderately coarse punctures in indistinct rows or scattered over surface; without indications of any striae except sutural stria ............................... 4
4. Elytra with discal area finely, sparsely punctate; moderately coarsely punctate laterally and toward apex. Brazil ................ *brasilia* Miller
– Elytra with discal area moderately coarsely, sparsely punctate; punctures becoming coarse laterally and toward apex. Male genitalia as illustrated (Figs. 3, 4). Venezuela .. ............ *ayacuchana,* new species

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# ANALYSIS OF STONE CRABS: *MENIPPE MERCENARIA* (SAY), RESTRICTED, AND A PREVIOUSLY UNRECOGNIZED SPECIES DESCRIBED (DECAPODA: XANTHIDAE)

Austin B. Williams and Darryl L. Felder[1]

*Abstract.*—The stone crab, *Menippe mercenaria* (Say, 1818) sensu lato, in the Caribbean and Carolinian Provinces of the western North Atlantic, is divisible into two morphologically distinct populations with almost separate, narrowly overlapping geographic ranges. These populations are here recognized as distinct species. The species differ in color, carapace morphometry, and stridulatory patches on chelae of the chelipeds. Five measured factors subjected to discriminant function analysis give good separation of the species at $P < 0.05$ for all specimens measured, and at $P < 0.01$ for specimens more than 15 mm in carapace length. *Menippe mercenaria,* restricted, ranges from Cape Lookout, North Carolina, through peninsular Florida, the Bahamas and Greater Antilles, to Yucatan peninsula, Mexico, and Belize. *Menippe adina,* new species, ranges from northwestern Florida around the Gulf of Mexico to Tamaulipas State, Mexico. The two species hybridize in the Apalachee Bay region of northwestern Florida.

Recent field studies in the Gulf of Mexico indicate that stone crabs assignable to *Menippe mercenaria* (Say, 1818), sensu lato, from the northwestern Gulf differ in color and morphometry from those found in peninsular Florida, and furthermore, that individuals exhibiting characters intermediate between these groups can be observed in the Apalachee Bay region of northwestern Florida. Questions arise from these recent surveys concerning variation over the range as a whole, i.e., whether the preliminary observations in the Gulf of Mexico were comprehensive enough to have validity, and whether still other populations within the range may exhibit character states with sufficient cohesion to be recognized as taxonomically distinct.

The chelipeds (claws) of this large crab are prized as a delicacy throughout a geographic range that extends through the Caribbean and Carolinian Provinces of the western North Atlantic Ocean from Cape Lookout, North Carolina, southward around peninsular Florida, through the Bahamas and Greater Antilles, to the Yucatan peninsula and Belize, and around the northern and western margin of the Gulf of Mexico to Tamaulipas State, Mexico, from intertidal burrows, crevices and pools, to a depth of 51 m (Williams 1984, in part). Through most of that range, the crabs are incidentally taken for human consumption as a byproduct of other fisheries, but along western and especially southwestern Florida, they are the basis for a seasonal commercial fishery (Costello et al. 1979). Since Florida recordkeeping began in 1962–63, the fishery grew to a peak annual landing of 2.6 million lb of claws during the 1981–82 season, and thereafter declined somewhat (preliminary estimate by National Marine Fisheries Service, Southeast Fisheries Center, 1.7 million

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[1] Order of authorship was decided by flip of a coin.

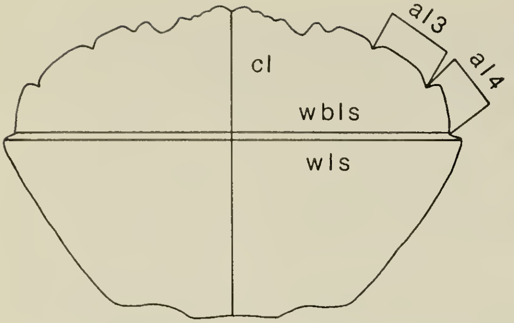

Fig. 1. Diagram of *Menippe mercenaria* (from Rathbun, 1884) showing carapace dimensions measured in mm: cl = carapace length in midline; wbls = width to base of lateral spine, wls = width between tips of lateral spines (wls − wbls = length of al5); al3 = width of anterolateral tooth 3, al4 = width of anterolateral tooth 4.

Fig. 2. Diagram showing inner surface of major chela bearing stridulatory patch, ♂ from USNM 7509, Key West, Florida.

lb for 1984–85). There is a sizeable fishery in Cuba as well where the crab is known as cangrejo moro (dappled crab).

Interrelationships of populations of these crabs seem important from standpoints of both biology and fisheries, and it is therefore the purpose of this paper to analyze the population structure from a systematic point of view. We have attempted to accomplish this by studying color and morphometry over selected parts of the range. Evaluation of these analyses demonstrates that two populations of the crabs can be distinguished. We interpret these populations to be two closely related species which hybridize in the panhandle region of northwestern Florida, and we give diagnostic characters for each in comparative tables, graphs, illustrations, and discussion.

## Materials and Methods

General observations of color over the entire geographic range of the species were accomplished by DLF, recorded photographically, and comparatively analyzed. Color pattern on the dactyl of the major chela was studied on specimens in the field, in museum collections, and on photographs by both of us. Measurements (Fig. 1) to the nearest 0.1 mm were recorded for carapace length in the midline, carapace width to the base of the notch between the 4th and 5th anterolateral teeth, carapace width including the 5th anterolateral tooth, and widths of the 3rd and 4th anterolateral teeth. Measurements of specimens from the northern Gulf of Mexico taken by DLF and of specimens in the crustacean collection of the National Museum of Natural History (USNM) taken by ABW were combined with a comparable data set from Charleston, South Carolina, plus a few measurements from specimens in other museums, photographs, and illustrations in literature, for combined statistical analysis. Density of parallel striae/mm in the stridulation patch on the inner surface of the major chela, and the maximum height of that chela, were recorded for representative populations by DLF (Fig. 2).

Statistical tests were performed on the Honeywell computer of the Smithsonian In-

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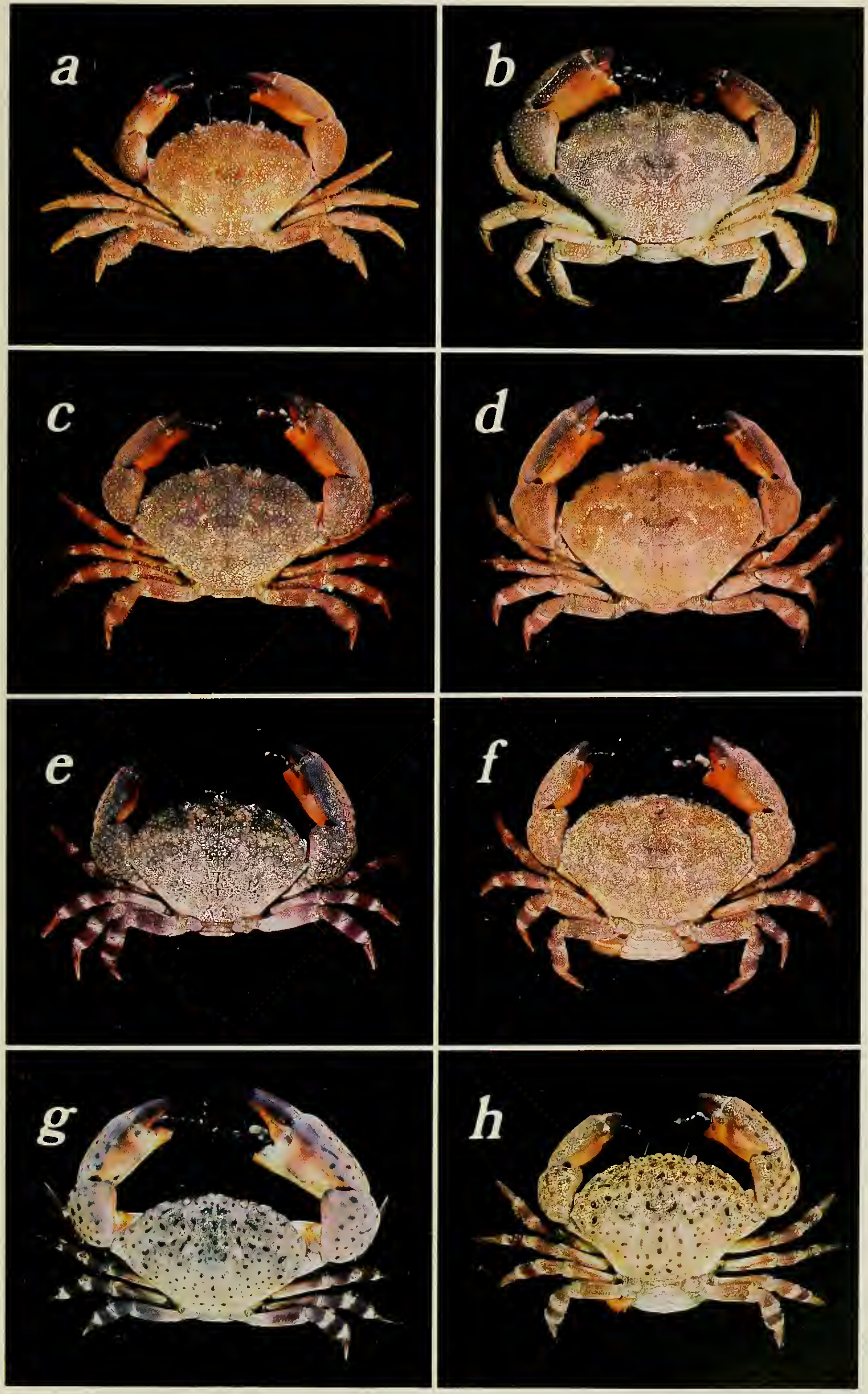
Fig. 3. *Menippe adina*. Louisiana.— a, ♂ cw 61.7 mm, Bayou Fourchon, Fourchon Parish; b, ♀ unmeasured, Cameron, Cameron Parish *M. adina* × *M. mercenaria*.—Florida: c, ♂ cw 92.2 mm, e, ♂ cw 64.6 mm, Wakulla Beach, Wakulla County; d, ♀ 102.7 mm, f, ♀ (ovig.) cw 86.8 mm, Turkey Point, Franklin County. *M. mercenaria*.—Florida: g, ♂ cw 99.4 mm, h, ♀ (ovig.) 92.6 mm, Turkey Point, Franklin County.


a
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stitution, using the SPSSx data analysis system. A stepwise discriminant analysis of morphological variables was used in an attempt to separate hypothesized populations. The analysis included up to five morphological variables, each of which was a ratio (R1–R5) determined as follows (see Figs. 1 and 2):

R1—AL3/AL4
R2—AL4/CL
R3—WLS − WBLS/CL; WLS − WBLS = length AL5 in Fig. 6C.
R4—WBLS/CL
R5—ln (no. striae per mm in stridulation patch/maximum height of chela); data for this ratio were log transformed because of strong curvilinear relationships.

Most specimens were assigned to either of two groups a priori on the basis of geographical distribution: Group 1, a warm temperate to tropical group ranging from North Carolina to Florida, Cuba, Yucatan-Belize, Saint Thomas, and perhaps Jamaica (*M. mercenaria*); Group 2, a northern Gulf of Mexico group ranging from extreme western Florida through the northwestern Gulf to northern Mexico (*M. adina*). The validity of these group assignments was investigated with discriminant analysis. The significance criterion used in this analysis was the overall multivariate F ratio for differences among group centroids. Morphological variables were selected stepwise for entry into the analysis on the basis of their partial F values. Unassigned specimens from two samples of questionable affinity (northwest Florida and Charleston, South Carolina) were independently entered into a classification analysis in order to determine their relationship to a priori groups on the basis of morphology. Most of the data set for the Charleston locality was limited to individuals larger than 15 mm carapace length and did not include counts of stridulatory ridges, so smaller individuals and R5 data were excluded from comparative analysis of that sample.

Coloration was not included in the discriminant analysis, although it was scoreable for all fresh and most preserved specimens. Within the sample from northwest Florida, specimens were scored as color morph a—legs not banded, carapace without dark spots (typical of *M. adina*), b—legs banded, carapace without dark spots or with weak spots (intermediate), or c—legs distinctly banded, carapace with distinct dark spots (typical of *M. mercenaria*). Means and deviations of the morphometrically determined discriminant scores were calculated independently for each of these color morphs in order to compare trends in color with those in morphometry.

*Specimens examined.*—1 ♂, 1 ♀ from the Academy of Natural Sciences of Philadelphia (ANSP). 113 ♂, 127 ♀, 194 juv, from the National Museum of Natural History (USNM) are represented in the following list by catalog numbers without alphabetical prefix; those recorded by catalog number only are listed in Rathbun (1930:475–477). 114 ♂, 134 ♀ from cataloged lots in the University of Southwestern Louisiana Museum collection are listed with the alphabetical prefix USLZ. 2 ♂, 3 ♀ from the Florida Department of Natural Resources are listed with the alphabetical prefix FDNR.

Specimens or photographs of 20 ♂, 53 ♀ from other sources are appropriately indicated.

*Synonymy.*—The synonymies that follow are selective in that no attempt has been made to search for all references to *M. mercenaria* in textbooks, technical reports, popular works, and encyclopedias. Many such references are included in the primary sources cited.

### *Menippe mercenaria* (Say), restricted
Figs. 1, 2, 3g–h, 4a–c

*Cancer mercenaria* Say, 1818:448.
*Xanthe mercenaria.*—H. Milne Edwards, 1834:399 (generic transfer).

*Pseudocarcinus ocellatus* H. Milne Edwards, 1834:409 (type locality unknown, type in Paris Museum).

*Xantho mercenaria.*—DeKay, 1844:4 (color, size, from South Carolina).

*Pseudocarcinus mercenarius.*—Gibbes, 1850:176 [12].

*Menippe mercenarius.*—R. Rathbun, 1884: 772–774, pl. 264 (part, North Carolina-Florida); 1887:650–651 (part, North Carolina-Florida); 1893:772–774, pl. 264 (part, North Carolina-Florida).

*Menippe mercenaria.*—Stimpson, 1859:53–54 [7–8] (comparison with *M. nodifrons* and *M. obtusa*).—Coues, 1871:120 (North Carolina).—Kingsley, 1878:318 (part, North Carolina-Florida, not Panama).—A. Milne Edwards, 1879:262, pl. 47 (colored); pl. 48, fig. 32.—Enders, 1905:37 (in *Chaetopterus* tube).—Binford, 1913:147–202, pls. 1–9 (gametogenesis, mating).—Pearse, 1913:102–103 (North Carolina); 1929:231–233 (ecology).—Hay and Shore, 1918:439, pl. 35, fig. 8 (description, distribution).—Schroeder, 1924:49–50, fig. 23 (part, North Carolina-Yucatan).—Hyman, 1925:14, pl. 13, figs. 163–170 (larvae).—Rathbun, 1930:472, text-fig. 78, pls. 191–193 (description, distribution); 1935:117 (Pleistocene fossil).—Lunz, 1937:11, 21 (South Carolina).—Ayers, 1938:523–537 (oxygen consumption).—Chace, 1940:38 (Cuba).—Miner, 1950: 522, pl. 167, unnumbered fig. (color description).—Siebenaler, 1952:99 ("trash" in trawls).—Stephenson and Stephenson, 1952:36 (in Carolinian region).—Menzel, 1956:80 (part, Apalachee Bay, Fla.).—Springer and Bullis, 1956:19 (part, sta 933 off W Florida).—Vernberg, 1956:227–ff. (oxygen consumption of tissues).—Gray, 1957:35–ff. (gill area).—Costlow and Bookhout, 1960:212 (method for hatching eggs).—Guinot-Dumortier and Dumortier, 1960:129–130, fig. 10 (stridulation structures).—Porter, 1960:168–ff., figs. 1–3 (larval development).—Manning, 1961:273–ff. (growth stages).—Tabb and Manning, 1961:600 (S Florida); 1962: 44–46, 48, 61 (S Florida).—Rees, 1963: 6, fig. 8 (general notes).—Dragovich and Kelly, 1964:83 (Tampa Bay).—Bullis and Thompson, 1965:12 (part, off SE Florida, Tampa Bay, and Golfo de Campeche).—Clark, 1965:52–54 (on turtle).—Gunter and Hall, 1965:64, 67 (SW Florida).—Williams, 1965:183, figs. 164D, E; 166 (part, not NW Gulf of Mexico).—Futch, 1966:1–6, figs. 1–3, 6 (part, not NW Florida).—Karandieva and Silva Lee, 1966: 5–19 (respiration & osmoregulation, Cuba); also translation 1973:292–310.—Sushchenya and Claro, 1966:217–230 (metabolism); also translation 1973:311–335.—Sushchenya and Claro Madruga, 1967:75–97 (energetics).—Bliss, 1968:369 (water loss in air).—Cheung, 1968:117–120, 1 pl. (sperm retention).—Savage and McMahan, 1968:1–17, figs. 9–11 (juvenile growth).—Cheung, 1969:327–346 (growth & reproduction in Florida).—Hartnoll, 1969:162–ff. (mating).—Herreid, 1969:831, ff. (water loss); 1969a:424–428 (integument permeability).—Suárez Alvarez and Xiqués Diaz, 1969:155 (physiology of feeding).—Ong and Costlow, 1970:17–29 (larval development).—Hudson et al., 1970:9 (list, Florida Bay).—Kurata, 1970:209–212, pls. 73–74 (development).—Rouse, 1970:144 (S Florida).—Bender, 1971:11 (abstract, oxygen consumption, juveniles).—Dudley and Judy, 1971:3–ff. (planktonic larvae).—Lyons et al., 1971:34 (Florida).—Savage, 1971:315–316, pl. 1 (mating); 1971a:1–19, fig. 3 (rearing experiments).—Suárez Alvarez and Xiqués Diaz, 1971:279–281 (physiology).—Bardach et al., 1972:672 (short review, culture).—Yang, 1971:53–54 (larval culture methods).—Bookhout and Costlow, 1972:1–13 (pollutant effect, larval development).—Bookhout et al., 1972:166–ff. (pesticide & larvae).—Stewart, 1972:173–178 (thermal effluent, mariculture).—Yang, 1972:183–184 (reproduction in Florida, general).—Cheung, 1973:1–11 (regeneration).—Collard and D'Asaro, 1973:fig. III G3 (part), fig. III G4, G7 (part) (habitats in eastern Gulf of Mexico).—Eguchi and Waterman, 1973: 146, 154 (retinular cell, comparison).—Leffler, 1973:1047, ff. (metabolic rate & body size).—Sushchenya and Claro, 1973: 311–335 (energy & growth).—Bland and Amerson, 1974:232–235 (experimental egg infection).—Bookhout and Costlow, 1974:77–87 (sublethal effects, mirex, larvae).—Duke and Dumas, 1974:152 (pesticide effect, larvae, review).—Grizzle, 1974:136 (Florida).—Mootz and Epifanio, 1974:44–55 (larval energy budget).—Payen, 1974:214–225, figs. 2, 4c (sexual morphogenesis in megalopa).—Sandifer et al., 1974:55–59 (aquaculture contaminants).—Savage et al., 1974:1–5, figs. 1–5 (molting).—Zeiller, 1974:94 (color photo).—Perry, 1975:55 (occurrence in *Callinectes* fishery).—Savage et al., 1975:1–37 (Florida fishery).—Cheung, 1976:138–144 (claw regeneration, functional change).—Gore et al., 1976:286 (Florida).—Iversen and Beardsley, 1976:195–196 (shell disease).—Miller, 1976:630 (Florida fishery).—Yang and Krantz, 1976:1–15 (culture manual).—Costlow, 1977:452–453 (pesticide & larvae).—Forward, 1977:331–341 (shadow response, larvae).—Kinne, 1977:839–840, 874, 876 (larval culture).—Livingston et al., 1977:90, Table 3 (part, Apalachicola Bay, Fla.).—Sinclair, 1977:193–207 (agonistic behavior).—Warner, 1977:174 (claws & trap fishery). Bert et al., 1978: 1–82 (biology).—Gore et al., 1978:225–ff. (reefs, SE Florida).—Savage and Sullivan, 1978:1–23 (growth & claw regeneration).—Tucker, 1978:169–172 (amino-acids, larvae).—Whetstone and Eversole, 1978:42–48 (predation on hard clams).—Young, 1978:182 (South Carolina).—Brown et al., 1979:143–159 (biomechanics, chelipeds).—Costello et al., 1979:19450–19496 (comprehensive review, part, from Cedar Key, Fla. S), fig. 1.—Costlow, 1979:356–357, 360–361 (pesticide & larvae).—Pérez Pérez and Ros, 1979:1–33 (regional Cuban fishery).—Roberts et al., 1979:419–430 (dinoflagellate toxic effects).—Schlieder, 1980:695–700 (desiccation, autospasy & egg production).—Sullivan, 1979:1–37 (population in SW Florida).—Williams and Duke, 1979:173, 183–185 (part, life history & ecology), 194, 200, 203, 205 (review pesticide effects).—Barnes, 1980: 728, fig. 14–55I (photo).—Davis et al., 1980:1–23 (mortality, declawing).—Factor, 1980:843 (larval development, mandibles & gastric mill).—Goy and Costlow, 1980:888 (larval nutrition).—McConaugha et al., 1980:544–547 (winter induced mating).—Ros and Suárez, 1980: 5–17 (epibiosis).—Ros et al., 1980:175–196 (polychromatism).—Ros Pichss et al., 1980:71 (reproduction, abstract).—Ros Pichss et al., 1980:72 (ovulation cycles, abstract).—Simonson and Steele, 1980:6 (abstract).—Sulkin and Van Heukelem, 1980:91–96 (larval diet).—Zuboy and Snell, 1980:1–32 (Florida fishery assessment).—Anger et al., 1981:199–212 (starvation, zoeae).—Anger et al., 1981a:518–525 (starvation resistance, zoeae).—Brine and Austin, 1981:283–286 (chitin variability).—Brine and Austin, 1981a:173–178 (chitin isolates).—Factor, 1981:253–258 (basement membrane, mid-gut); 1981a:1002 (basement membrane, midgut).—Meinroth, 1981:647 (part, not color pl. 642, N. America).—Pérez and Briquets, 1981:30–43 (size-class sampling methods).—Ros and Quiñones, 1981:92–102 (teratology).—Ros et al., 1981:1–29 (ovulation cycles).—Ros et al., 1981:73–91 (fecundity).—Simonson and Steele, 1981:21–28, figs. 1–5 (claw asymmetry, reversal & regeneration).—Factor, 1982: 299–312 (development & metamorphosis feeding apparatus).—Lee et al., 1982: 145–159 (oxygenase system).—Ortiz and

Pol Paredes, 1982:39–59 (symbionts & food).—Ramos Trujillo, 1982:97–115 (organic reserve in muscle).—Ros and Quiñones, 1982:17–24 (lipids in tissues).—Telford, 1982:166, fig. 5 (list, coral reef fauna).—Zuboy and Snell, 1982: 1–21 (Florida fishery assessment).—Wenner and Stokes, 1983:1–28 (experimental fishery, chela size & regeneration).—Lindberg and Marshall, 1984:1–18 (part, peninsular Florida population).—Roer and Dillaman, 1984:900, ff., pl. 2, figs. 9–12, pl. 3, figs. 15–20 (SEM views, cuticle).—Williams, 1984:420 (part, not NW Gulf of Mexico).—Felder et al., 1985:199 (color during development).—Simonson, 1985:281–293, figs. 1–2 (regeneration).—Bert et al., 1986:1–77 (South Florida population dynamics).—Salmon et al., 1986:29, Table 2 (hatching rhythms).

*Menippe rumphii.*—Stimpson, 1871:106 [6] (Florida, striations on inner palm). [Not *M. rumphii.*]

*Menippe ocellata.*—von Martens, 1872:87.

*Menipe ocellata.*—Gundlach and Torralbas, 1900:368 (not fig. G).—Gundlach et al., 1917:563 [23] (not fig. 15) (Cuba).

*Material.*—North Carolina: 17527, 62527.

South Carolina: 2089, 17170, 32250, 17171, 4906, 26144, 18195.—228714. 2 ♂, 1 ♀; Folly River, Charleston, M. Caldwell, 5–6 Apr 1986, 18.8–18.9° C, 30‰.—Uncataloged measured specimens from Charleston, 19 ♂, 51 ♀.

Georgia: 19474.—170782. 1 ♀; Sapelo Sound, M. Gray, 13 Dec 1962.—170784. 2 ♂, 1 ♀; same, 26 Jan 1962.—170783. 1 ♂, 3 ♀; Raccoon Bluff, M. Gray, 18 Feb 1961.

Florida: 56829, 20097, 2094, 20095, 42129, 53754, 6370, 8964, 18520, 7509 (6 ♂, 4 ♀ in 1985), 20096, 33463, 57007, 15101, 53756, 6948, 14988, 6439, 50465, 56359, 25607, 25608, 14995, 2017, 14991, 6432, 56830, 14989, 14997, 53757, 26145, 26146, 14992, 57843, 14994, 6409, 60973, 53755.—75792. 1 juv; Fernandina, rocks on jetty at Cumberland Sound, A. Pizzini, 13 Jul 1934.—170004. 1 ♂, 1 juv; Indian River County, Sebastian Inlet on intertidal sabellariid reef S side inlet bridge, R. H. Gore, 1 Nov 1974.—170005. 1 ♂; same, 15 Jul 1974.—170006. 1 ♂, 1 ♀, 1 juv; same, 9 Dec 1974.—170007. 1 ♀ (ovig.), 1 juv; St. Lucie County, Ft. Pierce Inlet intertidal sabellariid reef, R. H. Gore, 19 Aug 1974.—228511. 1 ♂; Biscayne Bay, Key Biscayne, SW Point flats, 25°41′18″N, 80°10′48″W, 2 ft, C. A. Child, summer 1962.—75785. 1 ♂ juv; Key West, W. C. Schroeder, 12 Nov 1919.—75786. 1 ♂, 2 juv; Key West, W. K. Butts, 28 Aug–4 Sep 1919.—75788. 1 ♂ juv; Key West in sponge, D.R.C. from USBF.—75796. 1 ♂, 1 ♀; Key West from USBF.—15570. 1 ♂; Lee County, Sanibel Island, N end beach, R. B. Manning, 3 Apr 1972.—97501. 1 ♂, Gulf of Mexico, 27°36′N, 83°18′W, 20 fm, *Oregon* sta 933, S. Springer, 18 Mar 1954.—101478. 1 ♂ juv; Gulf of Mexico, 27°30′N, 82°46′W, 3 fm, *Silver Bay* sta 59, 17 Jul 1957.—101479. 1 juv; Gulf of Mexico, 27°11′N, 82°33′W, 3 fm, *Silver Bay* sta 60, 17 Jul 1957.—72854. 9 juv (one soft shell); Lemon Bay, Englewood, S. Springer, Bass Biol. Lab., 2 Feb 1936.—75791. 1 juv; shore Sarasota Bay, W. W. Wallis, summer 1930.—FDNR, I-7654. 1 ♂, 2 ♀; Citrus County off Crystal River.—FDNR, I-7695. 1 ♂, 1 ♀; same.—99861. 1 ♂, Cedar Key, main channel, D. K. Caldwell, 23 Feb 1955.

Bahamas: 88662. 2 ♂, Bimini, A. S. Pearse, 10 Nov 1948.

Cuba: 61114.—47901. 1 ♀; Los Arroyos, Thos. Barreras, May 1914.—216981, 1 ♀; near Varadaro Beach, SE Hicacos Peninsula at 2 km marker, R. B. Manning et al., 2 Mar 1978.—216982. 3 ♀; E of Batabano, S shore, 4–5 m, R. B. Manning et al., 3 Mar 1978.—Museum of Comparative Zoology, Harvard University 10916. 1 ♀; Cienfuegos, off dock in fish trap, 30 Mar 1939.—Photographs of *M. ocellata* ♂ collected by M. Gundlach, Muséum National d'Histoire Naturelle, Paris.

St. Thomas, Virgin Islands: Photographs of *M. ocellata* ♀ collected by M. Souffait, Paris Museum.

Jamaica: 62528.

Mexico: 57067.—USLZ2945. 2 ♂, 1 ♀; near Progreso, State of Yucatan, D. L. Felder, 9 Jan 1978.—USLZ2946. 2 ♂, 2 ♀; same.—90343. 1 ♀, 1 juv; Campeche, State of Campeche, C. J. Goodnight, 20 Jul 1949.—USLZ2937. 1 ♂, 1 ♀; NE of Champoton, State of Campeche, T. C. Shirley and R. Tinnin, 3 Jan 1973.—USLZ2944. 1 ♂; just north of Seybaplaya, State of Campeche, D. L. Felder, 6 Jan 1978.—USLZ2940. 2 ♀; NE of Champoton, State of Campeche, D. L. Felder, 7 Jan 1978.—USLZ2943. 2 ♂, 3 ♀; same, 6 Jan 1978.—USLZ1413. 1 ♂; Isla Aguada, State of Campeche, D. L. Felder, 5 Mar 1981.—USLZ2939. 1 ♂; same, 5 Jan 1978.—USLZ2941. 2 ♂, 4 ♀; same.—USLZ2942. 2 ♂, 2 ♀; same.—USLZ2947. 1 ♂; same.—USLZ2948. 2 ♂, 1 ♀; same, 1 Jun 1982.

Belize: 204232. 2 ♂; Cay Caulker, Blue Hole, W side Cay Virgil, H. O. Wright, 8 Feb 1973.

*Diagnosis.*—See Table 1.

*Type locality.—"Inhabits* the southern states." Say's original account of *M. mercenaria* gave only a general indication of geographic origin for his material, but the last paragraph stated, "Esteemed as food and sold in the Charleston market, tied up in small parcels from four to eight together." Weiss and Ziegler (1931) recounted the collecting trip organized by Say and others in autumn 1817 for visits to the sea islands and adjoining coast of Georgia, and passage for an indeterminate distance up the St. John's River, Florida, that was cut short by bad feeling between the United States and Indian tribes in Florida, then still under control of Spain. The party retraced their route, touching Savannah and Charleston. The dates of this expedition and Say's descriptive account leave almost no doubt that his material came from the southeastern Atlantic coast of the United States.

*Types.*—Say listed his specimens as "Cabinet of the Academy." There are only two specimens of *Menippe mercenaria* in the ANSP. These are now numbered 3246 (dry). 1 ♀; cl 78 mm, cw 114.7 mm, maximum height of major right chela 50.1 mm, striae in patch 3/mm, maximum height of minor left chela 49.3 mm; 1 ♂, cl 64.8 mm, cw 96.2 (estimated, right lateral spine broken), maximum height of major right chela 45.1 mm, striae in patch 3/mm but very worn, maximum height left minor chela 19.6 mm (regenerated). The specimens each bear the number 26, printed by press in black ink on a tiny square of white paper that is affixed near the center of the carapace with sealing wax. This was the method of numbering individual specimens in early days of the Academy, and this was one of the very early numbers assigned.

The evidence indicates that these specimens are syntypes of Say's *Cancer mercenaria,* in both our opinion and that of curators at the ANSP. Say's original description was general with respect to morphology, but he did give details on color of the fingers, structure of the male abdomen, measurements of one specimen, and other comments. The female bears the handwritten words *Cancer mercenaria* in very old brownish colored ink on the upper outer propodal surface of the right cheliped. Measurements of this specimen are almost exactly those given in the original description, "Length three inches and one fourth, breadth four inches and a half," (the length measured by calipers is now ⅛ inch less). Say did not mention the sex of the measured individual. Other labels with these specimens, "*Pseudocarcinus mercenarius,* ♂ ♀ Southern coast of N.A.," "26a & b" (in brownish ink) along with the pencilled name "*Pseudocarcinus mercenaria,*" as well as other pencilled emendations, are attribut-

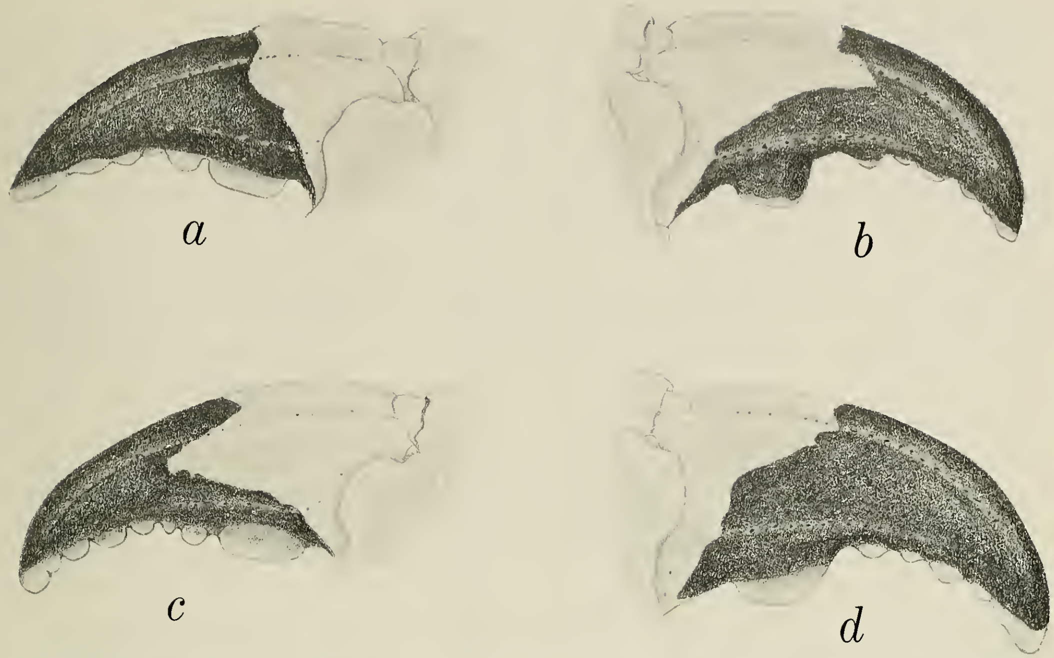

Fig. 4. Representative color patterns on frontal surface of dactyls of major chelae (see Table 1). *M. mercenaria,* light color preceding border between light and dark areas variously extended below punctate groove as broad tongue: a, 17171, Charleston, S.C.; b, 7509, Key West, Fla.; c, 47901, Cuba. *M. adina,* same extended along punctate groove as narrow point: d, 72139, Texas.

able to subsequent workers. No attempt has been made to determine who made such additions or changes.

Both specimens are in good condition for dry preservation of nearly 170 years. The chelipeds of both are still attached, although some of the succeeding pereopods are disarticulated, broken or missing. The exoskeleton of the female is clean. That of the male bears scattered barnacles on the carapace and on the carpus and propodus of the major cheliped which seems disproportionately large for a specimen with that size cephalothorax. Both the encrustation of the male and obvious wear on teeth of its major chela and stridulation patch indicate advanced duration of the instar. The major dactyl of each specimen has a color pattern about halfway intermediate between that shown in Fig. 4**a** and **c** for *M. mercenaria.* This alone testifies to origin in the Carolinian region.

*Known range.*—Cape Lookout, North Carolina, southward around peninsular Florida to Wakulla County, northwestern Florida, through the Bahamas and Greater Antilles to St. Thomas, Virgin Islands, Yucatan peninsula to southwestern State of Campeche, Mexico, and to Belize (Fig. 5). Intertidal to 51 m.

### *Menippe adina,* new species
Figs. 3a–b, 4d

*Menippe mercenarius.*—R. Rathbun, 1884: 772–774, pl. 264 (part, northern Gulf of Mexico); 1887:650–651 (part, northern Gulf of Mexico); 1893:772–774, pl. 264 (part, northern Gulf of Mexico).

*Menippe mercenaria.*—Cary and Spauld-

Table 1.—Comparisons between two species of *Menippe.*

| Structure | *M. mercenaria* | *M. adina* |
|---|---|---|
| | COLOR | |
| Carapace | Poorly defined light yellow spots on broken pattern of reddish-orange to reddish-violet, and often with additional dark spots; latter ocellated and near black in young. | Light yellow spots or flecks on broken pattern of reddish-orange to reddish-violet; spots edged with darker pigment in young. |
| Chelipeds | Frontal surface of major dactyl having border between light area at base and dark distal part *usually* with light area extended below punctate groove as broad tongue; often nearly vertical (see Table 2). | Frontal surface of major dactyl having border beween light area at base and dark distal part *usually* with light area extended along punctate groove as narrow point; rarely almost vertical (see Table 2). |
| Legs | Carpi and propodi distinctly banded with reddish-brown to orange (some bands maroon); ground color lighter (more broken mottling) between dark bands; without broken line of light spots at midwidth of merus 5. | Carpi and propodi lacking distinct bands; ground color reddish-orange to wine; pale yellow spots in longitudinal broken line at midwidth of merus 5. |
| | MORPHOLOGY | |
| Anterolateral tooth 3 | Almost always broader than 4, rarely equal to. | Usually broader than 4, but often narrower than and sometimes equal to. |
| Anterolateral tooth 5 | Weakly prominent, somewhat blunt; anterior margin shallowly concave, tip directed more laterally than anteriorly. | Strong, prominent, fairly acute; anterior margin rather strongly concave, tip directed more anteriorly than laterally. |
| Posterolateral margin of carapace | Usually weakly convex in anterior ⅓. | Usually straight to concave in anterior ⅓. |
| Setae on legs 2–5 | Dorsal margin of meri usually with few if any; sparse on propodus 5, restricted distally. | Dorsal margin of meri usually with well defined row; dense along most of ventral margin on propodus 5. |

ing, 1909:12 (Louisiana).—Schroeder, 1924:49–50, fig. 23 (part, Texas).—Reed, 1941:44 (as *Manippe*), 73 (Texas).—Behre, 1950:24 (Louisiana).—Gunter, 1950:38 (temperature, salinity, habitat, Tex.).—Whitten et al., 1950:59, 64, 71 (Texas jetties).—Hedgpeth, 1953:172, 175 (oyster biocoenosis, etc.).—Walker, 1953: 204 (Louisiana).—Hildebrand, 1954:276 (Texas).—Wass, 1955:157 (Alligator Harbor, Fla., color).—Menzel, 1956:80 (part, Apalachee Bay, Fla.).—Menzel and Hopkins, 1956:177–184, fig. 1 (predator on oysters).—Parker, 1956:319 (Miss. Delta).—Springer and Bullis, 1956:19 (part, Apalachee Bay, Fla.).—Simmons, 1957:179, 191 (in 25–35‰ S, upper Laguna Madre, Tex.).—Menzel and Nichy, 1958:125, 140–141, 144, fig. 6 (predator on oysters).—Parker, 1959:2123, 2161 (Texas).—Pounds, 1961:23, 46, figs. unnumbered on p. 23, 14, pl. 9, fig. 3 (natural history).—Richmond, 1962:75 (occ. Horn Is., Miss.).—Leary, 1964 (reissued 1967):23, 46, figs. unnumbered on p. 23, 39, fig. 14 (natural history).—Bullis and Thompson, 1965:12 (part, in and near Apalachicola Bay, Fla.).—Williams, 1965: 183 (part, not Carolina-Florida-Yucatan population).—Futch, 1966:1–6 (part, not peninsular Florida).—Menzel et al., 1966: 86, 90 (oyster predator).—Powell and Gunter, 1968:285–299 (natural history).—Lindner and Cook, 1971:157–162 (larval rearing, Texas).—Perret et al., 1971:62, appendix Tables 4, 7 (temperature, salinity, size trawl catch, La.).—Hoese, 1972:40 (Chandeleur Is., La.).—Collard and D'Asaro, 1973:fig. III G3 (part), fig. III G7 (part) (habitats, eastern Gulf of Mexico).—Christmas and Langley, 1973:295 (temperature, salinity, habitat, Miss.).—Day et al., 1971:23, 39 (Louisiana).—Felder, 1973:64–65, pl. 9, figs. 2–3 (NW Gulf of Mexico, key).—Fotheringham and Brunenmeister, 1975: 17, 26, 114, 136, 149, 167, figs. 2.3, 6.9 (mislabelled as *Panopeus herbstii*) (habitat, feeding).—Juneau, 1975:42 (low salinity, La.).—Perry, 1975:55 (occ. *Callinectes* fishery, Miss.).—Miller, 1976:630 (conservation, fishery).—Livingston et al., 1977:90, Table 3 (part, Apalachicola Bay, Fla.).—Burden, 1978:129 (temperature, salinity, habitat, La.).—Costello et al., 1979:19450–19496 (part, comprehensive rev., Apalachicola Bay, Fla. westward to Mexico).—Williams and Duke, 1979: 183–185 (part, life history, ecology).—Meinroth, 1981:647 (part, color pl. 642, N. America).—Mauro and Mangum, 1982:189–195 (temperature and respiratory physiology, specimens may be hybrids).—Kent, 1983:257–283 (predation on whelks, crabs may be hybrids).—Lindberg and Marshall, 1984:1 (northern Gulf of Mexico population).—Williams, 1984: 420 (part, not Carolina-Florida-Yucatan population).—Brooks and Mariscal, 1985: 112–116 (feeding on hermit crabs).—Horst and Bankston, 1986:1–20 (Louisiana fishery potential).

*Menippe nodifrons* Stimpson.—Rathbun, 1930:479 (part, USNM 30566 from Louisiana).—Scotto, 1979:359 (Louisiana).

*Material.*—Florida: USLZ1651. 1 ♂; Panama City, D. L. Felder.—USLZ258. 1 ♀; same.—USLZ2860. 1 ♂; same.—USLZ2676. 2 ♂; St. Andrew Bay, Panama City.—FDNR, I-2947. 5 ♂, 1 ♀; Saint Andrew Bay, Magnolia Beach to jetty and wreck N of jetty, Panama City, Bay County, 3 Jul 1966.—99871. 1 ♀ juv; Pensacola, Intracoastal Waterway 3.5 mi E Interarity Point, F. Berry and A. Mead, 15 Aug 1953.

Alabama: 19355.—81444. 1 ♂ juv; Mobile Bay, 30 Jan 1938. USLZ885. 1 ♀; Dauphin Island, J. W. Martin, 11 Nov 1977.

Louisiana: 26147.—64142. 1 ♂; Grand Pass, Lake Borgne, S. Springer.—USLZ83. 1 ♀; S Breton Island, Nov 1969.—USLZ2949. 1 ♂, 1 ♀, juvs; California Bay, D. L. Felder, 28 Mar 1972.—USLZ2685. 1 ♂; Lake Grande Ecaille, W. W. Forman and L. J. Kennair, 5 May 1972.—USLZ2686. 2 ♂, 2 ♀, juv; Lake Grande Ecaille, D. L. Felder, 8 May 1973.—USLZ2690. 1 ♂, 2 ♀; Grand Terre Island, C. Dugas, 12 Oct 1982.—USLZ 2691. 2 ♂, 7 ♀; same, 9 Nov 1982.—USLZ2692. 3 ♂, 2 ♀; same.—USLZ2693. 3 ♂, 7 ♀; same, 16 Nov 1982.—USLZ2694. 5 ♂, 4 ♀; same, 2 Dec 1982.—USLZ2696. 1 ♂, 7 ♀; same, 30 Nov 1982.—USLZ2697. 6 ♂, 6 ♀; same, 18 Nov 1982.—USLZ2698. 2 ♂, 6 ♀; same.—USLZ2699. 5 ♂, 11 ♀; same.—

Table 2.—Color pattern on frontal surface of dactyl of major chela in three populations expressed as percent of total sample. Patterns based upon shape of border between light proximal and dark distal coloration and classified by location of apical part of light coloration which may be: a corner or point marking punctate groove (on groove); a broad extension below punctate groove (below groove); or an irregular pattern without an apical extension (irregular/absent), in which border between colors may be nearly vertical (see Fig. 4).

| Population | On groove | Irregular/ absent | Below groove |
|---|---|---|---|
| Carolina-Belize | | | |
| n = 123 | 27.6 | 21.1 | 51.2 |
| Cedar Keys to Apalachicola Bay, Fla. | | | |
| n = 88 | 46.6 | 19.3 | 34.1 |
| NW Gulf of Mexico | | | |
| n = 156 | 94.9 | 5.1 | 0 |

USLZ2700. PARATYPES: 1 ♂; transferred to USNM 228864. 1 ♂, 5 ♀; same, 28 Oct 1982.—USLZ2701. PARATYPES: 1 ♂, 1 ♀; transferred to USNM 228861. HOLOTYPE ♂, (cl 75.4 mm, width between lateral spines 113.6, width to base lateral spines 106.5); USNM 228862. ALLOTYPE ♀ (cl 70.8 mm, width between lateral spines 102.8, width to base of lateral spines 98.7); PARATYPES: USNM 228863. 5 ♂, 7 ♀; same, 8 Oct 1982.—USLZ2695. 1 ♀; Grand Terre Island, J. M. Howell and F. M. Truesdale, Aug 1983.—USLZ1086. 1 ♀; Barataria Bay, L. P. Rozas, 21 Oct 1979.—USLZ1783. 1 ♂, 1 ♀; Barataria Bay.—102896. 2 juv; Barataria Bay, Grand Isle, E. H. Behre, 19 Aug 1943.—103756. 1 juv; from fouling collectors, 7.5 fm, S Grand Isle, E. H. Behre, 7 Jul 1959.—103757. 2 juv; same, C. E. Dawson, 3 Aug 1959.—103758, 3 juv; same, C. E. Dawson, 14 Sep 1959.—USLZ72. 1 ♀; Grand Isle, 1969.—USLZ2688. 1 ♂; near mouth of Bayou Fourchon, R. W. Heard III, Jun 1982.—USLZ2687. 1 ♂, 1 ♀; Freeport Sulphur Production Platform off Grand Isle, D. L. Felder, Nov 1971.—189917. 1 ♂; Bay Marchand Lease Area, 29°02'50"N, 90°09'46"W, 20 ft, SwRI for BLM, 19 Jun 1978.—187001. 1 ♀; South Timbalier Lease Area, 500 m N of platform, 28°48'19"N, 90°36'29"W, 18 m, SwRI for BLM, otter trawl, 25 Aug 1978.—30566. 1 ♂; Cameron (as *M. nodifrons* in Rathbun [1930]); R. P. Cowles.—USLZ2689. 1 ♀; Cameron rock jetties, J. Kavanagh, M. LaSalle, and T. Bishop, 30 Sep 1979.—USLZ1085. 1 ♀; same.—USLZ1818. 1 ♀; same.—USLZ358. 1 ♂; off Holly Beach, E. B. Stueben, trawl, 4 Aug 1973.—USLZ750. 2 ♀; between Holly Beach and Peveto Beach, C. Boudreaux, 9 Nov 1968.

Texas: 20637, 33032.—71664. 1 ♂; Texas, C. T. Reed.—72130. 1 ♀; Gulf Coast, South-Western Biol. Supply Co.—72139. 1 ♂; same.—78395. 1 ♂, 1 ♀; Galveston Bay, C. E. Burt, 9 Apr 1939.—USLZ96. 1 ♀; Freeport, J. Fruge, 1 Nov 1969.—USLZ686. 1 ♀; Port Aransas, J. Holmquist, 20 Jul 1977.—USLZ2681. 2 ♀; Port Aransas, T. C. Shirley and S. C. Rabalais, 14 Aug 1972.—62735. 1 ♀; Corpus Christi, M. E. Quisenberry, 1929.—72188. 1 ♀; Corpus Christi Bay, H. B. Parks, Oct 1936.—USLZ2935. 1 ♂; Corpus Christi Bay, T. C. Shirley, 18 Feb 1972.—USLZ2684. 1 ♀; jetty at Corpus Christi fish pass, D. L. Felder, 14 Aug 1972 USLZ685. 1 ♂, 3 ♀; S Padre Island rock jetty, Cameron County, J. Holmquist 22 Jul 1977.—USLZ2682. 1 ♀, many juv; same, S. C. Rabalais and N. N. Rabalais, 29 Jun 1973.—USLZ2683. 1 ♂; same, D. L. Felder, 28 May 1979.—USLZ2934. 1 ♂; Mansfield Pass rock jetty, S. C. Rabalais and N. N. Rabalais, 14 Jul 1973.—USLZ2932. 1 ♂, 1 ♀; S Padre Island rock jetty, Cameron Co., D. L. Felder, 28 May 1979.

Mexico: USLZ2938. 1 ♂; Barra del Tordo, mouth of Rio Carrizal, ca 75 km N Tampico, State of Tamaulipas, D. L. Felder, 24 May 1982.

*Diagnosis.*—See Table 1.

*Type locality.*—Grand Terre Island, Louisiana. See *Material.*

*Known range.*—Wakulla County in northwestern Florida, westward and southward around Gulf of Mexico to Tamaulipas State, Mexico (Fig. 5). Intertidal to 14.6 m (Hildebrand 1954).

*Etymology.*—From the Greek *adinus* (adinos), close, crowded, with reference to the patch of closely crowded striae on the inner palmar surface of the major chela.

### Introgressive Zone: *Menippe adina, M. mercenaria,* and *M. adina* × *M. mercenaria*

Fig. 3c–f

*Material.*—Florida: 56383.—92357. 1 ♀; Gulf of Mexico, 29°03'N, 84°24'W, 15 fm, *Oregon* sta 276, 23 Feb 1951.—USLZ2920. 4 ♂; Wakullah Beach, D. H. Wilber and D. L. Felder, 3 Apr 1985.—USLZ2921. 2 ♂; same.—USLZ2922. 1 ♂; same.—USLZ2923. 2 ♂; same.—USLZ2924. 4 ♂; same.—USLZ2925. 6 ♂; same.—USLZ2926. 1 ♂, 1

♀; Florida State Univ. Marine Lab., D. L. Felder and J. M. Felder, 6 Apr 1985.—USLZ2913. 3 ♀; approximately 3 mi W and offshore of Florida State Univ. Marine Lab., Turkey Point, Franklin County, D. H. Wilber and D. L. Felder, 4 Apr 1985.—USLZ2914. 1 ♂, 1 ♀; same.—USLZ2915. 1 ♂, 6 ♀; same.—USLZ2916. 3 ♀; same.—USLZ2917. 2 ♂, 2 ♀ (1 ovig.); same.—USLZ2918. 1 ♂, 4 ♀ (1 ovig.); same.—USLZ2919. 1 ♂, 5 ♀ (3 ovig.); same.—USLZ2677. 2 ♂, 2 ♀ (1 ovig.); Bay Mouth Bar, vicinity of Alligator Point, J. W. Martin, Oct 1982.—USLZ2929. 2 ♂, juv; same.—USLZ2928. 2 ♂; Alligator Point, D. H. Wilber, 5 Apr 1985.—USLZ2927. 3 ♂, 2 ♀; same.—75789. 1 juv; Apalachicola, A. S. Pearse, 5 Jun 1935.—75790. 2 juv; same, 16 Jun 1935.—228510. 2 ♀ (ovig.); Florida, from Florida State Museum.

## Results and Discussion

Our analysis suggests a highly significant morphological separation between two major populations that were formerly treated together as the species *M. mercenaria* (Table 3, Figs. 6–8). One of these populations—that ranging from North Carolina to peninsular Florida, the southeastern Gulf of Mexico and the western Caribbean Sea (Fig. 5)—has morphology and color pattern on the chelipeds like that of recently located syntypes designated by Say (1818) as *Cancer mercenaria*; it is to this group that we now restrict the name *M. mercenaria.* A second population, distinct from *M. mercenaria* in morphology and coloration, is distributed in Gulf of Mexico coastal waters from the northwestern Florida panhandle to Tamaulipas State, Mexico; it is this population that we assign to a new species, *M. adina.* Preliminary results from ongoing studies of this new species by ourselves and several collaborators indicate that it has unique characteristics in both physiology and larval development, but those topics will be reserved for future treatments.

Table 3.—Discriminant and correlation coefficients of variables listed in sequential pairings between Group 1 (*M. mercenaria*) and Group 2 (*M. adina*) by stepwise discriminant analysis. Analysis A corresponds to Fig. 8A, analysis B to Fig. 8B; statistics do not address ungrouped samples on upper axes of those figures. Values include unstandardized (Unstd. Disc. Coef.) and standardized (Std. Disc. Coef.) canonical discriminant function coefficients, along with pooled within-groups correlations between canonical discriminant functions and discriminating variables (Within-gps Correl. Coef.).

| Variable selected | Unstd. Disc. Coef.* | Std. Disc. Coef. | Within-gps Correl. Coef. |
|---|---|---|---|
| Analysis A: | | | |
| R2 | 51.713 | 0.670 | 0.747 |
| R4 | −3.699 | −0.355 | −0.690 |
| R1 | 26.094 | 0.502 | 0.575 |
| R3 | −7.577 | −0.412 | 0.083 |
| (Constant) | 6.757 | | |
| Analysis B: | | | |
| R4 | 2.616 | 0.257 | 0.675 |
| R2 | −49.508 | −0.799 | −0.590 |
| R5 | 0.588 | 0.753 | −0.159 |
| R3 | 8.488 | 1.227 | −0.090 |
| R1 | −48.038 | −1.226 | −0.477 |
| (Constant) | −3.789 | | |

* Group centroids: Analysis A, Group 1 = −2.109; Group 2 = 1.501. Analysis B, Group 1 = 2.307, group 2 = −1.523.

Scatterplots and regression analyses of variables comprising each of the ratios of morphological characters (Figs. 6 and 7) indicated that all ratios gave significant separation of the hypothesized populations, though R4 was least significant in making this separation.

Recent studies of isozyme variations in populations of stone crabs (T. Bert, Yale University, pers. comm.) have suggested that a genetically divergent population of *M. mercenaria* occurs along the coast of Georgia and South Carolina, perhaps extending as far north as Charleston. Our prior examinations of specimens had revealed no consistent differences in morphology and coloration between individuals we had observed in the Charleston area and elsewhere in the restricted range of *M. mercenaria.* Nevertheless, we classified a large sample

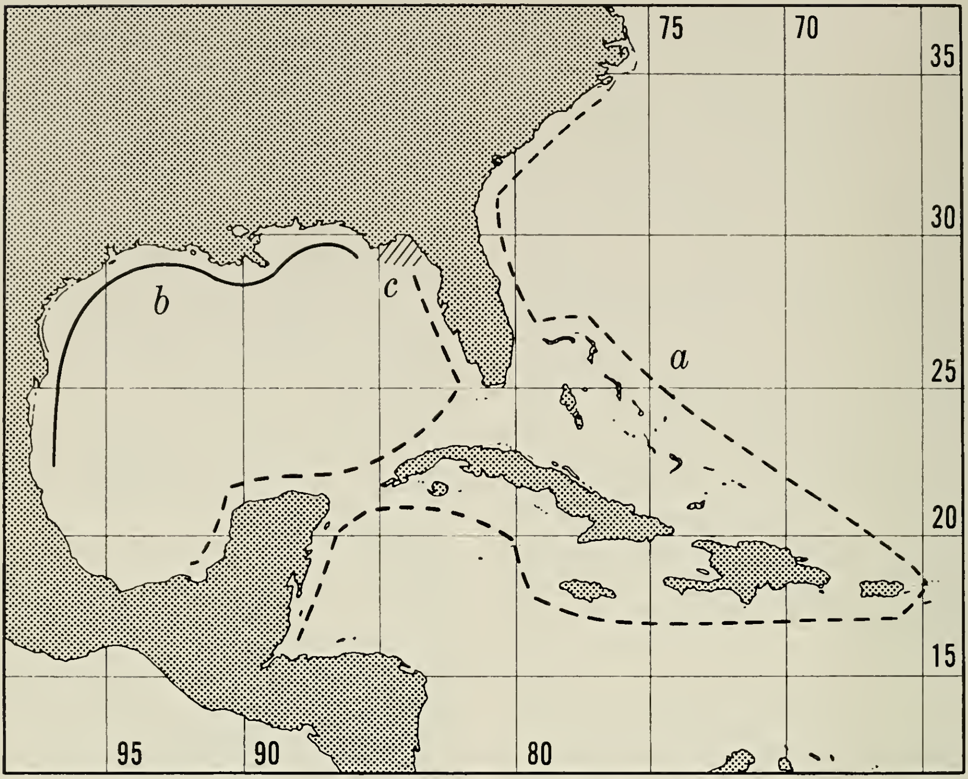

Fig. 5. Gulf of Mexico, parts of western North Atlantic Ocean and Caribbean Sea showing diagrammed geographic ranges of: a, *Menippe mercenaria* (Say), restricted, from Cape Lookout, North Carolina around peninsular Florida, through the Bahamas and Greater Antilles including Saint Thomas, Virgin Islands, to Yucatan Peninsula, Mexico, and Belize; b, *M. adina* new species from northwestern Florida, around Gulf of Mexico to Tamaulipas State, Mexico; c, zone of hybridization in Apalachee Bay region of northwestern Florida.

of specimens from Charleston on the basis of weighted morphological characters used in our discriminant analysis (Fig. 8A). We deemed such an analysis to be particularly important, as the Charleston area appears to be a likely source for Say's syntypes of *M. mercenaria.*

Both the distribution of discriminant scores and the resultant centroid for the Charleston sample closely approximated values for Group 1, which was the remainder of the population that we herein assign to *M. mercenaria.* Furthermore, both the Charleston sample and Group 1 diverged from values for Group 2, which was made up of samples that we assign to *M. adina.* This classification analysis was able to assign correctly over 98% of the Group 1 and Group 2 individuals to their a priori designations. From the resultant canonical correlation of 0.873, it is evident that about 76% of the separation between Groups 1 and 2 is explained by the four variables utilized in the analysis. Thus, on the basis of the morphological characters that we have analyzed, we find no support for taxonomic distinction of populations in the Charleston area from the remainder of materials assigned to *M. mercenaria.* However, our sample from further south, especially along the Georgia coast, was neither large nor extensive enough to exclude completely the possibility that divergent phenotypes occur in that region.

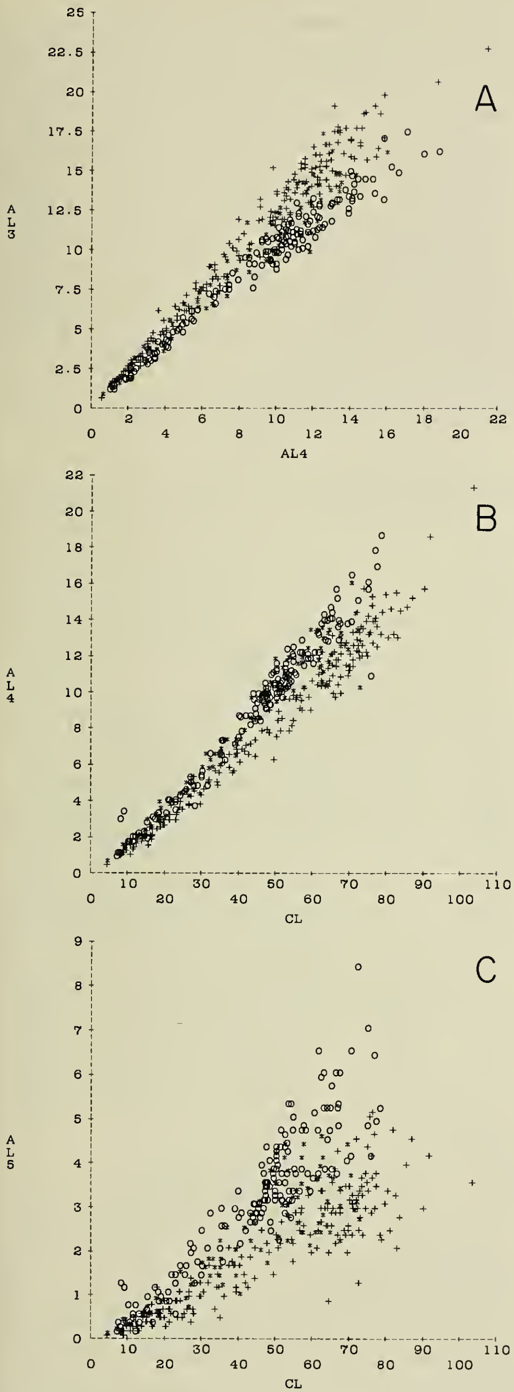

Fig. 6. Comparisons of morphological variables in *Menippe* populations assigned to *M. adina* (crosses), *M. mercenaria* (circles), and the hybrid zone (asterisks). A, Width anterolateral tooth 3 (AL3) as a function of width anterolateral tooth 4 (AL4); *M. mercenaria,* Y = 0.46776 + 1.18854 X; *M. adina,* Y = 0.66283 + 0.93972 X; *M.* hybrid, Y = 0.36809 + 1.05838 X; B, Width AL4 as a function of carapace length (CL); *M. mercenaria,* Y = −0.67632 + 0.18536 X; *M. adina,* Y = −0.73003 + 0.22309 X; *M.* hybrid, Y = −0.39580 + 0.20494 X; C, Length AL5 (equal to WLS − WBLS in Fig. 1) as a function of CL; *M. mercenaria,* Y = −0.25118 + 0.04756 X; *M. adina,* Y = −0.45164 + 0.08246 X; *M.* hybrid, Y = −0.11821 + 0.05568 X. All measurements in mm and taken as indicated in Fig. 1.

Atypical coloration of some specimens from the northeastern Gulf (Fig. 3c–f) first led us to suspect hybridization between populations in northwestern Florida. As early as 1979, we recognized the Apalachicola to Apalachee Bay region as the general area of transition or break between morphological extremes of "*M. mercenaria,*" and noted that these two extremes appeared to differ somewhat in life history and habitat. However, not until adequate samples were measured and photographed did we conclude that introgressive hybridization between species was occurring there; simultaneously, an independent study of isozyme variations in populations of *Menippe* resulted in similar conclusions regarding populations in northwestern Florida (Bert, in press). Also supportive of this conclusion was evidence that stone crab fishermen in northwestern Florida have long recognized that a hybrid is involved in the fishery there. When asked to comment on coloration of local stone crabs in his catch (but otherwise unprompted), Mr. Clint Wood of Taylor Co., Fla., volunteered the following: "There is the 'dominicker' . . . spotted and with marks on the legs, there is the 'stone crab' . . . more solid brown . . . they catch more of them further to the west, and there is the 'cross' . . . a mix of the other two." He further noted that the "dominicker" was the only kind found south of Cedar Keys.

Small juvenile to large adult specimens were included in our two-group discrimi-

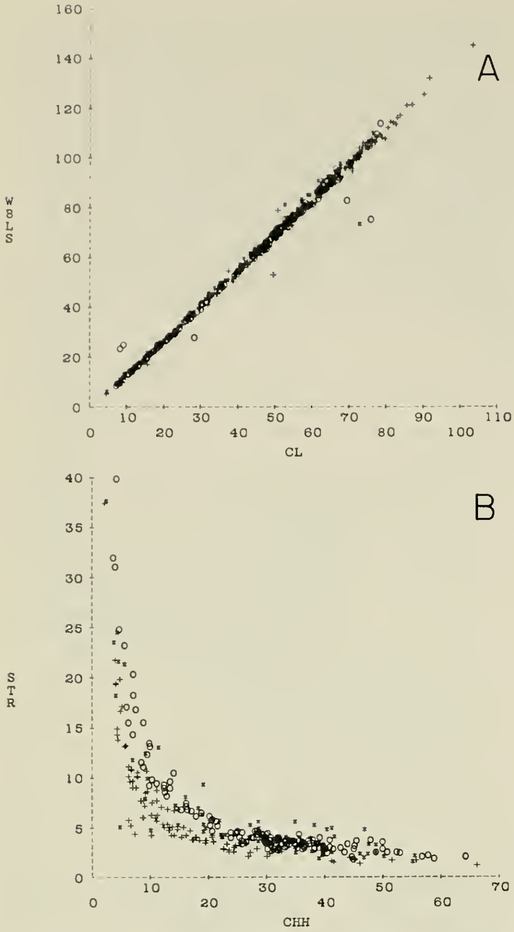

Fig. 7. Comparisons of morphological variables in *Menippe* populations assigned to *M. adina* (crosses), *M. mercenaria* (circles), and the hybrid zone complex (asterisks). All measurements in mm. A, Width of carapace excluding anterolateral tooth 5 (WBLS) as a function of carapace length (CL), taken as indicated in Fig. 1; *M. mercenaria*, $Y = -1.63382 + 1.42285 X$; *M. adina*, $Y = 0.04080 + 1.38674 X$; *M.* hybrid, $Y = -0.47386 + 1.40583 X$; B, Number of striae per mm (STR) in stridulatory patch on major chela as a function of maximum chela height (CHH), as shown in Fig. 2; *M. mercenaria*, $\ln Y = 4.07954 - 0.92235 \ln X$; *M. adina*, $\ln Y = 4.60272 - 0.94048 \ln X$; *M.* hybrid, $\ln Y = 4.07787 - 0.81343 \ln X$.

nant analysis of *M. mercenaria* and *M. adina*, and subsequent assignment of the sample from the hypothesized hybrid zone (Panama City to Steinhatchee, Fla.) (Fig. 8B). The analysis included five variables, all of which provided for an increase in group separation. The analysis correctly classified 97% of individuals assigned a priori to Group 1 (*M. mercenaria*) or Group 2 (*M. adina*), thus demonstrating morphological distinction of these species over a broad range of size classes. The resultant canonical correlation of 0.883 indicates that about 78% of the separation between Groups 1 and 2 is thus explained. Exclusion of individuals less than 15 mm carapace length from the analysis improved correct classification to over 99% on the basis of the same five variables (data not figured).

Superposition of a sample from the hypothesized hybrid zone (Fig. 8B, upper axis) on discriminant scores from populations assignable to *M. mercenaria* and *M. adina* (lower axis) defines a broadly intermediate but morphologically heterogeneous group which appears to include *M. mercenaria, M. adina,* hybrids of the two, and possible backcrosses. However, when discriminant scores for this group are independently separated into subgroups based upon color, they resolve into means a, b, and c as indicated, where color morph "a" matches color of *M. adina,* "c" matches color of *M. mercenaria* and "b" is intermediate. The significance of differences among these three morphs is made clear by statistical comparisons among sample means of their discriminant scores: a, $\bar{x}$ −.79063 ± SD .86266 vs b, $\bar{x}$ .51325 ± SD 1.2334, t = −5.071, 53 DF; b vs c, $\bar{x}$ 1.76489 ± SD .92149, t = −4.165, 40 DF; $P < .01$.

The sample comprising subgroup "a" (Fig. 8B) of the hybrid zone population in our analysis is slightly larger than those comprising subgroups "b" and "c," and likely includes a few individuals from just west of the area in which introgression of the two species occurs. This consists of 11 specimens from the vicinity of Panama City, Fla. In retrospect, all the latter are assignable to *M. adina,* and we have to date obtained no hybrid specimens from west of Cape San Blas. Thus, while we include specimens from

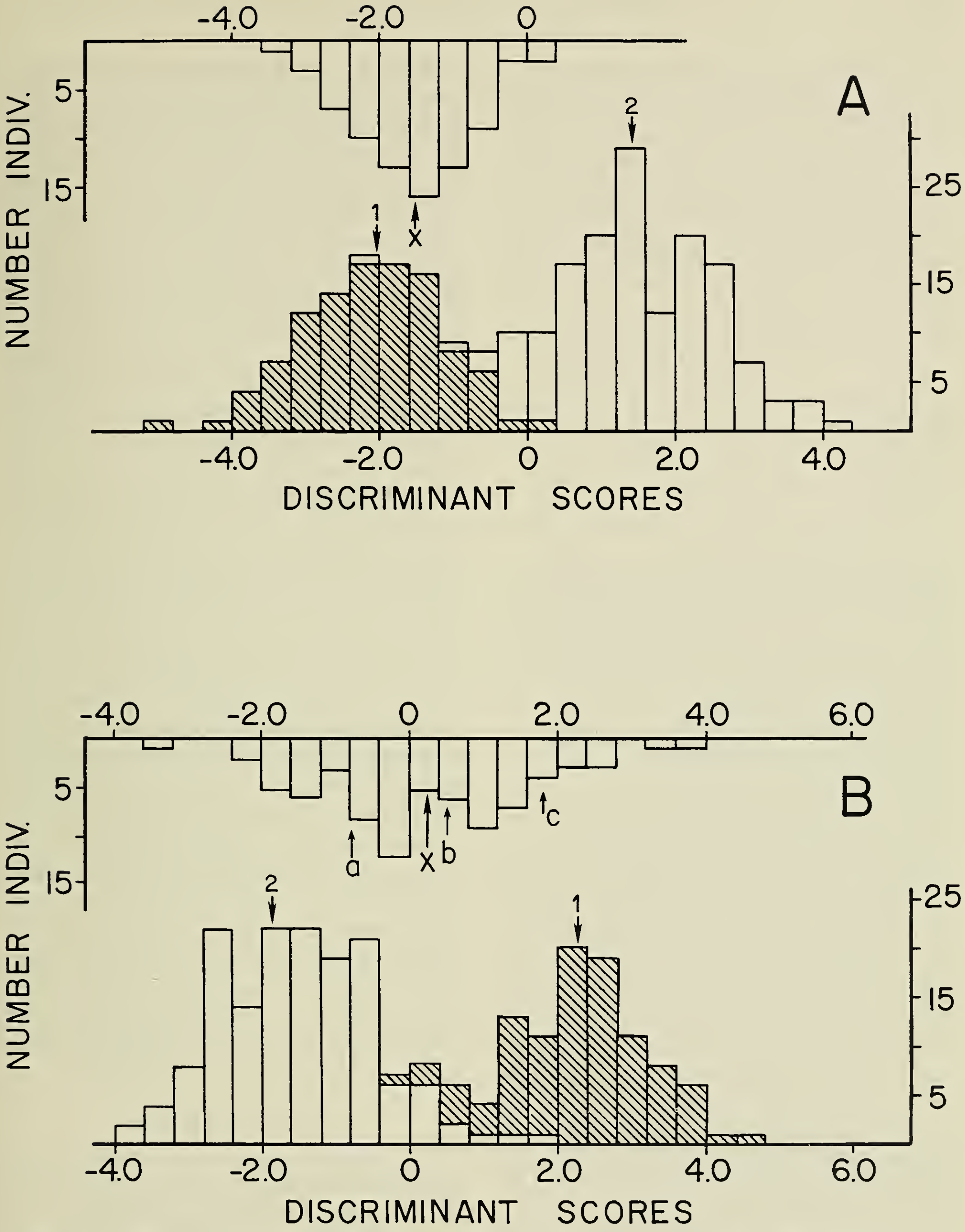

Fig. 8. A, Distribution of discriminant scores based upon R1, R2, R3 and R4 for specimens ≥15 mm carapace length: lower axis—a priori geographic Groups 1 and 2 (arrows mark centroids), assignable to *M. mercenaria* (cross-hatched bars) and *M. adina* (open bars), respectively; upper axis—ungrouped sample from Charleston, S.C. (arrow × marks mean); B, Distribution of discriminant scores based upon R1, R2, R3, R4, and R5 for all sizes (excluding only specimens that lacked R5 data): lower axis—a priori Groups 1 and 2 (arrows mark centroids), assignable to *M. mercenaria* (cross-hatched bars) and *M. adina* (open bars), respectively; upper axis—ungrouped sample from northwest Florida (arrow × marks overall mean; arrows a–c mark means for three color morphs.

Table 4.—Percentage of each color morph in samples of *Menippe* from two habitats in northwest Florida. Color morph "a" is that typical of *M. adina,* "c" is that typical of *M. mercenaria,* and "b" is intermediate and believed typical of hybrids; color patterns for morphs are described in Materials and Methods. Samples were taken on 3–4 April 1985; "oyster reef" habitat is located at Wakulla Beach, Wakulla Co.; "grass bed" habitat is located just west of the Florida State University Marine Laboratory, Turkey Point, Franklin Co.

| | Color morph | | |
|---|---|---|---|
| Habitat | a | b | c |
| Oyster reef<br>n = 18 | 67 | 33 | 0 |
| Grass bed<br>n = 29 | 31 | 31 | 38 |

Panama City in the hybrid zone sample from northwest Florida, as defined for our present analysis, the actual western extreme can only be defined after much more thorough collecting in that area.

Although detailed studies of ecological and physiological differences between *M. mercenaria* and *M. adina* have not as yet been completed, evidence for such differences emerges from observation of habitats in which these species have been collected. In the northwestern Gulf of Mexico, *M. adina* inhabits oyster reefs, rock jetties, and other debris-cluttered substrates in shallow waters where salinities range from 35‰ to distinctly less than 10‰. Throughout its distribution, *M. mercenaria* seems instead to be restricted to the upper extreme of this salinity range, inhabiting rubble and debris much as does *M. adina,* but in most cases preferring grass beds to inshore oyster reefs. In the course of sampling two habitats within the northwest Florida hybrid zone, we observed the hybrid or intermediate color morph (morph "b") to be about as common in an inshore oyster reef habitat as it was in rubble on a much less euryhaline grass bed (Table 4); however, the *M. adina* color morph (morph "a") was more common on the euryhaline oyster reef than in the grass bed, and the *M. mercenaria* color morph (morph "c") was common in our sample from the higher salinity grass bed but absent from the oyster reef. Although more extensive collections are needed to confirm the pattern suggested by these preliminary observations, it appears that genetic composition of a given sample from within the hybrid zone may, at least in part, be dictated by habitat. If so, systematic sampling from a full spectrum of habitats will be required in the course of further characterizing genetic trends within the zone of introgression, and characterizations of small or isolated samples cannot apply generally to the heterogeneous complex of the hybrid zone.

The recognition and separation of cryptic and sibling species among the Decapoda has been the subject of several recent investigations. For the most part, these are the subject of a forthcoming review (Knowlton, in press). In a number of cases, differences in coloration have provided the first evidence to support recognition of closely related siblings. This has been particularly true in recent studies of the pistol shrimp *Alpheus armatus* Rathbun and its near relatives (Knowlton and Keller 1985). In our studies, color not only facilitates the recognition of two closely related crab species; it also affords a character of use in recognition of what appear to be hybrids of these species. More detailed analysis of patterns may serve to distinguish simple hybrid crosses from possible backcrosses, and should afford a very useful phenological tool in future studies of genetic lineage.

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# INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD,
LONDON, SW7 5BD

14 April 1986

The Commission hereby gives six months notice of the possible use of its plenary powers in the following cases, published in the *Bulletin of Zoological Nomenclature*, volume 43, part 1 on 9 April 1986, and would welcome comments and advice on them from interested zoologists.

Correspondence should be addressed to the Executive Secretary at the above address, if possible within six months of the date of publication of this notice.

*Case No.*

2472 *Dasyurus hallucatus* Gould, 1842 (Mammalia, Marsupialia): proposed conservation by the suppression of *Mustela quoll* Zimmermann, 1783.

2485 *Cholus* Germar, 1824 (Insecta, Coleoptera): proposed conservation by the suppression of *Archarias* Dejean, 1821.

2486 *Dryophthorus* Germar, 1824 (Insecta, Coleoptera): proposed conservation by the suppression of *Bulbifer* Dejean, 1821.

2487 *Lachnopus* Schoenherr, 1840 (Insecta, Coleoptera): proposed conservation by the suppression of *Menoetius* Dejean, 1821 and *Ptilopus* Schoenherr, 1823.

2488 *Nemocestes* Van Dyke, 1936 (Insecta, Coleoptera): proposed conservation and designation of type species.

2489 *Zygops* Schoenherr, 1825 (Insecta, Coleoptera): proposed conservation by the suppression of *Eccoptus* Dejean, 1821.

2505 *Tylocidaris* Pomel, 1883 (Echinoidea, Cidaroidea): proposed designation of *Cidaris clavigera* Mantell, 1822 as type species.

2479 *Ammonites perarmatus* J. Sowerby, 1822 (Cephalopoda, Ammonoidea): proposed exemption from the Principle of Homonymy.

872 *Clausilia* Draparnaud, 1805 (Mollusca, Gastropoda): proposed correction of Opinion 119.

1985 De la Cépède, 1788–1789, "Histoire naturelle des Serpens" and later editions: proposed rejection as a non-binominal work.

2357 ATYIDAE De Haan, [1849] (Crustacea, Decapoda) and ATYIDAE Thiele, 1926 (Mollusca, Gastropoda): proposals to remove the homonymy.

2414 *Carcharias* Rafinesque, 1810 (Chondrichthyes, Lamniformes): proposed conservation by the use of the relative precedence procedure.

2468 *Pyralis nigricana* Fabricius, 1794 (Insecta, Lepidoptera): proposed conservation by the suppression of *Phalaena rusticella* Clerck, 1759.

2506 *Apanteles ornigis* Weed, 1887 (Insecta, Hymenoptera): proposed conservation by the suppression of *Microgaster robiniae* Fitch, 1859.

2492 *Strongylaspis* Spaeth, 1936 (Insecta, Coleoptera) *non Strongylaspis* Thomson, 1860: proposed designation of *Cassida atripes* LeConte, 1859 as type species.

2525 *Nomadacris* Uvarov, 1923 (Insecta, Orthoptera): proposed conservation by setting aside the first-reviser action of Jago.

637 Type species of the genus *Calymene* Brongniart (Trilobita) *in* Brongniart & Desmarest, 1822 and proposed suppression of the name *tuberculatus* Brünnich, 1781.

1094 *Tubulanus* Renier, [1804] and *T. polymorphus* Renier, [1804] (Polychaeta): proposed reinstatement under the plenary powers.

P. K. TUBBS
Executive Secretary

# INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD,
LONDON, SW7 5BD

14 April 1986

The following Opinions have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature,* volume 43, part 1 on 9 April 1986.

| *Opinion No.* | |
|---|---|
| 1369 (p. 15) | *Astacilla* Cordiner, 1793 (Crustacea, Isopoda): conserved. |
| 1370 (p. 17) | *Neadmete okutanii* Petit, 1974 designated as type species of *Neadmete* Habe, 1961 (Mollusca, Gastropoda). |
| 1371 (p. 19) | *Pachycephalosaurus* Brown & Schlaikjer, 1943 and *Troodon wyomingensis* Gilmore, 1931 (Reptilia, Dinosauria): conserved. |
| 1372 (p. 21) | *Donax hanleyanus* Philippi, 1847 (Mollusca, Bivalvia): conserved. |
| 1373 (p. 23) | *Panesthia saussurii* Wood-Mason, 1876 designated as type species of *Caeparia* Stål, 1877 (Insecta, Dictyoptera). |
| 1374 (p. 25) | *Boiga* Fitzinger, 1826 (Reptilia, Serpentes): conserved. |
| 1375 (p. 27) | *Glossodoris* Ehrenberg, 1831, *Hypselodoris* Stimpson, 1855 and *Chromodoris* Alder & Hancock, 1855 (Mollusca, Gastropoda): conserved. |
| 1376 (p. 30) | *Cuspidaria* (*Rhinoclama*) *adamsi* Morgan & Heppell, 1981 designated as type species of *Rhinoclama* Dall & Smith, 1866 (Mollusca, Bivalvia). |
| 1377 (p. 33) | *Chelydra osceola* Stejneger, 1918 given nomenclatural precedence over *Chelydra laticarinata* Hay, 1916 and *Chelydra sculpta* Hay, 1916 (Reptilia, Testudines). |
| 1378 (p. 35) | *Phalaena bellatrix* Stoll, 1780 designated as type species of *Crinodes* Herrich-Schäffer, 1855 (Insecta, Lepidoptera). |
| 1379 (p. 37) | *Gonodontis rectisectaria* Herrich-Schäffer, [1855] designated as type species of *Pero* Herrich-Schäffer, 1855 (Insecta, Lepidoptera). |
| 1380 (p. 39) | *Euphaedra* Hübner, [1819] (Insecta, Lepidoptera): conserved. |
| 1381 (p. 42) | *Ourocnemis* Baker, 1887 (Insecta, Lepidoptera): conserved. |
| 1382 (p. 45) | *Zeugophora* Kunze, 1818 (Insecta, Coleoptera): conserved. |

The Commission regrets that it cannot supply separates of Opinions.

P. K. TUBBS
Executive Secretary

# INFORMATION FOR CONTRIBUTORS

*Content.*—The *Proceedings* of the Biological Society of Washington contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers will be published in English (except for Latin diagnosis/description of plant taxa which should not be duplicated by an English translation), with a summary in an alternate language when appropriate.

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# A REVISION OF THE GENUS *NEPHASOMA* (SIPUNCULA: GOLFINGIIDAE)

Norma J. Cutler and Edward B. Cutler

*Abstract.*—The species in the sipunculan genus *Nephasoma* (formerly a subgenus of *Golfingia*) are reviewed and evaluated in light of a critical examination of 13 historically used morphological characters. Whenever possible, type material was examined. The monograph of Stephen and Edmonds (1972) was used as a starting point. Of the 46 putative species listed in that work or described since then, 23 remain as valid species, three are reduced to subspecific rank, five are considered either species inquirendum or incertae sedis, and the remainder are considered junior synonyms. One new subspecies is described (*N. diaphanes corrugatum*). The known distribution of each species is summarized. A key to all species is provided.

This paper is part of a continuing series begun in Cutler and Murina (1977) where all of the taxa then considered subgenera of *Golfingia* were reviewed in a preliminary fashion. The sipunculan genus *Golfingia* was created by Lankester in 1885 to commemorate a pleasant outing on the greens. In 1950 W. K. Fisher created five subgenera including *Phascoloides*. One of the species in the group was *G. (P). glacialis* which Cutler and Murina (1977) subsequently showed to be conspecific with *Nephasoma marinki* Pergament. This species name is a junior synonym but, unfortunately, the genus-group name is senior to *Phascoloides* and therefore must be retained as the name of this taxon. The retention of *Nephasoma* as a separate monotypic genus by Stephens and Edmonds (1972) is unfortunate and potentially confusing. When Cutler and Gibbs (1985) elevated *Nephasoma* to generic rank it had a different meaning, i.e., a polytypic taxon with the species formerly included within *Golfingia* (*Phascoloides*). This confusion is further compounded since Gibbs (1982) determined that *N. glacialis* is a junior synonym of *N. lilljeborgi.*

This review is one of a series critically examining the morphological characters used by taxonomists to characterize species within a genus and evaluating their meaningfulness within populations made up of varying size and age worms. We have examined the type material wherever possible and reevaluated the original descriptions based on our current understanding of a species as a group of reproductively isolated individuals within which there is variation. This effort has already been concluded for four of the six taxa considered *Golfingia* subgenera in Cutler and Murina (1977): *Mitosiphon* (Cutler 1979), *Golfingiella* and *Siphonoides* (Cutler et al. 1983), and *Thysanocardia* (Gibbs et al. 1983). The remaining group (*Golfingia* sensu stricto) is currently being revised and will be presented in the near future.

The genus *Nephasoma* is more difficult than many because of the small size of adult worms (many with diameters less than 1 mm) and the paucity of obvious characters. Many of the 'useful' features are located on the distal end of the introvert which is only rarely extended in preserved material (hook size/shape/arrangement and tentacle number/form). This genus is also very common (hundreds of individuals per sample) in deep-water collections made in recent years.

The need for a useful and biologically valid classification is especially pressing. This preliminary effort is directed towards this need.

In the following text we use these abbreviations for the indicated institutions: Zoological Museum, University of Bergen (ZMUB); British Museum of Natural History, London (BMNH); National Museum of Natural History, Washington (USNM); Zoological Institute, Academy of Sciences, Leningrad (ZIAS); Museum für Naturkunde, Berlin (MNHU); Irish National Museum, Dublin (INMD); Institut voor Taxonomische Zoölogie, Amsterdam (ZMUA).

### Remarks on the '*minutum*' Section

Since the early part of this century biologists have been confounded by one subset within this group of worms, i.e., those with reduced tentacular lobes, small, scattered, transparent, possibly deciduous hooks, normal body proportions, a nondistinct internal anatomy, and no unique external feature. This paper retains several names which have, at various times, been included in this complex. Now that *N. minutum* has been more narrowly defined (Gibbs 1975, 1977a) and *N. abyssorum* can be distinguished, we are left with *N. diaphanes* (with a new subspecies) and *N. lilljeborgi*. While these may be conspecific, only subsequent work using different methods of analysis will tell with any certainty. When one has only a few animals, some large and smooth and others small and papillated, it is easy to separate them into two sets. However, when one is working with hundreds of specimens the distinctiveness blurs and it becomes very difficult to draw a clear line. In terms of almost all the 'standard' characters, these taxa are identical, but after long deliberation we have decided to retain the two names (adding one subspecies) with much ambivalence. The written descriptons of these taxa cannot adequately communicate what one sees and is only an approximation.

Anyone conducting zoogeographical analyses of marine animals would be wise to exclude these species (as well as all their junior synonyms, especially *N. minutum*) from their works. There has been so much confusion over the years that it would be necessary to reexamine each collection in order to revalidate them within the current usage.

### *Nephasoma* Pergament, 1946

*Type species.*—*Nephasoma marinki* Pergament, 1946 [=*Onchnesoma glaciale* Danielssen & Koren: Cutler & Murina, 1977; =*Phascolosoma lilljeborgii* Danielssen & Koren: Gibbs, 1977] by monotypy.

*Diagnosis.*—Species generally small- to medium-sized (trunk less than 5 cm in length). Introvert about equal to, or shorter than, trunk. Hooks present, usually scattered (arranged in rings in *N. rimicola* (Gibbs), in spirals in *N. abyssorum* (Koren and Danielssen)). Body wall with continuous muscle layers. Oral disk carrying tentacles arranged around the mouth but tentacles may be reduced in both size and number and restricted to dorsal region. Two introvert retractor muscles often partially fused. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia.

This genus now contains all those species previously assigned to the *Golfingia* subgenus *Phascoloides* Fisher, 1950, since *Nephasoma* Pergament has been shown to have priority over *Phascoloides* (Cutler and Murina 1977). The endings of some species names have been modified in accordance with the ICZN as *Nephasoma* is a neuter name.

### Morphological Characters of *Nephasoma*

In their description of species, biologists have used a variety of morphological characters to differentiate these entities. These descriptions were legitimate attempts but not always based on a good understanding of possible variation within a population (species). In this section we evaluate these

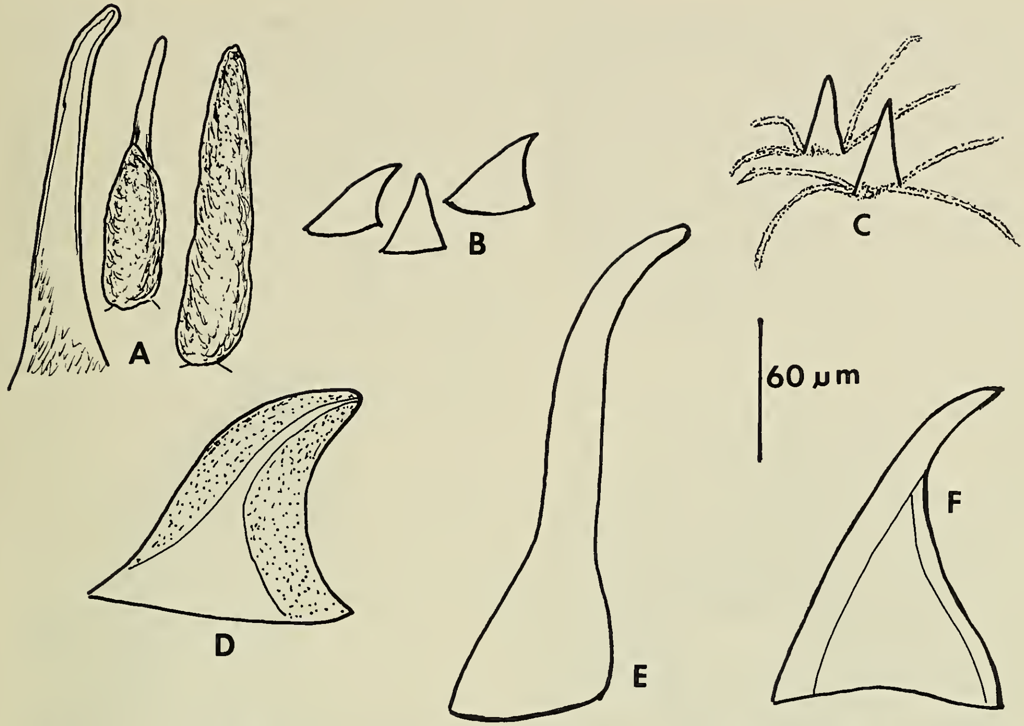

Fig. 1. Introvert hooks of *Nephasoma* species; A, *N. laetmophilum* (after Fisher 1952); B, *N. minutum*; C, *N. multiareneusa*; D, *N. confusum*; E, *N. constricticervix*; F, *N. abyssorum*. All drawn to same scale.

characters in light of our experience with large sample sizes.

*1. Introvert hooks.*—The presence or absence of hooks on the distal portion of the introvert throughout the life of a worm has been presumed to be a species–specific character by many, but not all authors (e.g., Gerould 1913; Selenka 1885; Southern 1913: 22). Our experience confirms the suggestions that while this may be true in some cases there are many species which have hooks as young individuals but lose them with age. For example, *N. abyssorum* seems to retain its hooks throughout its life and *N. eremita* is said to never have hooks. Our concern, which can only be answered by breeding and rearing worms, is: If one had young *N. eremita* in hand which did have hooks, one would probably put another name on it, i.e., that of a hooked species. Contrariwise, if there are large *N. abyssorum* without hooks, one would be inclined to identify these as some hookless species. An additional problem arises if one has an incomplete/damaged worm or one which is regenerating an introvert missing as the result of predation.

There are some useful attributes when hooks can be seen. A few species have very characteristic shapes or sizes (see *N. confusum, N. constricticervix,* or *N. multiaraneusa*) or unique arrangements (*N. abyssorum, N. rimicola*). However, most species have small, bluntly triangular, transparent, scattered hooks about 20–40 µm tall. There are six species with hooks 50–150 µm tall (*N. abyssorum, N. confusum, N. cutleri, N. laetmophilum, N. rimicola, N. schuttei*), and only two with hooks frequently more than 150 µm tall (*N. vitjazi* and *N. constricticervix*).

While we are uncertain and skeptical, our operational assumption is that three sets of species exist within this genus: Those which

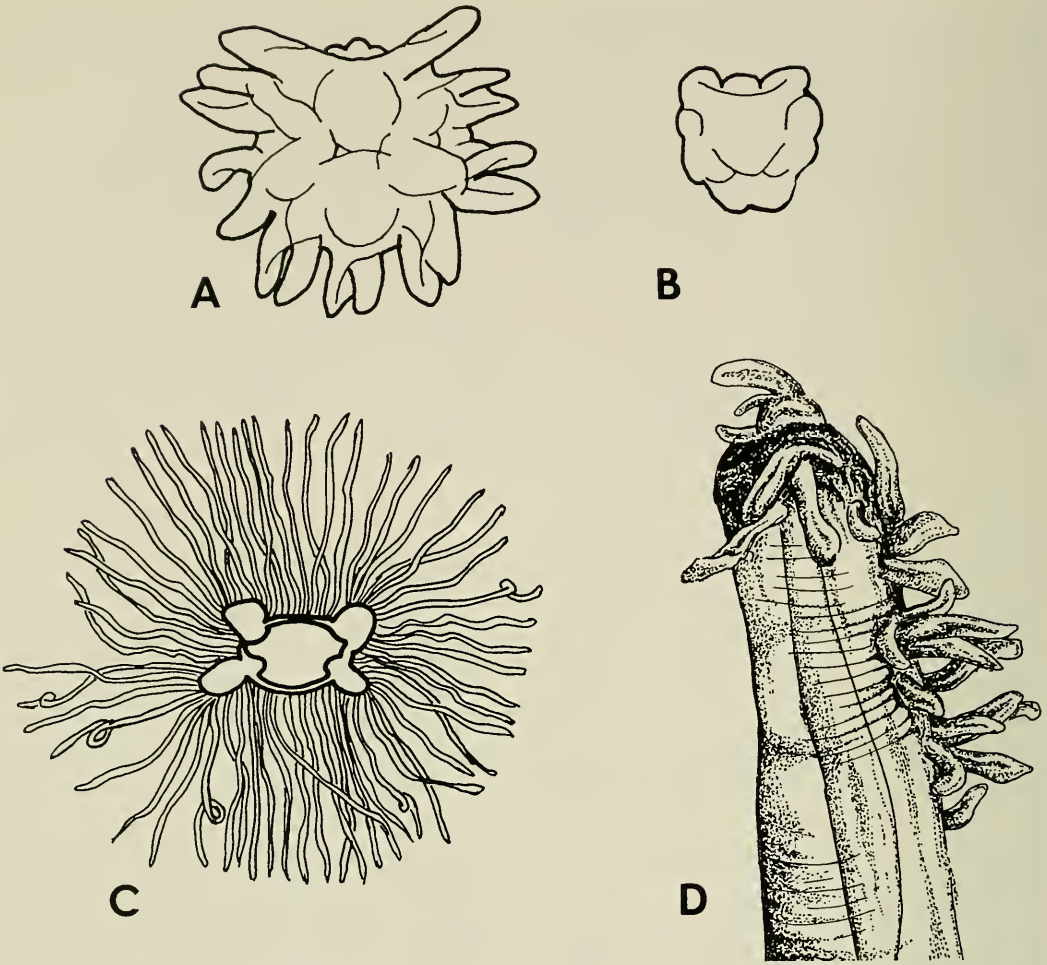

Fig. 2. Tentacles of *Nephasoma* species; A, *N. rimicola*; B, *N. minutum* (A and B from Gibbs 1977a); C, *N. novaezealandiae* (after Benham 1904); D, *N. rutilofuscum* (from Cutler and Cutler 1979a).

never have hooks, those which have hooks throughout their lives, and those with deciduous hooks. To use the absence of hooks in a few individuals, by itself, to establish a new species would be a mistake.

*2. Tentacles.*—Most members of this genus have one of two general types of tentacular arrays. About half the species have a 'normal' crown of flattened, digitate tentacles (more than 10, number increasing with age, Fig. 2A), while the other half have few (eight or less) short, lobate tentacles. Often these latter species exhibit only two tentacles plus four to six small lobes (Fig. 2B). There are two with unique arrangements (see *N. novaezealandiae* and *N. rutilofuscum,* Fig. 2C, D). In summary, this character can be helpful if it can be seen. A major problem is that most preserved specimens do not have their introverts extended and it is very difficult accurately to interpret the morphology of these structures in dissected material, especially since most have introverts less than 0.5 mm in diameter.

*3. Caudal appendage.*—This is an easily seen character. It is best exhibited in *N. flagriferum* as a thin, rat-like tail. In *N. bulbosum* it is less clearly set off and more like a narrowed tapered portion of the trunk, not an appendage. The posterior end of the trunk in the other species may form a conical point (like a blunt pencil) but not a tail.

*4. Trunk length to width ratio.*—These species fall into two general groups; elongate, slender worms (trunk length more than 10 times the width) and the shorter, stouter worms (length less than 6–8 times the width). Due to the ontogenetic or elastic properties of these worms there may be wide variation in this ratio. One must also be sure the trunk one is measuring has not been damaged/truncated. Except in a very general way, this measurement is of minimal value to the taxonomist and can be misleading if interpreted too narrowly.

*5. Introvert length.*—This body region ranges from ⅕ (in *N. constricticervix*) to twice the trunk length in a few species. Most species have introverts shorter than the trunk (0.4–0.8 ×). When the introvert is retracted or only partially extended, this measurement will be shorter than it would be if the introvert was completely extended due to its extreme elasticity. This character can have limited usefulness if accurately determined. Some confusion has resulted from how this measurement is made. Our practice is to use the nephridiopores to mark the anterior end of the trunk so that anything anterior to this point is considered introvert (in taxa where the anus is anterior to the nephridiopores the anus is used instead). Earlier authors have been less explicit and therefore one cannot be certain what they considered to be the introvert. Another often overlooked issue is an ontogenetic one. It is clear that the trunk grows faster than the introvert, so that as a worm ages, the introvert appears to get shorter, i.e., represent a smaller fraction of the total length (see Appendix).

*6. Anus/nephridiopores relationship.*—The middorsal anus usually is located at the anterior end of the trunk as are the pair of ventrolateral nephridiopores. There may be a small but measureable difference in the relative position of these openings. The nephridiopores are at essentially the level of the anus in most species in this genus. In six species these pores are anterior to the anus, commonly by 3–10% of the trunk length (see *N. flagriferum* in Appendix). Seven species are reported to have their nephridiopores posterior to the anus. In small worms where this distance is less than 1 mm the decision is subjective as to whether or not they are at the same level. This can be a useful character for some species.

*7. Papillae distribution, size, and shape.*—As with other genera these secretory organs are more concentrated and larger at the two ends of the trunk, sparser and smaller in the center. There are two basic morphs in these taxa; most species have low, inconspicuous 'skin bodies.' There are only a few species with well developed, obvious, mammiform papillae. The shape of these structures, when present, is quite variable and should not be considered taxonomically useful. It seems likely that a genetic potential for producing papillae exists and the degree to which this is expressed is determined by the nature of the microhabitat an individual occupies, i.e., analogous to human calluses.

*8. Shields.*—This term has caused much confusion within this phylum. In the Aspidosiphonidae there is a hardened epidermal structure (calcium or scleroprotein?) at the anterior end of the trunk (sometimes posterior also). This same term has been used to describe a very different situation in this genus, i.e., an aggregation of close-packed papillae around the distal ends of the trunk giving it a dark, rugose appearance. This condition is very different from a shield as used in other genera and the use of this term is misleading and should not be used in this taxon. These epidermal papillae may be gathered into longitudinal ridges and darkly pigmented (e.g., *N. vitjazi* or *N. wodjanizkii*). In addition, under certain conditions, the anterior end of the trunk is pulled in to give a flattened appearance accentuating this pseudoshield morph.

*9. Spindle muscle.*—In most sipunculans there is a thin thread-like muscle running through the gut coil and connecting to it at intervals. In some genera it extends through and out of the posterior end anchoring the coil to the posterior end of the trunk. In many, it extends out of the anterior end of the coil, along the rectum, and attaches to the body wall just anterior to the anus. However, there are several variations on this theme. In *Nephasoma* the muscle does not extend beyond the posterior end of the coil and in most species it does not extend beyond the anterior end either. In a few species one can see the muscle coming out the anterior end but it quickly terminates on the wall of the rectum. In a few (e.g., *N. flagriferum*) this muscle is well developed, sometimes branching, and extends from the rectum on to the body wall near or anterior to the anus. In a few species (e.g., *N. abyssorum, N. lilljeborgi*) one can rarely find any trace of the spindle muscle. One does find variation within a population (see *N. constrictum* in Appendix) and in small worms it is very difficult to find, even when present. Therefore, the taxonomic value of this character is limited as most species have a similar condition, it is not well developed in small individuals, and it is not consistently present within a population so that its apparent absence in an individual can be misleading.

*10. Retractor muscles' point of origin.*—The muscles that insert behind the 'head' and function to retract the introvert have their origins on the inner surface of the trunk wall. The position of this attachment along the anterior/posterior axis has been assumed to be of value. The most common condition is for these muscles to originate between 30–70% of the distance towards the posterior end of the trunk. Within a species this relative position may vary as the worm increases in size (appearing to move anteriad with an increase in trunk length, see Appendix). There are four species having these origins in the 15–30% range (*N. constricticervix, N. novaezealandiae, N. tasmaniense, N. vitjazi*) and three with their origins between 75–90% of the distance to the posterior end of the trunk (*N. filiforme, N. rutilofuscum, N. wodjanizkii*).

*11. Intestinal coiling.*—Most species have a tightly wound double helix but some of the elongate, slender species have this helix stretched out or loosely wound with space between the individual coils easily seen. This coiling seems to be a constant difference. What is not constant is the number of coils. This is clearly correlated to the size of the animal and not a species–specific character (see Appendix; also Ditadi and Migotto 1981).

*12. Intestinal fixing muscles.*—The number of fine, thread-like muscles attaching the gut coil to the body wall varies from 0–7 according to published accounts. This has been alleged to be a species–specific character but our experience suggests that A: these are very fragile structures and can be easily broken, and B: these are easily overlooked and even if present not mentioned by certain authors, and C: The number of muscles within one population does vary (see Appendix). In a population of 52 *N. confusum* examined by Ditadi and Migotto (1981) most had five of these muscles but the range was one to seven. Therefore, we place very little weight on this feature.

*13. Rectal caecum.*—This is not a useful character for two reasons. Given the small size of many of these worms and the difficulty of dissection, even if it was present it could be easily overlooked. Many authors simply do not mention its presence or absence. Also, in populations where this is present some individuals may lack it—which does not exclude the individual from this species; there is variation. However, there are species which consistently lack one (*N. constrictum*) while others seem to consistently have one (*N. flagriferum*) so in a few particular cases it may be helpful as a diagnostic character.

## Key to *Nephasoma* Species

1. Posterior end of trunk with caudal appendage (tail) ................ 2
– Posterior end of trunk rounded or bluntly pointed ................ 3

2. Posterior end of trunk with large papillae, and tail thin, whiplike ........................ *N. flagriferum*
– Posterior end of trunk without large papillae, and tail formed from narrowed portion of trunk .. *N. bulbosum*
3. Trunk rusty-red ..... *N. rutilofuscum*
– Trunk white, yellow, or brown; not red .......................... 4
4. Trunk with obvious, pigmented, raised papillae ................ 5
– Trunk may have papillae (skin bodies) but these are unpigmented and barely raised above the surface 7
5. Tentacles present, papillae uniformly distributed all over trunk, trunk length rarely exceeds width by more than 8 times (stout cylinder or flask shaped), shallow to bathyal depths ................ 6
– Tentacles reduced to lobes, papillae rare in midtrunk, trunk length commonly exceeds width by more than 8 times (slender cylinder), deep, cold water .. *N. diaphanes*
6. Trunk flask shaped, anus on narrowed anterior region which usually also exhibits an indented constriction, nephridia posterior to the anus ............... *N. constrictum*
– Trunk sausage shaped, nephridia not posterior to anus .. *N. pellucidum*
7. Elongate, very slender transparent trunk, sometimes threadlike (trunk width usually less than ⅒ the length), gut with separated coils and no spindle muscle ............. 8
– Cylindrical translucent or opaque trunk (trunk width rarely less than ⅒ the length), gut coils close together, spindle muscle usually present ...................... 13
8. About 30 dark longitudinal epidermal ridges at anterior end of trunk sometimes giving the impression of a hardened pseudoshield ..................... 9
– Anterior end of trunk without dark epidermal ridges .............. 10
9. Retractor muscles originate in anterior ⅓ of trunk, introvert less than ⅓ trunk length, distal hooks over 150 $\mu$m ................. *N. vitjazi*
– Retractor muscles originate in posterior third of trunk, introvert ½–7 times the trunk length, distal hooks less than 25 $\mu$m ............................. *N. wodjanizkii*
10. Anterior end of trunk in shape of short cone with epidermal ridge around base of cone (Fig. 3C) ........................ *N. tasmaniense*
– Anterior end of trunk not cone shaped but often swollen around nephridiopores ................ 11
11. Introvert longer than trunk (Fig. 3A), retractor muscles originate from 35–50% of distance to posterior end, hooks less than 30 $\mu$m ..................... *N. capilleforme*
– Introvert shorter than trunk, retractor muscles originate from 15–30% of distance to posterior end, distal hooks more than 100 $\mu$m 12
12. Introvert less than 25% trunk length, distal hooks exceed 200 $\mu$m ................ *N. constricticervix*
– Introvert 50–75% trunk length (Fig. 3B), distal hooks 150 $\mu$m or less .. ........................ *N. cutleri*
13. Hooks in distinct rows around introvert ................ *N. rimicola*
– Hooks, if present, not in rings .. 14
14. Hooks with unusual series of radiating filaments from base (Fig. 1C) .............. *N. multiaraneusa*
– Hooks, if present, without basal filaments ...................... 15
15. Retractor muscles originate in posterior ¼ of trunk ....... *N. filiforme*
– Retractor muscles originate in middle ⅓ of trunk ............ 16
16. Tentacular crown reduced to short lobes, dorsal pair largest ........ 17
– Normal array of digitiform tentacles present .................. 19
17. Hermaphroditic species from shallow, Northeastern Atlantic Ocean,

trunk length usually 4–5× diameter .................. *N. minutum*
- Dioecious species, trunk length 6–10× diameter .................. 18

18. Larger, opaque, from bathyal depths ................ *N. lilljeborgi*
- Smaller, transparent/translucent, bathyal and abyssal depths ........................... *N. diaphanes*

19. Medium sized (more than 50 $\mu$m) dark hooks present ............ 20
- Hooks apparently absent ....... 22

20. Hooks in spiral arrangement, unique shape (Fig. 1F) *N. abyssorum*
- Hooks scattered ................ 21

21. Hooks robust and blunt (Fig. 1D) ....................... *N. confusum*
- Hooks tall, spinelike with soft cortical layer (Fig. 1A) *N. laetmophilum*

22. Less than 50 digitiform tentacles, introvert 1–2 times trunk length .. ......................... *N. eremita*
- More than 50 threadlike tentacles, introvert less than ½ trunk length ................ *N. novaezealandiae*

## Taxonomic Section

This section has those species we consider to be valid arranged alphabetically. Following this is a section including the species placed in incertae sedis, species inquirendum or moved to other genera (see Table 1).

### *Nephasoma abyssorum* (Koren and Danielssen, 1875)

*Phascolosoma abyssorum* Koren and Danielssen, 1875:129–130.—1877:131–132.—Selenka et al., 1883:30–31.—Fischer, 1895:14; 1925:16; 1929:471–472.—Théel, 1905:78.—Gadd, 1911:88–89.—Southern, 1913:27–28.—J. Fischer, 1914:99–100.—Wesenberg-Lund, 1933: 9–11.

*Phascolosoma abyssorum* var. *punctatum* Herubel, 1925:261–262.

*Golfingia abyssorum.*—Wesenberg-Lund, 1955:201.—Murina, 1964a:220–221; 1964b:56–57; 1968:195.—Stephen and Edmonds, 1972:134–135.—Cutler and Cutler, 1980b:452.—Gibbs, 1982:121.—Cutler et al., 1984:268–269.—Saiz-Salinas, 1984:182–183.

Not *Physcosoma* (=*Phascolosoma*) *abyssorum* Southern 1913:12.

*Phascolosoma incompositum* Sluiter, 1912: 16–17, pl. 1, figs. 9–10.

*Golfingia incomposita.*—Stephen and Edmonds, 1972:145–146.

*Nephasoma incompositum.*—Gibbs, 1986: 339–340.

*Material examined.*—*N. abyssorum*: ZMUB, type; other recently collected North Atlantic specimens. *G. incomposita*: ZMUA, type. *G. benhami*: BMNH, type.

In general shape and appearance (smooth, white, sometimes iridescent trunk) this species resembles *N. lilljeborgi* and *N. minutum.* It is distinguished by having developed tentacles and unique, spirally arranged, medium-sized, dark hooks (50–150 $\mu$m). While this species is alleged to lack a spindle muscle we did observe a weakly developed muscle within the gut coil in two out of eleven specimens closely examined.

Herubel (1925) described a variety (*P. a. punctatum*) which Stephen and Edmonds (1972) elevated to subspecific rank. Since the reference material cannot be located and the putative difference (small elliptical papillae scattered thinly over the trunk) is so slight, we have reduced this taxon to the status of a junior synonym of the nominate form.

The single specimen of *N. incompositum* has the iridescent skin, dark recurved hooks and bathymetric range of *N. abyssorum.* Therefore, we concur with Gibbs (1986) in reducing it to the status of a junior synonym.

*Distribution.*—Common in northeast Atlantic and Arctic oceans, rare in northwest Atlantic and Pacific oceans, and Mediterranean Sea at bathyal and abyssal depths.

Table 1.—Species considered and proposed taxonomic changes.

| Present name | Proposed name |
|---|---|
| *Nephasoma abyssorum* (Koren and Danielssen, 1875) | No change |
| *Nephasoma benhami* (Stephen, 1948) | *N. abyssorum benhami* |
| *Nephasoma bulbosum* (Southern, 1913) | No change |
| *Nephasoma capilleforme* (Murina, 1973) | No change |
| *Nephasoma chuni* (Fischer, 1916) | incertae sedis |
| *Nephasoma cinctum* (Gerould, 1913) | *N. diaphanes diaphanes* |
| *Nephasoma cinereum* (Gerould, 1913) | *N. pellucidum pellucidum* |
| *Nephasoma confusum* (Sluiter, 1902) | No change |
| *Nephasoma constrictum* (Southern, 1913) | No change |
| *Nephasoma constricticervix* (Cutler, 1969) | No change |
| *Nephasoma cutleri* (Murina, 1975) | No change |
| *Nephasoma delagei* (Herubel, 1903) | incertae sedis |
| *Nephasoma depressum* (Sluiter, 1902) | species inquirendum |
| *Nephasoma diaphanes* (Gerould, 1913) | *N. diaphanes diaphanes* |
| *Nephasoma elachea* (Fisher, 1952) | *N. eremita* |
| *Nephasoma elisae* (Murina, 1977) | *N. wodjanizkii elisae* |
| *Nephasoma eremita* (Sars, 1851) | No change |
| *Nephasoma filiforme* (Sluiter, 1902) | No change |
| *Nephasoma fimbriatum* (Sluiter, 1902) | species inquirendum |
| *Nephasoma flagriferum* (Selenka, 1885) | No change |
| *Nephasoma glacialis* (Koren and Danielssen, 1880) | *N. lilljeborgi* |
| *Nephasoma improvisa* (Théel, 1905) | *N. minutum* |
| *Nephasoma incompositum* (Sluiter, 1912) | *N. abyssorum* |
| *Golfingia intermedia* (Southern, 1913) | *Phascolion strombus* |
| *Nephasoma laetmophilum* (Fisher, 1952) | No change |
| *Nephasoma lilljeborgi* (Danielssen and Koren, 1880) | No change |
| *Golfingia macra* (Sluiter, 1891) | *Aspidosiphon macer* |
| *Nephasoma marinki* Pergament, 1940 | *N. lilljeborgi* |
| *Nephasoma minutum* (Keferstein, 1863) | No change |
| *Nephasoma mucidum* (Sluiter, 1902) | *N. filiforme* |
| *Nephasoma multiaraneusa* (Murina, 1967) | No change |
| *Nephasoma nicolasi* (Thompson, 1980) | *N. wodjanizkii wodjanizkii* |
| *Nephasoma novaezealandiae* (Benham, 1904) | No change |
| *Golfingia pavlenkoi* (Ostroumov, 1909) | *Thysanocardia nigra* |
| *Nephasoma pellucidum* (Keferstein, 1865) | *N. pellucidum pellucidum* |
| *Nephasoma prioki* (Sluiter, 1881) | *Thysanocardia nigra* |
| *Nephasoma rimicola* (Gibbs, 1973) | No change |
| *Nephasoma rutilofuscum* (Fischer, 1916) | No change |
| *Nephasoma schuttei* (Augener, 1903) | No change |
| sensu Cutler and Murina | *N. diaphanes corrugatum* |
| *Nephasoma sluiteri* (tenBroeke, 1925) | *N. pellucidum pellucidum* |
| *Nephasoma subhamatum* (Sluiter, 1902) | *N. pellucidum subhamatum* |
| *Nephasoma tasmaniense* (Murina, 1964) | No change |
| *Nephasoma verrilli* (Gerould, 1908) | *N. pellucidum pellucidum* |
| *Nephasoma vitjazi* (Murina, 1964) | No change |
| *Nephasoma vitreum* (Roule, 1898) | incertae sedis |
| *Nephasoma wodjanizkii* (Murina, 1973) | *N. wodjanizkii wodjanizkii* |

### *Nephasoma abyssorum benhami* (Stephen, 1948), new status

*Phascolosoma benhami* Stephen, 1948:218–219, pl. 1, figs. 2–4.
*Golfingia benhami.*—Stephen and Edmonds, 1972:135–136.

The two bathyal Antarctic specimens of *G. benhami* are said to be similar to *N. lilljeborgi* differing only in papillae and hook size. However, our examination showed a much greater similarity to *N. abyssorum* with its larger, dark hooks and 'normal' tentacles. Stephen measured the body regions in the holotype from a point about 3 mm anterior to the nephridiopores. If one uses these pores to mark the anterior end of the trunk then the retractors are in the middle third, not posterior. The two specimens are 13 mm and 22 mm long. The presence of a spindle muscle within the gut coil (not extending out onto the rectum) and its location (no records of *N. abyssorum* in the southern latitudes) rule against combining these two taxa. Therefore, we have retained the name but reduced it to the rank of a geographically separated subspecies whose major morphological distinction is a strongly developed spindle muscle.

*Distribution.*—Off Kemp Land, Antarctica 600 m.

### *Nephasoma bulbosum* (Southern, 1913)

*Phascolosoma bulbosum* Southern, 1913:23–24, pl. 5, fig. 6.
*Golfingia bulbosa.*—Stephen and Edmonds, 1972:136.—Cutler, 1973:152–153.
*Nephasoma bulbosum.*—Gibbs, 1986:337.

*Material examined.*—INMD, Type material.

This taxon is similar to *N. flagriferum* in having a tail and papillae on the posterior end of the trunk but in both cases they are very much smaller in this species. The tail is not really a caudal appendage but more a narrowing of the trunk into a point. The nerve cord extends into the distal tip of this tail unlike the condition in *N. flagriferum.* Aside from the shape of the body this species is like *N. eremita* in many ways, including the apparent absence of hooks, and may be closely related.

*Distribution.*—Off Ireland and northeast United States at bathyal depths.

### *Nephasoma capilleforme* (Murina, 1973)

*Golfingia capilleformis* Murina, 1973a:943–944.—Frank, 1983:14–15.
*Golfingia glacialis.*—Murina, 1964b:57–59; 1974a:234.—Cutler and Cutler, 1980b:453–454.

*Material examined.*—ZIAS, Type material and other specimens identified by Murina; recently collected Atlantic Ocean worms.

This is one of the group of thin deep-water species with loosely wound gut coils. When present and extended the long introvert (1–2 times the trunk) and small hooks (20–25 μm) are diagnostic. In general this has the most elongate thread-like body of the genus and it is often irregularly contracted to give a beaded appearance. The anterior end of the trunk often is swollen and golden colored in the vicinity of the anus and nephridiopores.

*Distribution.*—Pacific and Atlantic oceans from 920–4900 m.

### *Nephasoma confusum* (Sluiter, 1902)

*Phascolosoma confusum* Sluiter, 1902:38–39, pl. 3, fig. 5.
*Golfingia confusa.*—Murina, 1957:993–994; 1972:298–299; 1974a:234; 1978:123.—Stephen and Edmonds, 1972:138–139.—Cutler and Cutler, 1980c:199–200.—Ditadi and Migotto, 1981:125–134.—Cutler et al., 1984:269.
*Golfingia confusa zarenkovi* Murina, 1974b:1716–1717, fig. 3.

*Material examined.*—ZMUA, Type specimen; 2 specimens from Japan; ZIAS, Murina's subspecies holotype.

This species has been redescribed in detail by Ditadi and Migotto (1981) on the basis of 106 specimens ranging in length from 2.5–25 mm. The scattered hooks are medium sized (up to 90 μm) and have a distinctive rim of reinforcing chitin. The skin lacks papillae but does have round skin bodies. In their paper Ditadi and Migotto (1981: 131–132) compare this species to *N. cinereum* but it is our belief, based on an examination of the type, that their interpretation of the papillae/skin bodies and hooks was in error. *Nephasoma cinereum* does not have this type of hook and does have distinct papillae. Therefore, following the lead of Cutler and Murina (1977) we consider it to be a junior synonym of *N. pellucidum.*

Murina's subspecies was described from two specimens of 4 mm and 5 mm. The supposed differences from the nominate form are due to its small size and these individuals do not warrant subspecific rank.

*Distribution.*—Around the Antarctic, off Brazil, southern Australia, Indonesia, and the northwest Pacific Ocean from 4–4600 m.

### *Nephasoma constrictum* (Southern, 1913)

*Phascolosoma constrictum* Southern, 1913: 25–27, pl. 6, fig. 7.

*Golfingia constricta.*—Stephen and Edmonds, 1972:139.

*Nephasoma constrictum.*—Gibbs, 1986: 337.

*Material examined.*—INMD, Type specimens; several recently collected specimens from near the type locality.

This species shares many attributes with *N. pellucidum* but differs most notably by the flask-shaped trunk, short stubby tentacles and the constriction at the introvert/trunk junction. The Appendix contains morphological information on 17 worms ranging in trunk length from 7–30 mm. The known distribution is distinct and limited.

*Distribution.*—Off Ireland at 1100–1300 m plus unpublished records in northeastern Atlantic (35–51°N) at 1900–4000 m.

### *Nephasoma constricticervix* (Cutler, 1969)

*Golfingia constricticervix* Cutler, 1969:215–217; 1973:153.—Cutler and Cutler, 1980b:452; 1980c:200.

*Material examined.*—Type material plus several recently collected specimens.

This is one of two species in this genus which has hooks exceeding 200 μm. It is one of several elongate, slender deep-water members of this genus and if the introvert is withdrawn or broken off it can be difficult to identify with certainty (see discussion of *N. cutleri*). The range in hook size is from 40–250 μm and only the more distal hooks exceed 200 μm. Therefore, if only the smaller hooks are seen it is possible to mistake this for another species e.g., *N. cutleri.*

*Distribution.*—North Atlantic at 1500–5500 m. Unpublished records extend this to 22°S in the eastern Atlantic.

### *Nephasoma cutleri* (Murina, 1975)

*Golfingia cutleri* Murina, 1975:1087–1088; 1978:123.

*Material examined.*—ZIAS, Type material.

On paper this species has many similarities to *N. constricticervix.* However, the hooks are considerably smaller (less than 150 μm) and paler, the introvert is longer (50–75% of the trunk length, not 20–25%) and the worm is much less robust. This species has only been recorded from the Pacific Ocean while the other appears to be an Atlantic Ocean species.

*Distribution.*—Pacific Ocean from 40°S–11°N at abyssal depths.

### *Nephasoma diaphanes diaphanes* (Gerould, 1913)

*Phascolosoma diaphanes* Gerould, 1913: 395.

*Golfingia diaphanes.*—Cutler and Cutler, 1980b:452–453; 1980c:201–202.—Frank, 1983:15–16.—Cutler et al., 1984:269–270.

*Phascolosoma improvisum.*—Gerould, 1913:395–396.—Wesenberg-Lund, 1930: 32–34; 1939:22–23.

*Golfingia improvisa.*—Wesenberg-Lund, 1955:11; 1963:110–111.—Murina, 1958: 1625–1628; 1968b:197; 1971b:42; 1972: 300; 1973b:69; 1978:123.—Stephen and Edmonds, 1972:145.—Amor, 1975:113–115.—Edmonds, 1976:222–224.

*Phascolosoma minutum.*—Théel, 1911: 31.—Sluiter, 1912:10–11.—Fischer, 1922a:34; 1922b:237; 1929:464–467 (partim).—Wesenberg-Lund, 1930:30; 1932:9–10; 1937a:9–10; 1937b:12–13.

*Golfingia minuta.*—Wesenberg-Lund, 1955: 11; 1963:110–111.—Murina, 1957:994–995; 1958:1628–1634; 1968b:197; 1971b: 42; 1972:300; 1973b:69; 1974a:235; 1976:65; 1978:124.—Stephen and Edmonds, 1972:149–150.—Cutler, 1973: 155–159; 1977a:143.—Cutler and Cutler, 1979a:957–958.—Saiz-Salinas, 1984:183.

*Golfingia sectile* Murina, 1974a:228–230.

*Phascolosoma anceps.*—Sluiter, 1912:10.—Wesenberg-Lund, 1925:90.

*Phascolosoma cinctum* Gerould, 1913:398–400, pl. 59, fig. 6, text–fig. 8.

*Golfingia cincta.*—Stephen and Edmonds, 1972:137–138.

*Phascolosoma sabellariae.*—Gerould, 1913: 392–395.

*Material examined.*—USNM #8584, Gerould's other material, *G. cincta* type; hundreds of specimens from the East Coast of North America; ZIAS, type specimen of *N. sectile.*

As noted in the introduction to this section this taxon is very similar to *N. minutum* and *N. lilljeborgi* but is generally small (less than 10 mm), with a transparent/translucent body wall, cosmopolitan in deep water, and dioecious. Gerould (1913) first suggested using the name *diaphanes* for the western North Atlantic animals that matched the description of *P. minutum* but were not hermaphroditic (he used the name *Phascolosoma sabellariae* for that collection). However, it was not until Cutler and Cutler (1980c:201) that this idea was discussed, adopted, and the name *G. diaphanes* was formally used. We recently examined Gerould's specimens of *P. sabellariae* which now serve as the type series for this species and selected one sample for a lectotype.

The single *N. sectile* from 6200 m in the South Atlantic is not as slender as most members of this species (1.6 × 6.7 mm) but is within the range of possible variation and does not exhibit any unique set of features. Thus, we consider it to be a junior synonym of this species. In Cutler (1973) *G. cincta* was placed in synonymy with *G. minuta* but since the recent redefinition of the latter, *G. cincta* must now be considered a junior synonym of this species.

*Distribution.*—Cosmopolitan, cold water, most from bathyal and abyssal depths.

### *Nephasoma diaphanes corrugatum,* new subspecies

*Golfingia schuttei.*—Murina, 1964a:238–242; 1967c:54; 1971a:81; 1971b:43; 1973b:69–70; 1974a:235; 1978:124.—Cutler and Cutler, 1980b:453; 1980c: 204.—Frank, 1983:17–18.

*Description.*—These pear- to cylindrical-shaped animals have trunks up to 10 mm long (occasionally up to 30 mm). The skin is tan to greyish-brown, translucent to opaque, with irregular, longitudinal epidermal ridges (wrinkles or folds) commonly on the base of the introvert and the anterior part of the trunk (occasionally extending to the posterior end). Often there are papillae on the posterior end which may be darker than the surrounding skin. The introvert is about equal in length to the trunk but may vary from 50–150% of the trunk length, and bears small (usually 20–30 μm tall), scattered, pale, triangular hooks. The tentacular crown is reduced to a few (6–8) short lobes plus two longer dorsal tentacles similar to that in *N. minutum.*

Internally the ventral pair of introvert retractor muscles originate near the posterior end (75–85%) in small worms (less than 4 mm) but in the middle (50–70%) in larger ones. The pair of short free nephridia are at the level of, or just posterior to, the anus. The gut forms a double helix with a weakly developed spindle muscle within the coil, not extending onto the rectum. No fixing muscles or caeca were seen.

*Differential diagnosis.*—The main difference from the nominate form is the nature of the epidermis, this one having rough, opaque skin with wavy ridges, *N. diaphanes diaphanes* having smoother, translucent/transparent skin, although some do have raised, pigmented papillae, especially on the posterior third. The subspecific name reflects its ridged epidermal appearance.

*Type material.*—Deposited at the National Museum of Natural History (USNM) Washington, D.C., holotype USNM 98775, 10 paratypes USNM 98776.

*Remarks.*—This subspecies is not well defined and future systematists using other characters may reach different conclusions. The use of the name *N. schuttei* in the several works by Cutler and Murina listed in the synonymy is the result of looking at the original description and interpreting it too broadly. The deep waters of the world's oceans are densely populated with small members of this genus which have been intensively collected over the past two decades. A dependable and universally applied classification of this fauna is desirable, but not yet in our hands.

*Distribution.*—Atlantic and Pacific oceans and the Mediterranean and Red seas from 80–5900 m.

### *Nephasoma eremita* (Sars, 1851)

*Sipunculus eremita* Sars, 1851:197.

*Sipunculus* (*Phascolosomum*) *borealis* Quatrefages, 865:620.

*Phascolosoma boreale* Keferstein, 1865: 437–438.—Baird, 1868:84.—Diesing, 1851:555; 1859:760.—Verrill, 1874: 387.—Koren and Danielssen, 1877:134.

*Phascolosoma digitatum* Théel, 1875:11; 1905:72.

*Phascolosoma eremita.*—Selenka et al., 1883:35–36.—Fischer, 1895:17; 1914:10; 1922b:237; 1925:17; 1929:463–464.—Théel, 1905:72–74.—Gadd, 1911:88.—Sluiter, 1912:8.—Gerould, 1913:385–387.—J. Fischer, 1914:98–99.—Chamberlain, 1920:4.—Wesenberg-Lund, 1930: 28; 1932:67; 1937b:11–12.—Leroy, 1936: 425.

*Golfingia eremita.*—Stephen and Edmonds, 1972:141–142.—Cutler, 1973:150–152.—Cutler and Cutler, 1980a:1–2; 1980c:202–204.—Frank, 1983:16–17.

*Phascolosoma eremita australis* Benham, 1922:17–18.—Fischer, 1929:483.

*Golfingia eremita* var. *australe.*—Wesenberg-Lund, 1963:111.—Stephen and Edmonds, 1972:14.—Murina, 1972:299–300; 1974a:234.—Not Wesenberg-Lund, 1959:182–183.

*Golfingia eremita californica* Fisher, 1952: 396–397.—Stephen and Edmonds, 1972: 142.

*Phascolosoma eremita scabra* Gerould, 1913:387–388.

*Golfingia eremita scabra.*—Stephen and Edmonds, 1972:142.

*Golfingia elachea* Fisher, 1952:399–400, pl. 25, figs. 1–3.

*Material examined.*—USNM, types of *G. eremita californica, G. eremita scabra, G. elachea*; MNHU, *P. boreale* type; recently collected North Atlantic specimens.

This species appears to be one of the few members of this genus to lack hooks. However, as pointed out earlier, if only the young worms do have hooks (as has been shown for other members of this phylum) they probably would be identified as some other species. A study of the early life stages of this species would be most valuable. Mature worms have a stocky nonpapillated trunk, often with transverse grooves in the thick body wall, and the tentacles are well developed.

Fisher's single example of *N. elachea* from Baja California presumably differs from this species because it has seven fixing muscles. The present condition of the type precludes any confirmation of this. Fisher did not provide a differential diagnosis but did put this item in italics thereby stressing its importance to him. The number of fixing muscles is quite variable throughout this phylum and especially within this genus. We see no real differences here and therefore consider *G. elachea* to be a junior synonym.

The three subspecies listed in Stephen and Edmonds (1972) are not considered by us to merit such rank and are hereby reduced to junior synonyms. We reaffirm Cutler's (1973) observations about Gerould's dark variety *scabra* being an environmentally (not genetically) determined attribute. Benham's (1922) variety *australis* was based on a single worm and the primary distinction was the distribution and relative size of the papillae, not a solid basis. Fischer's (1929) record was simply a repeat of Benham's, not new material. Fisher's (1952) variety *californica* has a 'strong' spindle muscle and no functional contractile vessel. Our comparison of this material showed these structures to be near one end of their particular continuum but not outside the range found in Atlantic populations.

*Distribution.*—Common in the Arctic and North Atlantic, present in South Atlantic and Antarctic, rare in the eastern Pacific Oceans from 20–2000 m.

### *Nephasoma filiforme* (Sluiter, 1902)

*Phascolosoma filiforme* Sluiter, 1902:37–38, pl. 4, figs. 1–4.

*Golfingia filiformis.*—Stephen and Edmonds, 1972:143.

*Phascolosoma mucidum* Sluiter, 1902:40.

*Golfingia mucida.*—Stephen and Edmonds, 1972:150.

*Material examined.*—ZMUA, Type material of *N. filiforme* and *N. mucidum.*

The three *N. filiforme* specimens vary more than the description suggests, especially in the form of their papillae on the two ends of the trunk. Only one of these has long hairlike papillae on the front end and the mushroomlike form of the posterior papillae is an oversimplification. One additional problem concerns the location of the anus and nephridiopores. Thompson (1980) said that these openings were on the introvert and Sluiter reported the introvert length to be half that of the trunk. This confusion results from the fact that the circular muscles in the anterior part of the trunk and the proximal part of the introvert have contracted in an atypical fashion. This situation has been the cause for confusion in *N. marinki* also (see Cutler and Murina 1977). Our operational definition of the trunk/introvert junction being that region just anterior to the nephridiopores resolves this problem so that the trunk is 40 mm long (not 60) with an introvert 1.2 times longer in this worm. In the other two type specimens (trunk lengths 15 mm and 45 mm) the introvert is about 0.8 and 0.3 times the trunk length, hardly a constant species-specific character. This is not a solidly based species and needs some clarification and a larger data base but we propose no changes at this time.

There are also some problems with *N. mucidum.* Our measurements of the two remaining specimens showed their length (6 mm and 7 mm) exceeds their width by only three times, not 10. It is clear that these specimens are damaged and incomplete so these measurements are of limited value. The long papillae Sluiter mentioned are very few in number. The grey felt-like covering does not seem to be a part of the animal but rather some adhering substrate and very easily rubbed off. These animals came from the same location and we see no significant differences. Since *N. mucidum* appears later in the publication it becomes the junior synonym.

*Distribution.*—Off Indonesia (6°S, 134°E) at 1788 m.

### *Nephasoma flagriferum* (Selenka, 1885)

*Phascolosoma flagriferum* Selenka, 1885: 13–16, pl. 3, fig. 17.—Sluiter, 1900:12.—Fischer, 1914:10.—Gerould, 1913:391–392.

*Golfingia flagrifera.*—Murina, 1968b:196; 1978:123.—Stephen and Edmonds, 1972: 144.—Cutler, 1973:153–155; 1977a:142–143.—Cutler and Cutler, 1980b:453.

*Material examined.*—BMNH, Type specimen; many recently collected specimens.

The large vesicular, bulbous papillae on the posterior end of the trunk and the distinct caudal appendage make this species easy to identify and there is no confusion about its validity. The Appendix contains morphological information on 27 worms ranging in trunk length from 3.5–120 mm.

*Distribution.*—An abyssal species (few bathyal records) common in the North Atlantic, present in the South Atlantic and Pacific.

### *Nephasoma laetmophilum* (Fisher, 1952)

*Golfingia laetmophila* Fisher, 1952:397–399, pl. 25, figs. 4–6.—Stephen and Edmonds, 1972:148.

*Material examined.*—USNM, Type specimen.

This single bathyal California specimen has many characters in common with the Atlantic Ocean *N. abyssorum.* The larger number of tentacles (40) and the strong wing muscle may be important or may be artifacts of its larger size. The one striking difference is the nature of the hooks; they have a spine-like form with a cortical layer which can be easily rubbed off. Whether this single specimen is an anomaly or part of a biological population is an open question. It is puzzling why no additional specimens from this heavily sampled region have been recovered in the intervening decades. Despite our reservations we propose no change in the status of this species at this time.

*Distribution.*—Off southern California, 1900 m.

### *Nephasoma lilljeborgi*
### (Danielssen and Koren, 1880)

*Phascolosoma lilljeborgii* Danielssen and Koren, 1880:463–464; 1881:63–64.—Selenka et al., 1883:40–41.—Fischer, 1895: 14; 1929:471–472.—Sluiter, 1912:9.—Théel, 1905:79–80.

*Golfingia lilljeborgi.*—Wesenberg-Lund, 1954:9–10.—Stephen and Edmonds, 1972:148.—Gibbs, 1982:121–122.—Frank, 1983:17.

*Onchnesoma glaciale* Danielssen and Koren, 1880:464; 1881:64.

*Phascolosoma glaciale.*—Roule, 1896: 474.—Théel, 1905:80–81.—Fischer, 1929:472.—Wesenberg-Lund, 1930:30; 1932:8–9.

*Golfingia glacialis.*—Stephen and Edmonds, 1972:144.—Gibbs, 1982:119–120.—Not Murina, 1964b: 57–59; 1974a: 234.—Cutler and Cutler, 1980b:453–454.

*Nephasoma marinki* Pergament, 1940:55–61.—Stephen and Edmonds, 1972:214–215.

*Material examined.*—ZMUB, Type specimens of *N. lilljeborgi* and *N. glaciale*; other recently collected specimens from near the type-locality.

This taxon has recently been revised by Gibbs (1982). On paper there is very little to differentiate this taxon from *N. diaphanes.* The type material is larger (10–30 mm), more opaque, does not live in foraminiferan tests as many *N. diaphanes* do, and was collected from shallower water. The posterior end of the trunk in many worms comes to a blunt point or has a posterior nipple on a rounded base. This name has only been used a few times and only for specimens collected in the northeast Atlantic Ocean. *Nephasoma marinki* was synonymized in Cutler and Murina (1977). Since the recent reevaluation of this species it has been determined that Cutler and Murina had used this name for some *N. capilleforme.*

*Distribution.*—Far northeast Atlantic Ocean from bathyal depths.

### *Nephasoma minutum* (Keferstein, 1863)

?*Sipunculus johnstoni* Forbes, 1841:254.
*Phascolosoma johnstoni.*—Southern, 1913: 28.—Lindroth, 1941:449–450.
*Phascolosoma minutum* Keferstein, 1863: 40, pl. 3, figs. 7–10; 1865:438.—Cuenot, 1922:9–10.—Fischer, 1925:19–20; 1929: 464–467(partim).—Wesenberg-Lund, 1939:20–22.—Stephen, 1934:167–168.
*Petalosoma minutum.*—Selenka et al., 1883: 129.—Southern, 1908:83–86.—Paul, 1909:1–50.
*Golfingia minuta.*—Åkesson, 1958:33–46.—Stephen and Edmonds, 1972:149–150.—Gibbs, 1973:73–86; 1975:69–82; 1977a:16–17.
*Phascolosoma anceps* Théel, 1905:84–86.—Wesenberg-Lund, 1925:90.
*Phascolosoma improvisum* Théel, 1905:82–83, pl. 5, figs. 51–58, pl. 12, figs. 177–178, pl. 14, figs. 202–203.—Wesenberg-Lund, 1939:22–23.
*Golfingia improvisa.*—Stephen and Edmonds, 1972:145.
*Phascolosoma sabellariae* Théel, 1905:81.

*Material examined.*—Several recently collected specimens identified by P. Gibbs collected near the type locality.

This name has been used in a variety of ways over the past century. Gibbs (1977a: 79–80) has been the most recent to examine this situation and he redefined the taxon in a narrow way including only those from shallow water in the northeastern Atlantic Ocean which are hermaphroditic (see also Paul 1910 and Åkesson 1958). It is often very difficult to differentiate between several populations as discussed in the introduction and it is likely that very often this name has been used as a taxonomic wastebasket. The present definition still includes *N. improvisa,* i.e., those with larger darker papillae. Some of the uses of this latter name may actually refer to *N. diaphanes* but as noted above, without reexamining the actual specimens one cannot be certain. We here divide the records based on location assuming that this is correct most of the time.

*Distribution.*—Northeast Atlantic Ocean from shallow water.

### *Nephasoma multiaraneusa* (Murina, 1967)

*Golfingia multiaraneusa* Murina, 1967b: 1332–1333, fig. 2.—Stephen and Edmonds, 1972:151.

*Material examined.*—ZIAS, Type material.

The hooks are the unique attribute of this species. They are 15–30 μm tall with a series of radiating filaments from the base giving each hook a spider-like appearance. The single 2 mm specimen is not a solid basis for a species but we propose no change at this time. If future collections in this region do not uncover additional specimens the status of this worm should be reconsidered.

*Distribution.*—Cuba at 4 m.

### *Nephasoma novaezealandiae* (Benham, 1904)

*Phascolosoma novae-zealandiae* Benham, 1904:301–303, pl. 15, figs. 1–2, pl. 16, fig. 8; 1909:82.
*Golfingia novae-zealandiae.*—Edmonds, 1960:162–163.
*Golfingia novaezealandiae.*—Stephen and Edmonds, 1972:151.

*Material examined.*—None.

The type of this species was taken from the stomach of a dogfish and five years later a second worm was found in ooze. Edmonds added two more specimens, all four coming from near New Zealand. The trunk length ranges from 25–235 mm with introverts much shorter than the trunks. As noted by Edmonds this species is morphologically similar to *N. eremita* but because of its geographic separation, the large number of thin, thread-like tentacles, and large size, it has been considered a separate taxon. Subspecific rank may be more appropriate but we propose no change at this time.

*Distribution.*—Off New Zealand and Chatham Is. from 65–70 m.

### *Nephasoma pellucidum pellucidum* (Keferstein, 1865)

*Phascolosoma pellucidum* Keferstein, 1865: 433, pl. 32, figs. 26–27.—Baird, 1868: 86.—Selenka et al., 1883:32–34.—Shipley, 1899:155.—Sluiter, 1902:34.—Augener, 1903:299–300.—Lanchester, 1905: 28.—Southern, 1913:6.—Fischer, 1914:8; 1919:281; 1922a:17; 1923:23.—tenBroeke, 1925:83.—Leroy, 1936:425.

*Golfingia pellucida.*—Murina, 1968a:421–422; 1972:302–303.—Stephen and Edmonds, 1972:152–153.—Cutler, 1973: 159–162; 1977a:143; 1977b:152.—Cutler and Cutler, 1979b:105; 1980a:2.—Cutler and Murina, 1977:177.—Thompson, 1980:258.—Cutler et al., 1984:270.

*Sipunculus* (*Phascolosomum*) *pellucidus* Quatrefages, 1865:620.

*Phascolosoma riisei* Keferstein, 1865:437.—Baird, 1868:96.

*Phascolosoma cinereum* Gerould, 1913: 396–398, figs. 6–7.

*Golfingia cinerea.*—Stephen and Edmonds, 1972:138.

*Phascolosoma sluiteri* tenBroeke, 1925:84–86.

*Golfingia sluiteri.*—Stephen and Edmonds, 1972:156–157.—Cutler and Murina, 1977:177, 182.

*Phascolosoma verrillii* Gerould, 1908:488–489; 1913:388–391.

*Golfingia verrillii.*—Murina, 1964a:243–246.—Stephen and Edmonds, 1972:158.

*Golfingia coriacea.*—Fisher, 1950:551; 1952:396.—Not Murina, 1972:298.

Not *Phascolosoma coriaceum* Keferstein, 1865:432.

*Golfingia eremita* var. *australe.*—Wesenberg-Lund, 1959:181–182.

*Material examined.*—MNHU, Type specimens; numerous recently collected specimens; USNM, *G. cinerea* type, Fisher's specimens of *G. coriacea*; ZMUA, *G. sluiteri*; ZIAS, Murina's *G. coriacea*; UZMK, Wesenberg-Lund's *G. eremita* var. *australe.*

This species with large uniformly distributed papillae is well founded and widely distributed. In Cutler and Murina (1977) *G. sluiteri* was reduced to a junior synonym since it turned out to be merely *N. pellucidum* with its esophagus everted through the mouth. *Golfingia verrillii* was reduced in status in Cutler (1973).

*Golfingia cinerea* was alleged to be distinct because of its stouter trunk (length 3 vs. 5–9 times the diameter), a greater variety of papillae shapes, and the relationship between the nephridiopores and anus. Our analysis of some large collections showed there to be sufficient variation within one population to include this species. When Gerould erected this species he did not compare it to *N. pellucidum* nor did he record any from the U.S. east coast. Ditadi and Migotto (1981) suggested that *G. cinerea* should be considered a junior synonym of *N. confusum.* As discussed above we disagree and place it here.

In Cutler (1973) *G. coriacea* was synonymized with this species based on an examination of Fisher's material. While we still believe Fisher's worms to be this species, Keferstein's species name has been transferred to *Themiste* with some uncertainty due to the loss of the type material (Gibbs et al., 1983). Murina's specimens of this species are without doubt a *Themiste.*

Wesenberg-Lund's *G. eremita* var. *australe* bears distinct hooks and in other ways clearly resembles this taxon. Murina's (1972) record from near Prince Edward Island (Subantarctic waters) is based on three worms all less than 6 mm long. We have been unable to confirm this record and question its validity. Edmonds (1982) questions the validity of earlier *N. pellucidum* records from Australian waters and suggests that they are probably *N. schuttei.* In Thompson (1980) *G. pellucidum* is listed in a brief checklist but no morphological or location data are given. This is the only suggestion that it occurs in the eastern Pacific and one hopes for a fuller statement in the near future.

*Distribution.*—Shallow-water species (few bathyal records) from the Western Atlantic and Caribbean down to Brazil, in the South Pacific (Indonesia/Australia), southern Japan, and one record from Cape Town.

### *Nephasoma pellucidum subhamatum* (Sluiter, 1902), new status

*Phascolosoma subhamatum* Sluiter, 1902: 35–36, pl. 3, figs. 10–12.
*Golfingia subhamata.*—Stephen and Edmonds, 1972:157.—Cutler et al., 1984: 270–271.

*Material examined.*—ZUMA, Type specimens.

This taxon compares with the nominate form in most ways but is a bathyal western Pacific population (not shallow warm water). The only morphological feature which differs is that the hooks in this form are larger (100 vs. 60 μm) and thinner. The type material has not been preserved well and the internal organs are macerated. One of the worms from Sluiter's Sta 126 is a *Thysanocardia.*

*Distribution.*—Indonesia and central Japan at 440–2050 m.

### *Nephasoma rimicola* (Gibbs, 1973)

*Golfingia rimicola* Gibbs, 1973:74–80; 1977a:18.—Saiz-Salinas, 1980:54–56.

*Material examined.*—Several specimens from type locality identified by P. Gibbs.

This is the only species in the genus to have its hooks arranged in distinct rings, which serves to differentiate it from species such as the very similar *N. minutum.* It also has its anus posterior to the nephridiopores; *N. minutum* has the reverse relationship.

*Distribution.*—Southwest England and northern Spain in intertidal waters.

### *Nephasoma rutilofuscum* (Fischer, 1916)

*Aspidosiphon rutilofuscus* Fischer, 1916:17.
*Phascolosoma aspidosiphonoides* Fischer, 1922c:11–12, pl. 2, fig. 8.
*Golfingia rutilofusca* Fisher, 1952:395.—Stephen and Edmonds, 1972:153–154.—Cutler, 1977a:143–144.—Cutler and Cutler, 1979a:958–961.

*Material examined.*—MNHU, Type specimen; many recently collected specimens.

This western Indian Ocean species is the most distinctive member of this genus and may well merit separate generic rank if one chose to weight the unique tentacular crown more heavily; we do not at this time. The rusty red color makes this form easy to identify. The posterior end of the trunk sometimes appears shield-like but this is not permanent as it varies with body wall contraction. It may be misleading as it was for Fischer who originally placed it in the genus *Aspidosiphon.* See Cutler and Cutler (1979a:958–961) for a redescription and illustrations.

*Distribution.*—Western Indian Ocean from 1–1562 m.

### *Nephasoma schuttei* (Augener, 1903)

*Phascolosoma schuttei* Augener, 1903:335–337, figs. 17–18.
*Golfingia schuttei.*—Stephen and Edmonds, 1972:156.—Edmonds, 1980:25–27.—Not as per Cutler, Cutler and Cutler, or Murina.

*Material examined.*—MNHU, Type specimen.

This name has been widely misapplied in recent decades by Murina and Cutler. They have used the name for a small deep-water species very common in two major oceans (see *N. diaphanes*). This error became obvious when we examined the type. Edmonds' (1980) material and excellent description are correctly based on Augener's species. The large dark papillae and coarse skin are distinctive. Edmonds gives a detailed description and discusses the similarities to *N. pellucidum.* This is a distinct and valid species but the unfortunate confusion may continue to be a problem for some time until all workers understand and accept this narrower, original definition.

*Distribution.*—South and West Australia from intertidal waters.

*Nephasoma tasmaniense* (Murina, 1964)

*Golfingia tasmaniensis* Murina, 1964a:242–243, fig. 13a–b.—Stephen and Edmonds, 1972:157.

*Material examined.*—ZIAS, Two type specimens and one additional specimen identified by Murina.

Both type specimens are incomplete and damaged worms lacking introverts. What were described as tentacles are actually the broken introvert retractor muscles. The third worm (unpublished record from 9°S, 71°E at 2218 m) is intact with an extended introvert. Small pale hooks and a few reduced tentacles are present on a swollen, bulb-like terminal part of the short introvert (less than half the trunk length). The anterior 4 mm of the trunk has the conical shape with a collar at the base of the cone, as figured by Murina (total trunk length is 18 mm). The trunk/introvert junction is constricted into a narrow neck. This species has an uncertain foundation being based on two incomplete worms and the flawed description. The absence of any differential diagnosis is another problem.

In general size, shape, looseness of gut coil, constricted neck, and short introvert with bulbous tip, it resembles *N. constricticervix.* The hooks are much smaller and the collar at the base of the anterior cone may be diagnostic. In several ways this species is similar to other long, slender, deep-water members of this genus. A more adequate description and diagnosis is needed. In anticipation of this by Murina, we propose no change in the status of this species.

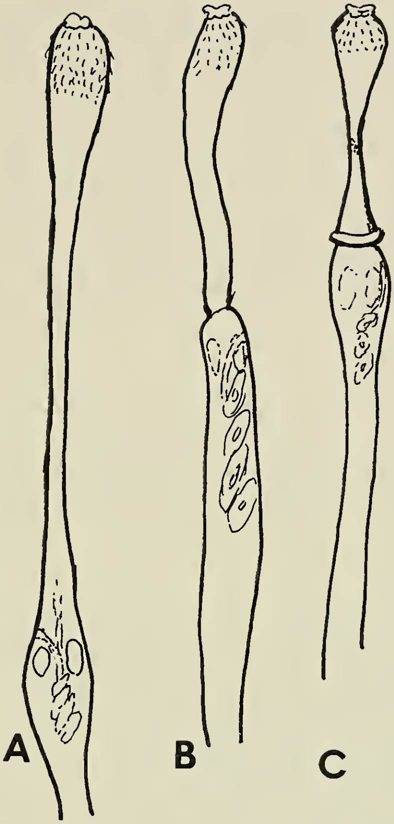

Fig. 3. Introvert and anterior end of three elongate, slender, deep-water *Nephasoma* species; A, *N. capilleforme*; B, *N. cutleri*; C, *N. tasmaniense.* Drawn as if trunk lengths were equal to show comparative lengths of introverts.

*Distribution.*—Tasman Sea at 1330 m.

*Nephasoma vitjazi* (Murina, 1964)

*Golfingia vitjazi* Murina, 1964a:246–248, fig. 16a–b.—Stephen and Edmonds, 1972:158.

*Material examined.*—ZIAS, Type specimen.

This single specimen is incomplete with a torn posterior end, and measures 15 × 0.08 mm. The anterior end has 30–35 parallel, longitudinal ridges forming what has been called a "shield." The 4 mm introvert bears large hooks (210–280 μm) which is unusual in this genus. While there is only this single specimen known, we propose no change in the status of this species.

*Distribution.*—Northwest Pacific Ocean at 4150 m.

### *Nephasoma wodjanizkii wodjanizkii* (Murina, 1973), new status

*Golfingia wodjanizkii* Murina, 1973a:944–945; 1973b:70.—Frank, 1983:18–19.
*Golfingia nicolasi* Thompson, 1980:951–956.

*Material examined.*—ZIAS, Type specimen and one other *N. wodjanizkii*; several specimens of *N. nicolasi* from type locality identified by B. Thompson.

This slender, bathyal species, with its two subspecies, has nephridia posterior to the anus, retractors originating in the posterior ⅕ and an introvert of varying lengths. In very young animals it is shorter than the trunk, it grows to two to three times the trunk in mature worms but in some populations, when completely extended, it may reach six to seven times the trunk length. Small hooks may be present and the tentacles are few and reduced.

The two *N. wodjanizkii* have 4 mm and 6 mm trunks with longitudinal lines along most of the trunk and part of the introvert. These worms were said to have indistinct shields at both ends of the trunk but we would not use this term. The introverts are about three times the trunk length but incompletely extended so nothing can be said about tentacles or hooks.

The California population of *Nephasoma nicolasi* is based on several hundred specimens with 7–36 mm trunks. The introverts range from 0.5 (in the smallest) to seven times the trunk length, longer than most species in this genus. No hooks have been seen. The introvert and the anterior end of the trunk have a series of longitudinally arranged fine brown lines (ridges in the epidermis).

A comparison of these two forms showed the differences to be artifacts of small sample size on the one hand and a failure to make a comparison on the other hand. When Thompson was analyzing his population he probably did not consider Murina's species since one had hooks and the other did not. There was also an apparent difference in trunk size and introvert length. Murina's use of the term shield could also have been misleading. It is our conclusion that these two taxa are conspecific and, despite the fact that Thompson's data base is superior his species must be submerged as a junior synonym.

*Distribution.*—Sea of Okhotsk, Peru-Chile Trench, and southern California from 1000–2400 m.

### *Nephasoma wodjanizkii elisae* (Murina, 1977), new status

*Golfingia elisae* Murina, 1977:133–134.
*Nephasoma elisae.*—Gibbs, 1986:338–339.

*Material examined.*—ZIAS, Type specimen; UZMK, cotypes; 2 specimens from the eastern Atlantic.

There are two problems with the description of this taxon: rather than the 11–13 longitudinal grooves forming the anterior shield there are 25–30; secondly, hooks have only been observed once (Murina) and appear to be deciduous, a feature shared with many species in this genus. A comparison of these two taxa, as corrected, shows them to be remarkably similar except that the introvert length in *N. w. elisae* is less than twice the trunk length. Our decision to retain this name at the subspecific rank was largely based on the fact that this represents the Atlantic Ocean population while the nominate form is a Pacific Ocean population.

*Distribution.*—Gulf of Guinea at 1520 m and from 43–58°N from 1600–2300 m in the northeast Atlantic Ocean.

## Species Names Transferred to Other Genera or Considered species inquirendum or incertae sedis

### *Nephasoma chuni* (Fischer, 1916)

*Phascolosoma chuni* Fischer, 1916:15; 1922c:9.

*Golfingia chuni.*—Stephen and Edmonds, 1972:136–137.—Murina, 1973b:68.

*Material examined.*—MNHU, Type specimen.

One of the two bottles in Berlin labelled *P. chuni* contained a poorly preserved nematode. The second bottle contained a worm with completely disintegrated internal organs except for the one pair of retractor muscles. Therefore, it is impossible to verify anything about its internal anatomy. Externally it resembles the *N. pellucidum* complex but there are too many unanswerable questions (see Stephen and Edmonds 1972:137) to do anything other than place this name on the list of incertae sedis.

### *Nephasoma delagei* (Herubel, 1903)

*Phascolosoma delagei* Herubel, 1903:100; 1907:115–117.

*Golfingia delagei.*—Stephen and Edmonds, 1972:139–140.

*Material examined.*—None.

In 1922 Cuenot treated this as a junior synonym of *Golfingia elongata.* Gibbs (1973) agreed but since the type has been lost he considered it to be indeterminable. We concur and place this name on the list of incertae sedis.

### *Nephasoma depressum* (Sluiter, 1902)

*Phascolosoma depressum* Sluiter, 1902:39–40.

*Golfingia depressa.*—Murina, 1964a:227–228.—Stephen and Edmonds, 1972:140.

*Material examined.*—ZMUA, Type specimen; ZIAS, Murina's (1964) specimen.

The type specimen has a 4 mm trunk, is poorly preserved, and the introvert is missing. Murina's worm is 2.5 mm long and she noted that her comparison was hampered by the 'poor intactness' of her worm and Sluiter's incomplete description. We place this name on the list of species inquirendum pending future clarification because of the poor condition of these two very small specimens and the puzzling nature of the descriptions.

### *Nephasoma fimbriatum* (Sluiter, 1902)

*Phascolosoma fimbriatum* Sluiter, 1902:34–35.

*Golfingia fimbriata.*—Stephen and Edmonds, 1972:143.—Murina, 1976:64.

*Material examined.*—ZMUA, Type specimen; ZIAS, two of Murina's worms.

This bathyal species is not solidly founded and the descriptions contain some discrepancies. The anterior part of the trunk is narrowed but by definition, the position of the nephridiopores coincide with the introvert–trunk junction. The nephridiopores open 2 mm posterior to the anus and not on the introvert. The introvert is retracted to an unusual degree so that the anterior 5 mm of the trunk is also retracted and while the introvert is shorter than the trunk (7 and 25 mm) this is not the normal condition. The papillae on the introvert are not unusually long. The retractor muscles originate very near the posterior end of the trunk (85–95%) which is not common in this genus.

Of greatest significance is the presence of contractile vessel villi. These structures are present but not on the free portion of the esophagus, only in the beginnings of the gut coil. We suspect that this is an artifact of the extreme state of contraction and in the extended state this portion of the gut would be uncoiled. This removes the ambiguity of earlier statements (Cutler and Murina 1977).

Although it is not extended the tentacular crown appears to be short festoons. These two features point towards *Thysanocardia* but the short introvert and anus–nephridiopore relationship do not fit that pattern. While we are inclined to place this in the synonymy of *T. nigra* we are hereby placing this name on the list of species inquirendum pending future clarification based on additional specimens.

### *Golfingia intermedia* (Southern, 1913)

*Phascolosoma intermedium* Southern, 1913: 3–5, pl. 1, figs. 1–8.—Stephen, 1948:219.

*Golfingia intermedia.*—Stephen and Edmonds, 1972:147.—Gibbs, 1977b:109–112.

*Material examined.*—None.

When Gibbs (1977b) examined the type material he concluded that these specimens are merely immature *Phascolion strombus.* We concur with that conclusion.

### *Golfingia macra* (Sluiter, 1891)

*Phascolosoma macer* Sluiter, 1891:114–115, pl. 2, figs. 13–14; 1902:34.

*Golfingia macra.*—Stephen and Edmonds, 1972:149.—Cutler and Murina, 1977: 183.

This species was discussed in Cutler and Murina (1977) after examining the type material. It clearly belongs in the genus *Aspidosiphon* and is an emended spelling of the original *P. macer.*

### *Golfingia pavlenkoi* (Ostroumov, 1909)

*Phascolosoma pavlenkoi* Ostroumov, 1909: 323.

*Golfingia pavlenkoi.*—Stephen and Edmonds, 1972:152.—Cutler and Murina, 1977:175.—Gibbs et al., 1983:301.

*Material examined.*—None.

Cutler and Murina (1977) discussed this species and concluded that it was a junior synonym of *Golfingia* (*Thysanocardia*) *catharinae.* However, when Gibbs et al. (1983) reviewed *Thysanocardia* and elevated it to generic rank, this species name went into the synonymy of *Thysanocardia nigra.*

### *Nephasoma prioki* (Sluiter, 1881)

*Phascolosoma prioki* Sluiter, 1881:152–153, pl. 1, figs. 5 and 9; 1891:115; 1902:34.—Selenka et al., 1883:37.—Selenka, 1885: 12–13.

*Golfingia prioki.*—Stephen and Edmonds, 1972:153.—Cutler, 1977b:153.

*Material examined.*—ZMUA, Type specimen.

This taxon has a very uncertain foundation. The first four references are all repetitions of the single holotype. Selenka's 1885 record was based on one additional worm. The three worms in Cutler (1977b:153) ". . . seem to fit this poorly known species." What has been overlooked is the presence of small but real contractile vessel villi and the nature of the tentacles which are withdrawn. At present, after our work on the genus *Thysanocardia,* it is clear that these four worms fit the criteria for that genus and are closest to *T. nigra.* The age and preservation history of the material makes positive identification difficult. The depth of Sluiter's worm (962 m) is also greater than other *T. nigra.* Nevertheless, *N. prioki* now becomes a junior synonym of *T. nigra.*

### *Nephasoma vitreum* (Roule, 1898)

*Phascolosoma vitreum* Roule, 1898:386; 1906:86–90.

*Golfingia vitrea.*—Stephen and Edmonds, 1972:158–159.

*Material examined.*—None.

The type and only representative of this species cannot be located and in the intervening 88 years no additional specimens fitting this rather peculiar description have been collected from these bathyal eastern

Atlantic waters. We therefore place this name on the list of incertae sedis.

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Appendix 1.—Certain morphological characters of *Nephasoma* species.

| Trunk length in mm | Introvert length as % trunk | # of gut coils | Nephridiopores anterior to anus by % of trunk | Origin of retractors (% of trunk) | Muscles | |
|---|---|---|---|---|---|---|
| | | | | | Spindle | Fixing |
| | | | *Nephasoma flagriferum* | | | |
| 120 | 108 | 70 | 8 | 23 | + | 0 |
| 97 | 75 | 45 | 4 | 28 | + | 1 |
| 90 | 51 | 70 | 1 | 22 | + | 0 |
| 85 | 67 | 6 | 4 | 27 | + | 2 |
| 83 | 87 | 80 | 2 | 37 | + | 0 |
| 82 | 52 | 60 | 4 | 29 | + | 0 |
| 77 | 130 | 70 | 4 | 35 | + | 0 |
| 77 | 56 | 60 | 1 | 23 | + | 1 |
| 75 | ? | 60 | 1 | 24 | 0 | 0 |
| 75 | 85 | 60 | 4 | 47 | + | 0 |
| 72 | ? | 85 | 7 | 22 | + | 0 |
| 63 | 106 | 60 | 3 | 28 | + | 1 |
| 61 | 162 | 80 | 2 | 48 | + | 0 |
| 58 | 121 | 25 | 2 | 16 | + | 1 |
| 55 | 89 | 50 | 4 | 33 | + | 0 |
| 54 | 111 | ? | 4 | 20 | + | 1 |
| 40 | 165 | 6 | 4 | 35 | + | 1 |
| 35 | 71 | 14 | 9 | 37 | + | 0 |
| 32 | 147 | 45 | 9 | 25 | + | 0 |
| 27 | 96 | ? | ? | ? | ? | 2 |
| 9 | 200 | 25 | 11 | 39 | + | 0 |
| 7 | 457 | 20 | 7 | 57 | + | 1 |
| 6 | 250 | 25 | 7 | 42 | + | 0 |
| 5 | 140 | 25 | 20 | 50 | ? | ? |
| 5 | 100 | 20 | 0 | 40 | ? | ? |
| 4 | 100 | 20 | 0 | 50 | ? | 0 |
| 3.5 | 143 | 15 | 14 | 43 | ? | ? |
| | | | *Nephasoma constrictum*<br>(posterior) | | | |
| 30 | 33 | 40 | 3 | 53 | 0 | 0 |
| 29 | 62 | 40 | 5 | 55 | 0 | 0 |
| 29 | 45 | ? | 7 | 69 | + | 1 |
| 25 | 88 | 30 | 4 | 64 | 0 | 0 |
| 23 | 104 | 25 | 7 | 57 | + | 0 |
| 22 | 59 | 40 | 9 | 59 | 0 | 0 |
| 20 | 60 | 35 | 3 | 55 | + | 0 |
| 20 | 80 | 30 | 10 | 50 | + | 0 |
| 18 | 78 | 35 | 6 | 56 | 0 | 1 |
| 17 | 82 | 28 | 18 | 59 | + | 1 |
| 15 | 60 | 35 | 3 | 67 | + | 1 |
| 13 | 77 | 30 | 12 | 38 | + | 0 |
| 12 | 83 | 20 | 8 | 67 | + | 0 |
| 10 | 80 | 30 | 10 | 50 | + | 0 |
| 8 | 113 | 20 | 6 | 50 | ? | ? |
| 7 | 157 | 15 | 11 | 71 | 0 | 0 |
| 7 | 214 | 20 | 14 | 57 | + | 0 |

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# ON THE SPECIES AND POPULATIONS OF THE GENUS *ACANTHOCEPHALUS* (ACANTHOCEPHALA: ECHINORHYNCHIDAE) FROM NORTH AMERICAN FRESHWATER FISHES: A CLADISTIC ANALYSIS

Omar M. Amin

*Abstract.*—Cladistic analysis provided greater understanding and further support of the evolutionary relationships among the species and populations of the genus *Acanthocephalus* from North American freshwater fishes outlined earlier by Amin (1985). It is proposed that *A. dirus, A. tahlequahensis* and *A. alabamensis* are monophyletic with *A. dirus* representing a probable successful and persistent general ancestor. The two southern species are more closely related to each other than either one is to *A. dirus,* probably evolved allopatrically, and now exhibit new restricted distributions. Within *A. dirus,* the Mississippi River and Wisconsin-Lake Michigan populations are more closely related to each other than either one is to the New England population, which may have been evolving in isolation longer than the former two.

The recent revision of the genus *Acanthocephalus* from North American freshwater fishes by Amin (1984) and Amin and Huffman (1984) established the presence of three species, *A. dirus* (Van Cleave 1931), *A. tahlequahensis* Oetinger and Buckner, 1976, and *A. alabamensis* Amin and Williams, 1983. *Acanthocephalus dirus* has the widest host and geographical distribution and exhibits the greatest morphological variability. It is found in 65 species and 16 families of fish mostly in the Mississippi River drainage system (or waters previously connected to it in Ohio and Lake Erie) in 13 states in the U.S. (Amin 1985). *Acanthocephalus tahlequahensis* is found in four species and two families of fish from Oklahoma and *A. alabamensis* in six species and four families from Alabama.

Three distinct populations are recognized within *A. dirus* by Amin (1984): the Mississippi River population; the Wisconsin-Lake Michigan population (=*A. parksidei* Amin, 1975) and the New England population (=*A. jacksoni* Bullock, 1962). The Mississippi River population has the widest geographical (in 10 states) and host (46 fish species in 11 families) distribution and is more variable morphologically than the Wisconsin-Lake Michigan population (in two states and 22 species and 10 families of fish) or the New England population (in two states and 14 species and nine families).

Meristogram patterns (unpublished) were distinctly different in each of the three species. Within *A. dirus,* the meristogram patterns were similar in all the populations studied by Amin (1984) except the Gleason population from Kentucky which showed some elements of uniqueness corresponding with certain peculiarities discussed by Amin (1984).

Based on geological evidence as well as on variability, host and geographical distribution, Amin (1985:214) proposed that "early *A. dirus* ancestors were probably found in the Mississippi River basin before the Wisconsin glaciation." The establishment of the geographically isolated Wisconsin-Lake Michigan population "must have taken place with Mississippi River elements from the Des Plaines-Illinois River system

Table 1.—Character distribution among species of genus *Acanthocephalus* from North American freshwater fishes and outgroups.

| Character distribution | Outgroups (Europe) | | North American species of *Acanthocephalus* | | |
|---|---|---|---|---|---|
| | $X_1$ *A. lucii*[1] | $X_2$ *A. anguillae*[1] | I *A. dirus* | II *A. alabamensis* | III *A. tahlequahensis* |
| (1) Mean male body length (mm) | Large (>5) | Large (>5) | Moderate (3–4) | Small (<3) | Small (<3) |
| (2) Mean female body length (mm) | Large (>10) | Large (>10) | Moderate (7–9) | Small (<6) | Small (<6) |
| (3) Body shape | Cylindrical | Cylindrical | Cylindrical | Cylindrical | Spindle |
| (4) Mean anterior testis length (μm) | Large (>800) | Large (>800) | Moderate (450–800) | Small (<450) | Small (<450) |
| (5) Mean anterior testis length/body (%) | Small (<15) | Small (<15) | Large (>19) | Large (>19) | Small (<15) |
| (6) Mean anterior testis width/body width (%) | Large (>50) | Moderate (42–46) | Large (>50) | Large (>50) | Small (<42) |
| (7) Mean no. proboscis hooks/row (males) | Small (<9) | Small (<9) | Moderate (9–10) | Small (<9) | Large (>11) |
| (8) Mean no. proboscis hooks/row (females) | Small (<9) | Small (<9) | Moderate (9–11) | Moderate (9–11) | Large (>11) |
| (9) Mean length of largest proboscis hooks (males) (μm) | Large (>60) | Large (>60) | Moderate (50–60) | Small (<50) | Small (<50) |
| (10) Mean length of largest proboscis hooks (females) (μm) | Large (>70) | Large (>70) | Moderate (60–70) | Small (<60) | Small (<60) |
| (11) Meristogram patterns | A[2] | B[2] | C | D | E |

[1] From Petrochenko (1956).
[2] Presumably.

(tributaries of the Mississippi River . . .” in post-glacial streams like the Pike River “. . . after the withdrawal of the Lake Michigan lobe of the Wisconsinan ice sheet from the area between 15,000 and 12,000 years B.P.” (before the present). Based on morphological evidence alone, the geographically isolated New England population appears to have also originated from a Mississippi River *A. dirus*-like source (Amin 1985). *Acanthocephalus tahlequahensis* has a limited distribution in an Oklahoma tributary of the Mississippi River and *A. alabamensis* is found in the Mobile Bay drainage system which had continuous fauna with the Mississippi River before barriers to recent dispersal arose. The two southern species are found more typically in certain species of *Etheostoma* not parasitized by other species of *Acanthocephalus*.

The above information provides a brief background of the inter- and intraspecific associations within the genus *Acanthocephalus* from North American freshwater fishes which lends itself to further analysis within a cladistic context. To date, cladistic analysis has not been used as an aid to the understanding of acanthocephalan evolutionary biology. This method, however, was found amenable to this study as it provided greater understanding of and further support for the evolutionary relationships briefly outlined above.

## Materials and Methods

Methods in Brooks et al. (1985) and Wiley (1981) as well as suggestions by Drs. D. R. Brooks and J. N. Caira were instrumental in the understanding of the findings pre-

Table 2.—Character distribution among populations of *Acanthocephalus dirus* and outgroups.

| | Outgroups | | | *Acanthocephalus dirus* populations | | |
|---|---|---|---|---|---|---|
| Character distribution | $X_1$ *A. alabamensis* | $X_2$ *A. tahlequahensis* | $X_3$ *A. lucii* | I Mississippi River | II Wisconsin-Lake Michigan | III New England |
| (1) Mean male body length (mm) | Small (<3) | Small (<3) | Large (>5) | Moderate (3–4) | Moderate (3–4) | Moderate (3–4) |
| (2) Mean female body length (mm) | Small (<6) | Small (<6) | Large (>10) | Moderate (7–9) | Moderate (7–9) | Moderate (7–9) |
| (3) Body shape | Cylindrical | Spindle | Cylindrical | Cylindrical | Cylindrical | Robust anteriorly |
| (4) Mean anterior testis length (μm) | Small (<450) | Small (<450) | Large (>800) | Moderate (450–800) | Moderate (450–800) | Moderate (450–800) |
| (5) Mean anterior testis length/body length (%) | Large (>19) | Small (<15) | Small (<15) | Large (>19) | Large (>19) | Moderate (17–18) |
| (6) Mean anterior testis width/body width (%) | Large (>50) | Small (<42) | Large (>50) | Large (>50) | Large (>50) | Moderate (42–46) |
| (7) Mean no. proboscis hooks/row (males) | Small (<9) | Large (>11) | Small (<9) | Moderate (9–10) | Moderate (9–10) | Small (<9) |
| (8) Mean no. proboscis hooks/row (females) | Moderate (9–11) | Large (>11) | Small (<9) | Moderate (9–11) | Moderate (9–11) | Small (<9) |
| (9) Mean length of largest proboscis hooks (males) (μm) | Small (<50) | Small (<50) | Large (>60) | Moderate (50–60) | Moderate (50–60) | Large (>60) |
| (10) Mean length of largest proboscis hooks (females) (μm) | Small (<60) | Small (<60) | Large (>70) | Moderate (60–70) | Moderate (60–70) | Large (>70) |
| (11) Meristogram pattern | A | B | C[2] | D | D | D |

[1] From Petrochenko (1956).
[2] Presumably.

sented in a cladistic context and in the construction and interpretation of cladograms.

## Results and Discussion

Cladograms were made with the assumption that the three North American species are each others' closest relatives, and that none has closer relatives on other continents (see following parts). Adequate data were available for four species of *Acanthocephalus*: *A. lucii* (Muller, 1776), *A. anguillae* (Muller, 1780), *A. clavula* (Dujardin, 1845), and *A. falcatus* (Frolich, 1789) for use as outgroups. Resolving all characters used in the analysis (Table 1) was possible by using the first two species, i.e., their plesiomorphic states satisfactorily polarized ingroup characters. These plesiomorphic states included large and cylindrical bodies, large testes, larger and fewer proboscis hooks per row. The choice of those characters was based on characteristics of body, testes, and proboscis hooks, the evolutionary significance of which was discussed by Amin (1984). Note that in the absence of other data (Tables 1, 2) a linear transformation series is to be preferred (Mickevich 1982). The data matrix is shown in Table 3. The resulting cladogram (Fig. 1) has a high overall consistency index (minimum number of steps/actual number of steps; see Farris et al. 1970a, b) of 95% and synapomorphic consistency of 100% indicating a low degree of parallel evolution in the characters used and giving a high degree of confidence in the pattern hypothesized. Two other cladograms with lower consistency values were excluded from consideration. The hypothesized pattern (Fig. 1) indicates that (1) the three North American species (ingroup) are monophyletic. $X_1$ and $X_2$ plus the three North American species are postulated to form a monophyletic group based on their shared possession of a suite of four derived traits (3, 5, 6, 7 in Fig. 1). Using the two "X" species as outgroups, I, II and III are postulated to be a monophyletic group based on traits 1, 2, 4, 8, 9, 10 in Fig. 1. The hypothesis of monophyly is supported by the very high goodness of fit statistics. (2) *A. alabamensis* and *A. tahlequahensis* are more closely related to each other than either one is to *A. dirus*. The two branching points on the cladogram indicate a north-south split (*A. dirus* and the ancestor of *A. alabamensis* and *A. tahlequahensis*). Prior to its differentitation into distinct populations, *A. dirus* was of the same age as the common ancestor of the two southern species.

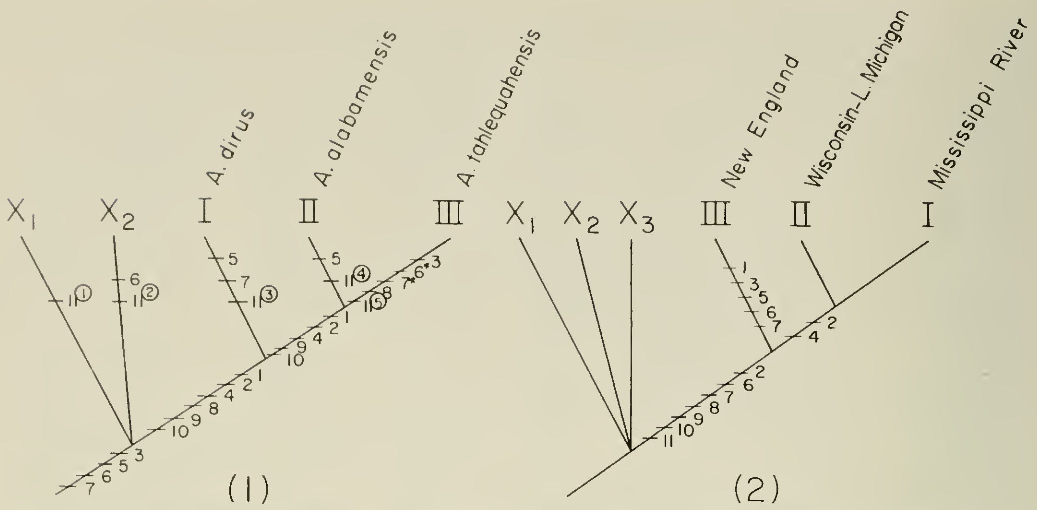
The most reasonable events are a widespread ancestor divided into a southern population giving rise to *A. alabamensis* and *A. tahlequahensis* and a more northern population forming *A. dirus*. Under the above conditions of monophyly, speciation would be allopatric. Figure 1 and Wiley's (1981) identical diagram (Fig. 2-10b) indicate allopatric speciation. While the identification of the persistent ancestral *A. dirus* population is possible, it is not easily detectable given available data above. It is proposed, however, that based on its broad geographical and host distributions and its great morphological variability. *Acanthocephalus dirus* appears to be a successful persistent general ancestor while *A. tahlequahensis* and *A. alabamensis* seem to exhibit new restricted distributions. *Acanthocephalus dirus* may also be interpreted as a successful adaptable new species with the other two species exhibiting relictual distributions. Some combinations of the two interpretations may also be theorized. The first interpretation is, however, preferred because of the ancestral position of *A. dirus* on the phylogenetic tree (Fig. 1). This is concordant with the contention that the anatomical diversity and the broad host and geographical distributions of this species do represent generalized persistent ancestral traits and that distinguishing states of the restricted *A. alabamensis* and *A. tahlequahensis*, e.g., small size, are more recently derived.

Table 3.—Data matrix of six taxa and 11 characters based on Table 1.

| Character state | Taxon | | | | |
|---|---|---|---|---|---|
| | $X_1$ | $X_2$ | I | II | III |
| 1 | 0 | 0 | 1 | 2 | 2 |
| 2 | 0 | 0 | 1 | 2 | 2 |
| 3 | 0 | 0 | 0 | 0 | 1 |
| 4 | 0 | 0 | 1 | 2 | 2 |
| 5 | 0 | 0 | 1 | 1 | 0 |
| 6 | 0 | 1 | 0 | 0 | 1 |
| 7 | 0 | 0 | 1 | 0 | 1 |
| 8 | 0 | 0 | 1 | 1 | 2 |
| 9 | 0 | 0 | 1 | 2 | 2 |
| 10 | 0 | 0 | 1 | 2 | 2 |
| 11 | 1 | 2 | 3 | 4 | 5 |

The evolutionary relationships among the three *A. dirus* populations are expressed in cladogram Fig. 2 based on data summarized in Tables 2 and 4. This cladogram has an overall and synapomorphic consistency index of 100%. It suggests that (1) the Mississippi River and the Wisconsin-Lake Michigan populations are more closely related to each other than either one is to the New England populations, (2) the latter population may have been evolving in isolation longer than the former two if equal rates of evolution of all characters are assumed. Of the three extant populations, the New England population is the most highly differentiated, and (3) the present Mississippi River population and that of Wisconsin-Lake Michigan are equally derived.

The above interpretation of cladogram



Figs. 1, 2. Cladograms showing the phylogenetic relationships among the three North American species of *Acanthocephalus* from freshwater fishes (Fig. 1, from Tables 1 and 3) and among the three populations of *A. dirus* (Fig. 2, from Tables 2 and 4). For asterisks see Tables 1 and 3. Circled numbers (A–E, Table 1 and A–D, Table 2) indicate specific meristogram patterns different in each species.

Fig. 2 provides additional evidence to those based on geological and morphological grounds (Amin 1985) supporting the proposition that the Wisconsin-Lake Michigan population of *A. dirus* dispersed from an early Mississippi River-based source and then became geographically isolated less than 15,000 years ago. Given sufficient time and continued isolation, this situation would be a classical example of Van Cleave's (1952) earlier proposition that in Palaeacanthocephala, isolation might allow the normal extremes in a highly variable species to become segregated as distinct species. The interpretation also provides further insights into those based on morphological and clinal variations suggesting a similar process for the New England population even though the origin of its source remains to be identified. Cladogram Fig. 2 indicates that this highly differentiated population may have been evolving in isolation longer than the other two.

At the present time, it is not known whether the dispersal of *A. dirus* led to the isolation of *A. alabamensis* and *A. tahlequahensis* due to competitive exclusion, or that some geological or host related changes which isolated the latter two species also allowed the dispersal of *A. dirus* after the fact. It is, however, clear that certain geological events affected other aspects of the distribution and evolution of these acanthocephalans, e.g., the geographically isolated northern populations of *A. dirus*, mak-

Table 4.—Data matrix of six taxa and 11 characters based on Table 2.

| Character state | Taxon | | | | | |
|---|---|---|---|---|---|---|
| | $X_1$ | $X_2$ | $X_3$ | I | II | III |
| 1 | 0 | 0 | 1 | 2 | 2 | 2 |
| 2 | 0 | 0 | 1 | 2 | 2 | 2 |
| 3 | 0 | 1 | 0 | 0 | 0 | 2 |
| 4 | 0 | 0 | 1 | 2 | 2 | 2 |
| 5 | 0 | 1 | 1 | 0 | 0 | 2 |
| 6 | 0 | 1 | 0 | 0 | 0 | 2 |
| 7 | 0 | 1 | 0 | 2 | 2 | 0 |
| 8 | 0 | 1 | 2 | 0 | 0 | 2 |
| 9 | 0 | 0 | 1 | 2 | 2 | 1 |
| 10 | 0 | 0 | 1 | 2 | 2 | 1 |
| 11 | 1 | 2 | 3 | 4 | 4 | 4 |

ing the proposed geological scenario the best hypothesis presently possible.

## Acknowledgments

I am grateful to Drs. D. R. Brooks, University of British Columbia, Vancouver, and J. M. Caira, University of Maine, Orono, for help with the cladistic analysis. The support and inspiration of Michele Meinert are gratefully noted.

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# A NEW SUBSPECIES OF *TURDUS SWALESI* (AVES: PASSERIFORMES: MUSCICAPIDAE) FROM THE DOMINICAN REPUBLIC

Gary R. Graves and Storrs L. Olson

*Abstract.*—A new subspecies, *Turdus swalesi dodae,* is described from the Sierra de Neiba and Cordillera Central of the Dominican Republic. The arid Cul-de-Sac/Valle de Neiba Depression forms a barrier between *T. s. swalesi* of the Massif de la Selle and Sierra de Bahoruco and *T. s. dodae.*

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The La Selle Thrush, *Turdus swalesi,* one of the last species of birds to be described from the island of Hispaniola (Wetmore 1927, Wetmore and Swales 1931), was long believed to be endemic to the Massif de la Selle in southeastern Haiti. Within the past fifteen years, however, populations have been found in several localities in the Dominican Republic (Fig. 1). One of these near the Haitian border in the Sierra de Bahoruco was not unexpected, as this is only an eastward extension of the La Selle ridge (Bond 1977). Of greater interest was the subsequent discovery of two populations in the mountains north of the arid Cul-de-Sac/Valle de Neiba Depression.

Although *T. swalesi* may be locally common (Bond 1928, Bond 1978), it is evidently represented by fewer than a dozen specimens in museums. From the small series at hand, there appears to be no geographic variation among specimens of the nominate form from the mountains south of the Cul-de-Sac Depression. The two specimens collected north of the depression, in the Sierra de Neiba and the Cordillera Central, however, represent a distinctive new subspecies.

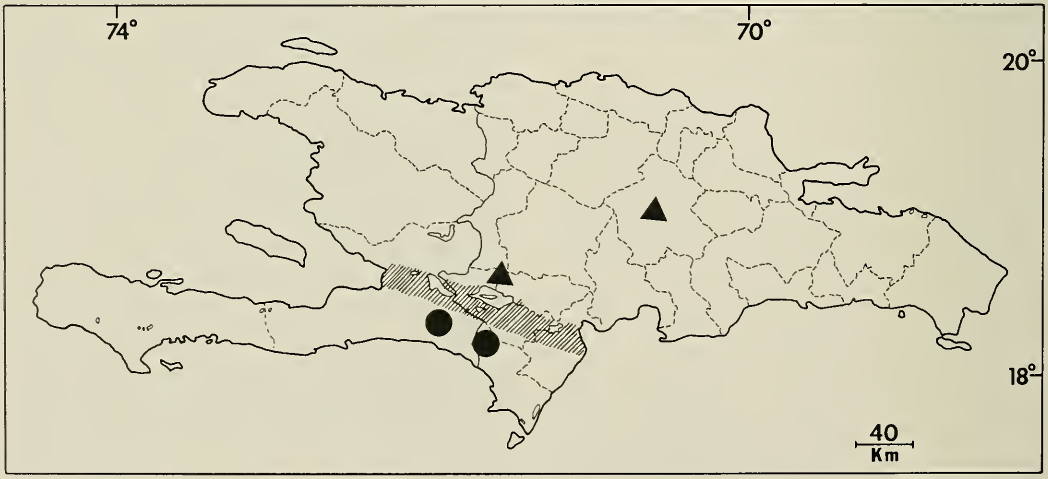

Fig. 1. Distribution of collected specimens of *Turdus s. swalesi* (circles) and *T. s. dodae* (triangles) on Hispaniola. Hatched area represents the Cul-de-Sac/Valle de Neiba Depression, which forms a low arid barrier between the "north" and "south" montane islands.

Fig. 2. Dorsal view (from left to right) of *Turdus s. dodae* (MNHN 647 ♀; USNM 536701 ♂) and *T. s. swalesi* (USNM 264705 ♀; USNM 264704 ♂; MNHN 197 ♀, subadult).

### *Turdus swalesi dodae,* new subspecies
Fig. 2

*Holotype.*—National Museum of Natural History, USNM 536701; male, from near divide between Río Baiguate and Río Jimenoa, about 15 miles (ca. 24 km) NE of Constanza, La Vega Province, Dominican Republic, elevation 5900 ft (1800 m); coll. 6 Mar 1976 by Francis M. Greenwell and William M. Perrygo.

*Diagnosis.*—*Turdus swalesi dodae* differs from *Turdus s. swalesi* in having an olivaceous brown black (Saccardo's Umber to Umber-Brown; Ridgway 1912) contrasting sharply with the black of the hindneck and wings, whereas the dorsum of *T. s. swalesi* is uniformly black (Fig. 2).

*Range.*—Montane forest in the Sierra de Neiba and Cordillera Central, Dominican Republic.

*Measurements.*—See Table 1.

*Specimens examined.*—*Turdus s. swalesi*: Haiti: Massif de la Selle (USNM 264704 ♂, 13 Apr 1927; 264705 ♀, 13 Apr 1927;

Table 1.—Measurements (in mm) of *T. s. swalesi* and *T. s. dodae.* Wing and tail measured to nearest mm. Culmen measured from anterior edge of nostril.

| | Wing (chord) | Tail | Tarsus | Culmen |
|---|---|---|---|---|
| *swalesi* | | | | |
| Massif de la Selle | | | | |
| USNM 264707 ♂ (type) | 128 | 105 | 42.2 | 17.4 |
| USNM 264704 ♂ | 131 | 105 | 44.7 | 15.4 |
| USNM 264705 ♀ | 125 | 99 | 43.0 | 16.2 |
| Sierra de Bahoruco | | | | |
| MNHN 197 ♀ (subadult) | 121 | 94 | 40.5 | 13.2 |
| MNHN 879 ♀ | 128 | 100 | 44.0 | 16.4 |
| *dodae* | | | | |
| Sierra de Neiba | | | | |
| MNHN 647 ♀ | 125 | 99 | 43.5 | 15.7 |
| Cordillera Central | | | | |
| USNM 536701 ♂ | 129 | 108 | 42.0 | 16.3 |

Fig. 3. Dorsal plumage of subadult (top) and adult (sexes nearly identical) *T. s. swalesi.* Note the exposed apteria near the rictus and on the sides of the throat in the subadult.

264707 (type) ♂, 15 Apr 1927). Dominican Republic: Loma de Toro, Sierra de Bahoruco (Museo Nacional de Historia Natural, Santo Domingo [MNHN] 197 ♀ subadult, 1 Sep 1972; 879 ♀, 15 Apr 1976). *Turdus s. dodae*: Dominican Republic: Sierra de Neiba (MNHN 647 ♀, 15 May 1975); NE Constanza (USNM holotype).

*Etymology.*—We take pleasure in naming this subspecies for Annabelle Dod, in recognition of her contributions to ornithology in the Dominican Republic.

## Variation in Plumage

The type specimen of *T. s. dodae* was erroneously reported as an "immature specimen" (Bond 1977:12), possibly because of its olivaceous brown black. Unfortunately, the collectors did not include gonad or skull ossification data on the specimen tag. The unspotted, sleek glossy plumage and silvery auriculars indicate that the holotype is an adult in a definitive plumage; the only evidence that could be construed as indicating immaturity are the pointed rectrices and faint brownish edgings of the greater wing coverts.

The juvenal plumage of *T. swalesi* is unknown. One of the specimens from the Sierra de Bahoruco (MNHN 197) appears to be a subadult in prebasic molt—the rictus is enlarged and fleshy, the plumage is lax and fluffy, especially on the breast and flanks, and apteria are exposed along the sides of the throat (Fig. 3). Compared with an adult female (MNHN 879) from the same locality, the plumage of the immature is similar in pattern, but duller and less glossy. Otherwise, faint spotting across the pectoral region of the immature is the only age-related difference. The presence of a "black back" in immature and definitive plumages of *T. s. swalesi* precludes the possibility that the olivaceous back, the diagnostic character of *T. s. dodae,* is just a feature of immature plumage in the species. It should be noted that the distal ⅓ to ½ of the dorsal feathers of *T. s. dodae* are olivaceous, not merely the edges or tips.

The two examples of *T. s. dodae* differ from one another in several details: (1) the posterior margin of the black hindneck is V-shaped in the holotype but is rounded in the Sierra de Neiba specimen; (2) the olivaceous brown portion of the dorsum in the holotype is more restricted in distribution and contrasts more with the adjacent black plumage than in the Neiba specimen. We are unsure as to whether these differences represent intra- or inter-populational differences or sexual dichromatism. Given a larger sample, the Sierra de Neiba and Cordillera Central populations may be taxonomically separable from one another as well as from *T. s. swalesi.*

## Discussion

The pattern of distribution of the two subspecies of *Turdus swalesi* is similar to that of numerous other Hispaniolan vertebrates, with the low arid areas of the Cul-de-Sac/Valle de Neiba presumably forming a barrier to gene flow between the southern peninsula of Haiti and the remainder of Hispaniola. During periods of marine transgression, this valley formed a channel separating the two land areas into discrete islands. The two-island theory has been used to explain the origin of a variety of species-pairs of birds, reptiles and amphibians (Pregill and Olson 1981). In some instances, members of these pairs have spread beyond their island of origin and co-occur in some regions (e.g., *Todus subulatus* and *T. angustirostris*). In other cases, allopatric taxa are still restricted either to the "north" or "south" island. Variance in the degree of differentiation or sympatry among former isolates doubtless reflects differences in the time of splitting of ancestral populations, in dispersal ability, and in habitat preference.

## Acknowledgments

We thank Steve Cardiff, Annabelle Dod, Frank Greenwell, George Reynard, and Mark Robbins for information. Sixto Inchaustegui, Antonio Domingo Siri, and Manuel Campora of the Museo Nacional de Historia Natural, Santo Domingo, were instrumental in providing specimens. Photographs were provided by Victor Krantz.

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# A NEW ACTINOPTERYGIAN FISH (PALEONISCIFORMES) FROM THE UPPER MISSISSIPPIAN BLUESTONE FORMATION OF WEST VIRGINIA

Robert E. Weems and John F. Windolph, Jr.

*Abstract.*—A new genus and species of deep-bodied paleonisciform fish, *Tanypterichthys pridensis,* is described from near the base of the Pride Shale Member of the Bluestone Formation of the Upper Mississippian Series (Namurian A equivalent) in West Virginia. Its unusually large size (roughly 0.5 m), diamond-shaped deep body, very large pectoral fins, and the details of its scale ornamentation demonstrate that this is a new and unique paleonisciform. The type specimen of *Tanypterichthys,* found immediately above a basal rubble zone representing a marine transgressive event, is associated both with goniatitic cephalopods and with plant and tree fragments. This association indicates that it was entombed in a shallow coastal marine or marginal marine deltaic depositional environment. The functional morphology of *Tanypterichthys* and its burial environment suggest that this fish may have inhabited quiet waters along the coastal reaches of rivers and brackish estuaries, where kelplike colonial algae or canelike aquatic plants grew in dense stands.

A large fossil fish, missing most of the skull and the caudal and dorsal fins, was discovered in an ellipsoidal carbonate concretion in a roadcut near Princeton, West Virginia (Fig. 1), by John Windolph during geologic investigations in the U.S. Geological Survey Upper Mississippian/Pennsylvanian stratotype project (Englund et al. 1979). The concretion is one of many, mostly unfossiliferous, in a discrete zone near the base of the Pride Shale Member of the Bluestone Formation (Upper Mississippian Series) (Fig. 2).

The fish was discovered by splitting the concretion, whereupon an internal view of the scale pattern and left posterior skull elements (Fig. 3) was revealed. Much of the scale pattern and the conformation of the anal fin was discernible from this internal view, but nothing could be ascertained about the pelvic fins and little about the pectoral fins or the external ornamentation of the scales. For this reason, we decided that the left side of the fish should be acid prepared to try to determine something about its external appearance. The exposed parts of the left side first were photographed by Deborah Dwornik of the U.S. Geological Survey, then the left half of the fish was taken to the National Museum of Natural History where Arnold Lewis and Daniel Chaney impregnated the exposed part of the left side of the fish in plastic. After the plastic polymerized, they removed all but a 1-inch slab of the concretion with a diamond saw. The authors then immersed the block in a formic acid bath to remove most of the external concretionary covering. Unfortunately, some layers were rich in pyrite and were nearly unaffected by the formic acid. In those areas, material could not be removed without dislodging fragments of scales. This caused a certain amount of breakage to the specimen, but most of the outer nodular coating was successfully removed by the acid treatment to reveal a complex papillate to stoutly ridged pattern on the scales and the outlines of the pectoral and pelvic fins (Fig.

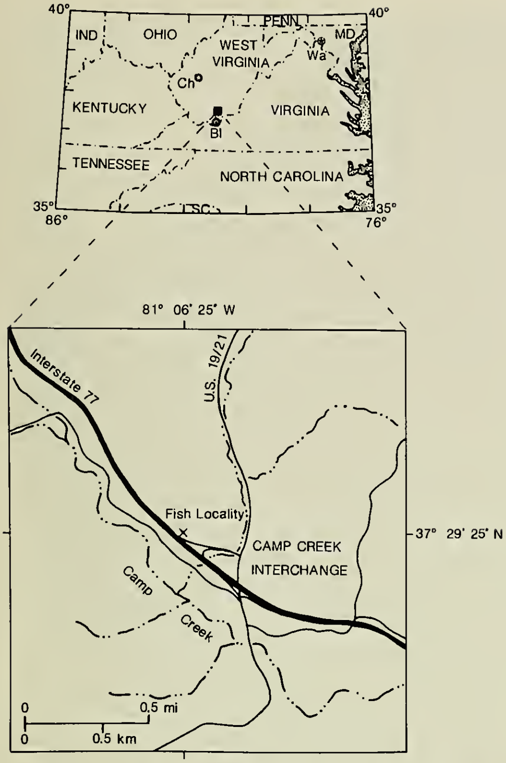

Fig. 1. Map showing the locality in West Virginia (marked by X) of the type specimen of *Tanypterichthys pridensis.* Bl = Bluefield, W. Va.; Ch = Charleston, W. Va.; Wa = Washington, D.C.

4). The right half of the fish remains in its original concretionary coat.

The pectoral fin, pelvic fin, most of the anal fin, posterior skull margin, and central body region are present and well preserved, but the caudal fin, dorsal fin, upper body outline, and much of the skull are missing. The nearly perfect articulation of the fossil fish suggests that the entire animal probably was once in the rock, but that the parts of the skeleton not enclosed by the concretion were destroyed by weathering and erosion.

## Geologic Setting

*Tanypterichthys* was discovered in a large ellipsoidal limestone concretion collected from a zone of concretions that lies approximately 6 inches above the base of the

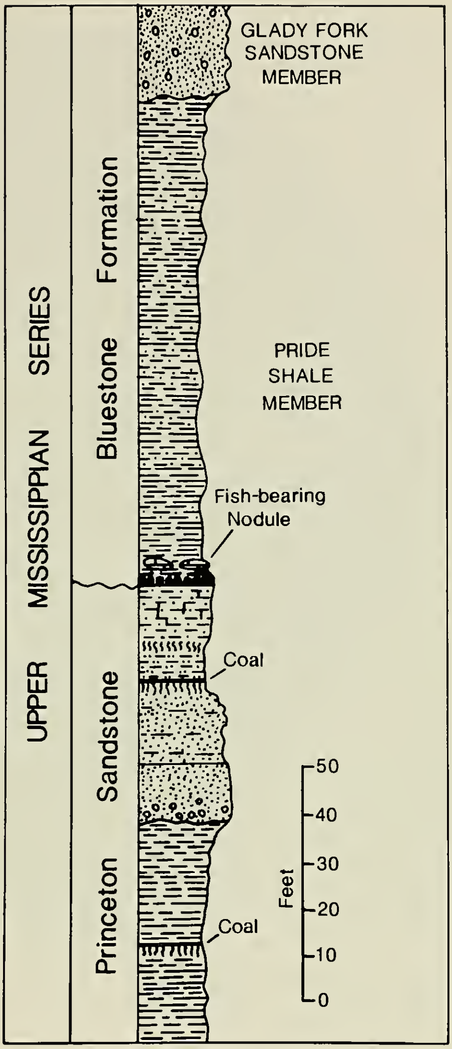

Fig. 2. Detailed stratigraphic column of the upper Princeton Sandstone and lower Bluestone Formation at the discovery locality for *Tanypterichthys pridensis.* The fish-bearing concretion zone occurs near the base of the Pride Shale Member of the Bluestone Formation. The unconformably underlying Princeton Sandstone and the conformably overlying Glady Fork Sandstone Member of the Bluestone Formation were formed in deltaic environments, as shown by the presence of coal and root casts, but at least the basal Pride Shale Member formed in a marginal-marine environment of deposition as shown by the successive presence of cone-shaped nautiloid and coiled goniatitic cephalopod shells in the 6-inch interval below the fish-bearing nodule zone, and the presence of inarticulate brachiopods and wood fragments within the fish-bearing nodule zone.

Fig. 3. Internal view of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) before it was mounted in plastic and exhumed from the matrix on the other side with formic acid. These and the following photographs were taken by Deborah Dwornik (U.S. Geological Survey, Reston).

Pride Shale Member (Fig. 2). The Pride Shale Member is the basal member of the Bluestone Formation (Upper Mississippian Series) and is correlative with late Chesterian age rocks of the midcontinent and with Namurian A strata of western and central Europe.

The Princeton Sandstone immediately underlies the Pride Shale Member and is approximately 60 feet thick at the fossil site. Outcrops of the Princeton extend for more than 100 miles along the southeastern edge of the Appalachian Basin, forming a belt of clastic wedges and deltaic sequences that thin to the northwest. The Princeton Sandstone, which resulted from erosion after a widespread tectonic event, consists of lenses of medium-light-gray to medium-gray polymictic conglomerate, coarse- to fine-grained conglomeratic subgraywacke, sandstone, siltstone, shale, underclay, and coal. Basal conglomerate and sandstone beds grade coarse to fine upward, are massive to thin-bedded, and form impressive bluffs to the southeast along the Bluestone River. The clasts are diverse in size and source, consisting of well-rounded to angular fragments of quartz sandstone, siltstone, shale, lime-

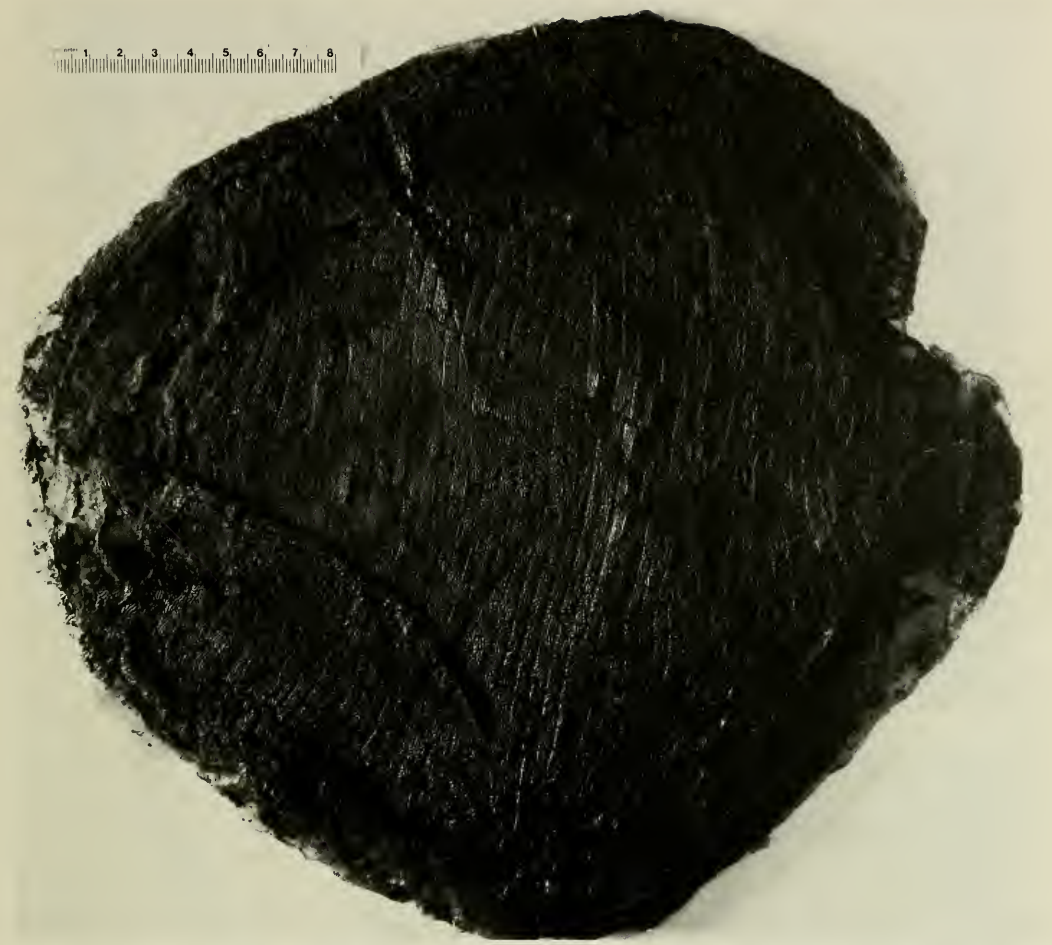

Fig. 4. External view of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) after being treated with formic acid.

stone, ironstone, chert, and coalified plant and tree-trunk fragments. Many of the lithic fragments were derived from limestone and clastic sediments immediately underlying the Princeton, but others came from more distant sources of older Paleozoic sedimentary and Proterozoic to Paleozoic metamorphic and igneous rocks that occur to the southeast. Sandstone beds, located at distal parts of clastic wedges and locally at the upper part of deltaic sequences, are light-gray, moderately quartzose, and lenticular. This description suggests the formation of beach and barrier-bar deposits by winnowing and reworking of sediments through high-energy coastal and long-shore processes. The Princeton Sandstone locally includes thin-bedded to nonbedded medium-gray to greenish-gray siltstone, shale, limestone concretions, coal, and underclay. The several rooted underclays, overlain by thin coalbeds no more than 2 inches thick, indicate periods of protected and stable swamp-forming conditions. Thin roof shales above the coal beds contain partially abraded plant fossils (identified by W. H. Gillespie in Englund et al. 1985) including *Sphenophyllum tenerrimum, Stigmaria stellata,* *Pecopteris aspera, Archaeocalamites* sp., and *Sphenopteris elegans.* These floral elements are characteristic of the Upper Mississippian of North America and the Namurian A of western and central Europe. They occur in zone 3A, above the Upper Mississippian *Fryopsis* zone (zone 3 of Read and Mamay 1964) and below the *Neuropteris pocahontas* zone (zone 4 of Read and Mamay 1964), which marks the base of the Pennsylvanian System.

Locally, the Princeton Sandstone is overlain by an irregularly bedded rubble zone that ranges from an inch to more than a foot in thickness. It consists of a polymictic conglomerate in a silty sandstone matrix and includes well rounded quartz pebbles and other diverse lithic fragments as much as 1 inch in diameter. This rubble zone forms an extensive resistant ledge at the base of the Pride Shale Member, and it has been traced for more than 5 miles to the southeast of the locality where the type specimen of *Tanypterichthys* was found. This zone marks a disconformable contact that was formed by a widespread marine-transgressive event at the beginning of Bluestone deposition.

The Pride Shale Member is the basal unit of the Bluestone Formation and is approximately 100 feet thick at this locality. It is dark-gray, very fissile, carbonaceous, and silty. In places, it is bioturbated and includes thin, silty lenticular beds and flaser bedding. A few thin grayish-red units are present at the base, beneath the more widespread zone of sparsely fossiliferous limestone concretions in which the fossil fish was found. Exposed in roadcuts northwest of the fossil site are several large slump, scower, and channel features that are overlain and underlain by horizontal bedding. These unrooted features suggest the action of strong tidal influences and submarine currents. Associated with these beds are marine and brackish invertebrate fossil assemblages, which were collected by T. W. Henry of the U.S. Geological Survey and which are consistent with a shallow bayfill or lagoonal depositional environment for the Pride Shale Member. Above the Pride, coarse clastic rocks characterize the succeeding Glady Fork Sandstone Member of the Bluestone Formation. These clastic rocks are similar to those previously described from the underlying Princeton Formation.

## Taxonomic Description

The fish described here (see Figs. 5, 6, 7, 8) would seem to be readily assigned to the Paleonisciformes in view of the persistent development of branchiostegal rays in its cheek region and the unreduced number of rays in its fins. The order Paleonisciformes traditionally has been divided into two suborders (Moy-Thomas 1971), one (Paleoniscoidei) for normally shaped, fusiform types and the other (Platysomoidei) for deep-bodied forms reminiscent of our fish. Up to four families (Amphicentridae, Platysomidae, Bobasatranidae, and Dorypteridae) have been recognized, though variations on this theme have been proposed. The Amphicentridae and Platysomidae were combined into a single family by Berg et al. (1964). Fowler (1958) suggested that the term Uropterygidae should be favored over the term Platysomidae because the latter name is pre-empted, but this practice has not been followed by any subsequent worker. Berg (1940b) suggested placing the Bobasatranidae into a separate order, the Bobasatraniformes. This practice generally has been followed.

In recent years, this relatively simple taxonomy has collapsed. Campbell and Phuoc (1983) have pointed out that the skull of the type species of *Platysomus,* the Permian *P. gibbosus,* shows derived characteristics which indicate that it, and by definition the genus *Platysomus,* belong in the Bobasatraniformes. But it is unlikely that Mississippian and Pennsylvanian species which have been classified in *Platysomus* (or any of the other genera formerly classified in the Platysomidae and Platysomoidei) share these derived traits. Therefore, although

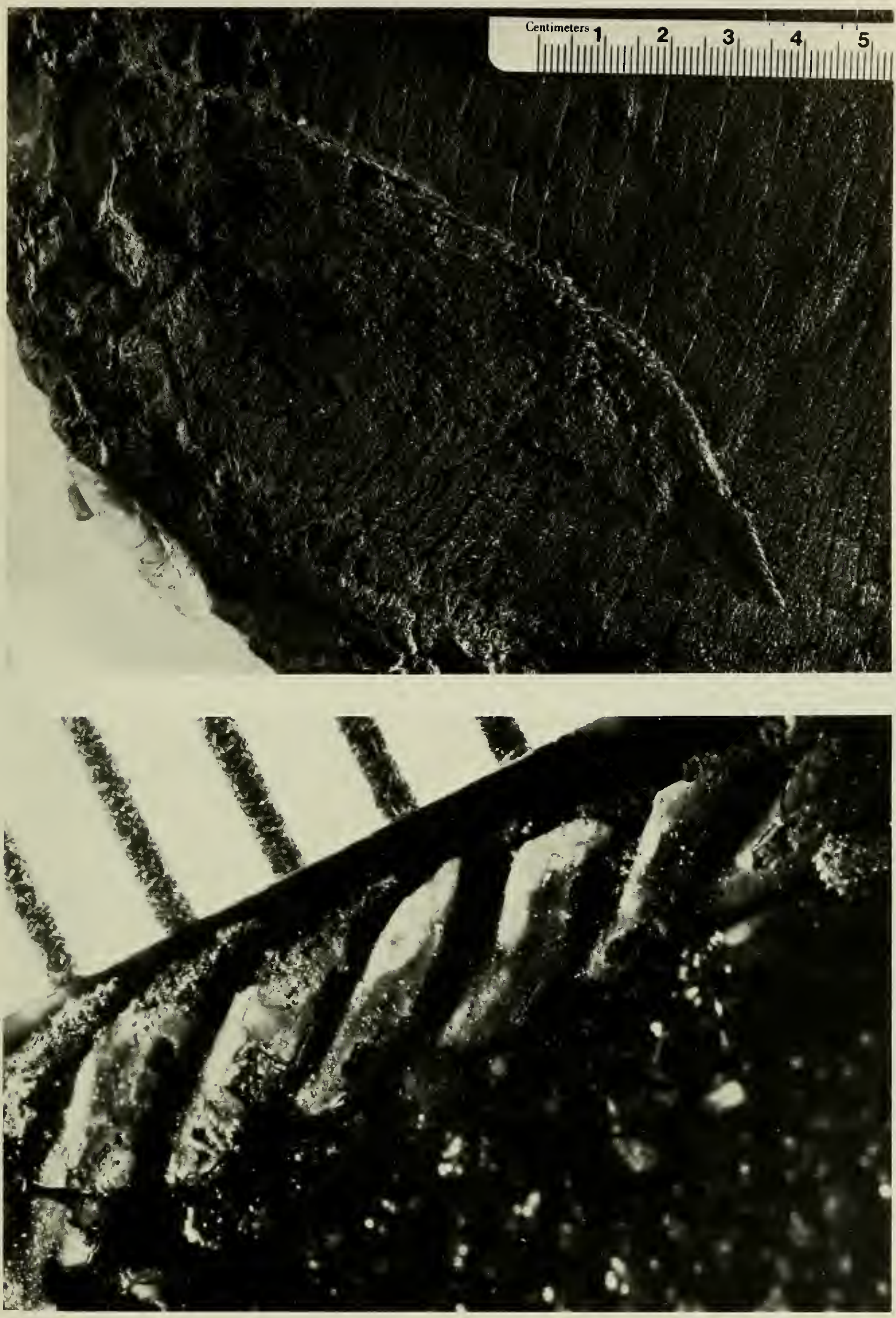

Fig. 5. (Top) Detail of the left pectoral fin of the type specimen of *Tanypterichthys pridensis* (USNM 391949). Note that the dorsal edge of the fin is lined by an enlarged row of scales, which are shown in more detail below. (Bottom) Detail of dorsal scale row on the pectoral fin of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949). Scales are near distal end of fin.

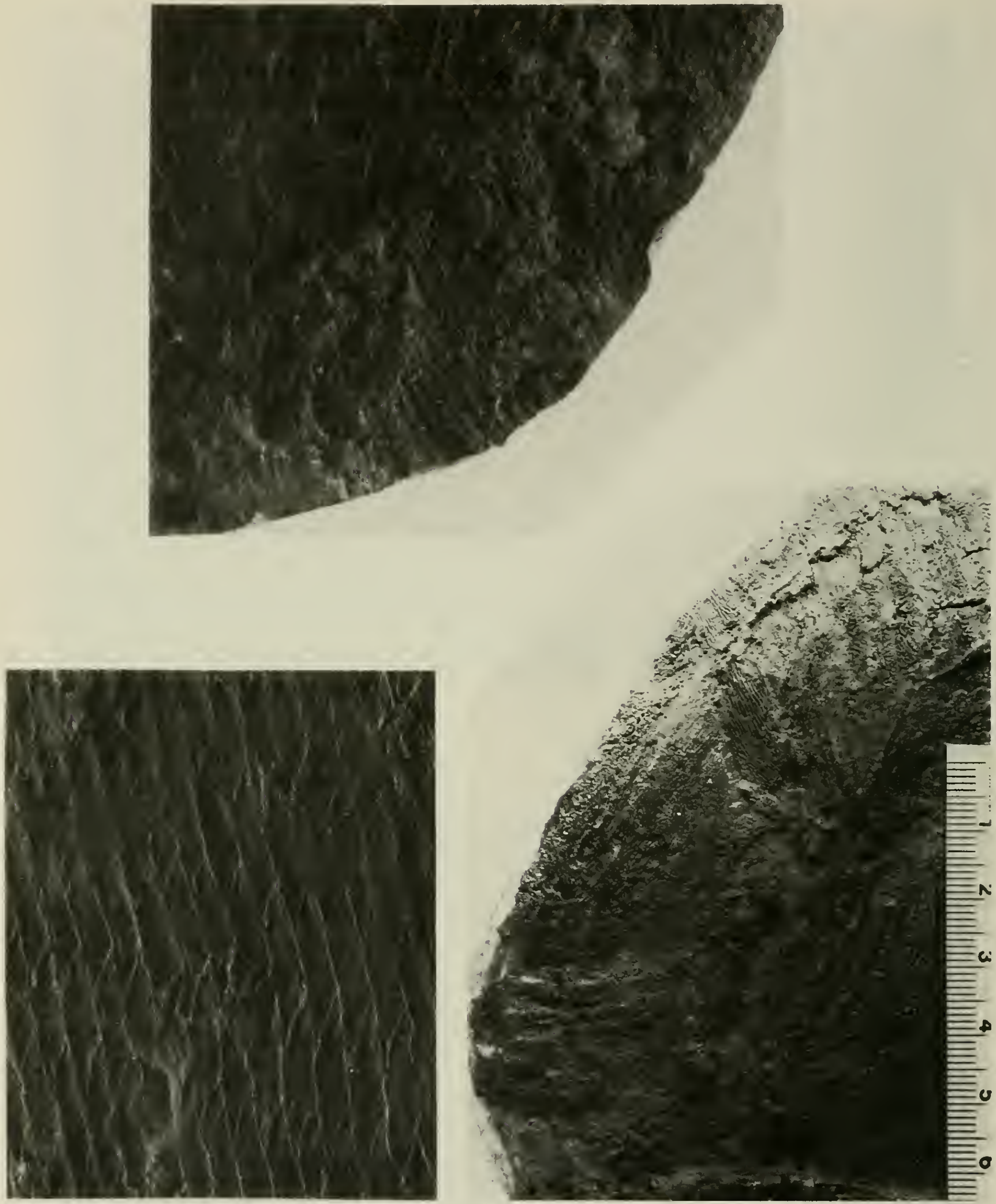

Fig. 6. (Top) Detail of anterior scale pattern on the anal fin of the type specimen of *Tanypterichthys pridensis* (USNM 391949), seen in internal view on the left side before acid preparation. (Lower left) Detail of internal flank scale pattern on the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) before acid preparation. (Lower right) Detail of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) showing the vermiform sculpture on the posterior cranial elements, and the pustulose pattern on the anterior flank scales.

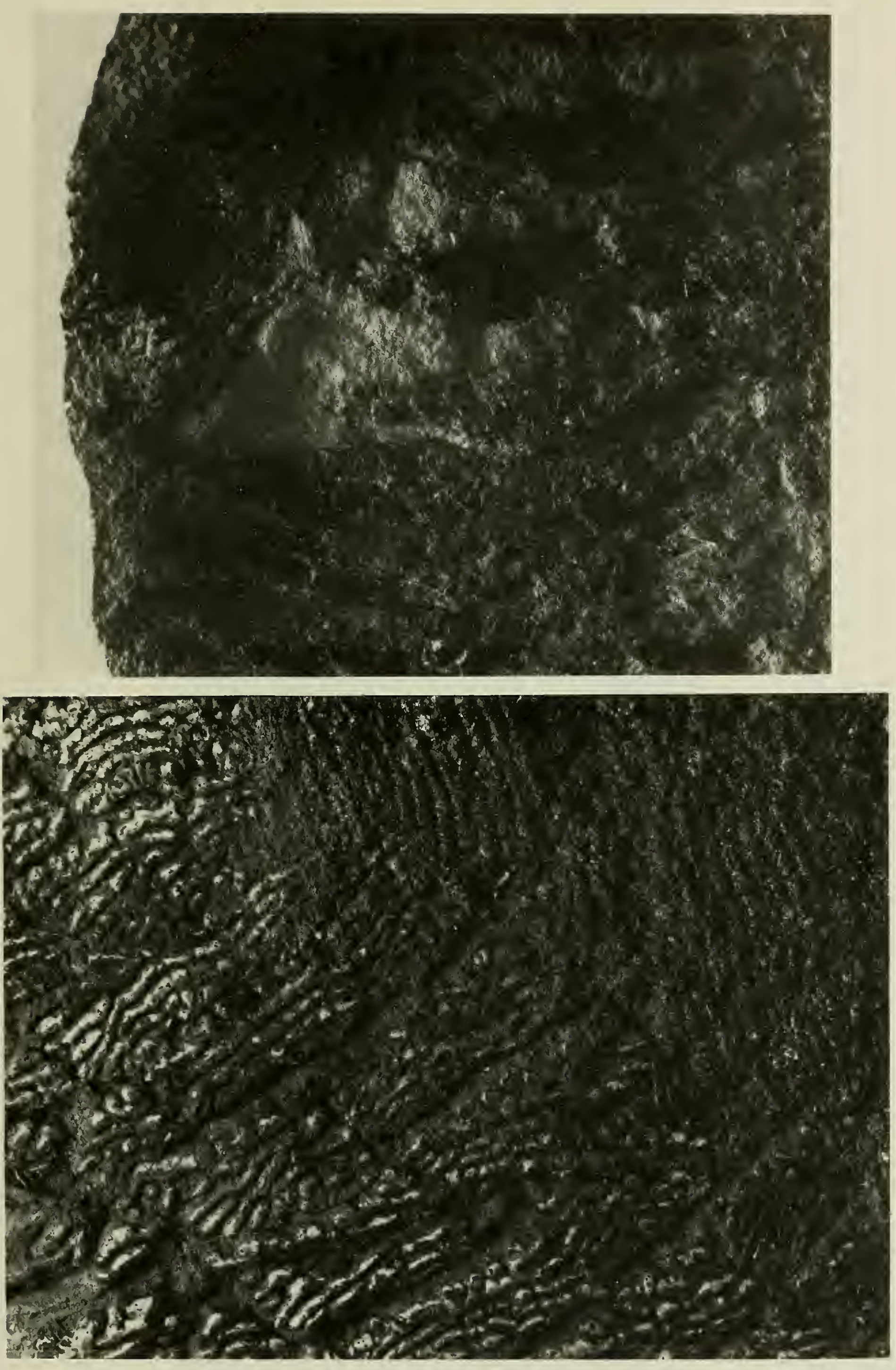

Fig. 7. (Top) Detail of internal ventral skull element pattern on the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) before acid preparation. (Bottom) Detail of lower anterior flank region of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949), showing the ventral pectoral fin rays (upper right diagonal) and the ridgelike texture on the ventral flank scales beneath the pectoral fin (lower left diagonal).

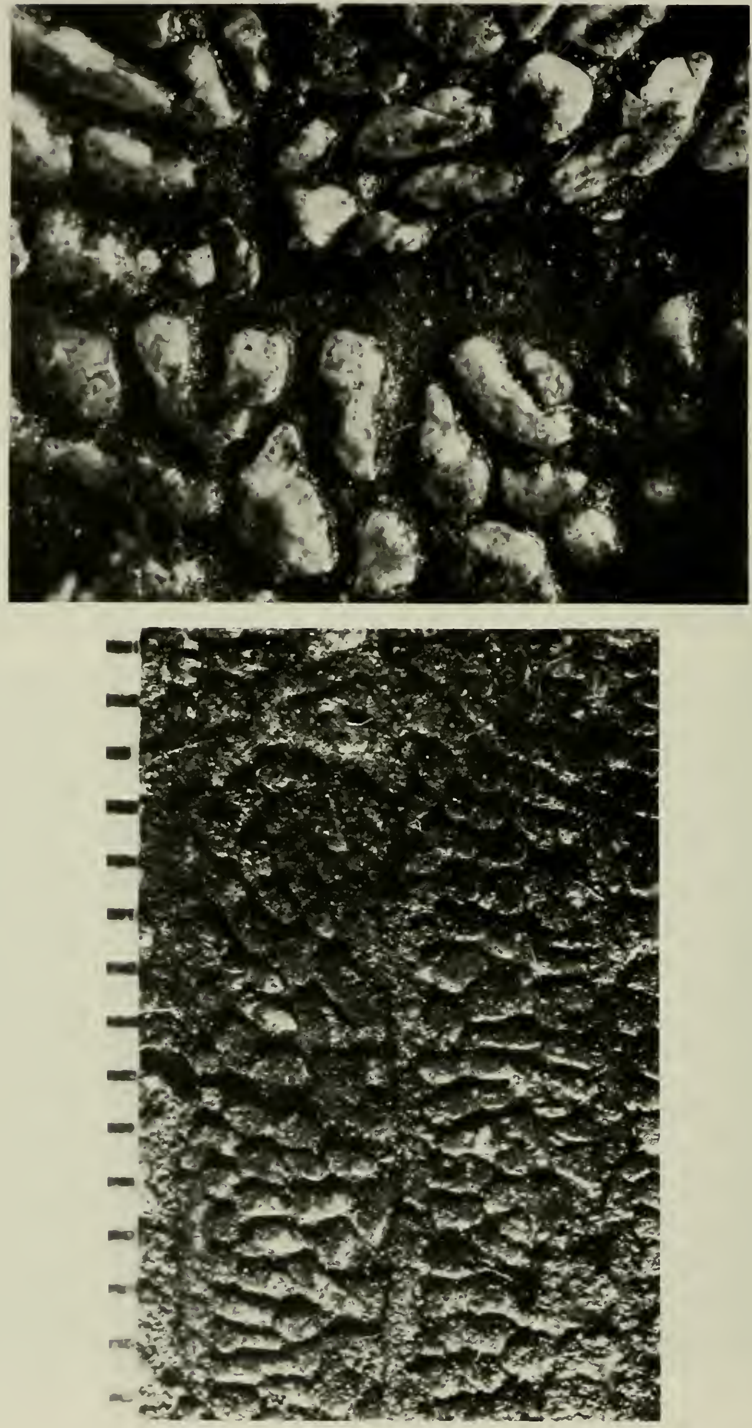

Fig. 8. (Top) Detail of the ornamentation pattern on a single antero-medial flank scale from the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949). (Bottom) Detail of papillate ornamentation on a single postero-medial flank scale from the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949).

these older forms can be properly retained within the Paleonisciformes, the type genus for the family Platysomidae and suborder Platysomoidei now is removed so that the taxonomy of the remaining deep-bodied paleonisciforms is near chaos. It is beyond the scope of this paper to sort through the various phylogenetic pathways in this complex of genera and to classify them correctly, so for now our new form is simply placed in Paleonisciformes without familial assignment. Future work could even demonstrate that it deserves its own familial assignment.

Because a meaningful classification for deep-bodied paleonisciform fishes has not been worked out, the genera which have been described from rocks of Early Mississippian to Middle Triassic age simply are considered in seriatim. These are *Mesolepis, Paramesolepis, Platysomus* (in part), *Schaefferichthys, Soetendalichthys, Wardichthys, Cheirodopsis, Cheirodus* (=*Amphicentrum*), *Eurynotus, Paraeurynotus, Proteurynotus, Adroichthys, Globulodus* (=*Lekanichthys*), *Eurynotoides,* and *Caruichthys.*

Most of these fish are extremely deep bodied and narrow, but *Mesolepis* (Young 1866, Traquair 1879, Ward 1890, Traquair 1907, Pruvost 1919, Van der Heide 1943) and *Eurynotus* (Agassiz 1833–43, Koninck 1878, Traquair 1879) evolved into only slightly deep-bodied forms and even *Proteurynotus* (Moy-Thomas and Dyne 1938) is not nearly so deep bodied as *Tanypterichthys. Adroichthys* (Gardiner 1969), *Paramesolepis* (Traquair 1881, Moy-Thomas and Dyne 1938), *Cheirodopsis* (Traquair 1881, Moy-Thomas and Dyne 1938), and *Wardichthys* (Traquair 1874, 1879, 1907) all have a short-based and posteriorly located anal fin; this contrasts sharply with the elongate, anteroventrally expanded anal fin in *Tanypterichthys.*

*Soetendalichthys* (Gardiner 1969) is somewhat similar to *Tanypterichthys* in body shape and possibly in anal fin elongation, but it contrasts with our form in that its flank scales are not nearly so vertically elongated. Additionally, it has a much more tubercular scale ornamentation, and the pin and socket connections between scales in each column are at the center of each scale rather than along the front or back margin.

*Cheirodus* (Newberry and Worthen 1870; Hancock and Atthey 1872; Traquair 1879; Ward 1890; Pruvost 1919, 1930; White 1937; Dyne 1939; Van der Heide 1943; Bardack 1979) is markedly distinct from *Tanypterichthys* in its small size (5–15 cm), tubercular scale ornamentation, the extreme constriction between the tail and body, and the presence in at least some forms of body "horns" drawn up before the dorsal and anal fins like keels.

*Platysomus* has been used as a generic name for more species of deep-bodied paleonisciforms than any other (Agassiz 1833–43; Eichwald 1857; Hancock and Atthey 1872; Ward 1890; Cope 1891; Pruvost 1930; Moy-Thomas and Dyne 1938; Van der Heide 1943; Wilson 1950; Zidek 1972; Simpson 1979; Schaumberg 1976, 1980). As noted above, the type species of *Platysomus* now is considered to be bobasatraniform, so at least part of the Permian species assigned to that genus belong in that order. Mississippian and Pennsylvanian species assigned to *Platysomus* are grossly similar to *Tanypterichthys,* but they differ consistently from our fish in their possession of a finely vermiform scale-ornamentation pattern (aligned in parallel vertical rows), possession of a more constricted region between the body and the tail, much smaller pectoral fins, and pelvic fins which are never drawn forward far enough to lie beneath the pectorals.

*Schaefferichthys* (Dalquest 1966) is a poorly known form from the Permian of Texas. It is generally platysomid in form and has a finely vermiform scale-ornamentation pattern aligned in parallel vertical rows as in *Platysomus.* It may be possible that this species is a primitive bobasatraniform, but the scale-ornamentation pattern debars it from any close relationship with *Tanypterichthys.*

*Paraeurynotus* (Obruchev 1962) is poorly known, but the scale proportions (only two times higher than wide) and ornamentation (nearly smooth) are markedly different from those of *Tanypterichthys.* Additionally, it is remote in time from our form (Early Permian).

*Eurynotoides* (Berg 1940a) has very nearly a normal fish shape and scale structure, and it is also remote in time (Late Permian) from *Tanypterichthys*; obviously it is not closely related to our specimen.

*Caruichthys* (Broom 1913, Lehman 1966) of the Early Triassic is remote in time from *Tanyperichthys,* a smaller form (about 20 cm long), and covered with scales that are ornamented by irregular prominent transverse ridges.

*Globulodus* (Munster 1842, King 1850, Young 1866, Traquair 1879, Woodward 1891, Brough 1934, Westoll 1941, Berg et al. 1964, Schaumberg 1980) shows some obvious similarities to *Tanypterichthys.* The scales are coarsely striated and their pin and socket arrangement is located along the edge of the scale, the size is large (a maximum of 40 cm), and the constriction between the body and the tail is persistently thick for a deep-bodied paleonisciform fish. Yet the anal fin is not nearly so elongated and the adjacent postero-ventral flank scale columns are not turned downward and forward as they are in *Tanypterichthys.* In these characteristics, *Globulodus* is persistently the more primitive form, even though it is much younger in age (Late Permian). This temporal progression in specialization from derived to primitive seems to debar any direct lineage between these two forms. Probably the similarity in tail structure is a shared primitive trait retained in both forms and should not be considered to be of phylogenetic signficance; the position of the pin and socket arrangement also is shared by many other forms in this family. Large size (40 cm) and a relatively thick tail constriction also are characteristics of *Adroichthys,* which otherwise is not especially close in its morphology to either *Globulodus* or *Tanypterichthys.*

Some other forms formerly placed among the deep-bodied paleonisciforms ("*Eurynotus*" *uspallatensis* (Rusconi 1946a), "*Platysomus*" *pehuenchensis* (Rusconi 1946b) and "*Platysomus*" *cajonensis* (Rusconi 1948), from the Triassic and Jurassic of Argentina) probably do not belong there. What little that is known of them suggests that their scales are not so elongate as those of *Tanypterichthys* and not similarly ornamented. The unnamed platysomid from the Triassic of Australia mentioned by Banks (1978) is, if correctly identified, probably the youngest representative of this family.

Two other recognized families, also deep bodied and frequently considered to be paleonisciforms, are the Dorypteridae and the Dorsolepidae. The monogeneric Dorypteridae (Westoll 1941, Schaumberg 1980) is known only from Late Permian marine beds. This family is characterized by a very unusual body shape and the loss of nearly all trace of a scale coat, characteristics that are not remotely similar to those found in our fish. The monogeneric Dorsolepidae, known only from the Early Triassic, is represented only by the form *Dorsolepis* (Jorg 1969a, b; Gall et al. 1974). It has been associated with the platysomids, but only its narrow and deep body form strongly suggests any affinity. Its scales are greatly reduced and it is very small (5 cm), so it has no close similarity to *Tanypterichthys.*

The marine-going Bobasatraniformes, which includes *Bobasatrania canadensis* (Schaeffer and Mangus 1976), *B. groenlandica* (Stensio 1932, Nielsen 1952, Lehman 1957), *B. mahavavica* (White 1932, Lehman 1957), *B. nathorsti* (Stensio 1921), *Ebenaqua ritchiei* (Campbell and Phuoc 1983), *Ecrinesomus dixoni* (Woodward 1910, Lehman 1957), *Lambeichthys canadensis* (Lambe 1914, Russell 1951, Lehman 1966), "*Platysomus*" *brewsteri* (Warren 1936, Lehman 1966), *Tompoichthys abramovi* (Berg et al. 1964, Lehman 1966), and *Sinoplatysomus meishanensis* (Wei 1980), are all forms that are grossly similar in appearance to *Tanypterichthys.* However, their scale ornamentation, where described, is finely vermiform in vertically parallel ridges, and the constriction between the body and tail is extreme, being only about four scale rows thick. *Sinoplatysomus* and *Ebenaqua* are from the Late Permian, and the other members of this family are from the Early Triassic. The pectoral fin of *Tanypterichthys* is similar to that of *Bobasatrania*, but otherwise shows no special similarity to any member of this family except in its relatively large size. Moreover, the preserved portion of the cheek region in *Tanypterichthys* shows that it contains numerous branchiostegal rays. In contrast, bobasatraniforms have the cheek region highly modified from the primitive paleonisciform condition and the branchiostegal rays have been largely or wholly removed from lateral view (Schaeffer and Mangus 1976). Its gross similarities to the bobasatraniform fishes are considered here to be the result of convergence rather than any intimate relationship.

Thus *Tanypterichthys*, although it falls within the definition of the Paleonisciformes and bears some resemblance to the Bobasatraniformes, cannot be shown to have a clear and close affinity to any other genus so far described within either of those two orders. *Tanypterichthys* therefore warrants recognition as a new and separate genus that can be defined as follows:

### Order Paleonisciformes

### *Tanypterichthys*, new genus

*Diagnosis.*—*Tanypterichthys* differs from all other paleonisciforms by the following combination of characters. Scales vertically elongate (as much as 4 times longer than wide), ornamented with a complex pattern consisting of globular papillae and randomly oriented, short, thick ridges reminiscent of the scale ornamentation in *Wardichthys*; scales arrayed in about 50 columns (from behind the head to the constricted portion of the tail) and in rows of 15 (near the tail) to no more than 26 (near the middle of the body). Posterior skull elements ornamented with a fine, vermiform, vertically aligned pattern of parallel ridges very different from the body scale pattern. Pectoral fins greatly elongated and expanded as in *Eurynotus, Caruichthys*, and *Bobasatrania*, more than half as long as the body. Pelvic fins long, thin, subcylindrical, and inserting far forward on the body beneath the distal part of the pectoral fins, length about one-third that of the body. Anal fin greatly elongated, bordering along the entire length of the back half of the body and turning the adjacent postero-ventral scale columns forward in a manner similar to that seen in *Platysomus striatus*. Constriction between the body and the tail pronounced, but less so than in other deep-bodied members of this order except *Adroichthys* and *Globulodus*. Size very large, as much as 0.5 m.

*Type species.*—*Tanypterichthys pridensis*, new species.

### *Tanypterichthys pridensis*, new species

Figs. 3–11

*Type specimen.*—USNM 391949, a large calcareous concretion containing the bulk of the body, the back edge of the skull, pectoral fins, pelvic fins, and the anal fin.

*Type locality.*—At the northwest end of the Camp Creek Interchange along the West Virginia Turnpike, Mercer County, West Virginia, at latitude 37°29′25″N and longitude 81°06′25″W.

*Horizon.*—About 6 inches above a rubble zone at the base of the Pride Shale Member of the Bluestone Formation (Upper Mississippian Series).

*Collector.*—John F. Windolph, Jr., 20 Nov 1982.

*Diagnosis.*—As for the genus.

*Etymology.*—The pectoral fin is unusual in appearance, being very large and elongate, and it is this striking characteristic to which the generic name alludes (*tany-* = stretched out, *pteryx* = fin or wing, *ichthys* = fish). The specific name reflects the occurrence of the specimen in the Pride Shale Member of the Bluestone Formation.

*Discussion.*—Electron photomicrographs were made of a fragment of one bony scale

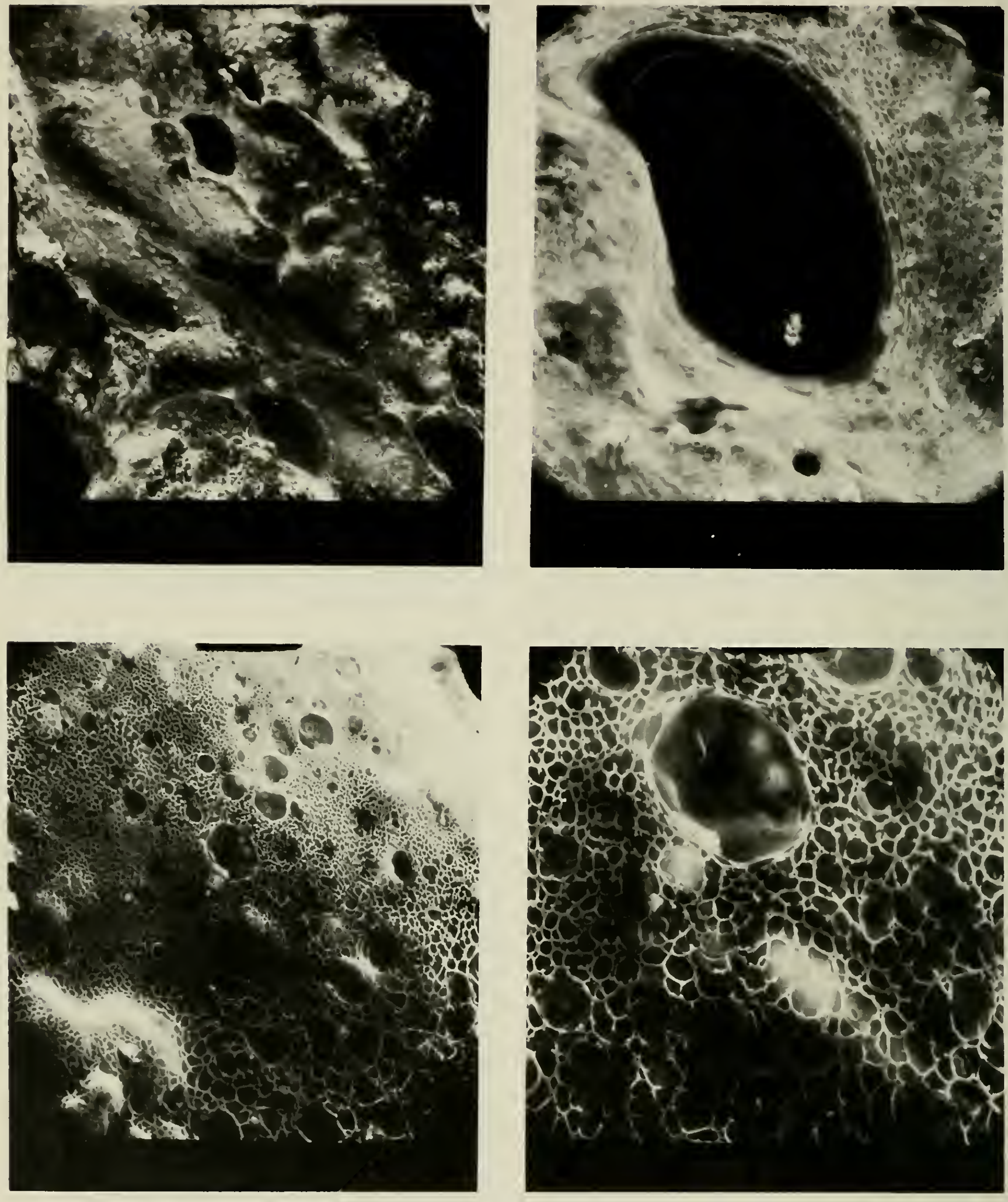

Fig. 9. Electron photomicrographs of details of a single scale from the postero-medial region of the left flank of the type specimen of *Tanypterichthys pridensis* (USNM 391949). Upper left, scale surface showing ridges (running from upper left to lower right) and nutrient foramina (top center); upper right, detail of the nutrient foramina in the top center of the upper left picture; lower left, more detailed view showing the cellular structure of the scale; lower right, more detailed view showing the central region of the lower left picture. Photos by Richard Larson (U.S. Geological Survey, Reston).

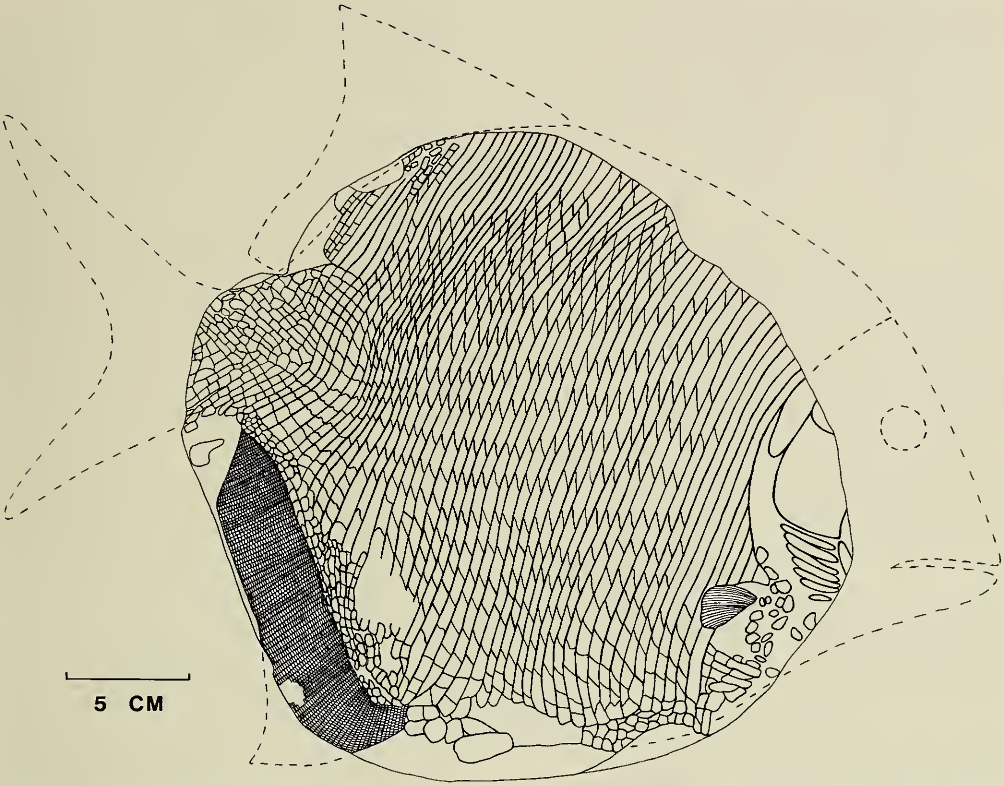

Fig. 10. Sketch showing the scale pattern and anal fin shape as seen from the internal view of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) before acid preparation.

by Richard Larson (U.S. Geological Survey, Reston), and details of the well preserved bone structure and nutrient channels are shown at four different magnifications (Fig. 9). SEM spectral analysis of the fragment showed calcium and phosphorus as major elements, and silicon, aluminum, iron, and sulfur as minor elements.

No trace of the appendicular skeleton was observed. Possibly the concretion split through the scales on one side of the body, so that the remains of a bony skeleton were not revealed. If so, there is no trace of the shapes of such bones revealed by warpage of the visible internal scale surfaces. Therefore, it seems more likely that the concretion split through the middle of the fish, and the appendicular skeleton had left no trace of its former presence. The proportions of the bones at the back of the skull are normal for a platysomid and require no special discussion, though their parallel vermiform pattern (reminiscent of *Platysomus*) is strikingly different from the scale-ornament pattern. Parts of the front, top, and back of the body are missing, but general proportions can be estimated from the available remains. Deep-bodied paleonisciform fishes are known to have 15 (*Paramesolepis tuberculata*) to 26 (*Eurynotus, Soetendalichthys*) rows of scales present in each vertical column near the deepest part of the body. Because about 22 scale rows are preserved in the type specimen of *Tanypterichthys,* the top of the body almost certainly did not extend any higher than 4 more short scale-

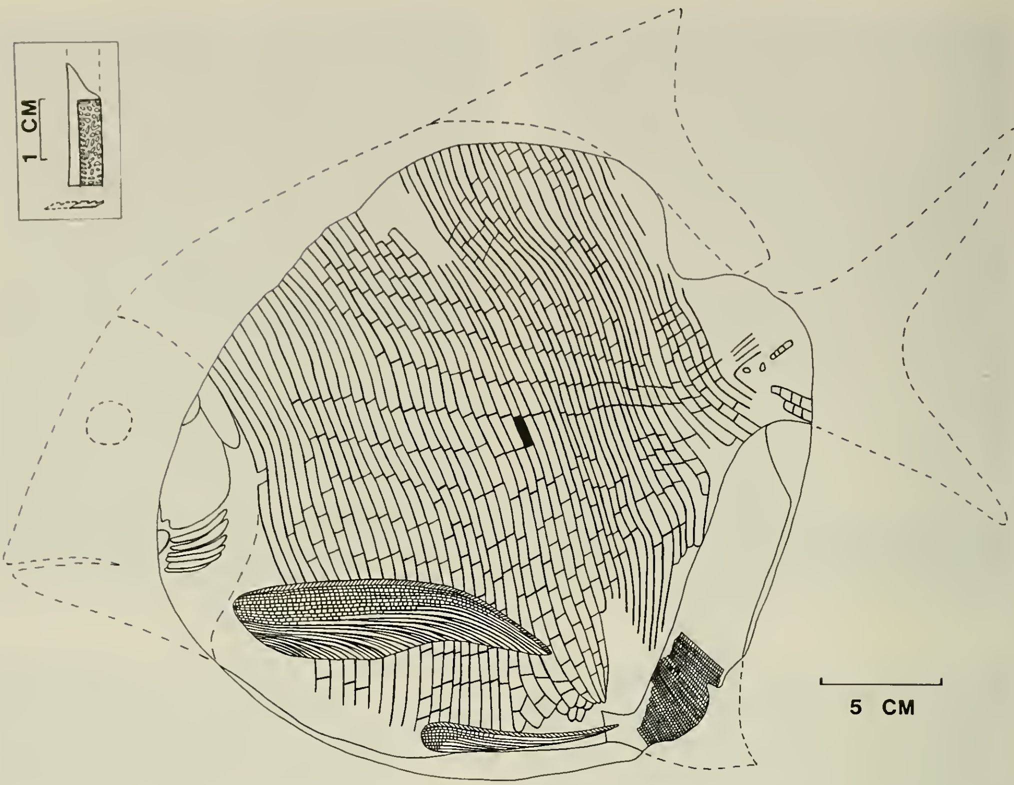

Fig. 11. Sketch showing scale pattern, pectoral fin, and pelvic fin as seen from the external view of the left side of the type specimen of *Tanypterichthys pridensis* (USNM 391949) after acid preparation. Shape of the anal fin was derived from Fig. 10; the general body form is assumed to be typically platysomid. Inset shows the details of the construction and ornamentation of a single flank scale (shaded black on the fish body) and its relationships to surrounding scales.

heights above the level of the preserved upper margin. Likewise, when a large anal fin is found in other fishes in this family, it is matched by an equally large or larger dorsal fin (for example, *Platysomus superbus* or *Ebenaqua ritchiei*). The gross shape of the skull and the shape of the tail are not greatly variable in known members of this group; therefore, the rough outlines of the body reasonably can be surmised in addition to the observable detailed patterns of the preserved parts (Figs. 10, 11).

## Functional Anatomy

The outline of the flank scales is markedly different in internal and external aspect (see Figs. 3, 4). This is because the scales are hinged along their dorsal and ventral borders in such a manner that the internal anterior dorsal border forms a pinlike slip. This slip inserts beneath the internal anterior ventral border of the next scale above it where it is embayed from the internal side to form a socket (see Fig. 11). This general kind of structure is probably normal among deep-bodied paleonisciform fish, though in *Eurynotus* (Traquair 1879) and *Soetendalichthys* (Gardiner 1969) the pins and sockets are in the center of the scales, and in *Adroichthys* (Gardiner 1969) they are slightly off-center. In *Globulodus* (Agassiz 1833–43, King 1850), *Platysomus* (Traquair 1879), *Cheirodus* (Traquair 1879), and *Tanypter-*

*ichthys,* the pin is formed by an upper corner of the scale. The function of this arrangement seems to have been to strenghten the ganoid scale coating and thus to form a chain-mail effect through a combination of antero-posterior overlapping and vertical interlocking of the scales. Such an interlocking arrangement would be mobile only around a vertical axis, and the body movement of these fishes would be restricted to lateral flexure. Such restriction in body motion is probably correlated with the very deep body form of the animal. The fact that the body armor did not evolve to a greater rigidity suggests that these fishes did need to preserve their ability to move in a laterally undulatory, normal piscine fashion.

The dorsal fin of *Tanypterichthys* is unknown, but in better known members of the family that also have expanded anal fins (for example, *Platysomus superbus* (Moy-Thomas and Dyne 1938) and *Ebenaqua ritchiei* (Campbell and Phuoc 1983)) great expansion and elongation of the anal fin is matched by an equal or greater development of the dorsal fin. Such well developed sets of anal and dorsal fins in modern fishes usually function to propel their bearer at slow speeds by undulations of these two fins without marked undulation of the body as a whole. The well-developed anal fin, present in *Tanypterichthys* and in many of the other deep-bodied paleonisciforms and bobasatraniforms, suggests that a similar mode of propulsion probably was employed.

The pectoral and pelvic fins are strongly modified from the generalized actinopterygian condition, which suggests that they were specialized in function. The large pectorals were braced along their dorsal border by an enlarged row of scales (see Fig. 5), which probably afforded them exceptional strength for an actinopterygian. These large fins could have poled the fish forward while it cruised near the bottom or functioned as oars for maneuvering the body fore, aft, and in tight circles. The pelvic fins are long but very thin. They could have functioned in murky water as feelers to keep the fish slightly above the bottom or as claspers during mating as similarly shaped pelvic fins do in many modern actinopterygians.

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# LARVAE OF *XIPHOPENAEUS KROYERI* (HELLER, 1862) (CRUSTACEA: DECAPODA: PENAEIDAE) FROM OFFSHORE WATERS OF VIRGINIA, U.S.A.

Robert C. Maris

*Abstract.*—A range extension is provided for the shrimp *Xiphopenaeus kroyeri* (Heller, 1862). Larvae of *X. kroyeri* were collected from offshore waters of Virginia, U.S.A. near the Chesapeake Light Tower (36°54′N, 75°43′W). Zoeal stages I–III, V–VII, and IX were obtained at depths ranging from neuston to epibenthic, during the day and night, with a maximum concentration of 6.8 per cubic meter. This report extends the known range of *X. kroyeri* about 190 km northward from Cape Hatteras, North Carolina.

Zooplankton collections taken off the coast of Virginia were found to contain larval specimens of *Xiphopenaeus kroyeri* (Heller, 1862). This species was previously known to occur from capes Hatteras and Lookout, North Carolina, through the Gulf of Mexico and Caribbean Sea to Brazil (Williams 1984).

A station near the Chesapeake Light Tower (36°54′N, 75°43′W) was occupied for a continuous 72-hour period, 13–16 August 1985, (Maris 1986). Quantitative plankton samples were collected at three-hour intervals from the following depths: neuston (0.10–0.15 m), 1 m, 3 m, 6 m, epibenthic (12.8 m).

A total of 125 samples were collected, of which 12 (9.6%) contained specimens of *X. kroyeri.* Zoeal stages I, II, III, V, VI, VII, and IX were obtained and identified using descriptions provided by Kurata (1970). The larvae were found at all depths sampled, during both day and night collections, with a maximum concentration of 6.8 per cubic meter. A summary of the entire collection of larval *X. kroyeri* can be found in Table 1.

The occurrence of larval *X. kroyeri* might indicate breeding populations in Virginia waters, but possible transport from the south cannot be eliminated. However, the presence of early zoeae casts doubt on long-distance transport as the sole dispersal mechanism. Also, the abundance and variety of later zoeal stages seems to imply that at least limited metamorphosis is occurring off Virginia. Thus, this report extends the known range of *X. kroyeri* about 190 km northward from Cape Hatteras, North Carolina.

Table 1.—Offshore Virginia collections of larvae of *Xiphopenaeus kroyeri* (Heller, 1862).

| Date (1985) | Time (EDT) | Depth (m) | Stage | Density (no./m³) |
|---|---|---|---|---|
| 13 Aug | 1500 | 6 | II | 0.7 |
| 14 Aug | 0000 | 1 | III | 2.2 |
| 15 Aug | 0000 | 0 | IX | 0.8 |
| 15 Aug | 0000 | 6 | VI | 2.0 |
| 15 Aug | 0300 | 6 | III | 1.1 |
| 15 Aug | 0300 | 6 | VII | 1.1 |
| 15 Aug | 0900 | 6 | I | 1.1 |
| 15 Aug | 1500 | 6 | II | 1.0 |
| 15 Aug | 1500 | 6 | V | 1.0 |
| 16 Aug | 0000 | 0 | V | 1.8 |
| 16 Aug | 0300 | 13 | I | 0.7 |
| 16 Aug | 0600 | 3 | II | 6.8 |
| 16 Aug | 0900 | 6 | II | 1.1 |
| 16 Aug | 0900 | 6 | VII | 1.1 |
| 16 Aug | 1200 | 6 | II | 2.2 |
| 16 Aug | 1200 | 6 | III | 2.2 |

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99(4), 1986, pp. 604–611

# TWO NEW CRABS, *PARAPAGURISTES TUBERCULATUS* AND *PALAEOXANTHO LIBERTIENSIS*, FROM THE PRAIRIE BLUFF FORMATION (MIDDLE MAASTRICHTIAN), UNION COUNTY, MISSISSIPPI, U.S.A.

Gale A. Bishop

*Abstract.*—Two new genera and species of fossil crabs, *Parapaguristes tuberculatus* and *Palaeoxantho libertiensis,* occur in the Prairie Bluff Formation in Union County, Mississippi. Associated with these taxa are *Prehepatus harrisi* Bishop, 1985, *Raninella*? sp., *Protocallianassa* sp., an indeterminate claw of a portunid, and claw fragments of a large lobster. The genus *Parapaguristes* is erected to include *P. tuberculatus* n. sp. and *P. whitteni* (Bishop, 1983). The new genus *Palaeoxantho* is morphologically similar to the xanthid genera *Xanthosia, Xantho,* and *Syphax.*

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During October 1982, I was guided to a fossil echinoderm locality by Mr. Ralph Harris, a paraprofessional collector working with me in studies of fossil Cretaceous Mississippi decapod crustaceans. The exposure is situated just west of and below the Liberty School and Church in the SW ¼, SW ¼, Sec. 3, T 8S, R 3E, Union County, Mississippi. This locality, herein called The Liberty School Locality (Gale A. Bishop Locality 52 indicated herein GAB 52), is a scraped area just off the road to the northeast of a small ridge perpendicular to Sand Creek (Fig. 1). The rocks exposed in the scraped area consist of a few centimeters of marlstone overlain by three meters of sandy, fossiliferous limestone assignable to the Prairie Bluff Formation (Fig. 2), which is laterally equivalent to the clastic Owl Creek Formation. The Prairie Bluff Formation is unconformably overlain by the Paleocene Clayton Formation and unconformably overlies the Ripley Formation (Russell et al. 1982:11). The age of the Prairie Bluff Formation is Middle Maastrichtian (Russell et al. 1982:24).

The fauna from the Prairie Bluff appears to be diverse (Stephenson and Monroe 1940:204). At the Liberty School Locality, the fauna (Fig. 3) is dominated by the heart urchin *Linthia variabilis* Slocum but includes numerous other taxa including *Baculites* sp., *Scaphites* sp., *Turritella* sp., *Exogyra costata, Pinna* sp., *Urceolabrum* sp. and numerous other molluscs. A small but integral part of this fauna are the decapods *Protocallianassa* sp., *Parapaguristes tuberculatus* n. gen., n. sp., *Palaeoxantho libertiensis* n. gen., n. sp., *Prehepatus harrisi* Bishop, 1985; *Raninella*? sp., claw fragments of *Hoploparia* sp., and an indeterminate claw of a portunid crab. Stephenson and Monroe (1940:208a) presented a faunal list for the Prairie Bluff Formation that included *Callianassa* sp., *Avitelmessus* n. sp., *Prehepatus* n. sp., *Raninoides ovalis* Rathbun, a portunid, and crab claws. These specimens are in the collections of the United States National Museum of Natural History but could not be located during a visit in 1984.

Order Decapoda Latreille, 1803
Infraorder Anomura
H. Milne-Edwards, 1832
Superfamily Paguroidea Latreille, 1803
Family Paguridae Latreille, 1803

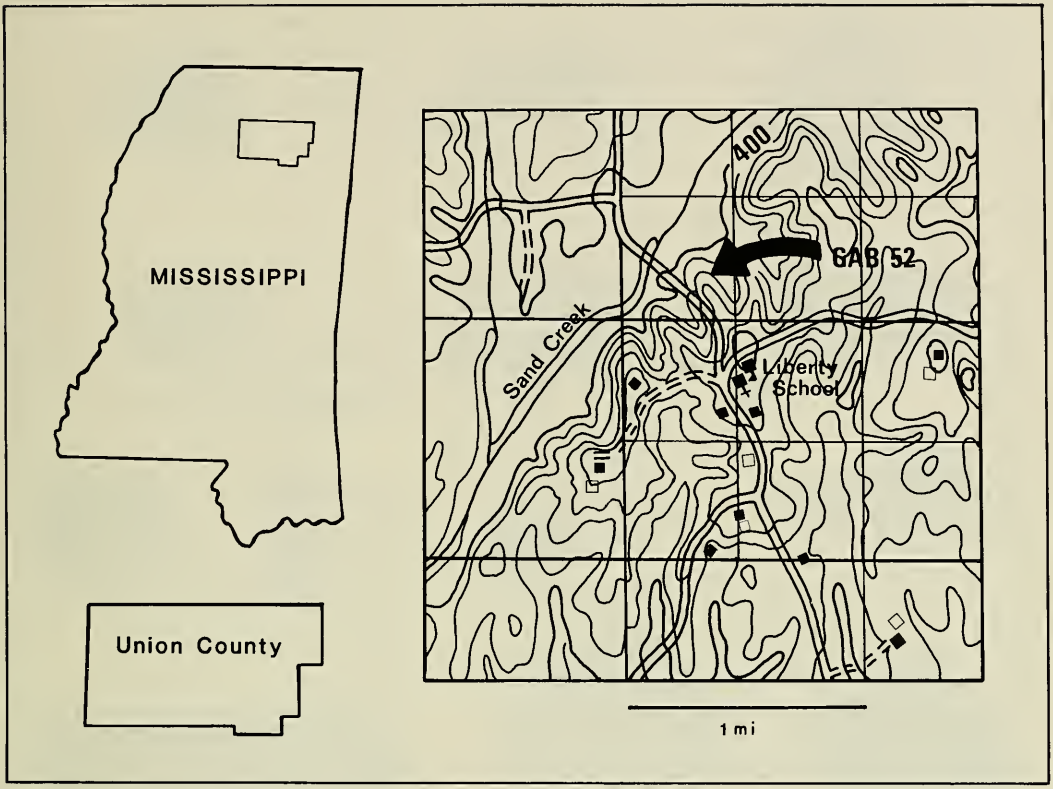

Fig. 1. Geographic setting of the Liberty School Locality.

### Subfamily Pagurinae Latreille, 1803

### *Parapaguristes,* new genus

*Type species.*—*Paguristes whitteni* Bishop, 1983.

*Diagnosis.*—Claws large, equal, longer than high, thick and biconvex; upper and lower margins convex, proximal margin strongly oblique, distal margin vertical, paralleled by furrows on front and back; fixed finger short, blunt, and downturned; top margin on inner face more or less overturned into horizontal crest; surface ornamented by coarse tubercles.

*Etymology.*—*Parapaguristes* is derived from *Para* (Greek, near to) + *Paguristes* (Greek, a genus of (hermit) crab); gender masculine.

*Occurrence.*—The two species that comprise *Parapaguristes* are both from the east-central Mississippi Embayment occurring in the Coon Creek Formation (*P. whitteni* Bishop, 1983) and Prairie Bluff Chalk (*P. tuberculatus* n. sp.) and range from early to middle Maastrichtian in age.

### *Parapaguristes whitteni* (Bishop, 1983)

Fig. 5B

*Synonymy.*—*Paguristes whitteni* (Bishop, 1983:420–424, figs. 3F, 4.

*Diagnosis.*—Chelipeds large, equal, similar, biconvex and inflated, upper margin overturned into horizontal crest; finger downturned; ornamented by longitudinal rows of tubercles on outerface.

*Remarks.*—*Parapaguristes whitteni* is well known, being represented by nearly all elements of the chelipeds. In my assignment to *Paguristes,* I pointed out (Bishop 1983) the relatively poor concurrence of this species with the genus *Paguristes,* with the

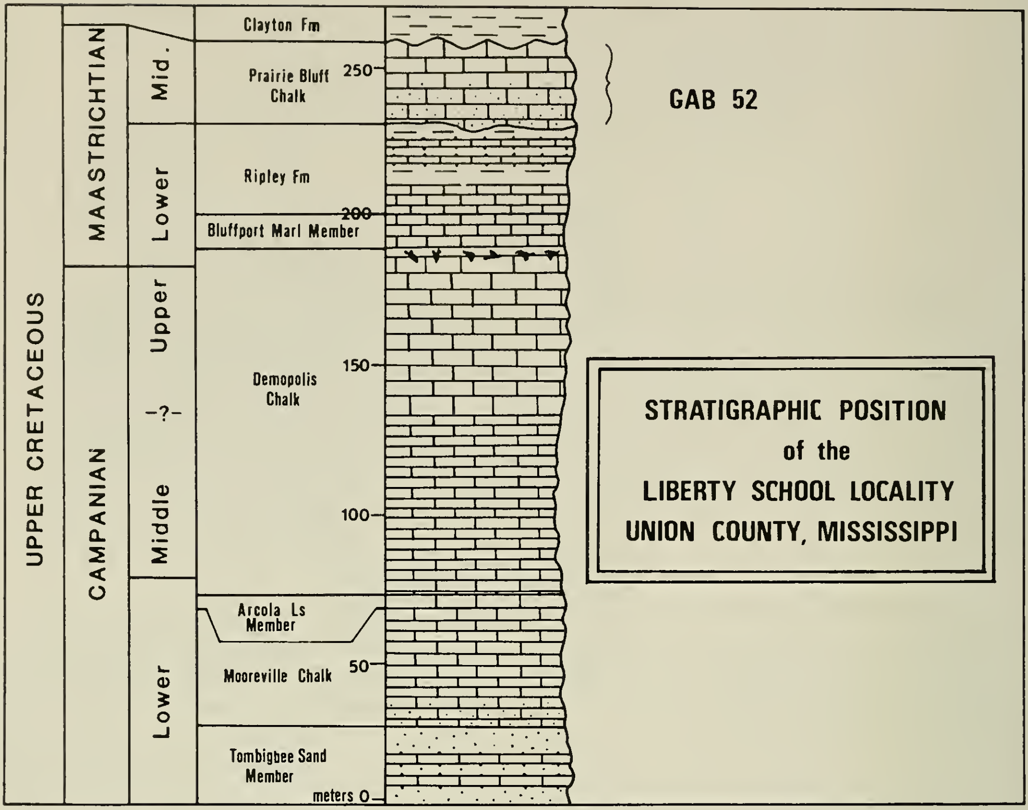

Fig. 2. Stratigraphic setting of the Liberty School Locality.

suggestion of Forest (Bishop 1983:419) and now myself that it is better to erect a new taxon for fossils such as *Paguristes whitteni* than to try to assign them to existing taxa in which they really do not fit. The description of taxa based solely upon claws is necessary because certain taxa have differentially mineralized exoskeletons leading to preferential preservation, as in the hermit crabs.

*Parapaguristes whitteni* was described from a sample of 30 specimens, all claws.

*Parapaguristes tuberculatus*, new species
Figs. 3D, 4, 5A

*Diagnosis.*—Claws large, biconvex, equal, palm longer than high; overturned horizontal crest on top margin of inner face reduced to subtle ridge paralleling margin; entire claw ornamented by random pattern of large tubercles alternating with granules.

*Description.*—Claws large, biconvex, longer than high (L/H = 1.4), highest at distal third, upper and lower margins convex; distal margin vertical, paralleled by shallow furrows; proximal margin oblique, rounding evenly onto upper margin. Entire surface covered by coarse tubercles interspersed with very small granules in random pattern except for relatively smooth area on inner face along proximal articulation and bottom of distal marginal grooves. Tubercles conical; those on upper and lower margins tilted slightly distally; fixed finger apparently downturned.

*Comparison.*—*Parapaguristes tuberculatus* differs from *Parapaguristes whitteni* by being ornamented more richly and evenly, by its less well developed overturned crest

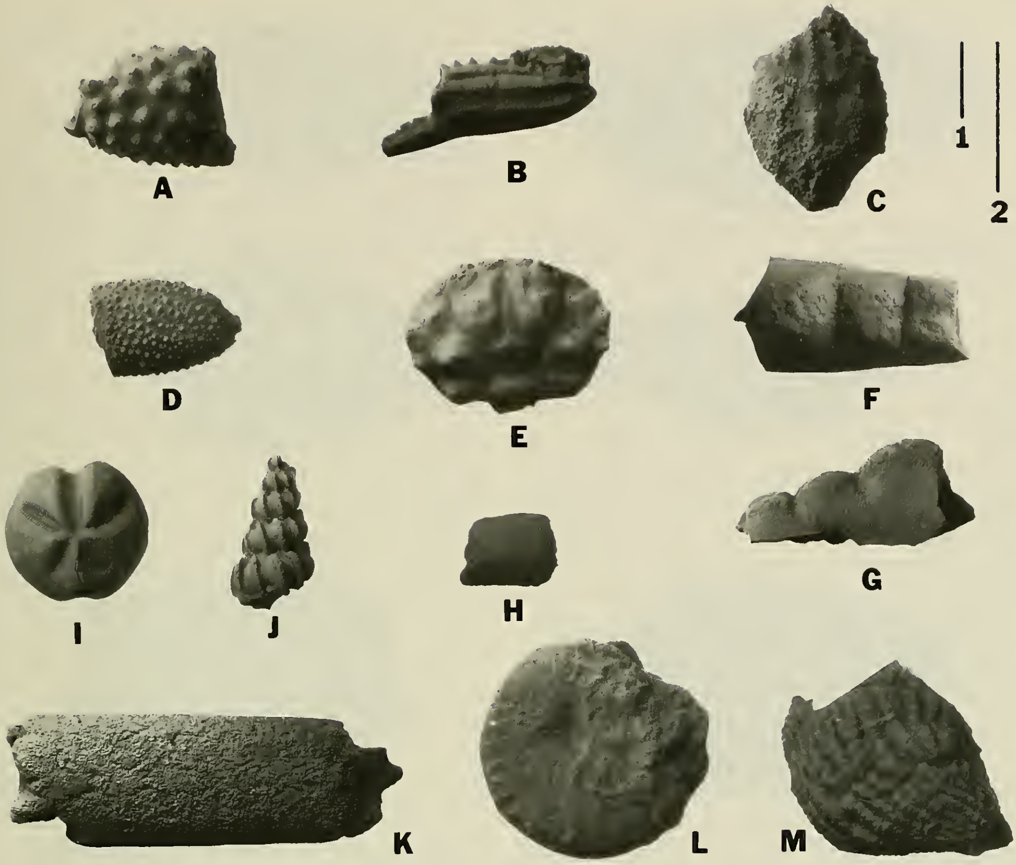

Fig. 3. Important elements of the Liberty School fauna. A, *Prehepatus harrisi* Bishop, 1985 (GSCM 1687); B, Portunid(?) claw (GAB 52-14); C, *Raninella*? sp. (GAB 52-13); D, *Parapaguristes tuberculatus* n. sp. (GSCM 1690); E, *Palaeoxantho libertiensis* n. sp. (GSCM 1692); F–G, Occulusional surface of crushing claw of lobster or crab (GAB 52-5); H, *Callianassa* sp. (GAB 52-4); I, *Linthia variabilis* Slocum, 1909 (GAB 52-6); J, *Urceolabrum* sp. (GAB 5207); K, *Baculites* sp. (GAB 52-8); L, *Scaphites* sp. (GAB 52-9); and M, *Exogyra costata* Say, 1820 (52-10); exhibiting healed predation breaks. (Bar scales—1 cm; Scale 1, Figs. A, D, F–G, I–M; Scale 2, Figs. B–C, E, H.)

on the upper part of the inner face, and its smaller size (Fig. 5).

*Etymology.*—Named for the exceedingly tuberculate claws.

*Types.*—The holotype (GSCM 1690) and paratype (GSCM 1691a, b) of *Parapaguristes tuberculatus* are deposited in the collection of the Georgia Southern College Museum, Georgia Southern College, Statesboro, Georgia 30460.

*Occurrence, sample size, and preservation.*—Four specimens were collected from the Liberty School Locality: the holotype, a single left claw; the paratypes, a pair of claws found in close proximity to one another and a single right claw. The exoskeleton is preserved intact and the claws are filled with sediment.

Section Brachyrhyncha Borradaile, 1907
Superfamily Xanthoidea MacLeay, 1838
Family Xanthidae MacLeay, 1838
*Palaeoxantho,* new genus

*Type species.*—*Palaeoxantho libertiensis* n. sp.

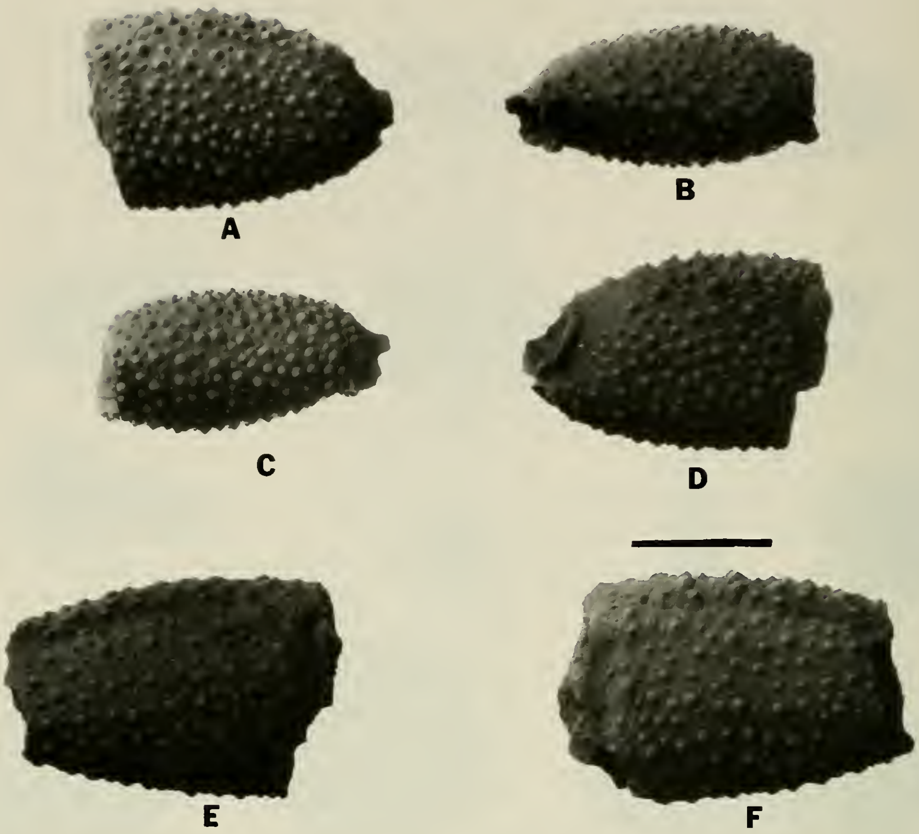

Fig. 4. Photographs of *Parapaguristes tuberculatus.* A–D, Outer, top, bottom, and inner views of holotype left claw (GSCM 1680); E–F, Outer view of paratype claw pair (GSCM 1691a, b). (Bar scale = 1 cm.)

*Diagnosis.*—Carapace oval-pentagonal, wider than long, widest across epibranchial lobes; anterolateral margins upturned, front rounded; posterolateral margins relatively straight; converging posteriorly; posterior margin unknown; rostrum bilobed and sulcate; orbits small, bifissured above; fronto-orbital width 58% of carapace width. Carapace well differentiated into tumid lobes by well defined grooves.

*Etymology.*—From the combination of *Paleo* (Greek, old) + *Xantho* (Greek, one of Cyrene's attendant nymphs).

*Occurrence.*—*Palaeoxantho* is known only from the middle Maastrichtian Prairie Bluff Formation at the Liberty School Locality (GAB 52) in Union County, Mississippi.

*Remarks.*—*Palaeoxantho* is similar to the xanthid genera *Syphax* A. Milne-Edwards, 1863 (Eocene France), *Xantho* Leach, 1804 (Miocene-Pleistocene, Europe and Fiji; Recent, Indopacific, Mediterranean, Eastern Atlantic), and *Xanthosia* (Albian- ? Paleocene, Europe, North America, ? W. Africa). *Palaeoxantho* has the same general shape and groove morphology as *Syphax* but has better differentiated, more tumid regions, a trend carried even further by *Xantho* with its more differentiated but less tumid carapace. *Palaeoxantho* differs from these by its upturned lateral margins, its general flatness, and the tumidity of its carapace. *Palaeoxantho* is relatively narrower and thicker than *Xanthosia* but bears a resemblance to that genus (and many other xanthids).

### *Palaeoxantho libertiensis,* new species
Figs. 3E, 6

*Diagnosis.*—Carapace ovate-pentagonal, wider than long, widest near middle. Anterolateral margin and frontal margins broadly rounded, anterolateral margins upturned; front short, bilobed, medially sulcate, 10% of carapace width; orbits small, bifissured above, upturned; frontal-orbital width 58% of carapace. Posterolateral margins relatively straight, converging posteriorly; hind margin unknown. Carapace well differentiated by grooves into tumid lobes.

*Description.*—Carapace small, rounded pentagonal, wider than long (L/W = 0.80), widest across epibranchial lobes near midlength. Frontal and anterolateral margins broadly rounded, upturned, posterolateral margins fairly straight, convergent posteriorly, posterior margin unknown. Front short, medially grooved, bilobed, 10% of carapace width; frontal region between inner angles of orbits 33% of carapace width; orbits small, upturned, bifissured above, distance between outer edges of orbits 58% of carapace width. Four anterolateral lobes present (frontal, hepatic, and 2 epibranchial), hepatic placed at anterior of convergent posterolateral margin. Carapace well differentiated by grooves into tumid regions; scapular arch separated from cephalic arch by sinuous cervical furrow. Cephalic arch differentiated into mesogastric lobe, triangular behind with narrow anterior tongue; very large, tumid protogastric lobes; small longitudinally elongate epigastric lobes; slightly tumid hepatic lobes, and poorly defined frontal areas. Scapular arch well differentiated into tumid regions; cardiac lobe rounded-hexagonal, separated from mesogastric lobe by broad transverse depression (continuing across entire dorsal shield), epibranchial regions differentiated into 3 bosses, 2 marginal, anterior at widest part of carapace and both produced into upturned wings, and one large boss forming most of region; epibranchial region separated from mesogastric lobe by aforementioned broad, transverse depression; mesobranchial lobe developed into transverse ridge, in line with cardiac region, with slight tumid area along margin of dorsal shield; intestinal and metabranchial regions unknown. Carapace finely and sparsely granulate over entire surface, especially on summits of bosses. Sides of carapace downturned, nearly vertical, slanting slightly under dorsal shield; sides granulate, faint grooves present on sides in line with ends of cervical groove and groove separating marginal epigastric bosses.

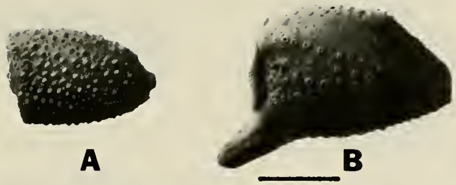

Fig. 5. Comparison of outer views of left claws of (A) *Parapaguristes tuberculatus* (GSCM 1690) and (B) *Paraguristes whitteni* (Bishop, 1983) (GSCM 1683). (Bar scale = 1 cm.)

*Comparison.*—*Palaeoxantho libertiensis* resembles *Syphax crassus* (A. Milne-Edwards, 1864) from the Lower Tertiary of southern France in carapace outline but differs significantly from it by having straighter posterolateral margins, a better areolated carapace, and upturned anterolateral margins. *Palaeoxantho libertiensis* is similar to *Titanocarcinus serratifrons* A. Milne-Edwards in carapace outline but differs in having a better areolated carapace, upturned anterolateral margins, and lacking the pronounced dentate anterolateral margins. *Palaeoxantho libertiensis* resembles *Xantho impressus* (Lamark) from the Recent in its general carapace shape and areolation but differs from it by being relatively narrower, having a better areolated carapace, and by its lack of differentiation of the protogastric and epibranchial lobes. *Palaeoxantho libertiensis* differs from species of *Xanthosia* by being relatively more oval, thicker (i.e., not flattened), narrower, by having a more rounded front, a better areolated carapace,

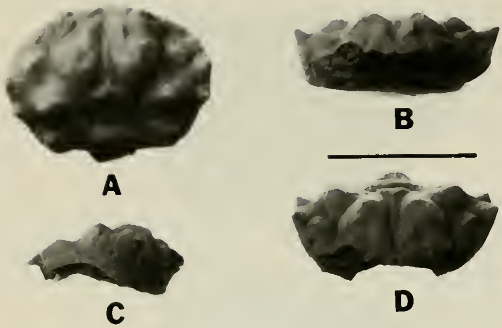

Fig. 6. *Palaeoxantho libertiensis* seen in: A, dorsal; B, anterior; C, right lateral; and D, oblique anterior views, holotype (GSCM 1692). (Bar scale = 1 cm.)

and upturned anterolateral margins. In spite of these major differences, *P. libertiensis* resembles species of *Xanthosia* in a general way, and specifically is more similar to *Xanthosia granulosa* (McCoy) and *Xanthosia buchii* (Reuss) but still very different from them as expressed above.

*Etymology.*—The trivial name *libertiensis* is derived from the type locality near the Liberty School and Church.

*Type.*—The holotype (GSCM 1692) of *Palaeoxantho libertiensis* is deposited in the collection of the Georgia Southern College Museum, Georgia Southern College, Statesboro, Georgia 30460.

*Occurrence.*—One partial carapace has been collected from the Prairie Bluff Formation near the Liberty School and Church in Union County, Mississippi.

## Conclusions

The decapods of the Prairie Bluff Formation represent the youngest Late Cretaceous fauna known in North America. As more of this fauna is described and compared to the older and younger Gulf Coast crab faunas, it may be possible to document the presence or absence of a mass extinction event among decapods of the Gulf Coastal Plain at the Cretaceous-Tertiary boundary.

The decapods of the Prairie Bluff occur as rare elements in the fossil assemblages dominated by echinoids and molluscs, not as decapod-dominated assemblages. It is anticipated that few new additional taxa will be discovered; hence, the importance of describing the known decapods becomes more significant. To attain this end, I have described a new *Prehepatus* from the Prairie Bluff (Bishop 1985) and in this paper have described two new species (*Parapaguristes tuberculatus* and *Palaeoxantho libertiensis*). Three additional Prairie Bluff decapod taxa are known and in hand. One of those is represented by large claw fragments of a shell-crushing decapod (Fig. 3F, G). This taxon is known from many localities ranging from the Demopolis Formation through the Prairie Bluff in Mississippi and Alabama and will soon be described. The fauna also includes a raninid crab assigned to *Raninella*? (Fig. 3C) which may be the same taxon reported by Stephenson and Monroe (1940:208a) as *Raninoides ovalis* Rathbun. The collection also contains a claw of a brachyuran (Fig. 3B) which probably belongs to a portunid crab. A similar claw, from the Coon Creek Formation, was named and assigned as a lobster, *Eryma flecta* Rathbun, 1926, and maintained in that taxon in 1935 (Rathbun 1935:21). Both claws appear to belong to portunid crabs. I hesitate to name and make such reassignment until the portunid cited by Stephenson and Monroe (1940:208a) is examined. A callianassid claw (Fig. 3J) is likewise not named, because it is difficult to make even a generic assignment based on unique claws of the callianassids (Rathbun 1935:29). *Prehepatus harrisi* Bishop, 1985, may prove to be the same as *Prehepatus* n. sp. cited by Stephenson and Monroe (1940:208a). I am also looking forward to seeing the specimen of *Avitelmessus* n. sp. cited by them.

The decapods now known from the middle Maastrichtian Prairie Bluff Formation of Northern Mississippi include:

Fig. 3F–G Claw fragments indet.
Fig. 3J *Callianassa*? sp.
Fig. 3D *Parapaguristes tuberculatus* n. sp.
Fig. 3C *Raninella*(?) sp. (?=*Raninoides*

*ovalis* Rathbun: Stephenson and Monroe, 1940)

Fig. 3A *Prehepatus harrisi* Bishop, 1985 (?=*Prehepatus* n. sp. Monroe)

Fig. 3E *Palaeoxantho libertiensis* n. sp.

Fig. 3B Portunid claws indet. (?=*Eryma* cf. *flecta* Rathbun and ?=portunid of Stephenson and Monroe 1940)

No Fig. *Avitelmessus* n. sp. (Stephenson and Monroe, 1940)

## Acknowledgments

The assistance of Mr. Ralph Harris in collecting decapods from the Cretaceous of Mississippi is gratefully acknowledged. Direct support of this research was received from the National Science Foundation (Grant DEB 8011570) and the National Geographic Society (Grant NGS 1629). Indirect support was received from the Department of Geology and Geography and the Faculty Research Committee, Georgia Southern College. The manuscript was typed by Phyllis Wiggins, Donna Cain, and Judith Underwood. The manuscript was strengthened considerably by R. M. Feldmann and J. S. H. Collins, whose constructive criticism is especially appreciated.

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# A NEW SPECIES OF *TUBIFICOIDES* LASTOCHKIN (OLIGOCHAETA: TUBIFICIDAE) FROM BERMUDA AND THE BAHAMAS

Berit Råsmark and Christer Erséus

*Abstract.*—*Tubificoides bermudae,* new species, is characterized by (1) papillated body wall in postclitellar segments, (2) possession of only bifid setae, 2–3 per bundle anteriorly, 1–2 per bundle in postclitellar segments, (3) vasa deferentia that are about as long as atria, and (4) conical penis sheaths with smooth outline and slightly distended distal end. The species appears closely related to *T. brownae* Brinkhurst and Baker, and *T. motei* Brinkhurst, but is easily distinguished from these by the characteristic shape of its penis sheaths.

While studying the marine oligochaete fauna of Bermuda, the second author encountered a new species of *Tubificoides* Lastochkin at several subtidal stations of muddy sand. The same species was also found in material collected in Bermuda and the Bahamas by Dr. Meredith L. Jones, National Museum of Natural History (USNM), Washington, D.C.

## Material and Methods

Specimens were sorted from sand collected at various sites in Bermuda in 1977 and were fixed in Bouin's fluid. Seventeen specimens were sectioned and stained in Azan or Heidenhain's hematoxylin and eosin. The bulk of the individuals were, however, stained whole in paracarmine; 6 of these were dissected, the remaining 33 mounted whole in Canada balsam. Three additional whole-mounted specimens, one from Bermuda and two from the Bahamas, were kindly placed at our disposal from the USNM. The type-series of *T. bermudae* is deposited in the USNM.

## *Tubificoides bermudae,* new species
Figs. 1, 2

*Holotype.*—USNM 98945, whole-mounted specimen from Smith's Sound (SE end of Smith's Island), Bermuda, 32°22′08″N, 64°39′25″W, 5 m, muddy fine sand (coll. C. Erséus, 2 Dec 1977).

*Paratypes.*—USNM 98946–98951, 1 sectioned, 1 dissected and 4 whole-mounted specimens from type locality.

*Other material.*—USNM 98954, 1 whole-mounted specimen from Blue Hole area, base of causeway, Bermuda, sand (coll. M. L. Jones, Aug 1975). USNM 98952–98953, 2 whole-mounted specimens from Andros Island, Bahamas (coll. M. L. Jones, Mar 1966): 1 from S shore of Fever Cay, Middle Bight, lower intertidal, sand; and 1 from S side of Fresh Creek, "deeper flats with filamentous algae." Second author's collection: 12 sectioned, 5 dissected and 28 whole-mounted specimens collected in Bermuda by C. Erséus (Aug and Dec 1977); 9 worms from type locality, others from 4 different stations, 0.2–15 m depth, largely muddy sands (often with slight smell of $H_2S$).

*Etymology.*—The name *bermudae* refers to the geographic origin of most of the material studied.

*Description.*—Body wide anteriorly, particularly at sexual maturity, behind clitellum abruptly narrower; postclitellar part slender with elongated segments (Fig. 1A). Color greyish red. Length (8 complete, fixed specimens) 6.4–12.3 mm, about 50–60 seg-

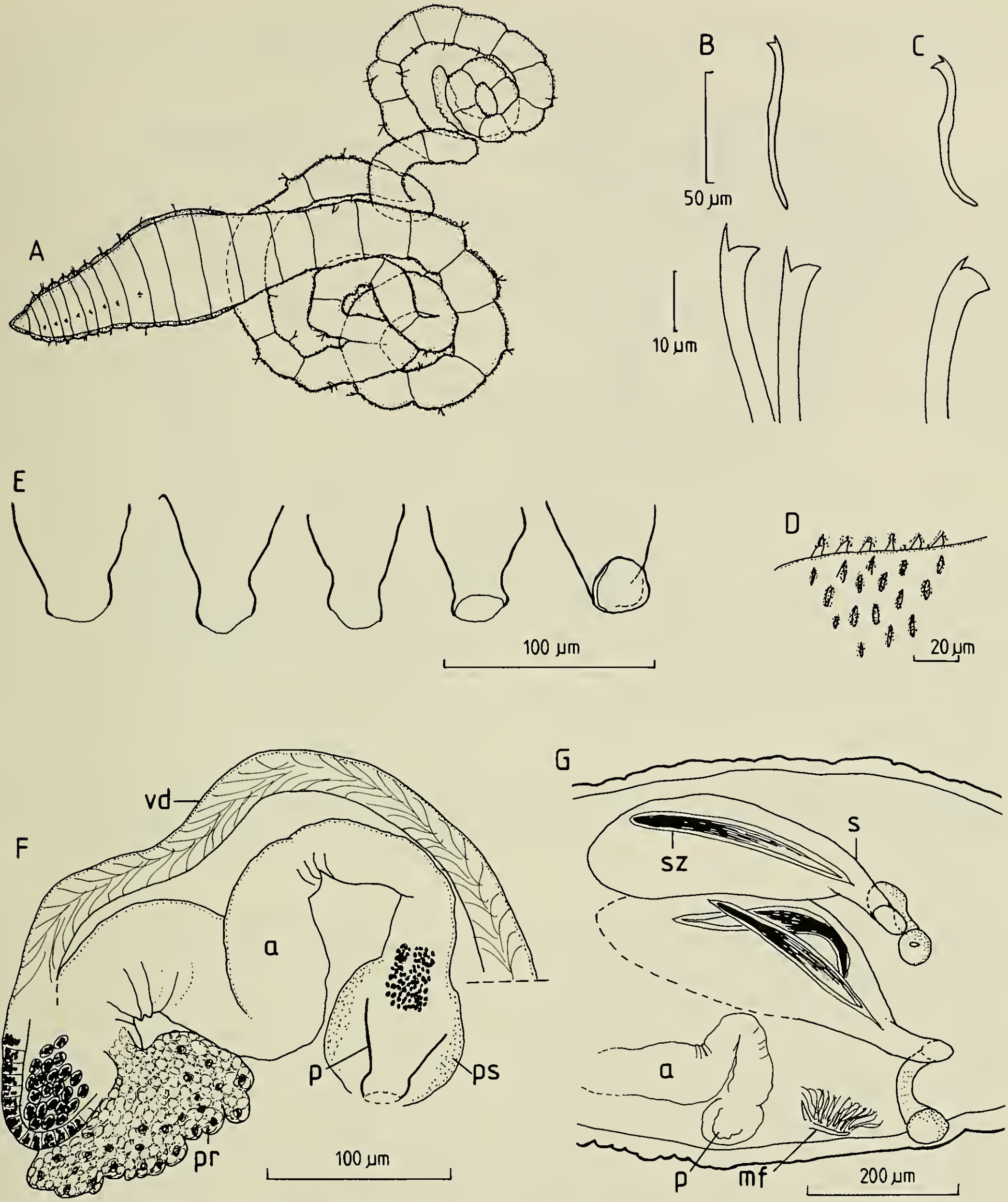

Fig. 1. *Tubificoides bermudae*: A, General outline of whole-mounted, fixed specimen; B, Anterior setae; C, Posterior setae; D, Body wall papillae; E, Penis sheaths from different specimens; F, Male duct from a dissected specimen; G, Spermathecae and parts of male duct, whole-mounted specimen. (a = atrium; mf = male funnel; p = penis; pr = prostate gland; ps = penial sac; s = spermatheca; sz = spermatozeugma; vd = vas deferens.)

ments; posterior end generally not fully differentiated. Width (slightly compressed specimens) 0.26–0.43 mm in V–VI, 0.43–0.78 mm at clitellum, about 0.2–0.3 mm in XIV–XV. Prostomium conical, shorter than width at base, sometimes partly retracted within peristomium. Clitellum indistinct, extending over XI–½XII. In postclitellar

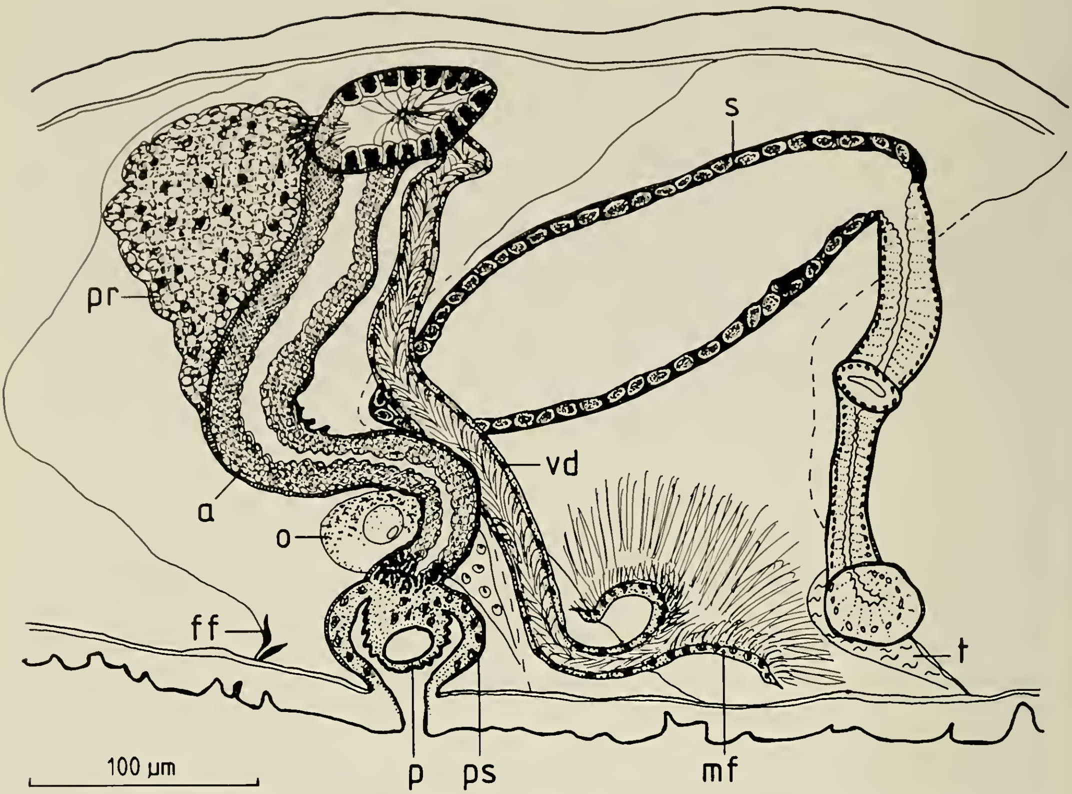

Fig. 2. *Tubificoides bermudae,* lateral view of male duct and spermatheca; reconstruction from a few longitudinal sections. (ff = female funnel; o = ovary; t = testis; other abbreviations as in Fig. 1.)

segments body wall with small, leaf-shaped papillae encrusted with particles of unknown origin (Fig. 1D). Setae (Fig. 1B, C) all bifid; 2–3 per bundle both dorsally and ventrally in II–IX; dorsal, and sometimes ventral, bundles of X–XII represented by 1 seta only, ventrally however, setae often absent; 1–2 per bundle from XIII. Bifids with upper tooth thinner and shorter than lower, more pronounced in posterior segments. Anterior bifids 50–95 $\mu$m long, 2–3 $\mu$m thick at node, posterior ones 55–75 $\mu$m long, 3–4 $\mu$m thick. Spermathecal and male pores paired in line with ventral setae, in middle of X and XI, respectively.

Pharyngeal glands in IV–V, poorly developed. Esophagus enlarged in IX. Male genitalia (Figs. 1F, 2) paired. Male funnel large. Vas deferens thin-walled, 22–26 $\mu$m wide, about as long as atrium, entering atrium subapically, opposite to entrance of moderately large, stalked prostate gland. Atrium tubular, about 440 $\mu$m long, 33–62 $\mu$m wide (measurements from one dissected specimen), apical end ciliated and wider than remaining parts. Atrium histologically tripartite; ental and ectal parts granulated, middle (largest) part not so. Muscle fibers in rings around atrium. Atrium somewhat constricted near base of penis. Penis with conical, distally slightly distended, cuticular penis sheath (Fig. 1E, F, p), enclosed in penial sac. Sheaths with smooth outline, 51–61 $\mu$m long, 44–59 $\mu$m wide at base, distally 25–31 $\mu$m wide; terminal opening round. Spermathecae (Figs. 1G, 2, s) with slender, somewhat coiled duct near opening bearing bulbous swelling, and oblong sac-like ampulla; sperm trap present. Spermatozeugmata (Fig. 1G, sz) slender, spindle-shaped, generally with one end less pointed than other.

*Remarks.*—This species appears closely related to *T. motei* Brinkhurst, 1986, known from Florida, and the widely distributed *T. brownae* Brinkhurst and Baker, 1979, and *T. wasselli* Brinkhurst and Baker, 1979. *Tubificoides motei* and *T. brownae,* however, do not have body wall papillae which characterize the postclitellar segments of *T. bermudae,* and their penis sheaths are clearly different from those of *T. bermudae. Tubificoides motei* has conical sheaths tapering to a very narrow distal end, apparently with an oblique opening (cf. Brinkhurst 1986, fig. 3). The sheaths of *T. brownae* are somewhat conical too, but they have an uneven outline and are not smoothly funnel-shaped as those of the new species (cf. Brinkhurst 1986, fig. 2). *Tubificoides wasselli,* which has body wall papillae both anteriorly and posteriorly (not only in postclitellar segments as in *T. bermudae*), is also distinguished from the new species by its penial sheaths; the latter are cone-shaped but have a lateral opening.

*Distribution and habitat.*—Bermuda and Bahamas. Lower intertidal and subtidal, generally muddy sands, down to at least 15 m depth.

## Acknowledgments

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# FOUR NEW GENERA OF DORVILLEIDAE (ANNELIDA: POLYCHAETA) FROM THE GULF OF MEXICO

Paul S. Wolf

*Abstract.*—Four new genera, each with one new species, are described from the Gulf of Mexico. One new genus, *Ougia,* is diagnosed to include two species formerly placed within *Schistomeringos* Jumars, 1974. Maxillary morphology is considered herein to be the primary diagnostic character at the generic level.

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Major taxonomic treatments of the dorvilleids were done by Pettibone (1961) and Jumars (1974). Pettibone (1961) used only external morphological characters to separate the five genera known at that time. Fauchald (1970) and Jumars (1974) also used, to a certain extent, the morphology of the mouth-parts, in addition to traditional characters, to separate genera and some species. Recent descriptions of new species have relied heavily on maxillary morphology in specific diagnoses (e.g., Oug 1978; Westheide 1977, 1982; Blake 1979; Wainwright and Perkins 1982).

Wolf (1984) employed maxillary morphology as the primary generic and specific diagnostic character. Other generic characters included the degree of development of the head appendages, the distribution and degree of development of the notopodia, and the presence or absence of notopodial internal acicula. Westheide and Nordheim (1985) also used the above characters in describing four new genera and showed the importance of the pygidium as a diagnostic character.

Wolf (1984) identified three possible new genera and a fourth possible new genus was placed, with reservations, within *Schistomeringos.* The purpose of this study is to describe those four genera and four new species and to propose new combinations for *Schistomeringos macilenta* and *S. subaequalis,* both described by Oug (1978), in one of the newly proposed genera, *Ougia.*

The bulk of the material examined for this study was collected as part of a U.S. Bureau of Land Management (now Minerals Management Service) Outer Continental Shelf baseline study conducted during 1975–1981. MAFLA stations were those designated within the Mississippi-Alabama-Florida portion of the program; SOFLA stations were those located off southwest Florida; STOCS stations were located off the Texas coast (see Uebelacker and Johnson 1984). The remaining material was collected under the auspices of the Environmental Protection Agency (EPA) during a contract issued to Science Applications International Corp. through JRB Associates, McLean, Virginia (EPA stations).

Type material and some additional specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Other specimens are in the laboratory museum of Barry A. Vittor & Associates, Inc., Mobile, Alabama.

## Figure Abbreviations

an—antenna
anC—anal cirrus
bPl(supR)—basal plate (superior row)
br—branchia
D1, D2, etc.—free denticle 1, free denticle 2, etc.
Li—ligament
mC—maxillary carrier
mvC—midventral cirrus
neAc—neuroaciculum
noAc—notoaciculum
noto—notopodium

pa—palp
vC—ventral cirrus
vSetLo—ventral setigerous lobe

### *Ougia,* new genus

*Type species.*—*Ougia tenuidentis,* new species.

*Diagnosis.*—Maxillae in 4 rows; superior rows with basal plates and free denticles; inferior rows without basal plates, with free denticles. Maxillary carrier present. Palps long, slender, biarticulate. Antennae long, sometimes articulated. Notopodia with or without distal article, with internal acicula throughout. Supra-acicular setae include simple forms, with or without furcate setae. Subacicular setae include compound falcigers and occasionally inferior simple setae in far posterior setigers.

*Remarks.*—*Ougia* is distinguished from the genus *Schistomeringos* Jumars, 1974, by lacking basal plates in the inferior maxillary rows. As defined here, *Ougia* now contains *O. macilenta* (Oug, 1978) and *O. subaequalis* (Oug, 1978) both formerly included within *Schistomeringos.*

*Etymology.*—The genus is named in honor of Dr. Eivind Oug, who described several *Schistomeringos* species from Scandinavia, and suggested they be removed to new genera. His excellent figures and descriptions made this task relatively painless.

### Key to the Species of *Ougia*

1. Maxillae with anteriormost inferior free denticles with long, slender, arista-like process; furcate setae, when present, pseudocompound, with entire tips ........ *O. tenuidentis*
– Maxillae with anteriormost inferior free denticles otherwise; furcate setae, when present, simple, with hispid tips ........................ 2
2. Notopodia small, without distal article; maxillary carriers poorly developed ................ *O. macilenta*
– Notopodia long, with distal article; maxillary carriers well-developed ....................... *O. subaequalis*

### *Ougia tenuidentis,* new species
Figs. 1, 2

*Schistomeringos* sp. B, Wolf, 1984:44–18, fig. 44-11, 44-12a-i.

*Material examined.*—FLORIDA, off St. Petersburg: MAFLA Sta 2209J, Nov 1977, 27°52′30.5″N, 83°33′59.0″W, 34 m, clayey-sandy silt, 1 paratype (USNM 89566); MAFLA Sta 2211F, JUL 1976, 27°56′29.5″N, 83°52′59.5″W, 43 m, coarse sand, 1 specimen; MAFLA Sta 2211E, Aug 1977, same data, 1 paratype (USNM 89567). Off Apalachicola River: MAFLA Sta 2423C, Jul 1976, 29°37′00.8″N, 84°17′00.2″W, 19 m, silty-fine sand, 1 specimen (USNM 89568). Off Port St. Joe: EPA Sta 1-2, Nov 1983, 29°53.1′N, 85°31′W, 13.8 m, fine sand with shell, 1 paratype (USNM 98925); EPA Sta 4-1, Nov 1983, 29°52.2′N, 85°30.65′W, 12.6 m, fine sand with shell, 1 paratype (USNM 98926); EPA Sta 5-2, Nov 1983, 29°52.2′N, 85°30.5′W, 14.7 m, fine sand with shell, 1 paratype (USNM 98927); EPA Sta 14-1, Nov 1983, 29°47.05′N, 84°26.55′W, 11.4 m, fine sand with shell, 1 paratype (USNM 98929); EPA Sta 24-2, Nov 1983, 29°50.4′N, 84°28.45′W, 12 m, fine sand with shell, HOLOTYPE (USNM 98924); EPA Sta 27-1, Nov 1983, 29°51.4′N, 84°29.95′W, 13.2 m, fine sand with shell, 1 paratype (USNM 98928); EPA Sta 27-2, Nov 1983, same data, 1 specimen. Off Panama City: EPA Sta 3-1, Nov 1983, 30°07′03″N, 85°45′30″W, 15 m, medium to fine sand with shell, 2 specimens; EPA Sta 8-1, Nov 1983, 30°07′08″N, 85°45′38″W, 12.6 m, sand with shell, 1 specimen.

*Description.*—Length to 3.0 mm, width to 0.37 mm (including parapodia). Largest specimen complete with 40 setigers; one specimen (USNM 98927) incomplete but with 46 setigers, 2.7 mm long. Prostomium broadly rounded anteriorly, eyes absent (Fig. 1A). Antennae deciduous, when present with

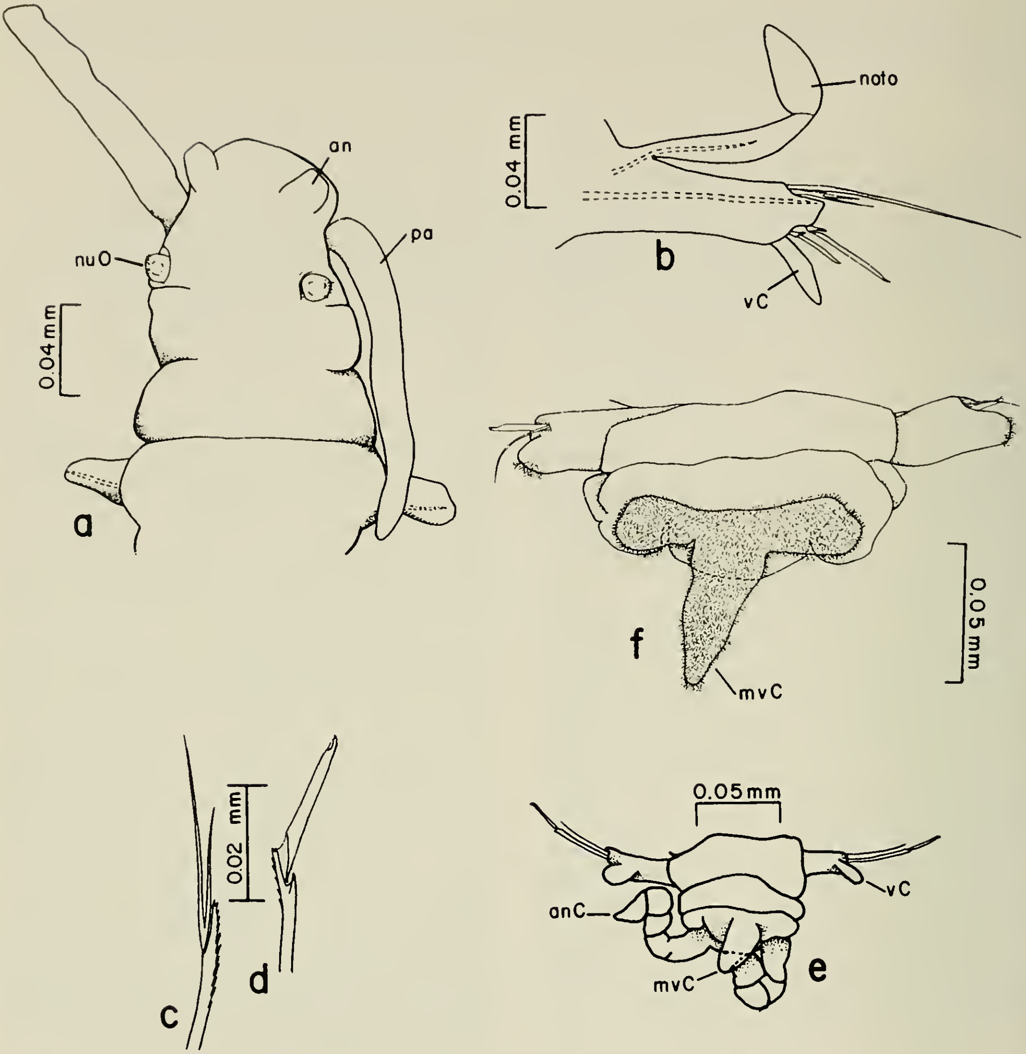

Fig. 1. *Ougia tenuidentis*: a, Anterior end, dorsal view (antennae broken); b, Anterior parapodium, posterior view; c, Furcate seta; d, Middle compound falciger; e, Posterior end, ventral view; f, Same, lateral anal cirri missing. (Figures a–d from Wolf 1984:fig. 44-12a–d.)

9 particles, terminal article pear-shaped. Palps also deciduous, when present indistinctly articulated with palpostyle. One specimen (USNM 98929) with both palps and antennae present; antennae about 1.5 times length of palps. Single pair of ciliated nuchal organs present, often inverted.

Notopodia present from setiger 2, each long, slender, with terminal article (Fig. 1B). Neuropodia without distinct pre- and postsetal lobes. Supra–acicular neurosetae simple, serrate, tapering to fine tips; 5–6 per parapodium in 2 rows in anterior setigers; anterior row of 2–3 short, gently curved setae; posterior row with 3–4 long, gently curved setae. Number of supra-acicular setae reduced to 3–4 per parapodium after about setiger 13–15. Furcate setae present on a few parapodia in some specimens, absent entirely in other specimens. When present, furcate setae pseudocompound, with long, thin tines, with serrations below short

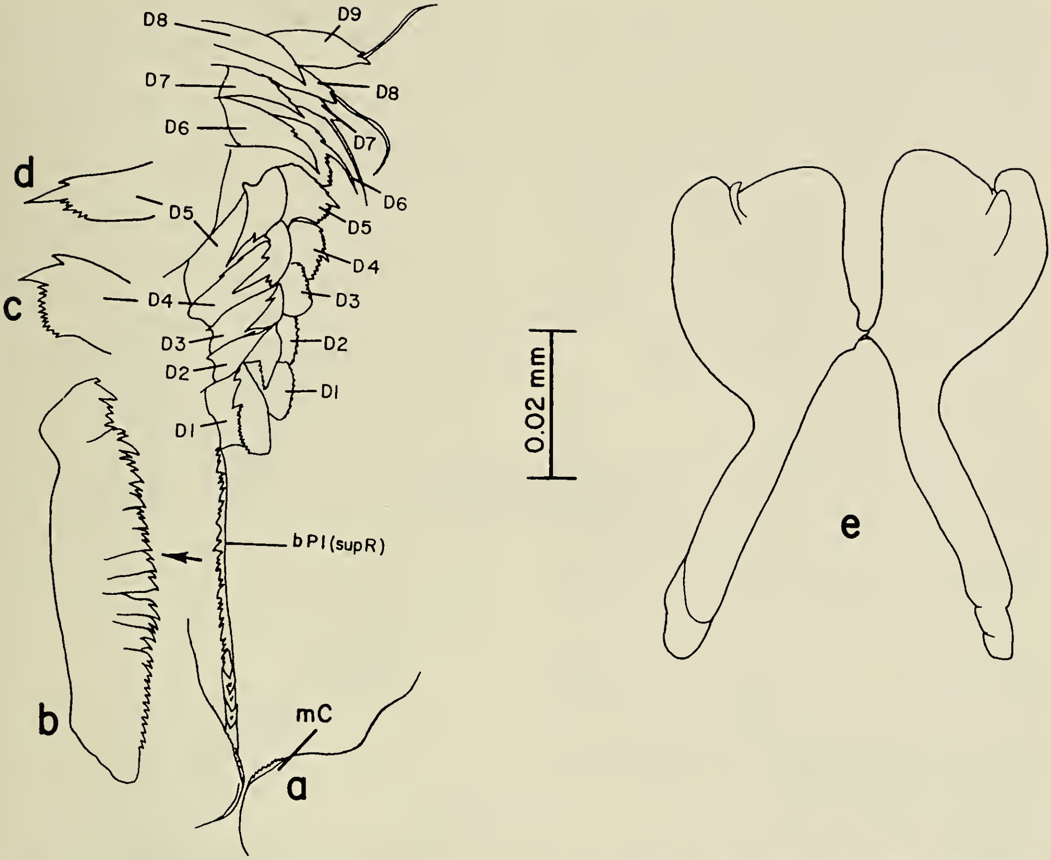

Fig. 2. *Ougia tenuidentis*: a, Entire left side of maxillae, dorsal view; b, Left basal plate, lateral view; c, Free denticle 4 from superior row; d, Free denticle 5 from superior row; e, Mandibles, dorsal view. (Figures a–e from Wolf 1984:fig. 44-12e–i.)

tine (Fig. 1C). Subacicular setae entirely compound, bidentate falcigers with minute serrations on concave margins (Fig. 1D); about 6 per parapodium arranged in 2 ill-defined rows; blade length ratio 2.1:1. Far posterior neuropodia occasionally with single long, very thin, inferior simple seta.

Pygidium with 2 articulated, terminolateral anal cirri and a single digitiform, subterminal, midventral cirrus (Fig. 1E). Enlarged ventral view reveals median cirrus heavily ciliated and located on a ventral ciliated pad (Fig. 1F).

Maxillae with weakly chitinized serrate, maxillary carriers (Fig. 2A) extending ventrolaterally as a weak ridge. Superior row basal plates (Fig. 2B) with about 12 large teeth and 33 smaller teeth; up to 9 free denticles present. Denticles with large main fang, numerous medial teeth and 1 lateral tooth (Fig. 2C, D); anteriormost denticles long, sharply pointed. Inferior maxillary row without basal plates (Fig. 2A); with up to 9 free denticles. Denticles 1–3 oval, with broad cutting edge composed of numerous minute teeth. Anteriormost free denticles each with long main fang and very long, thin, arista. Mandibles (Fig. 2E) broad anteriorly, widely divergent posteriorly; anterior edge of each mandible trilobed.

*Remarks.*—The most notable variation found among material examined concerned the presence of furcate seta. In most specimens only one furcate seta could be found on the entire worm. Several specimens did not have any furcate setae at all, and examination of excised cleared parapodia did not reveal any internal developing furcate setae. It is concluded that the presence of furcate setae in any parapodia is entirely random and may not occur at all. This variable appearance of furcate setae is also described for *O. subaequalis* but not for *O. macilenta* (see Oug 1978:294, 296).

*Ougia tenuidentis* differs from other members of the genus in having maxillae with its anteriormost inferior free denticles bearing long, terminal, arista-like projections; having pseudocompound instead of simple furcate setae with tines tapering to fine tips instead of hispid tips; and in having mandibles each with three anterior lobes instead of a single lobe. *Ougia tenuidentis* differs from *O. macilenta* in having long notopodia with a distal article instead of short ones without a distal article. *Ougia tenuidentis* differs from *O. subaequalis* in having poorly-developed instead of well-developed maxillary carriers.

*Etymology.*—The specific epithet is taken from the Latin *tenuis,* thin, and *dens,* a tooth, referring to the long, thin appearance of the anterior free denticles of the inferior maxillary rows.

*Distribution.*—Gulf of Mexico, off Florida, 11.4–43 m.

## *Diaphorosoma,* new genus

*Type species.*—*Diaphorosoma magnavena,* new species.

*Diagnosis.*—Maxillae in 4 rows, each row composed entirely of free denticles; basal plates lacking. Maxillary carriers absent. Antennae long, articulated. Palps biarticulate. Anterior notopodia long, slender with internal acicula; posterior ones small, without internal acicula. Branchiae present on anterior parapodia. Supra-acicular setae simple, tapering to bidentate tips. Furcate setae absent. Subacicular setae include bidentate compound and pseudocompound falcigers.

*Remarks.*—Among the genera with four rows of maxillae, *Diaphorosoma* is unique in lacking maxillary carriers and in having each of its maxillary rows composed entirely of free denticles, thus lacking basal plates entirely. It differs additionally in having well-developed notopodia with acicula anteriorly which are replaced by small, globular ones without acicula posteriorly. The presence of pseudocompound falcigers is also unknown among other dorvilleid genera.

*Etymology.*—From the Greek *Diaphoros,* divided, and *soma,* body, referring to the divided appearance of its body into anterior and posterior regions characterized by the presence of long notopodia anteriorly and small notopodia posteriorly.

## *Diaphorosoma magnavena,* new species
Figs. 3, 4

Genus B, Wolf, 1984:44-32, fig. 44-23, 44-24a–k.

*Material examined.*—FLORIDA, Southwest: SOFLA Sta 25E, Nov 1980, 24°47′57″N, 82°13′16″W, 24 m, silt/clay, HOLOTYPE (USNM 89577); SOFLA Sta 25D, Jul 1981, same location, 1 paratype (USNM 89578). Off St. Petersburg: MAFLA Sta 2208H, Jul 1976, 27°56′00.5″N, 83°27′29.6″W, 30 m, clayey-sandy silt, 1 specimen; MAFLA Sta 2208J, Aug 1977, same location, 1 paratype (USNM 89576). Off Apalachicola River: MAFLA Sta 2422H, 29°30′N, 84°27′W, 24 m, medium fine sand, 1 specimen; MAFLA Sta 2422I, same date and location, 1 specimen.

*Description.*—Length to 8.5 mm, width to 0.25 mm. Largest specimen incomplete with about 65 setigers. Prostomium (Fig.3A) conical, broadly rounded anteriorly, with 2 slightly raised, longitudinal lobes dorsally. Eyes absent. Antennae each with up to 20 distinct articles; each about 2.25 times length

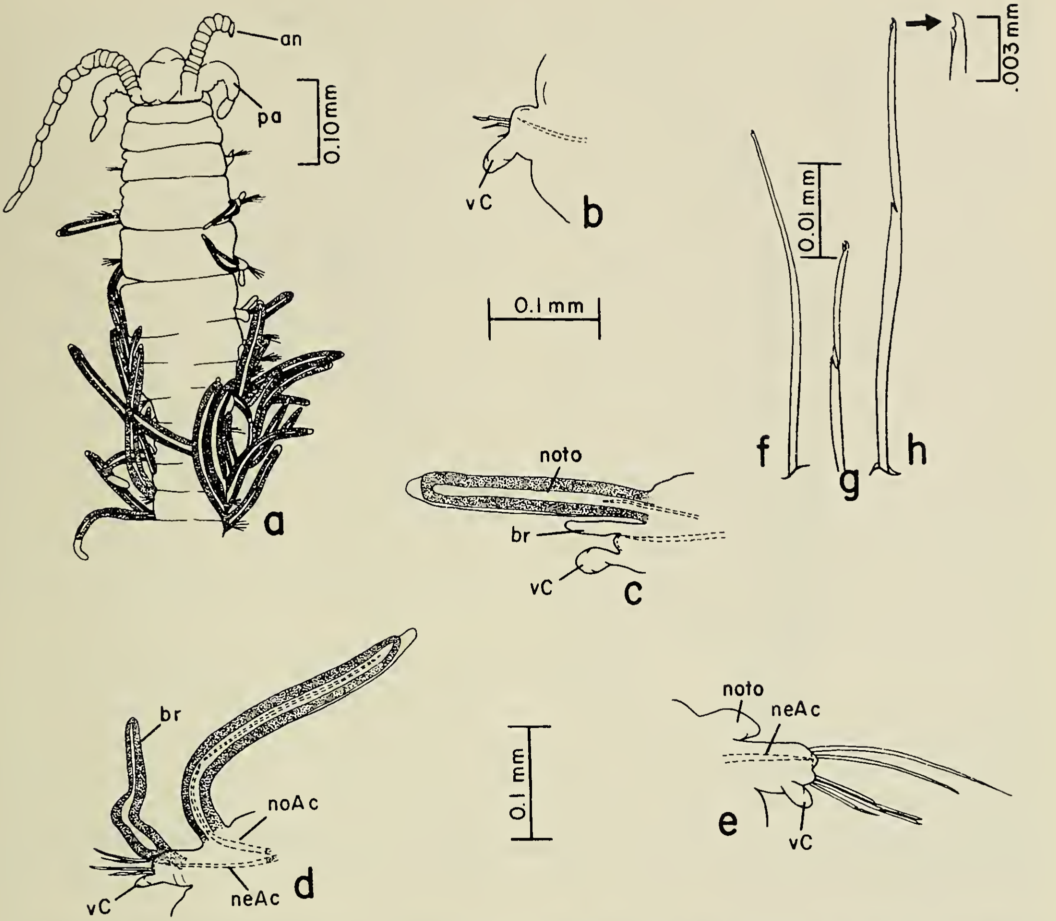

Fig. 3. *Diaphorosoma magnavena*: a, Anterior end, dorsal view; b, Parapodium from setiger 1, anterior view; c, Parapodium from setiger 4, anterior view; d, Parapodium from mid-branchiate region, anterior view; e, Posterior parapodium, posterior view; f, Simple supra-acicular seta; g, Subacicular compound falciger; h, Subacicular pseudocompound falciger from far posterior region. (Figures a–h from Wolf 1984:fig. 44-24a–h.)

of palps. Palps stout with distinct palpostyles.

Setiger 1 without notopodia, with large, digitiform ventral cirri (Fig. 3B). Notopodia of setigers 2–18 to 20 longer than body width, with internal acicula and obvious internal vascular loop (Fig. 3C, D). Notopodia posterior to setigers 18–20 small, papilliform, without internal acicula or vascular loop (Fig. 3E). Branchiae present from setigers 4–18 to 20, arising distally on dorsal side of neuropodia; beginning as small digitiform lobes without vascular loops (Fig. 3C), gradually becoming larger and obviously vascularized (Fig. 3D). Neuropodia each with 1 presetal lobe and 1 or 2 postsetal lobes depending on state of contraction. Supra-acicular setae simple with small, bidentate tips and minute serrations along one margin (Fig. 3F). Furcate setae absent. Subacicular compound falcigers with long to short bidentate blades (Fig. 3G), becoming pseudocompound on far posterior setigers (Fig. 3H).

Pygidium missing on all specimens examined.

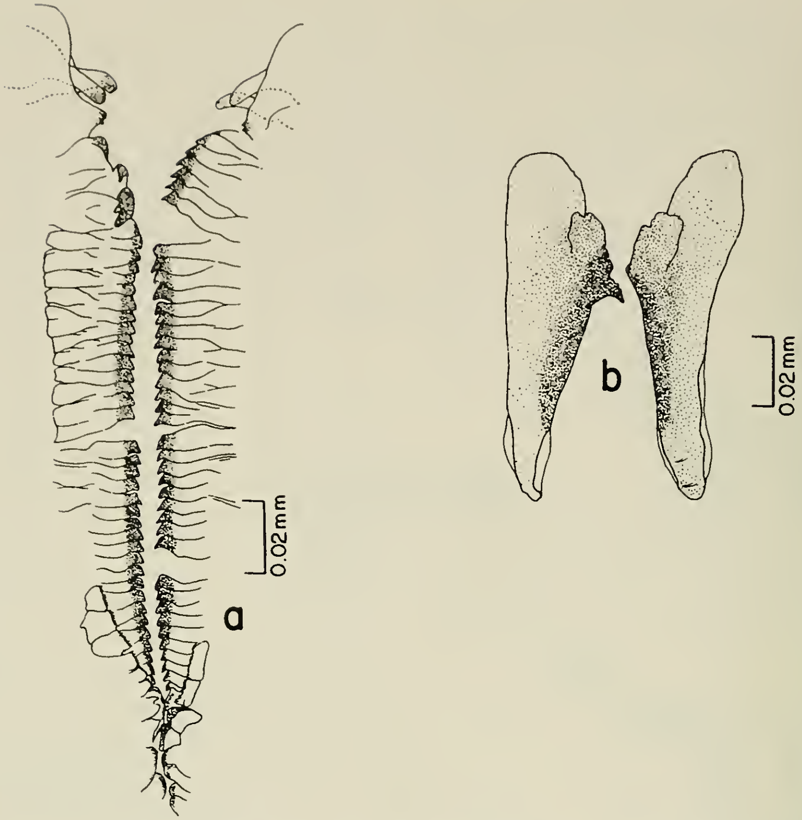

Fig. 4. *Diaphorosoma magnavena*: a, Entire maxillae, dorsal view; b, Mandibles, dorsal view. (All figures from Wolf 1984:fig. 44-24i–k.)

Maxillae (Fig. 4A) in 4 rows composed only of free denticles, basal plates entirely absent. Maxillary rows not fused posteriorly. Superior maxillary rows asymmetrical; left side with 6 dentate free denticles anteriorly and 1 smooth denticle posteriorly; right side with 2 dentate denticles anteriorly and 2 smooth denticles posteriorly. Inferior maxillary rows symmetrical, each composed of 30–40 beaked free denticles, each denticle bearing 1 tooth; 4 anteriormost denticles digitiform, smooth to slightly dentate (broken?); 2–4 posteriormost denticles smooth. Maxillary carriers absent. Mandibles large, anterior portions each with 1 large lobe and smaller lobe on inner margin; each mandible tapering posteriorly to narrow, slightly divergent tips (Fig. 4B).

*Remarks.*—*Diaphorosoma magnavena* is unique among dorvilleids in having distinctly vascularized branchiae and notopodia. Development of such appendages may be in response to the low oxygen conditions in clay habitats, from which four of the six specimens were collected.

*Etymology.*—The specific epithet is taken from the Latin *magnus,* large, and *vena,* blood vessel, referring to the obvious vascular loops present in the anterior notopodia and branchiae.

*Distribution.*—Gulf of Mexico, off Florida; 24–30 m.

## *Eliberidens,* new genus

*Type species.*—*Eliberidens forceps,* new species.

*Diagnosis.*—Maxillae in 4 rows, each row with superior and inferior basal plates only, free denticles entirely lacking. Maxillary rows fused posteriorly to very small and thin maxillary carriers apparently fused to posteriorly directed ligament. Palps and antennae similar to each other in size and shape, each simple, smooth, digitiform. Notopodia absent. Supra-acicular setae include simple, serrate, tapering forms; with or without furcate setae. Subacicular setae compound, unidentate falcigers.

*Remarks.*—The actual presence of maxillary carriers is somewhat questionable. A pair of very small, thin, lateral projections is found in the area where maxillary carriers are to be expected. These projections are here interpreted to be reduced maxillary carriers similar to those described for *Gymnodorvillea floridana* Wainwright and Perkins, 1982.

Among the genera having four rows of maxillae, *Eliberidens* is unique in that each row is composed of only a basal plate, thus lacking free denticles entirely. *Eliberidens* is similar to *Meiodorvillea* Jumars, 1974, in lacking notopodia while possessing both antennae and palps; but differs in having four rather than two rows of maxillae; in having each maxillary row composed entirely of a single basal plate instead of only free denticles; and in having very reduced maxillary carriers fused to a posteriorly directed ligament instead of a pair of dorsally placed, small carriers not fused to a ligament.

*Etymology.*—From the Latin *e,* without, *liber,* free, and *dens,* teeth, referring to the complete absence of free denticles in the maxillary rows. Gender: masculine.

### *Eliberidens forceps,* new species
Fig. 5

Genus A, Wolf, 1984:44-29, fig. 44-21, 44-22a–g.

*Material examined.*—FLORIDA, off Cape Romano: MAFLA Sta 2958I, Aug 1977, 25°40′N, 83°50′W, 120, medium fine sand, HOLOTYPE (USNM 89575). Off St. Petersburg: MAFLA Sta 2212C, Jun 1976, 27°57′00.0″N, 84°47′59.6″W, 189 m, silty-very fine sand, 1 paratype (USNM 89574).

*Description.*—Length to 3.5 mm, width to 0.2 mm. Largest specimen incomplete with about 43 setigers. Prostomium (Fig. 5A) conical, rounded anteriorly. Eyes absent. Antennae and palps similar in size and shape, each smooth, digitiform.

Parapodia without well-developed pre- and postsetal lobes (Fig. 5B). Supra-acicular setae include long, simple, serrate setae tapering to fine tips. Furcate setae (present in only one specimen) with long tine about twice as long as short tine (Fig. 5C), spines present below short tine; furcate setae replaced by shorter simple setae in some fascicles. Subacicular compound falcigers with long to short unidentate blades; long extension of shaft-head bifid (Fig. 5D, E). Blade ratio approximately 5.9:1.

Pygidium missing from all specimens examined.

Maxillae in 4 rows, each row composed entirely of basal plates; free denticles entirely lacking (Fig. 5F). Plates of superior row appearing as blunt pincers; each plate thin, clear, with rounded tooth bearing minute, subterminal, brush-like hairs anteriorly. Plates of inferior row with numerous, fine teeth. Superior and inferior plates fused to each other posteriorly and to very small, thin maxillary carriers; carriers fused to a long, posteriorly directed ligament. Anterior portion of ligament dark brown. Mandibles (Fig. 5G) poorly developed, only slightly divergent posteriorly, produced into curved arms anteriorly.

*Etymology.*—The specific epithet is from the Latin *forceps,* pincers, referring to the pincer-like shape of the superior maxillary rows, and is a noun in apposition.

*Distribution.*—Florida, Gulf of Mexico, 120–189 m.

### *Westheideia,* new genus

*Type species.*—*Westheideia minutimala,* new species.

*Diagnosis.*—Maxillae in 2 rows, each row

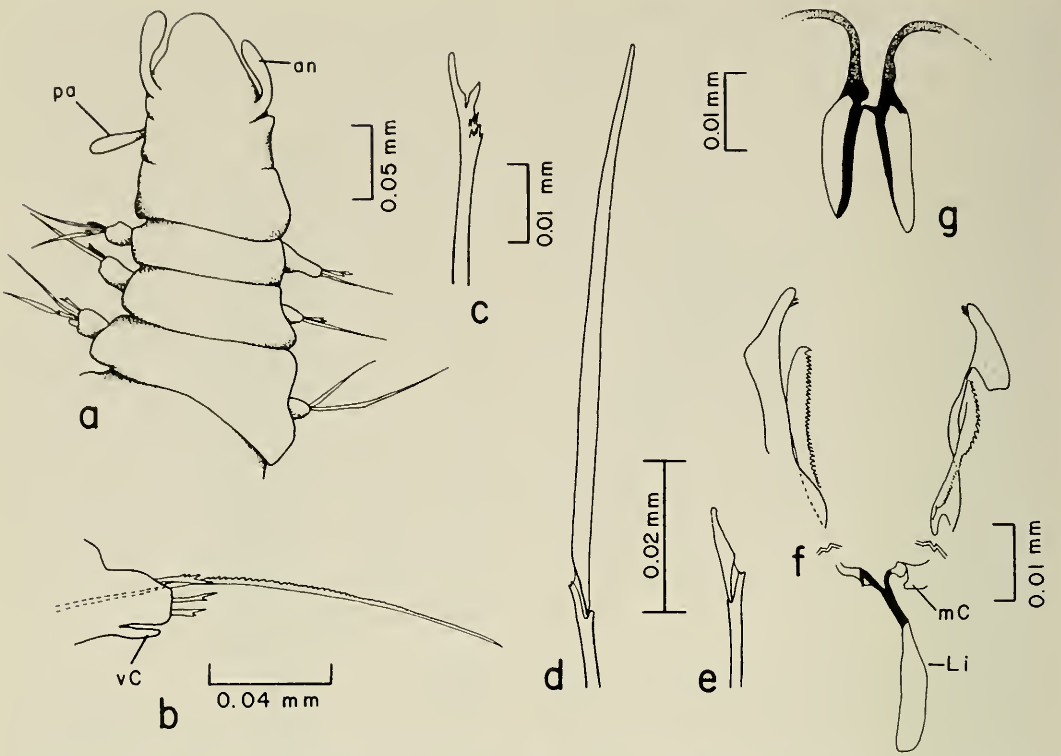

Fig. 5. *Eliberidens forceps*: a, Anterior end, dorsal view; b, Anterior parapodium, posterior view; c, Furcate seta; d, Upper compound seta; e, Lower compound seta; F, Entire maxillae, dorsal view (broken); g, Mandibles, dorsal view. (All figures from Wolf 1984:fig. 44-22a–g.)

composed of single plate, serrate posteriorly, with denticles anteriorly; maxillary carriers present, fused to posteriorly directed ligament. Palps biarticulate. Antennae indistinctly articulated, similar in length to palps. Notopodia present on anterior setigers only, each without distal article but with internal acicula. Branchiae present on anterior parapodia. Supra-acicular setae simple including long, evenly tapered forms and furcate forms. Subacicular setae compound, unidentate falcigers.

*Remarks.*—The maxillae of *Westheideia* are similar to those of *Ikosipodus* Westheide, 1982. In *Westheideia,* however, the maxillae are carried on narrow maxillary carriers instead of broad carrier plates. *Westheideia* differs primarily from *Ikosipodus* in having instead of lacking antennae, in having notopodia anteriorly instead of lacking them throughout, in having instead of lacking furcate setae, and in having more than 87 setigers instead of no more than 10.

*Westheideia* is similar to *Eliberidens* and *Gymnodorvillea* in having reduced maxillary carriers fused to a long posterior ligament. *Westheideia* differs from *Eliberidens* in having two instead of four rows of maxillae and in having notopodia with internal acicula intead of lacking notopodia entirely. *Gymnodorvillea* lacks head appendages and notopodia and has four rows of maxillae.

*Etymology.*—I am pleased to name this genus in honor of Dr. Wilfried Westheide who has published numerous detailed and careful works on the Dorvilleidae.

### *Westheideia minutimala,* new species
Fig. 6

Genus C, Wolf, 1984:44-32, fig. 44-25, 44-26a–i.

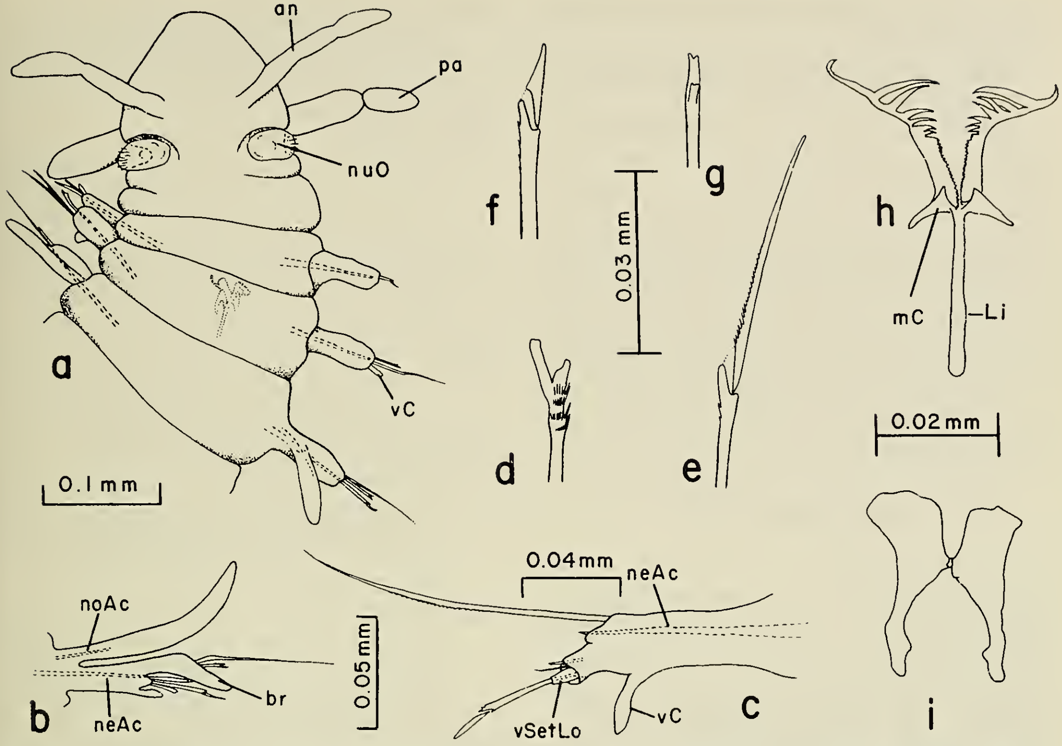

Fig. 6. *Westheideia minutimala*: a, Anterior end, dorsal view; b, Anterior parapodium, posterior view; c, Posterior parapodium, posterior view; d, Furcate seta; e, Upper compound falciger; f, Lower compound falciger; g, Shaft of compound seta, edge-on view; h, Entire maxillae, dorsal view; i, Mandibles, dorsal view. (All figures from Wolf 1984:fig. 44-26a–i.)

*Material examined.*—FLORIDA, off Cape Romano: MAFLA Sta 2960G, Sep 1977, 25°40′N, 82°20′W, 27 m, fine sand, HOLOTYPE (USNM 89579). Off St. Petersburg: MAFLA Sta 2211F, Nov 1977, 27°56′29.5″N, 83°52′59.5″W, 43 m, coarse sand, 1 paratype (USNM 98923). Off Crystal River: MAFLA Sta 2316C, Nov 1977, 28°42′00.3″N, 84°20′00.7″W, 35 m, silty fine sand, 1 paratype (USNM 89581). Off Apalachicola River: MAFLA Sta 2423C, Jul 1976, 29°37′00.8″N, 84°17′00.2″W, 19 m, silty fine sand, 1 specimen. TEXAS, off Matagorda Island: STOCS Sta 6-1, transect I, Spring 1976, 27°39′N, 96°12′W, 100 m, silty clay, 1 paratype (USNM 89580).

*Description.*—Length to 5 mm, width to 0.6 mm. Largest specimen incomplete with 87 setigers. Prostomium (Fig. 6A) conical, rounded anteriorly, eyes absent. Antennae indistinctly articulated. Palps smooth, biarticulate, similar in length to antennae. Single pair of large ciliated nuchal organs present at dorsal postectal margins of prostomium.

Setiger 1 without notopodia, with small ventral cirri. Notopodia present on setigers 2–29 only, each long, cylindrical, about half as long as body width, without terminal article (Fig. 6B). Neuropodia without distinct pre- and post-setal lobes, with superior branchial lobe on setigers 5–28 (Fig. 6B), and with strongly eversible ventral setal lobe, especially in posterior parapodia (Fig. 6C). Supra-acicular neurosetae include simple serrate setae tapering to fine tips, and furcate setae having blunt tines with cusps below short tine (Fig. 6D). Subacicular compound falcigers with long to short unidentate blades

(Fig. 6E, F), long extension of shaft-head bifid (Fig. 6G).

Pygidium missing from all specimens examined.

Maxillae (Fig. 6H) in 2 rows, each row as single plate, serrate posteriorly, with 6–7 long, sharp teeth anteriorly. Anteriormost portion of maxillae sharply pointed, curved. Maxillary , carriers thin and triangular, fused to dorsal face of maxillae and to posteriorly directed ligament. Mandibles broad anteriorly, fused medially, tapering posteriorly to narrow, widely divergent tips (Figs. 6I).

*Distribution.*—Off western Florida and Texas, 19–100 m.

## Acknowledgments

I wish to thank Drs. Kristian Fauchald, National Museum of Natural History, Washington, D.C.; Brigitte Hilbig, Battelle New England Marine Research Laboratory, Duxbury, Massachusetts; and Barry A. Vittor, Barry A. Vittor & Associates, Inc., for their reviews of the manuscript. Dr. Kristian Fauchald arranged the loan of some material. Some of the material examined was obtained under contract from Environmental Protection Agency to JRB Associates, McLean, Virginia, contract number 68-01016388. Barry A. Vittor & Associates, Inc., provided monetary and material support for this research.

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# THREE NEW SPECIES OF DORVILLEIDAE (ANNELIDA: POLYCHAETA) FROM PUERTO RICO AND FLORIDA AND A NEW GENUS FOR DORVILLEIDS FROM SCANDINAVIA AND NORTH AMERICA

Paul S. Wolf

*Abstract.*—Three new species of *Dorvillea* Parfitt, 1866, are described from Puerto Rico and the east and west coasts of Florida. *Dorvillea* and *Schistomeringos* Jumars, 1974, are here combined under *Dorvillea* which is further divided into two subgenera: 1) *Dorvillea,* which contains species Jumars (1974) retained within the genus *Dorvillea s.s.* primarily because they lack furcate setae; and 2) *Schistomeringos* which contains species Jumars (1974) placed in the genus *Schistomeringos* primarily because they have furcate setae. A new genus, *Parougia,* is proposed for a suite of *Schistomeringos* species from Scandinavian and northeast American waters (Oug 1978). A key to the species of *Parougia* is also provided.

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*Dorvillea* Parfitt, 1866, and *Schistomeringos* Jumars, 1974, are two closely related genera that have complete maxillary apparatus (i.e., with basal plates and numerous free denticles in both the superior and inferior maxillary rows), well-developed head appendages, and well-developed notopodia with internal notoacicula. The two genera have been separated primarily by the presence of furcate setae in species of *Schistomeringos.* The continued separation of *Dorvillea* and *Schistomeringos* based on the presence of furcate setae has been questioned by Blake (1975:81), Oug (1978:302), Westheide (1982:123), and Wolf (1984:44-15). All seem to agree the genera should not be distinguished using that character, but to date, *Dorvillea* and *Schistomeringos* have remained split. This paper proposes that all species heretofore placed in those two genera be placed within the genus *Dorvillea.* Those species that do not possess furcate setae are placed within the subgenus *Dorvillea.* Those species that always possess furcate setae are placed within the subgenus *Schistomeringos.*

*Schistomeringos caeca* (Webster and Benedict, 1884), *S. eliasoni* Oug, 1978, and *S. nigridentata* Oug, 1978, are here placed within the newly proposed genus *Parougia.*

Wolf (1984) identified a possible new species of *Dorvillea* and a new species of *Schistomeringos* from the Gulf of Mexico. Both species are here introduced as new species of *Dorvillea.* Additionally, another new species of *Dorvillea* is described from benthic samples collected off Tampa Bay and Port Everglades, Florida.

The bulk of the material examined for this study was collected as part of a U.S. Bureau of Land Management (now Minerals Management Service) Outer Continental Shelf baseline study conducted during 1975-1981. MAFLA stations were those designated within the Mississippi-Alabama-Florida portion of the program; SOFLA stations were those located off southwest Florida (see Uebelacker and Johnson 1984). The remaining material was collected under the auspices of the Environmental Protection Agency (EPA) during contracts issued to Battelle, Columbus Laboratories

(EPA/Bat stations) and to Science Applications International Corp. through JRB Associates (SAI stations) for studies located off Puerto Rico and the east and west coasts of Florida (see Acknowledgments).

The type material and some additional specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Other specimens are in the laboratory museum of Barry A. Vittor & Associates, Inc., Mobile, Alabama.

### Figure Abbreviations

an—antenna
bPl(infR)—basal plate (inferior row)
bPl(supR)—basal plate (superior row)
ciT—ciliary tract
DanC—dorsal anal cirrus
lT—lateral tooth
mC—maxillary carrier
mT—medial tooth
neAc—neuroaciculum
noAc—notoaciculum
D1, D2, etc.—free denticle 1, etc.
fD(infR)—free denticle, (inferior row)
fD(supR)—free denticle, (superior row)
noto—notopodium
VanC—ventral anal cirrus
vC—ventral cirrus
vSetLo—ventral setal lobe

### *Dorvillea* Parfitt, 1866

*Type species.*—*Staurocephalus rubrovittatus* Grube, 1855.

*Diagnosis.*—Maxillae arranged in 4 rows, each having a prominent basal plate and several free denticles; posterior free denticles usually with large curved teeth flanked by smaller teeth; anterior free denticles usually long with more numerous but smaller teeth. Prostomium with well-developed palps usually having palpostyles; antennae articulated, similar in length to palps. Notopodia present throughout from setiger 2, with acicula and terminal article. Furcate setae absent in adults (subgenus *Dorvillea*) or always present in adults (subgenus *Schistomeringos*).

*Remarks.*—The subgeneric split proposed above is introduced strictly for utilitarian purposes. While I agree that the presence of furcate setae does not warrant separate generic status for *Schistomeringos* Jumars, it cannot be overlooked that a discrete group of species exists whose members always have furcate setae in every setiger as adults, yet share other diagnostic characters of *Dorvillea*. s. s.

### *Dorvillea* (*Dorvillea*) *largidentis,* new species
Figs. 1, 2

*Dorvillea* sp. A.—Wolf, 1984:44-27, fig. 44-19, 44-20a–k.

*Material examined.*—PUERTO RICO, off San Juan: SAI Sta SJ3-1, Mar 1984, 18°30.24′N, 66°09.8′W, 224 m, clayey silt, 2 paratypes (USNM 98914).—Off Yabucoa: SAI Sta Y27-1, Mar 1984, 18°02.6′N, 65°23.5′W, 642 m, clayey silt, 1 paratype (USNM 98915). FLORIDA, off Port Everglades: EPA/Bat Sta PE1-2, Feb 1984, 26°06′N, 80°04.2′W, 111 m, silty sand and rubble, 2 paratypes (USNM 98913).—EPA/Bat Sta PE 3-3, Feb 1984, 26°06.0′N, 80°03.4′W, 108 m, silty sand, 1 paratype (USNM 98912).—EPA/Bat Sta PE10-2, Nov 1984, 26°00.4′N, 80°04.0′W, 158 m, muddy sand, 1 paratype (USNM 98911).—Off Southwest Florida: SOFLA Sta 18A, Apr 1981, 25°45′22″N, 83°42′13″W, 87 m, medium sand, 2 specimens (USNM 89569-70).—SOFLA Sta 20, Nov 1980, 25°17′20″N, 82°09′44″W, 22 m, coarse sand, 2 specimens (USNM 89571-2).—Off Northwest Florida: MAFLA Sta 2316I, Jun 1975, 28°42′00.3″N, 84°20′00.7″W, 35 m, silty fine sand, 1 specimen.—MAFLA Sta 2534, Jun 1975, 29°40′59.9″N, 86°17′28.6″W, 73 m, coarse sand, 1 specimen.—MAFLA Sta 2643, Jun 1975, 29°36′31.0″N, 87°27′00.8″W, 69 m, fine sand, 1 specimen.—MAFLA Sta 2644D, 5 Jun 1975, 29°36.2′N, 87°23.5′W, 75 m, medium sand, HOLOTYPE (USNM 98910). ALABAMA, off Mobile Bay: MAFLA Sta 19G, May 1974, 26°36′12″N, 87°23′30″W,

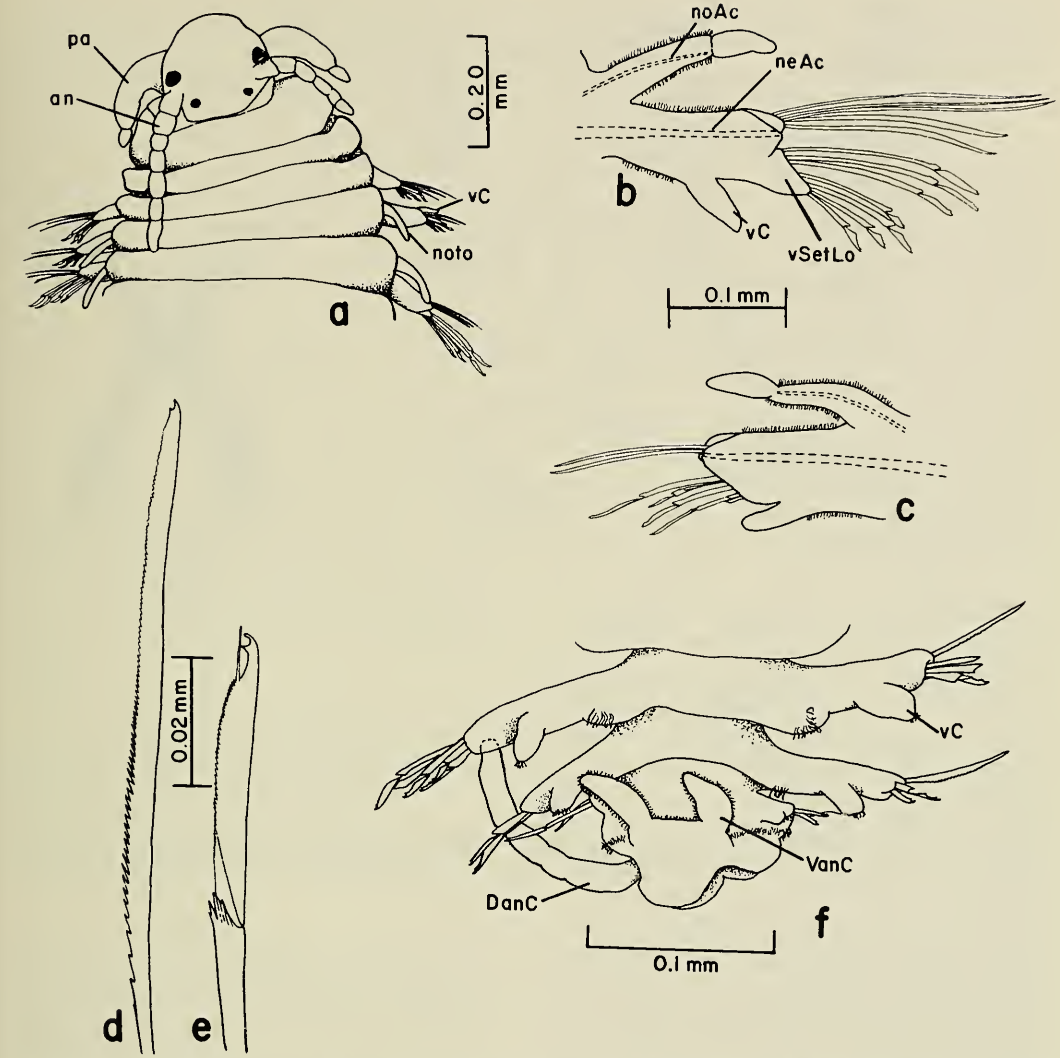


Fig. 1. *Dorvillea largidentis*: a, Anterior end, dorsal view; b, Parapodium from setiger 4, posterior view; c, Parapodium from setiger 5, posterior view; d, Supra-acicular simple seta; e, Compound falciger; f, Posterior end, ventral view (left dorsal anal cirrus missing). (Figures a–e from Wolf 1984:fig. 44-20a–e.)

75 m, medium sand, 1 specimen (USNM 89573), 2 additional specimens.

*Description.*—Length to 7 mm, width to 0.25 mm. Largest specimen complete with 45 setigers. Prostomium (Fig. 1a) rounded with 4 eyes, anterior pair largest. Antennae with about 7 articulations. Palps stout, biarticulate, shorter than antennae.

Notopodia present from setiger 2, each extending to end of neuropodial lobe, with internal acicula and terminal article (Fig. 1b, c). Neuropodia without distinct presetal lobes, with small postsetal lobes (Fig. 1b, c). Ventral setigerous lobes long when everted (Fig. 1b). Ciliary tracts present on dorsal and ventral margins of noto- and neuropodia (Fig. 1b, c). Small bundle of cilia also present on tips of ventral cirri of far posterior setigers (Fig. 1f).

Supra-acicular neurosetae simple, ser-

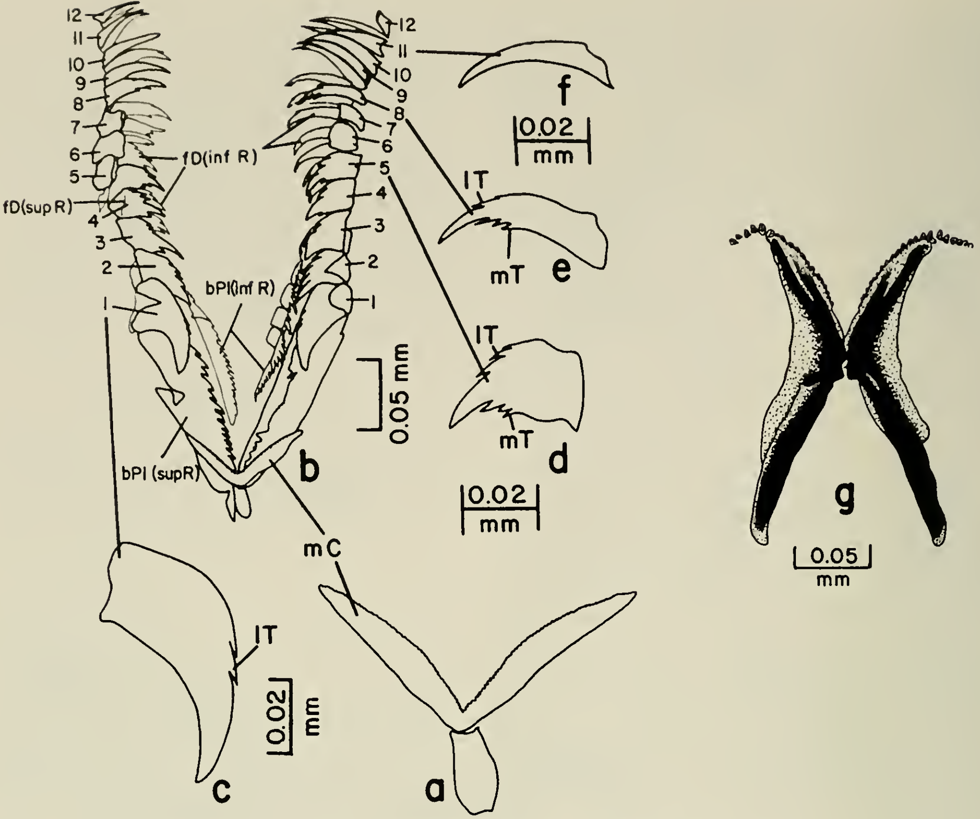


Fig. 2. *Dorvillea largidentis*: a, Maxillary carriers; b, Entire maxillae, dorsal view; c–f, Superior row denticles: c, D1; d, D5; e, D8; f, D11; g, Mandibles, dorsal view. (Figures a–f from Wolf 1984:fig. 44-20g–k.)

rate, with bidentate tips (Fig. 1d), 4–5 per neuropodium. Subacicular compound falcigers with long to short bidentate blades having thin guard extending slightly beyond teeth (Fig. 1e).

Pygidium (Fig. 1f) damaged, apparently with 2 pairs of anal cirri. Dorsal anal cirri of specimens examined about twice as long as ventral anal cirri, indistinctly wrinkled, devoid of cilia. Ventral anal cirri short, digitiform, with lateral ciliary tracts. Ventral cirri appear connected by low, cilated ventral ridge (Fig. 1f).

Maxillary carriers fused to oval-shaped base, serrate along anterior margins (Fig. 2a). Basal plates of superior and inferior maxillary rows apparently connected posteriorly by thin, clear ligament. Maxillae (Fig. 2b) with 12 free denticles in superior row, 15–17 free denticles in inferior row. Basal plates of superior row each with about 14 teeth. D1 with large main fang sharply curved and posteriorly directed; with 2 small, lateral teeth (Fig. 2c). D5 with large main fang, 3 lateral and 3 medial teeth (Fig. 2d). D8 with sharply pointed main fang, 1 lateral and 3 medial teeth (Fig. 2e). D11 sharply pointed, curved, without lateral or medial teeth (Fig. 2f).

Basal plates of inferior row each with about 16 teeth (Fig. 2b). Posterior free denticles short, squared, with main fang flanked by 2–3 teeth on either side; anterior denticles becoming long and sharply pointed by D9–10.

Mandibles (Fig. 2g) symmetrical, fused

medially, each with about 5–7 small, free denticles anteriorly and 14 small teeth on inner margin; darkened area bifurcate anteriorly; posterior stems widely flaring.

*Remarks.*—Among the described species of the genus, *Dorvillea* (*Dorvillea*) *largidentis* closely resembles *D.* (*Dorvillea*) *sociabilis* (Webster, 1879) but differs from the latter in having 12 instead of 17–20 free denticles in each superior row, 15–17 instead of 23–31 free denticles in each inferior row, in having D1 of each superior row strongly curved and posteriorly directed, and in having D5 of each superior row broader and with three instead of one lateral teeth. Also, *D. largidentis* has palpostyles, antennae longer than palps, and short postsetal lobes, all of which differ from *D. sociabilis.* There is a significant size difference, with *D. largidentis* measuring up to 7 mm in length compared to a reported 20 mm for *D. sociabilis.*

*Etymology.*—The specific epithet is taken from the Latin, *largus,* large, and *dens,* a tooth, referring to the characteristically large D1 of the superior maxillary row.

*Distribution.*—Puerto Rico, east coast of Florida, Gulf of Mexico; 22–642 m.

### *Dorvillea* (*Dorvillea*) *clavata,* new species

Figs. 3, 4

*Schistomeringos* sp. A.—Wolf, 1984:44-15, fig. 44-9, 44-10a–j.

*Material examined.*—FLORIDA, off Port Everglades: EPA/Bat Sta PE4-2, Feb 1984, 26°06.0′N, 80°04.4′W, 33 m, sand and coral rubble, 1 paratype (USNM 98918).—Off Tampa Bay: EPA/Bat Sta 1111-III-5-3, Dec 1984, 27°28.7′N, 83°06.5′W, 24.7 m, sand, HOLOTYPE, ripe male (USNM 98916), 1 paratype (USNM 98917).—EPA/Bat Sta 1111-III-8-3, Dec 1984, 27°32′N, 83°05′W, 23.5 m, sand, 2 paratypes (USNM 98919).—Off St. Petersburg: MAFLA Sta 2207G, Nov 1977, 27°57′00″N, 83°09′00″W, 19 m, fine-very fine sand, 1 specimen (USNM 89561).—Off Crystal River: MAFLA Sta 2852E, Aug 1977, 28°30′00″N, 83°29′58″W, 22 m, medium sand, 1 specimen (USNM 89565).—MAFLA Sta 2315A, Feb 1978, 28°33′59″N, 84°20′09″W, 38 m, silty fine sand, 3 specimens (USNM 89562-4).

*Description.*—Length to 6 mm, width to 0.96 mm. Largest specimen complete with 58 setigers. Prostomium small, rounded, with 2 pairs of eyes, anterior pair largest (Fig. 3a). Antennae with up to 5 articles. Palps stout, with palpostyles, about equal in length to antennae. Ciliated nuchal organs located at dorsal postectal corners of prostomium, usually covered by anterior margin of first apodous ring in preserved specimens. Additional ciliated areas present on prostomium and laterally on both apodous rings and subsequent segments (Fig. 3a).

Setiger 1 without notopodia, with large digitiform ventral cirri. Subsequent anterior setigers each with large, clavate notopodium bearing small, pear-shaped, distal article and internal acicula (Fig. 3b). Notopodia of posterior setigers more slender (Fig. 3c). All notopodia with dorsal and ventral ciliary tracts that connect anterior to distal article (Fig. 3a–c).

Neuropodia of anterior setigers with large, rounded presetal lobe and small postsetal lobe (Fig. 3b). Neuropodia of posterior setigers with 2 small, rounded presetal lobes and 1 large, rounded postsetal lobe (Fig. 3c). Neuropodia with dorsal and ventral ciliary tracts. Ventral cirri devoid of cilia (Fig. 3b, c).

Supra-acicular setae simple, bidentate, narrow to cultriform, serrate along convex margin (Fig. 3d); furcate setae absent in adults (see *Remarks*). Subacicular compound falcigers with long to short bidentate blades, with small, thin guards (Fig. 3e, f).

Pygidium with 2 pairs anal cirri (Fig. 3g). Dorsal anal cirri very long, indistinctly articulated. Ventral anal cirri short, digitiform, may be ciliated and connected ventrally by small ciliated ridge.

Maxillary carriers asymmetrical, fused,

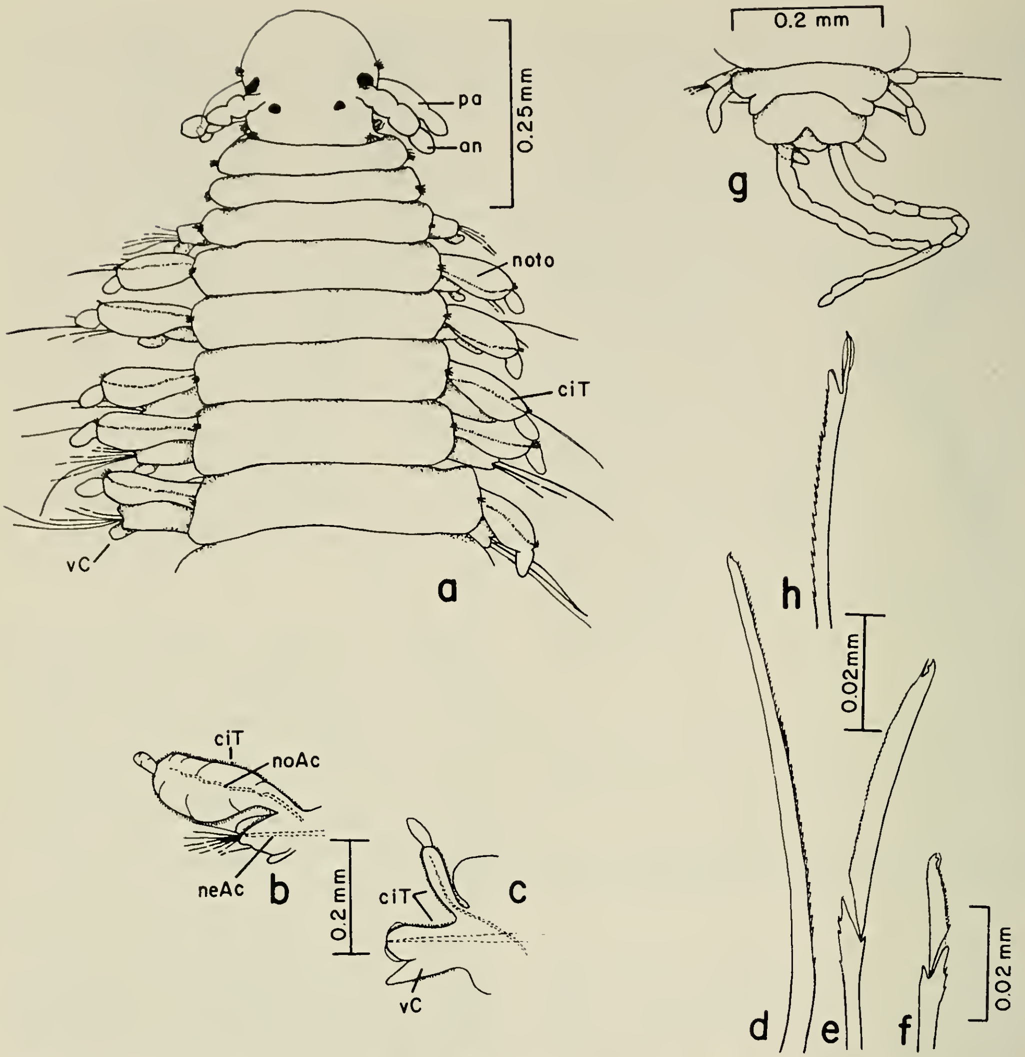


Fig. 3. *Dorvillea clavata*: a, Anterior end, dorsal view; b, Anterior parapodium, posterior view; c, Posterior parapodium, posterior view; d, Supra-acicular cultriform seta; e, Subacicular superior falciger; f, Subacicular inferior falciger; g, Posterior end, dorsal view; h, Furcate seta from juvenile. (Figures b–f, h from Wolf 1984: fig. 44-10b–f, j.)

serrate; right carrier slightly longer than left (Fig. 4a). Basal plates of superior and inferior rows apparently connected posteriorly by thin, clear ligament. Superior row basal plates with 12 large teeth, each large tooth with smaller subapical tooth and 3–5 smaller teeth anteriorly. Superior row with up to 25 free denticles. D1 with 1 large tooth, 4 medial and 4 lateral teeth; subsequent denticles with increasing number of lateral and medial teeth as denticles become long and narrow (Fig. 4b) until anterior-most denticles which become shorter, more broad and with only a few minute apical teeth (Fig. 4c).

Inferior row basal plates with numerous small teeth (Fig. 4a). Up to 21 free denticles present in inferior row. D1 with large main tooth, 7 medial and up to 7 lateral teeth; subsequent denticles somewhat squared,

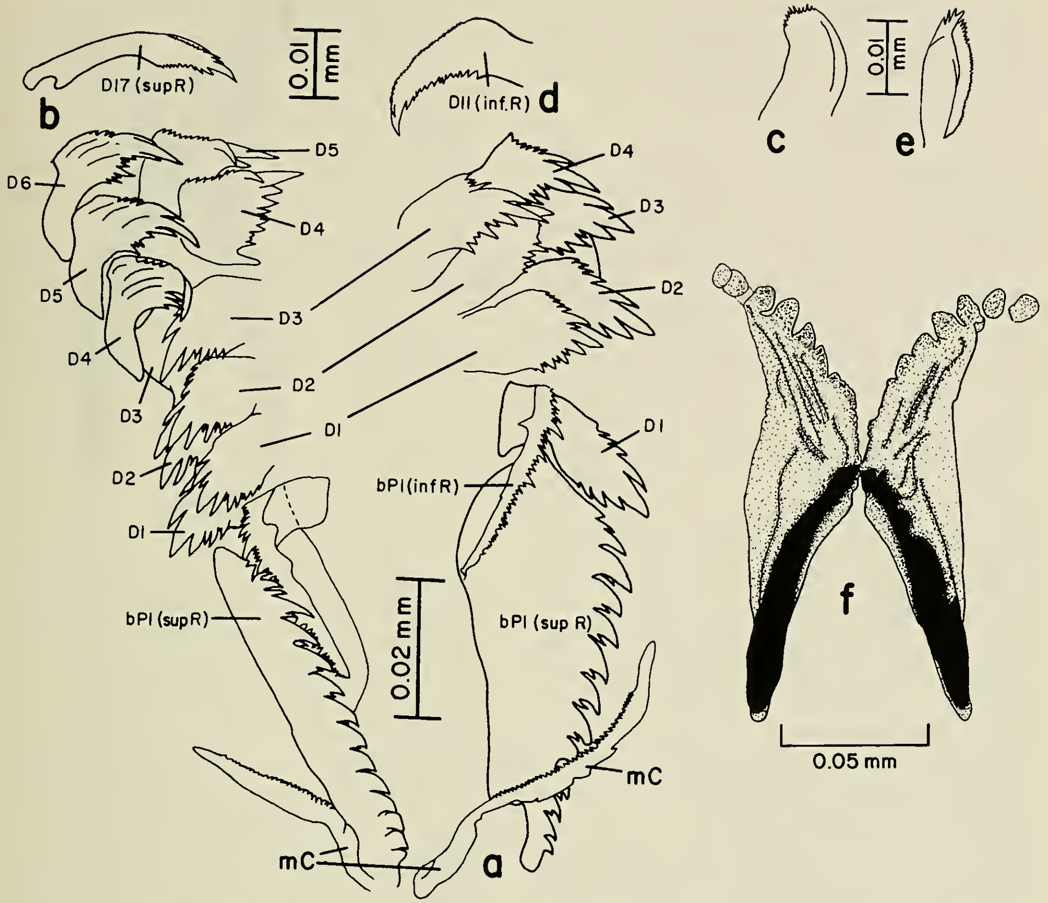


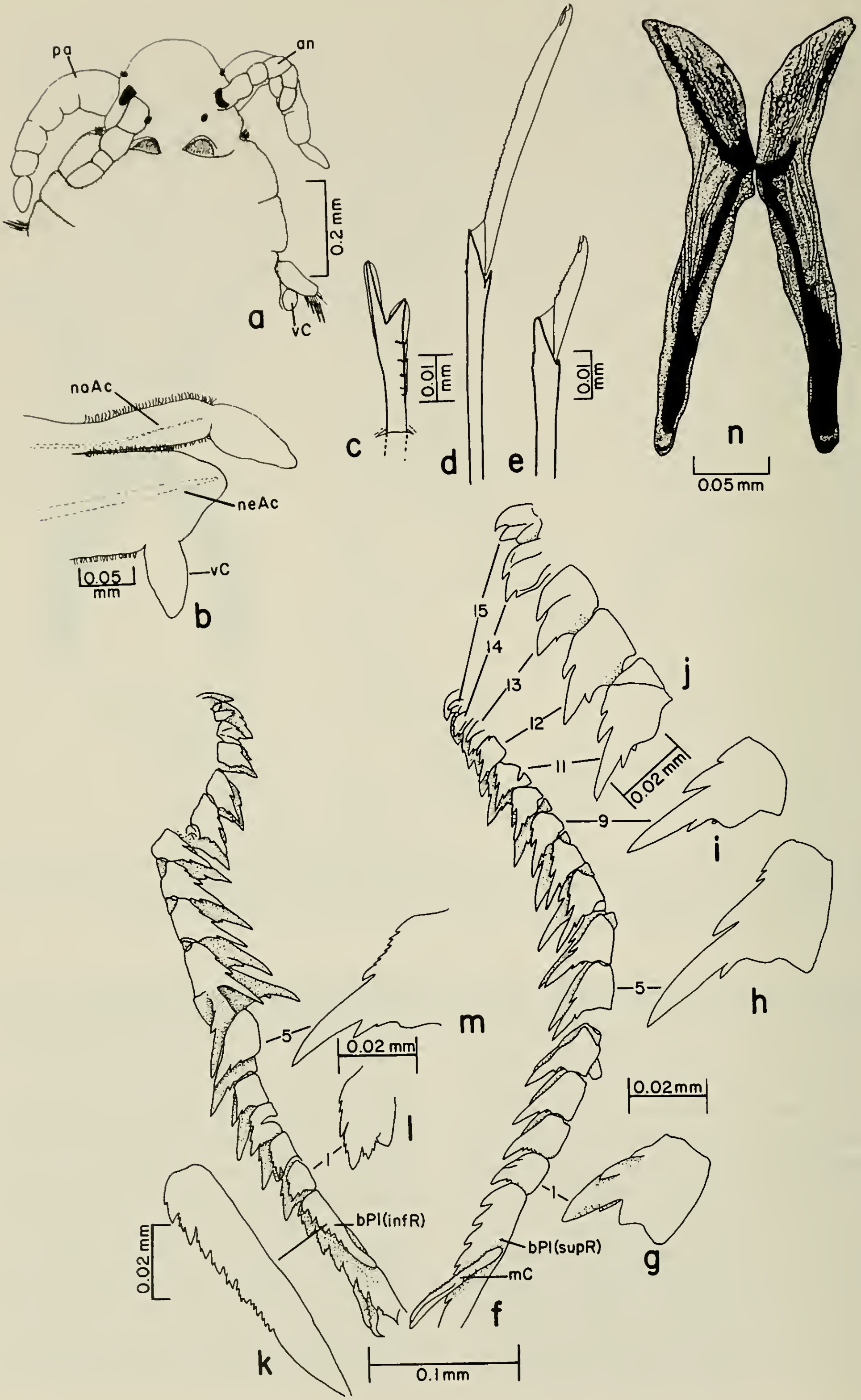
Fig. 4. *Dorvillea clavata*: a, Posterior portion of maxillae, dorsal view (maxillary carriers broken posteriorly); b, D17, superior row; c, Anteriormost free denticle, superior row; d, D11, inferior row; e, Penultimate free denticle, inferior row; f, Mandibles, dorsal view. (Figures a, b, d from Wolf 1984:fig. 44-10g–i.)

then becoming longer with medial teeth becoming more numerous and lateral margin becoming serrate (Fig. 4d) until anteriormost denticles which have about 4 apical teeth and thin, serrate margin (Fig. 4e).

Mandibles (Fig. 4f) symmetrical, fused medially, each with 2 free denticles anteriorly and about 5 large teeth on inner margin; posterior stems flaring slightly.

*Remarks.*—A juvenile specimen of *Dorvillea* (*Dorvillea*) *clavata* differs from the other specimens examined only by the presence of furcate setae (Fig. 3h) after setiger 15. All other morphological characters are identical including the maxillae. The presence of furcate setae would normally place *D. clavata* within the subgenus *Schistomeringos*; however, since the furcate setae are absent in adults, the species is more properly placed within the subgenus *Dorvillea.*

The maxillary morphology of *Dorvillea* (*D.*) *clavata* is quite similar to that of *Dorvillea* (*Schistomeringos*) *rudolphi* (Delle Chiaje, 1828) (see Fauchald 1970:156) and *D.* (*S.*) cf. *rudolphi* (see Wolf 1984:44-21) particularly with respect to the anteriormost free denticles. *Dorvillea* (*S.*) *rudolphi,* however, differs in having furcate setae in the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adult, longer antennae and palps, more numerous free denticles, and symmetrical maxillary carriers.

*Dorvillea clavata* differs from all other described species of the genus in having large, clavate notopodia anteriorly and more slender, digitiform ones posteriorly.

*Etymology.*—The specific epithet is taken from the Latin, *clavatus,* club-shaped, referring to the clavate notopodia present in anterior setigers.

*Distribution.*—East and west coasts of Florida; 19–38 m.

### *Dorvillea* (*Schistomeringos*) *perkinsi*, new species

Fig. 5

*Material examined.*—FLORIDA, off Port Everglades: EPA/Bat Sta Dive 1, Nov 1984, 26°07.7′N, 80°05.0′W, 17 m, sand, HOLOTYPE (USNM 98920).—Off Tampa Bay: SAI Site 4, Sta 26-3, Oct 1983, 27°36′N, 83°12′W, 24 m, sand, 1 paratype (USNM 98921).—EPA/Bat Sta 1111-III-5-3, Dec 1984, 27°28.7′N, 83°06.5′W, 24.7 m, sand, 1 paratype (USNM 98922).

*Description.*—Length to 6.0 mm, width to 0.4 mm. All specimens incomplete, largest one with 39 setigers. Prostomium broadly rounded anteriorly (Fig. 5a). Two pairs of eyes present; anterior pair large, slightly reniform; posterior pair small, round. Antennae about ⅔ as long as palps; each antenna with about 5 articulations. Palps large, indistinctly articled, with pear-shaped palpostyle. Ciliated nuchal organs located at dorsal postectal corners of the prostomium. Additional paired ciliary patches present dorsally anterior to palps and laterally just anterior to nuchal organs.

Notopodia present from setiger 2, each long, slender, with distinct terminal article (Fig. 5b). Neuropodia without distinct pre- and postsetal lobes. Noto- and neuropodia with dorsal and ventral ciliary tracts (Fig. 5b).

Supra-acicular neurosetae include 1–2 furcate setae (Fig. 5c) and 1–2 long, simple, serrate, tapered setae. Each furcate seta with long tine about twice length of short tine. Both tines sheathed, serrations present below short tine. Subacicular setae entirely compound, bidentate falcigers with long to short blades, each blade serrate along inner margin (Fig. 5d, e).

Pygidium missing from specimens examined.

Maxillae with slender, serrate maxillary carriers (Fig. 5f) probably fused posteriorly (broken in figure). Basal plates of superior and inferior rows connected posteriorly by thin, clear ligament. Superior row basal plates each with 6 large teeth and about 15 small teeth; up to 15 free denticles present. D1 with 1 main fang, 4 medial teeth, and 2 lateral teeth (Fig. 5g). D2-9 with main fang becoming longer and more slender, accompanied by reduction in number of medial and lateral teeth (Fig. 5h, i). D11-15 with main fang becoming shorter, accompanied by loss of medial teeth and retention of only 1 lateral tooth (Fig. 5j); main fang and lateral tooth equal to each other in size and shape on D15 (Fig. 5j).

Inferior row basal plates each with about 25 irregular teeth, anterior teeth appear as main fang with 2–3 lateral teeth (Fig. 5f, k). Inferior maxillary rows each with about 14 free denticles. D1 with main fang, 4 medial teeth and 5 lateral teeth (Fig. 5l). D2-6 with main fang becoming very long and slender, accompanied by reduction in number of medial teeth to 2 and increase in lateral teeth

←

Fig. 5. *Dorvillea perkinsi*: a, Anterior end, dorsal view; b, Anterior parapodium, posterior view; c, Furcate seta; d, Superior compound falciger; e, Inferior compound falciger; f, Entire maxillae, dorsal view (left side twisted posteriorly); g–j, Superior row free denticles: g, D1; h, D5; i, D9; j, D11-D15; k, Basal plate, inferior row; l, m, D1 and D5, inferior row; n, Mandibles, dorsal view.

to about 7, giving serrate appearance to anterior edge of the denticles (Fig. 5m). From D7-14 all teeth becoming reduced in size and number (Fig. 5f).

Mandibles long, slender, moderately flared, without free denticles or teeth (Fig. 5n). Anterior portions of each mandible with scalloped lines.

*Remarks.*—*Dorvillea* (*Schistomeringos*) *perkinsi* is unique among species of *Dorvillea* in having mandibles with scalloped lines and without denticles.

*Etymology.*—The species is named in honor of Mr. Thomas H. Perkins, whose numerous publications have contributed greatly to our knowledge of polychaete taxonomy.

*Distribution.*—East and west coasts of Florida; 17–24.7 m.

### *Parougia,* new genus

*Type species.*—*Schistomeringos nigridentata* Oug, 1978.

*Diagnosis.*—Maxillae in 4 rows; superior rows with basal plates and free denticles; basal plates composed of 5–7 fused free denticles; inferior rows without basal plates, with free denticles. Maxillary carriers absent. Mandibles dentate anteriorly. Antennae well-developed, articulated. Palps well-developed, stout, biarticulate, shorter than antennae. Notopodia present throughout, well-developed, biarticulate, with internal notoacicula. Supra-acicular setae include simple minutely bidentate forms; furcate setae, when present, with long thin tines. Subacicular setae as compound, bidentate falcigers. Pygidium with 2 dorsal anal cirri and single midventral cirrus.

*Remarks.*—*Parougia* as defined above contains *P. caeca* (Webster and Benedict, 1884), *P. eliasoni* (Oug, 1978), and *P. nigridentata* (Oug, 1978) which are separable using the key provided below.

*Parougia* is very similar to *Coralliotrocha* Westheide and Nordheim, 1985, but differs in having internal notoacicula in the notopodia and in having dentate mandibles instead of smooth ones.

*Parougia* is very similar to *Ougia* Wolf (1986) in lacking basal plates in the inferior row, in having well-developed head appendages and notopodia, and in having a pygidium with two dorsal anal cirri and a midventral cirrus. *Parougia* differs from *Ougia* in lacking, instead of having, maxillary carriers, in having superior row basal plates composed of fused free denticles rather than being a serrate plate, and in having dentate mandibles rather than smooth ones.

The above diagnosis as well as the key to species below was compiled from the excellent descriptions given in Oug (1978). As a result of the detail and completeness of his work, it was deemed unnecessary to reexamine his material.

### Key to the Species of *Parougia*

1. Neuropodium without suprasetal lobe; tines of furcate setae with pointed, entire tips .......... *P. caeca*
– Neuropodium with dorsal, suprasetal lobe; tines of furcate setae blunt, pubescent ...................... 2
2. Maxillary denticles of superior row with large, hook-shaped main fangs; free denticles of inferior row widest medially; neuropodial suprasetal lobe of anterior setigers shorter than postsetal acicular lobe ..... *P. eliasoni*
– Maxillary denticles of superior row with main fangs not hook-shaped; free denticles of inferior row widest distally, at dentate margin; neuropodial suprasetal lobe of anterior setigers about equal in length to postsetal acicular lobe ..... *P. nigridentata*

*Discussion.*—Jumars (1974) divided the genus *Dorvillea* into *Dorvillea* and *Schistomeringos.* He identified three diagnostic characters: 1) presence of furcate setae, 2) basal plates of inferior maxillary rows fused to or free from those of the superior maxillary rows, and 3) ratio of the length of the inferior row basal plate to the length of the basal plate's longest tooth. Each is discussed below.

The increased biological sampling of marine benthic environments has brought to light a greater diversity of dorvilleid taxa than was available at the time of Jumars' (1974) revision (e.g., Oresanz 1973; Oug 1978; Wainwright and Perkins 1982; Westheide 1982; Westheide and Riser 1983; Westheide and Nordheim 1985; Wolf 1984, 1986, and the present study). Some of these studies (Oug 1978; Westheide and Nordheim 1985; Wolf 1984, 1986) have shown the furcate setae may appear randomly in some taxa (e.g., *Ougia* Wolf, 1986; and *Parougia,* n. gen.), or only in posterior setigers (*Coralliotrocha natans* Westheide and Nordheim, 1985), or only in juveniles (*Dorvillea* (*Dorvillea*) *clavata,* n. sp.). These findings certainly indicate that the usefulness of furcate setae as a diagnostic character at the generic level has diminished. Indeed, the finding of furcate setae in a juvenile *Dorvillea* may lead one to predict its presence in other juvenile species of *Dorvillea.*

The fusion of the inferior maxillary basal plates to those of the superior rows is somewhat difficult to assess. From my observations of members of both *Dorvillea* and *Schistomeringos,* I believe it is more accurate to describe these plates as being connected by a thin, clear ligament which is attached posteriorly on the inferior maxillary basal plates, then extends back to near the posterior region of the superior maxillary basal plates. At any rate, this feature is extremely difficult to see in small species, and it is subject to damage and other limitations when viewing slide mounts under light microscopy.

In *Dorvillea* sensu Jumars, the inferior basal plates may be free from or fused to the basal plates of the superior rows, and when they are free, the length of the inferior basal plates are less than three times the length of the longest teeth on the plate itself. In *Schistomeringos* sensu Jumars, the inferior basal plates are always free and always three times the length of the longest teeth present on the basal plate. This may be an important taxonomic distinction and one that, along with the possibility of fusion itself, has been overlooked in past discussions of the *Dorvillea-Schistomeringos* split. This diagnostic feature is, however, difficult to assess in view of the problem of determining whether or not the inferior basal plates are free from or fused to the superior plates. Again, in slide preparations of the maxillary apparatus, this feature can be very difficult to measure accurately, and judging from Jumars' (1974) figures of the maxillae of *Dorvillea rubrovittata* (Fig. 4) which has free inferior basal plates, the measurements must be extremely accurate. By my measurements of the inferior basal plate within the figure, the plate appears to be exactly three times the length of the longest tooth.

In summary, the only consistently useful diagnostic character is the presence of furcate setae, if they are always present in every setiger in adult worms. The species placed by Jumars (1974) in *Schistomeringos* fit that description, but, as has already been stated above, this one character does not seem to be sufficient to maintain the *Dorvillea-Schistomeringos* split. At best, the presence of furcate setae does appear useful for subgeneric distinctions as has been suggested herein.

## Acknowledgments

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# REDESCRIPTION OF *SHEINA ORRI* HARDING, 1966, A MYODOCOPID OSTRACODE COLLECTED ON FISHES OFF QUEENSLAND, AUSTRALIA

Louis S. Kornicker

*Abstract.*—*Sheina orri* Harding, 1966 (Myodocopina: Cypridinidae), an ostracode collected on the gills of fishes from Heron Island, Queensland, Australia, and type species of the genus, is redescribed from type specimens. The coxa of the mandible does not lack an endite as stated in the original description, but the endite is reduced. The endite is also sexually dimorphic, a condition not previously observed in the Cypridinidae. Several other morphologic characters are described and illustrated, and the diagnosis of the genus is emended.

While examining two paratypes of *Sheina orri* Harding, 1966, that had been deposited at the National Museum of Natural History by Dr. Harding, I observed some interesting morphologic characters not mentioned in the original description. Additional types borrowed from the British Museum (Natural History) showed the characters to be consistent, and they are described and illustrated herein. In addition, appendages of the male, female, and a juvenile, are described, but in general, the description is intended to supplement that of Harding (1966:371). The specimens are from gills of the fishes *Taeniura lymna,* a ray, and *Hemiscyllium oscellatus,* a shark, captured in the vicinity of Heron Island, Queensland, Australia.

## *Sheina* Harding, 1966

*Type species.*—*Sheina orri* Harding, 1966, by monotypy.

*Type locality.*—Heron Island, Queensland, Australia, from the gills of either *Taenirua lymna,* a ray, or *Hemiscyllium oscellatus,* a shark.

*Diagnosis* (emended).—Harding (1966: 374) stated that the diagnostic features of *Sheina* are: "The short, strong claws on the end of the maxilla, the absence of an endite on the coxa of the mandibles and the shape of the upper lip." Because the present study revealed a reduced endite on the coxa of the mandible, it is necessary to revise the part of the diagnosis pertaining to the mandible as follows: Endite of coxa reduced to a backward-pointing process with a single terminal spine on adult males and with many spines on adult females and juveniles.

## *Sheina orri* Harding, 1966
Figs. 1, 2

*Sheina orri* Harding, 1966:371, figs. 8–20.

*Type material.*—British Museum (Natural History): 1965.11.9.1, holotype, adult male in alcohol; 1965.11.9.2 (B), adult male in alcohol; 1965.11.9.3 (specimen 1), 1 partly dissected juvenile in alcohol + 1 slide with right 1st antenna, right maxilla, both mandibles, and both 7th limbs; 1965.11.9.3, 9 adult males and 2 juveniles in alcohol; 1965.11.9.4, 1 adult male in alcohol; 1965.11.9.5, 4 adult females and 5 juveniles in alcohol; 1965.11.9.6 (A), 1 empty carapace in alcohol; 1965.11.9.7, adult male appendages on 2 slides; 1965.11.9.8 (female D), 1 female body and shell in alcohol (2 vials) + 1 slide with left mandible; 1965.11.9.9, 1 slide with left 1st antenna and left 2nd antenna; 1965.11.9.10 (C), 1 empty carapace and 1 body in separate vials with alcohol; 1965.11.9.11, 1 slide with a 1st and 2nd antenna, a right mandible, and copulatory limb of a male. National Museum of Natural History: USNM 112675, adult male and adult female in alcohol and on slides.

*Description of male and female appendages.*—First antenna, male: 1st joint bare. 2nd joint with abundant medial spines forming rows. 3rd joint short with 2 bristles (1 ventral, 1 dorsal). 4th joint about 3 times length of 3rd and broader, with 2 terminal bristles (1 ventral, 1 dorsal). 5th joint trapeziform, about same length as 4th but broader; sensory bristle stout in proximal part, with 9 or 10 long, narrow, proximal filaments, 2 long slender filaments near midlength, and 1 short subterminal filament (all filaments on dorsal margin of bristle). 6th joint with short medial bristle near dorsal margin. 7th joint: a-bristle about same length as bristle of 6th joint; b-bristle with short stout proximal filament (with bulbous base, large sucker, and small process near pointed tip) followed by 2 short filaments each with 4 or 5 minute suckers; c-bristle with stout proximal filament (similar to that of b-bristle except for sucker having twice diameter of large sucker of b-bristle) followed by 2 filaments with 4 minute suckers followed by about 9 slender filaments; c-bristle more than twice length of b-bristle. 8th joint: d- and e-bristles about same length as b-bristle, bare with blunt tips; f-bristle with about 9 bare marginal filaments (proximal 3 shorter than others); g-bristle with 11 marginal filaments (proximal 4 shorter than others).

First antenna, female: Joints 1–3 similar to those of male except 3rd joint not as short. Joint 4 about twice length of 3rd joint and about same width, with 2 terminal bristles (1 ventral, 1 dorsal). 5th joint rectangular (not trapeziform as on male); sensory bristle with 10 long, narrow, proximal filaments, 2 long slender filaments near midlength, and 1 short subterminal filament (all filaments on dorsal margin of bristle). 6th joint with short medial bristle near dorsal margin. 7th joint: a-bristle similar to short bristle of 6th joint; b-bristle almost twice length of a-bristle, with 4 slender, short, hair-like, proximal filaments on dorsal margin (tip broken on specimen examined); c-bristle reaching past tip of sensory bristle of 5th joint, with about 11 marginal filaments. 8th joint: d- and e-bristles similar to those of male; f-bristle only slightly shorter than c-bristle, with about 9 marginal filaments; g-bristle about same length as c-bristle, with about 11 marginal filaments.

Second antenna, male: Protopodite with small, distal, medial bristle. Endopodite 3-jointed (Fig. 1a, b): 1st joint with 4 proximal bristles (3 short, 1 longer) and 1 long distal bristle; 2nd joint with short terminal bristle; 3rd joint with long terminal filament. Expodite: bristle of 2nd joint reaching to 6th joint, with 6 or 7 ventral spines (small proximal spine followed by 2 to 4 stout curved spines, then few small spines); bristles of joint 3-8 long, with natatory hairs but no spines; 9th joint with 4 bristles (3 long with natatory hairs, 1 small, bare); 3rd joint with minute basal spine; joints 4–8 with large basal spines increasing in length on distal segments (basal spine of 8th joint about twice length of 9th joint; dorsal edge of spines with minute tooth near midlength); 9th joint with lateral spine about same length as basal spine of 8th joint; minute, indistinct spines forming row along distal lateral edge of 2nd joint.

Second antenna, female: Same as that of male.

Mandible, male (Figs. 1c, 2): Coxal endite consisting of backward-pointing process with stout spine at tip and with or without 2 additional marginal spines; small bristle present ventral to process on some specimens. Basis: ventral margin with 2 a-bristles (1 unusually long), 1 small lateral b-bristle, and 4 c- and d-bristles (distal d-bristle long, hirsute); dorsal margin with 3 distal bristles (1 subterminal, 2 terminal). Exopodite hirsute reaching past midlength of dorsal margin of 1st endopodial joint, with 2 bare sub-

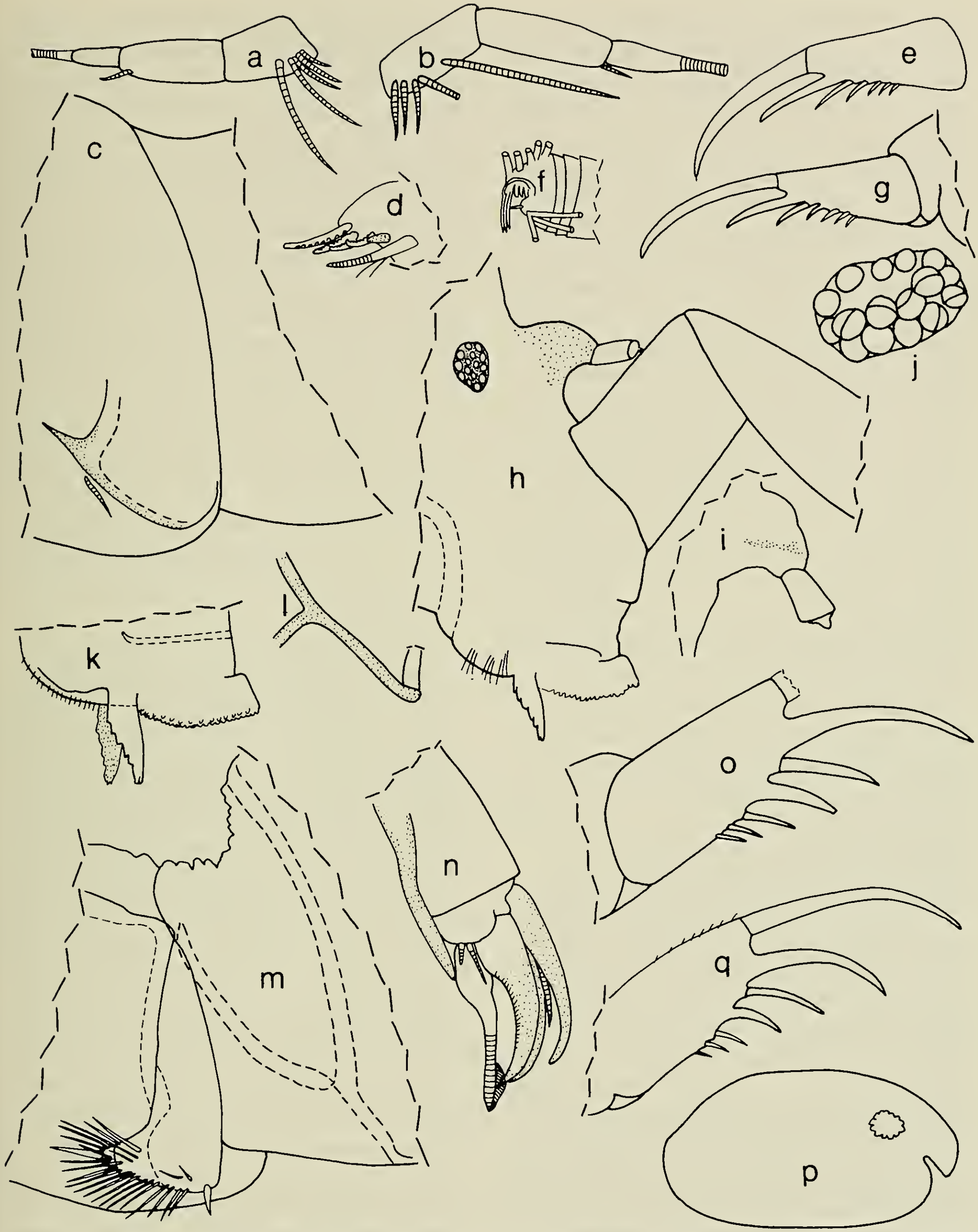

Fig. 1. *Sheina orri,* male, paratype, BM 1965.11.9.11: a, b, Medial views of endopodites of left and right 2nd antennae. Male, paratype, BM 11965.11.9.7: c, Medial view of coxa of left mandible showing endite; d, Posterior view of 1st exopodial joint of 5th limb; e, Furcal lamella. Male, paratype, USNM 112675: f, Tip of 7th limb; g, Lateral view of left furcal lamella; h, Anterior of body showing lateral eye, medial eye and bellonci organ, upper lip, 1st and 2nd joints of right 1st antenna, and anterior end of esophagus (dashed); i, Medial eye and bellonci organ; j, Right lateral eye; k, Upper lip, anterior towards right; l, Left Y-sclerite, anterior towards left. Female, paratype, BM 1965.11.9.8: m, Medial view of coxa of left mandible showing endite; n, Medial view of tip of left mandible. Female, paratype, USNM 112675: o, Lateral view of right lamella. A-1 instar, paratype, BM 1965.11.9.3: p, Lateral outline of complete specimen showing right lateral eye as seen through shell; q, Right furcal lamella.

terminal ventral bristles (distal about ¾ length of proximal). 1st endopodial joint with 4 bare bristles (2 short, 1 medium length, 1 long). 2nd endopodial joint with distinct ventral curvature; ventral margin with bristles forming 3 groups (proximal group of single small bristle just distal to joint midlength; middle group of single small bristle; and subterminal group of small, ringed, lateral bristle, and stout, unringed medial bristle (process) reaching well past end of joint); dorsal margin with 8 proximal bristles (including distal bristle about twice length of next longest bristle, and 1 short medial bristle with stout marginal spines). End joint with 3 strongly curving claws (dorsal claw bare, only slightly shorter than paired, finely dentate, ventral claws and with narrower base), and 4 bristles (dorsal bristle lateral to dorsal claw and not as long; 2 ventral medial bristles, very small; lateral ventral bristle coarsely ringed and with broad tip with dorsal hirsute pad).

Mandible, female (Fig. 1m, n): Coxal endite consisting of backward-pointing process with stout spine at tip and slender spines mostly along ventral edge; small ventral spine-like bristle at base of process. Limb otherwise similar to that of male.

Maxilla, male: Coxa with dorsal fringe of hairs. Endite I with 7 spinous and pectinate bristles; endite II with 4 spinous and pectinate bristles; endite III with 4 spinous and pectinate bristles (1 proximal, 3 terminal). Basis with 2 terminal bristles (1 dorsal, 1 lateral). Exopodite well developed, reaching midlength of 1st endopodial joint, with 3 hirsute bristles (1 subterminal, 2 terminal). 1st endopodial joint with hairs along anterior margin, 2 alpha-bristles (longer plumose, shorter bare), and 2 beta-bristles (outer bristle pectinate); cutting tooth bifurcate. 2nd endopodial joint with 3 bare, hook-like claws and 8 bristles (including 3 pectinate a-bristles).

Maxilla, female: Similar to that of male.

Fifth limb, male (Fig. 1d): Epipodite with 50 bristles. Protopodite with short anterior tooth. Endites I and II each with 5 bristles; endite III with 6 bristles. 1st exopodial joint: main tooth with proximal, smooth, tapering peg and 4 constituent pectinate teeth (Fig. 1d); bristle proximal to smooth peg with few, long, proximal spines and many, short, distal spines; anterior side with 2 stout bristles (with long spines near middle) proximal to main tooth, and stout hirsute bristle near tooth of protopodite. 2nd exopodial joint with 4 pectinate a-bristles (proximal bristle short, ringed, others stout, unringed, claw-like), 9 ringed and pectinate b′- and b″-bristles, 1 hirsute c-bristle, and 1 hirsute d-bristle. 3rd joint: inner lobe with 3 bristles (proximal with long hairs proximally and short spines distally, others bare); hirsute outer lobe with 2 equilength terminal bristles (1 or both with long proximal hairs). Fused 4th and 5th joints hirsute, with total of 2 bristles.

Fifth limb, female: Not examined in detail, but, in general, similar to that of male.

Sixth limb, male: 5 small bare bristles in place of epipodite. Endite I with 2 small hirsute bristles and 1 long terminal bristle with long marginal spines; endite II with 2 hirsute medial bristles and 1 long terminal bristle with long proximal spines; endites III and IV each with 1 small, distal, medial bristle with long proximal spines, and 2 long stout, terminal bristles with long proximal and short distal spines. End joint with 6 bristles (with long proximal and short distal spines) on anterior half (bristles 2–6 decreasing in length posteriorly) followed by wide space and then 3 hirsute bristles at posterior corner. Medial surface of end joint hirsute, with long hair-like spines along ventral edge, and shorter spines forming short rows just within edge of posterior half.

Sixth limb, female: Not examined in detail but, in general, similar to that of male.

Seventh limb, male (Fig. 1f): Each limb with 20–21 bristles, each with 3–6 bells. Limbs of USNM 1123675 with 20 bristles on each limb, 10 on each side (comb side with 5 proximal and 5 terminal; peg side with 6 or 7 proximal, 3 or 4 terminal); terminal comb with about 12 teeth (3 short on each side of about 6 long); side opposite comb with single straight peg.

Seventh limb, female: Not examined in detail but, in general, similar to that of male.

Furca, male (Fig. 1e, g): Each lamella with 7 or 8 claws; claws 2 and 4 fused to lamella, others separated from lamella by suture; all claws with tiny teeth along posterior margins: claws 3 and 4 about same width and length, otherwise, claws decrease in length and width posteriorly; claw 2 reaching to about midlength of claw 1.

Furca, female (Fig. 1o): Claw 4 broader than claw 3; limb otherwise similar to that of male.

Bellonci organ, male (Fig. 1i): Short, cylindrical with tapering tip.

Bellonci organ, female: Similar to that of male.

Eyes, male: Lateral eyes with black pigment and about 16 ommatidia (Fig. 1j). Medial eye light amber (Fig. 1h, i).

Eyes, female: Similar to those of male.

Upper lip, male (Fig. 1k): In ventral view, unpaired anterior part narrow, wedge-shaped, with several rows of small glandular tubercles; posterior part consisting of paired tusks with 4 or 5 glandular openings along posterior margin and 2 or 3 at tip.

Upper lip, female: Similar to that of male.

Genitalia: Copulatory limbs of male well developed, lobate, with several small bristles on lobes (Harding, 1966:fig. 18). Genitalia of female not observed.

Posterior of body, male and female: Smooth, without folds, spines, or posterodorsal process.

Y-Sclerite, male (Fig. 1l): Ventral branch forming right angle with posterior end of middle branch, typical for subfamily Cyridininae.

Eggs: No eggs observed.

Description of juvenile (Fig. 1p, q): Carapace similar in shape to that of adult (Fig. 1p).

Size: BM 1965.11.9.3, specimen 1, length 2.21 mm, height 1.15 mm.

First antenna: 1st and 2nd joints without bristles; 3rd and 4th joints each with 2 bristles (1 ventral, 1 dorsal); 5th and 6th joints broad and with same number of bristles as on adult (armature of bristles not examined in detail).

Second antenna: Protopodite and exopodite similar to those of adult. Endopodite 3-jointed: 1st joint with 3 proximal bristles (2 short, 1 longer) and 1 long distal bristle; 2nd and 3rd joints similar to those of adult.

Mandible: Similar to that of adult female, with 3 recurved terminal claws.

Maxilla: Similar to that of adult, with 3 recurved terminal claws.

Fifth and sixth limbs: Not examined in detail but well developed.

Seventh limb: With 11 strongly tapering proximal bristles, each with single terminal bell; terminal part fragmented on examined specimen, remaining part with 4 slightly tapering bristles on one side, each bearing up to 4 terminal bells.

Furca (Fig. 1q): Similar to that of adult except claw 2 reaching well past midlength of claw 1.

Bellonci organ: Similar to that of adult.

Eyes (Fig. 1p): Medial and lateral eyes similar to those of adult.

Upper lip: Similar to that of adult.

Genitalia: Not observed.

Sex: Unknown, but broad 5th and 6th joints of 1st antenna resemble those of adult male.

*Discussion.*—The three terminal claws of the end joint of the endopodite of the mandible of *Sheina orri* (Figs. 1n, 2b, c) are more recurved than those on other species of Cypridinidae and may be used by the ostracodes, along with three recurved claws of the maxilla, to cling to the gills of the fish, but no direct evidence is available. The stout lateral bristle of the end joint of the endopodite also differs from those of other species in terminating in a broad flattened pad (Fig.

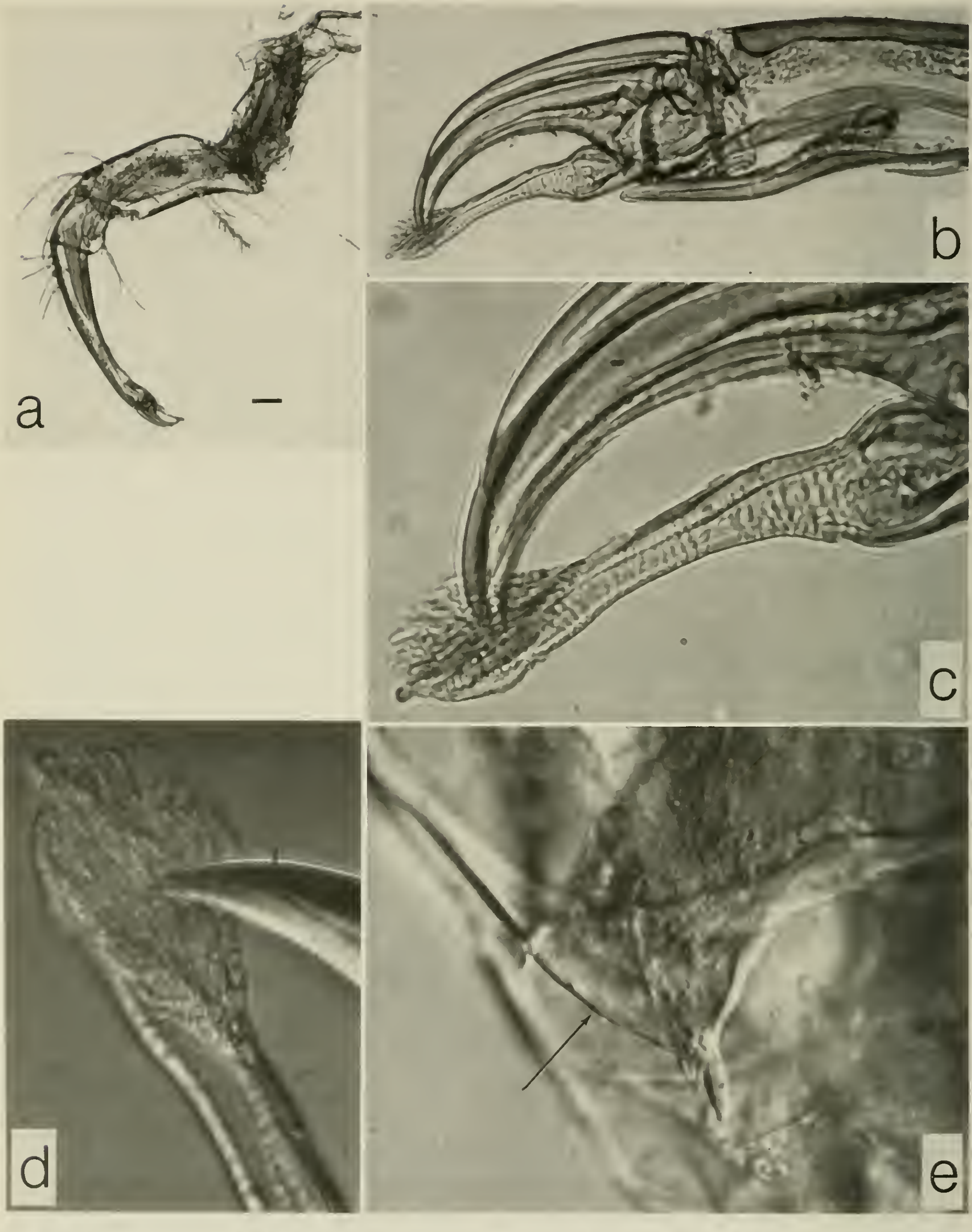

Fig. 2. *Sheina orri,* male, paratype, USNM 112675, medial views of left mandible: a, Complete limb (length of scale bar 0.10 μm): b, Detail of tip of endopodite in a; c, Detail from b; d, Detail from c showing pad at tip of lateral bristle; e, Coxal endite (arrow) from a (interference contrast). Photographs by Dr. Robert P. Higgins.

2c, d). The function of this peculiar bristle is unknown.

The coxal endite of the mandible of *S. orri* is reduced to a small process with 1–3 spines in the male (Figs. 1c, 2e) and many spines in the female (Fig. 1m). In other species of Cypridinidae the coxal endite is not sexually dimorphic, but in the Philomedidae and Rutidermatidae the male coxal endite is always poorly developed. The similarity of the dimorphism in *S. orri* and the Philomedidae and Rutidermatidae is attributed to convergence, and the dimorphism in *S. orri* is interpreted to be an autapomorphic character state within the Cypridinidae. It is possible that adult males of *S. orri* in the collection are not conspecific with adult females and juveniles, having more spines on the coxal endite, but it seems unlikely because of similarities in many other morphologic characters.

The above description of *S. orri* differs in several details from that of Harding (1966: 371). Some differences are: (1) Proximal filaments of the 5th joint of the 1st antenna are shown to be short instead of long. (The short filaments in the illustration of Harding (1966:fig. 8) probably represent remnants of longer bristles.) (2) The four bristles of joints 3 and 4 of the 1st antenna are not shown on the limb illustrated by Harding (1966: fig. 11). (3) Harding (1966:373, fig. 12) described the 2nd joint of the endopodite of the 2nd antenna as not having a bristle. (4) Harding (1966:373) described the mandibles of both the male and female as lacking an endite on the coxa. (5) The illustration of the maxilla (Harding 1966:fig. 7) shows the base of the proximal bristle to be at the base of the exopodite rather than subterminal. (6) The illustration of the 6th limb (Harding 1966:fig. 17) does not show the long terminal bristle of the 1st endite (the bristle is missing on one of the limbs on Harding's slide but was clearly torn off and is present elsewhere on the slide). (7) Harding (1966:373) described the furca as having only the 2nd claw fused to the lamella, but both the 2nd and 4th are fused, although this is not clearly shown on the single lamella on the slide prepared by Harding.

Specimens interpreted to be adult females herein do not have eggs in the marsupium, nor were they observed within the ovaries but these could have been obscured on some of the specimens. Genitalia also were not observed. Because of the possible absence of the adult characters, it may be that the females, interpreted to be adults are, in fact, next-to-last instars. On the other hand, the bristles of the 7th limbs are cylindrical (not strongly tapered) and have several distal bells, all characteristic of adults. Also, the relative lengths of the "adult" females and adult males are consistent with differences in other Cypridininae. Therefore, the large females in the collection are treated as adults here.

The gut of all specimens examined is gorged with a fine-grained, brownish, unidentified substance. The full gut of the males suggests that the relatively few spines of the coxal endite of the male mandible does not result in a decrease in feeding by the male, as seems to occur in the Philomedidae and Rutidermatidae, families in which the coxal endite of the male is also reduced.

*Sheina orri* is closely related to *Vargula,* which it resembles in the endopodite of the 2nd antenna having a bristle on the 2nd joint, in the mandible having a stout medial bristle (process) at the distal end of the ventral margin of the 2nd endopodial joint, and in having long tusks on the upper lip. It differs from *Vargula* in having reduced and sexually dimorphic endites on the coxa of the mandible.

Skogsberg (1920:262–265), Harding (1966:369), and Cohen (1983:255) have discussed occurrences of Cypridinidae associated with fish and other organisms. Only with *Sheina orri* is there the suggestion that appendages are adapted for a commensal habit. The hook-like terminal claws of the maxillae and mandibles of *S. orri* would seem to be useful for clinging to fish gills.

But if the ostracodes had been collected in the substrate or swimming freely in the water column rather than on the gills of fish, the hook-like claws would probably have been associated with predatory feeding rather than with commensalism. The recorded occurrences of ostracodes in orifices of fish may be instances of the ostracodes attacking the fish after it has been caught, while it is suspended in the water, a hypothesis previously advanced by Cohen (1983:255). Dr. Gavin Naylor, University of Maryland, (in litt. 1985) has reported such an occurrence in a shark about 1 meter long that had been captured on a long line in about 7 meters of water off Curlew Cay, Belize. The line had been set at 6 pm, 21 Aug 1985, and retrieved at 6 am, 22 Aug 1985. The heart and gill filaments were absent, apparently eaten by a swarm of ostracodes and a few isopods found in the vicinity of those organs as well as in the anterior part of the liver. The ostracodes, which I identified as *Skogsbergia lerneri* Kornicker, 1958, had previously been studied in Belize by Cohen (1983: 243) who found that they ate dead fish and did not attack uninjured invertebrates (amphipods, copepods, tanaids, worms). Attacks of the ostracode *Vargula tsujii* Kornicker and Baker, 1977, on live fish have recently been described by Stepien and Brusca (1985). The ostracodes appeared to feed on mucus and small pieces of fish skin, and remained on the fishes without harming them for long periods and in large numbers, especially along the dorsal and anal fin bases, around the anus, and along the opercula (Stepien and Brusca 1985:96). Thus, a relationship between members of the family Cypridinidae and both live and dead fish appears established, but whether or not the ostracodes are true commensals must remain open.

## Acknowledgments

I thank Dr. Roger Lincoln, British Museum (Natural History) for the loan of types of *Sheina orri,* and Dr. I. G. Sohn, Dr. Roger F. Cressey, and Dr. T. E. Bowman for reviewing the manuscript.

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# THE FIRST *ANILOCRA* AND *PLEOPODIAS* ISOPODS (CRUSTACEA: CYMOTHOIDAE) PARASITIC ON JAPANESE FISHES, WITH THREE NEW SPECIES

Ernest H. Williams, Jr. and Lucy Bunkley Williams

*Abstract.*—*Anilocra prionuri,* new species, is described from *Prionurus scalprus, Girella punctata,* and *Stephanolepis cirrhifer* from the Kii Peninsula to Miyakejima; *Anilocra clupei,* new species, from *Sardinella zunasi* from Matsushima Bay to Hiroshima; *Pleopodias superatus,* new species, from off Yui, Japan. *Anilocra prionuri* is distinguished by a slightly produced third segment on antenna 1, and by the length of antennae, uropods, and lobe of head; *A. clupei* by a produced third segment on antenna 1, swellings in both sides of the anterior dactyls, and pleotelson shape; *Pleopodias superatus* by length of antennae, pereonite 7 extending over pleonite 1 and 2, and a posteriorly notched pleotelson. *Anilocra prionuri* apparently has multiple broods interspersed with vegetative growth stages. An injury to the third segment of antenna 1 in *A. clupei* apparently triggered the partial regeneration of the flagellum segments.

Isopods in the genera *Anilocra* and *Pleopodias* have not been reported from Japanese waters. We studied fish parasitic isopods and fish collections for isopods at 20 marine and fisheries laboratories throughout Japan (Hokkaido through the Yaeyama Islands). We identified two new species of *Anilocra* and one of *Pleopodias* from this material.

## Materials and Methods

Hosts were measured for standard, fork, and total length to the nearest mm. Isopods were measured for total length and maximum width to the nearest 0.1 mm and placed in 70% ethanol. Mouthparts and appendages were mounted in glycerine jelly and drawn with the aid of a Nikon projection microscope. Whole specimens were drawn using a Nikon SMZ-10 stereoscope and built-in camera lucida. Pleotelsons of the illustrated specimens were drawn in a natural or slightly depressed position; therefore, the length of pleotelsons in illustrated dorsal views do not represent the actual total lengths. Measurements are given in mm, means in parenthesis. Isopods and hosts loaned by Mukishima Marine Biological Station, Hiroshima University (MMBS) are deposited in their collection. All other specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Common and scientific names of the hosts follow Masuda et al. (1984).

## *Anilocra prionuri,* new species
Figs. 1–23

*Type-host and locality.*—Nizadai, *Prionurus scalprus* Valenciennes (Perciformes: Acanthuridae), Shikine Island, Izu Islands Japan, 34°19.1′N, 139°12.4′E, 25 Jul 1960 (host not examined by us).

*Additional hosts and localities.*—*P. scalprus,* off Seto Marine Biological Laboratory, Kii Peninsula, Wakayama Prefecture, Honshu, Japan, 7 Feb 1951, 7 Feb 1953, 15 Nov 1957; Miyakejima, Izu Islands, Japan (J. T.

Figs. 1–15. *Anilocra prionuri,* 1, 2, 13. Female holotype with oostegites; 3–12, 14, 15. Female paratype lacking oostegites: 1, Dorsal view; 2, Lateral view; 3, Incisor process of mandible; 4, Mandible and palp; 5, Apex of distal segment of mandibular palp; 6, Distal lobes of maxilla 2; 7, Maxilla 2; 8, Apex of maxillipedal palp; 9, Maxilliped; 10, Scales on maxilliped; 11, Apex of maxilla 1; 12, Maxilla 1; 13, Head, ventral view; 14, Antenna 1; 15, Antenna 2. (Scale of 4, 7, 9, 12 equal; scale bars in mm.)

Moyer, pers. comm.); mejina, *Girella punctata* Gray (Girellidae), off Seto Marine Biological Laboratory, 4 Apr 1954; kawahagi, *Stephanolepis cirrhifer* (Temminck and Schlegel) (Tetradontiformes: Monacanthidae); off Seto Marine Biological Laboratory, 19 May 1956; unknown host, off Seto Marine Biological Laboratory, 1958 (hosts not examined by us).

*Site of infection.*—Beneath eye or on side of head of host (not observed by us).

*Specimens studied.*—11 (all females).

*Type specimens.*—Holotype (female), USNM 231071; 10 paratypes, USNM 231072-231078.

*Description.*—Body elongate-oval, length-width ratio 2.69–3.46 (2.96). Antennae 1 compressed, third segment slightly enlarged, extending to just before to just beyond posterior margin of head, 8-merous. Antennae 2 extending to just anterior of to just posterior of posterior margin of pereonite 1, 10-11-merous. Anterior margin of head truncate, flexed and produced into lobe between bases of antennae 1 and anterior portion of antennae 2. Head only slightly constricted at level of antennae. Head width-length ratio 1.4–1.6 (1.5). Distance between eyes 38–49% (45%) of head width. Distal portion of incisor process of mandible slender, proximal portion expanded. Distal segment of mandibular palp with 12 setae, 1 seta at distal outer corner of second segment. Maxilla 1 with 4 stout recurved spines at distal end. Maxilla 2 with 1 long spine on inner lobe and 2 smaller spines on outer lobe. Maxillipedal palp with 3 recurved spines at distal end. Posteroventral angle of pereonite 7 produced ventrally into rounded lobe. Pereonite 7 extending over approximately ⅔ to almost all of pleonite 1. Shortest pereonite 2, longest 6. Dactyls of pereopods 1–4 without swellings on margins. Pereopod 7 abruptly longer than other pereopods. Pleotelson with low median ridge, 1.1–1.3 (1.2) times longer than wide (damaged ones as wide as long to slightly wider than long). Uropods extending posterior of posterior margin of pleotelson, endopod extending beyond posterior end of exopod. Endopods of pleopod 2 with simple proximomedial lobe; endopods of pleopods 3–5 with complexly folded proximomedial lobes, increasing in size and complexity from 3 to 5.

*Male.*—Unknown (see *Anilocra* sp.).

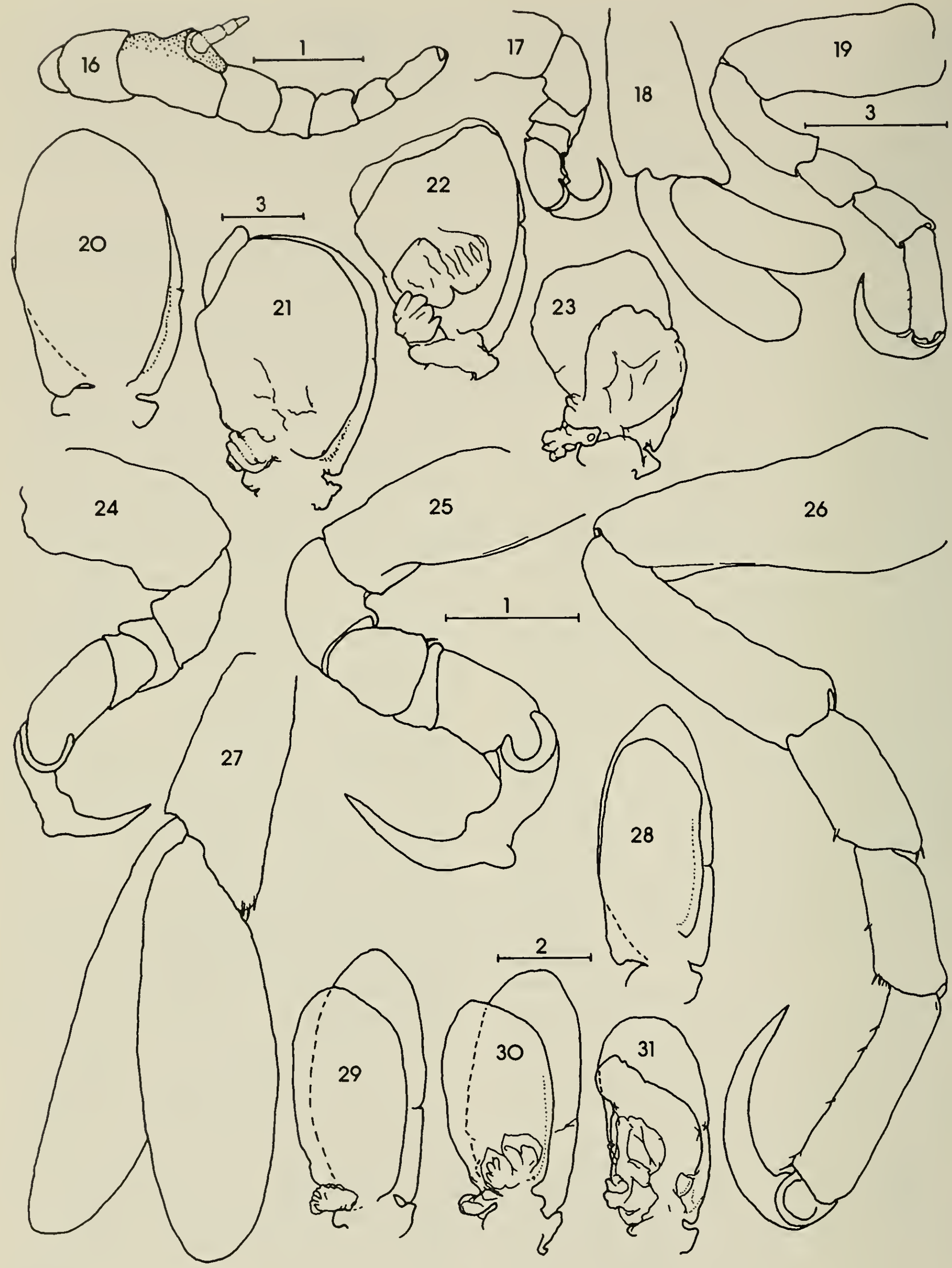
*Female* (N = 11).—Total length 32.6–47.2 (39.1), maximum width 9.1–16.8 (13.4). The longest, widest, shortest, and most narrow females lacked oostegites. Length-width ratios of the 5 females with oostegites varied from 2.75 to 3.20, the 6 without oostegites 2.69 to 3.46. Both groups averaged 2.96.

*Geographic distribution.*—*Anilocra prionuri* is known to occur from the Inland Sea to the Izu Islands of Japan (along the southern Pacific coast of Honshu). It was not observed in the Ryukyu Islands. The type and most frequently reported host has a temperate distribution from Matsushima Bay, Miyagi Prefecture to Taiwan (Masuda et al. 1984). This isopod may also be restricted to temperate areas.

*Etymology.*—The specific name is from the genus of the host.

*Japanese standard common name.*—Nizadai-yodori-mushi (shin-shô) = parasitic isopod attaching to nizadai.

*Remarks.*—*Anilocra prionuri* seems to be intermediate between the species of *Anilocra* with geniculate or produced third segment of antennae 1, and those species with no enlargement of this segment. By being consistently intermediate, *Anilocra prionuri* differs from all other species of this genus, all having this segment either distinctly produced or not produced. *Anilocra prionuri* most closely resembles *A. acanthuri* Williams and Williams, known from Puerto Rico, British and U.S. Virgin Islands, Dominican Republic, Cuba, Jamaica, Bahamas, and south Florida, U.S.A. (Williams and Williams 1981), in body shape (length-width ratio 2.9 vs. 2.96) and size (29 to 40 vs. 32.6 to 47.2), and primary host family (Acanthuridae). *Anilocra prionuri* differs



Figs. 16–23. *Anilocra prionuri,* female paratype lacking oostegites: 16, Antenna 1 with damaged third segment and auxiliary flagellum; 17, Pereopod 1; 18, Uropod; 19, Pereopod 7; 20, Pleopod 2; 21, Pleopod 3; 22, Pleopod 4; 23, Pleopod 5. (Scale for 17–19 equal; 20–23 equal; scale bars in mm.)

Figs. 24–31. *Anilocra clupei,* female paratype with oostegites: 24, Pereopod 1; 25, Pereopod 4; 26, Pereopod 7; 27, Uropod; 28, Pleopod 2; 29, Pleopod 3; 30, Pleopod 4; 31, Pleopod 5. (Scale for 24–27 equal; 28–31 equal; scale bars in mm.)

from *A. acanthuri* by having a temperate distribution instead of a tropical to subtropical distribution, attaching to the face of its host instead of beneath the pectoral fin, having longer antennae 1 and 2, having uropods which extend to or beyond the posterior margin of the pleotelson instead of not extending to the posterior margin, having an elongate instead of a broad lobe of the head which extends between bases of antennae 1 and 2 instead of only between antennae 1.

Dr. Jack T. Moyer (pers. comm.) has frequently observed what appear to be specimens of *Anilocra prionuri* on the face of *Prionurus scalprus* at Miyakejima. He observed three and four isopods on one side of the face of a single host.

The largest females of *A. prionuri* lack oostegites. These probably represent vegetative growth stages between broods and indicate this species has multiple broods on its host and a long term host association. The condition is similar to that found in females of *Mothocya bohlkeorum* Williams and Williams (1982).

One female (35.8 × 12.4) without oostegites has an antenna 1 on the left with nine segments and one on the right with a miniature, auxiliary flagellum on the third segment (Fig. 16). The condition appears to be the result of a partial regeneration after an injury.

### *Anilocra clupei*, new species
Figs. 24–45

*Type-host and locality.*—Sappa, *Sardinella zunasi* (Bleeker) (Clupeiformes: Clupeidae), Matsushima Bay, Miyagi Prefecture, 39°50.6′N, 141°07.9′E, 10 Sep 1951 (host not examined by us).

*Additional locality.*—*S. zunasi*, shore of Mukaishima Marine Biological Station, Hiroshima Prefecture, Japan, 1973 (MMBS—no numbers).

*Site of infection.*—Along side of head of the host.

*Specimens studied.*—5 (females).

*Type specimens.*—Holotype, USNM 231070; 4 paratypes (MMBS—no numbers).

*Description.*—Body elongate, length-width ratio 3.30–3.57 (3.44). Antennae 1 compressed, 8-merous, extending from middle to ¾ length of eye, third segment enlarged. Antennae 2 extending onto pereonite 2, 10-merous. Anterior margin of head truncate, flexed and produced into lobe between bases of antennae 1 and anterior portion of antennae 2. Head slightly constricted at level of antennae. Head width-length ratio 1.2. Distance between eyes 35–44% (39%) of head width. Distal portion of incisor process of mandible slender, proximal portion expanded. Mandibular palp with 11 setae on distal segment. Maxilla 1 with 4 slightly recurved spines at distal end. Inner lobe of maxilla 2 with 1 large and 1 small recurved spine, 2 small spines on outer lobe. Distal segment of maxillipedal palp with 3 recurved spines. Anteroventral angle of pereonite 1 produced ventrally and slightly anteriorly. Posteroventral angle of pereonite 7 slightly produced ventrally. Pereonite 7 extending over approximately ⅓ of pleonite 1. Shortest pereonite 2, longest 6. Dactyls of pereopods 1–4 with swellings on both sides, swellings on outer margin higher than those on inner margin. Pereopod 7 abruptly longer than other pereopods. Pleotelson expanded along lateral margin to a width greater than width of pleonite 5, with low median ridge, 1.32–1.40 (1.36) times longer than wide, lateral margins up-turned so that pleotelson scoop-shaped. Uropods extending beyond posterior end of pleotelson, endopods and exopods subequal in length. Endopods of pleopod 2 with simple proximomedial lobe; endopods 3–5 with complexly folded proximomedial lobes and pockets, much larger and more complex in pleopod 5.

*Male.*—Unknown (see *Anilocra* sp.).

*Female* (N = 5).—Total length 27.4–28.3 (27.7), maximum width 7.7–8.3 (8.1), all gravid. No remnants of appendix masculinum present.

*Geographic distribution.*—*Anilocra clupei* is known to occur from the western portion of the Inland Sea of Japan to the northern Pacific coast of Honshu (approximately ¾ of the length of the Pacific coast of Honshu). We did not find this isopod on *Sardinella zunasi* in the Ryukyu Islands. This isopod may be restricted to the temperate portion of Japan.

*Etymology.*—The specific name is from the family of the host.

*Japanese standard common name.*—Sappa-yadori-mushi (shin-shô) = parasitic isopod attaching to sappa.

*Remarks.*—Only three known species of *Anilocra* have both a produced third segment in antennae 1 and swelling in both sides of the dactyls of the anterior pereopods. *Anilocra leptosoma* Bleeker, known from Indonesia to the Gulf of Suez and South Africa (Bowman and Tareen 1983), has a more slender body than *A. clupei,* a head more abruptly narrowed at the level of the antennae, and a pleotelson with parallel sides for the proximal ⅔ and a sharply angular distal end, instead of sub-oval with a concave dorsal surface. *Anilocra cavicauda* Richardson, 1910, known only from the Philippines, has a head and pleotelson shape similar to *A. leptosoma.* The lateral margins of the pleonites are up-curved in *A. cavicauda* but not in *A. clupei*; the pleotelson is more narrow (1.8 length width ratio vs. 1.45); the median ridge is absent; coxae of pereonites 6–7 extend to middle instead of ⅔ or more length of lateral margin of pereonites; and the uropods extend only to the posterior end of the pleotelson instead of well beyond. *Anilocra alloceraea* Koelbel, 1879, known only from Sumatra, has a head and body shape very similar to *A. leptosoma* and different from *A. clupei,* the pleotelson does not have the concave dorsal surface of *A. clupei,* and posterior ends of the basis, endopod and exopod of the uropods are not acute in *A. clupei.*

The four *Sardinella zunasi* hosts for the paratypes of *A. clupei* were 92–94 (93.3) in fork length. Host size was not available for the holotype.

### *Anilocra* species
Figs. 47–53

*Host and locality.*—Katakuchi-iwashi, *Engraulis japonicus* Temminck and Schlegel (Clupeiformes: Engraulidae), Kagoshima Bay, Kagoshima Prefecture, Kyushu, Japan, 7 Feb 1978 (hosts not examined by us).

*Male* (N = 3).—USNM 231083, total length 13.8–14.6 (14.2), maximum width 2.4–2.7 (2.6). Antennae 1 8-merous, antennae 2 10-merous. Penes lobes not discernable. Appendix masculina of pleopod 2 linear with unmodified apex, as long as endopod. No pigment spots apparent. Attached on body of host.

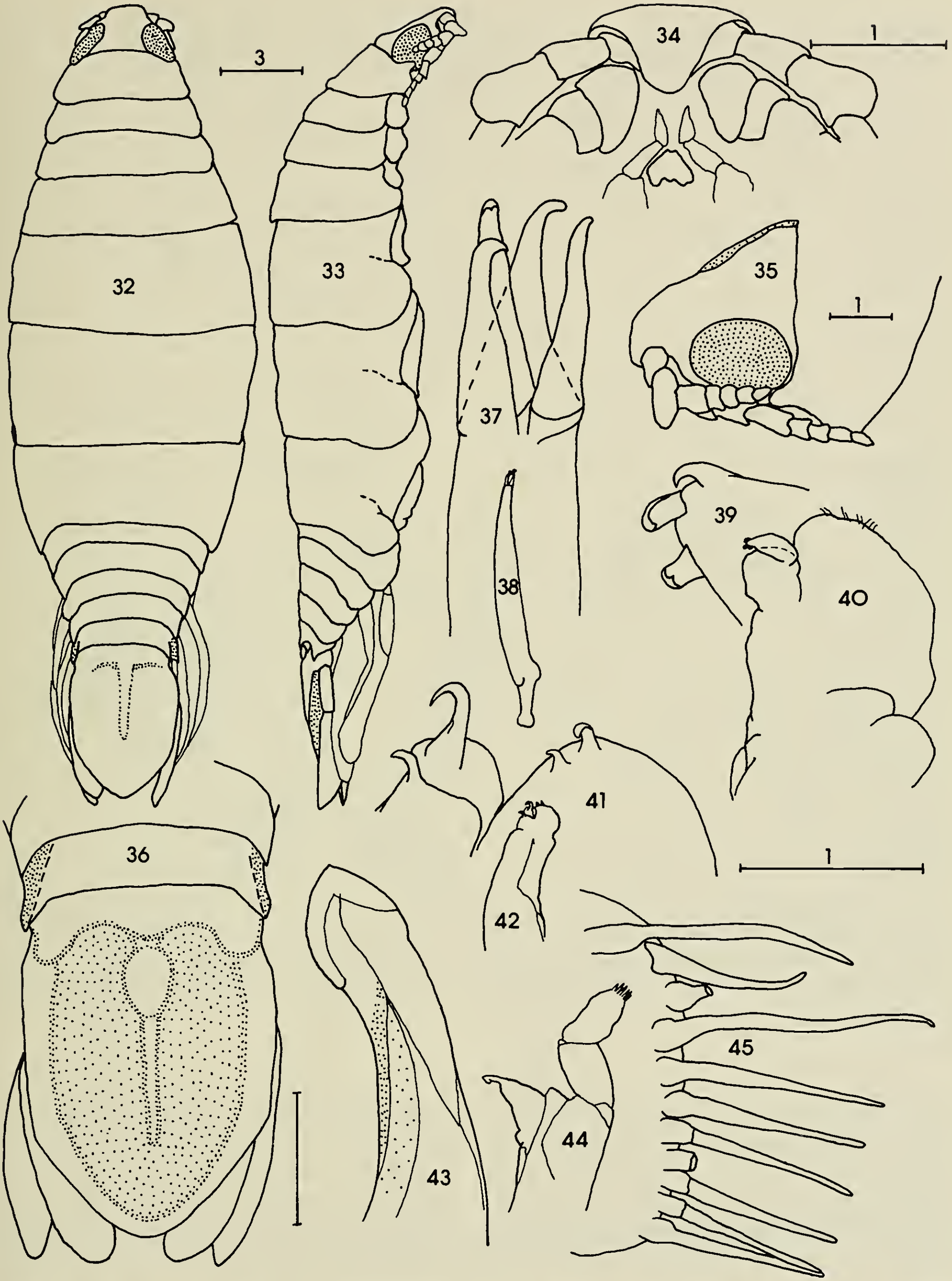
### *Anilocra* species
Figs. 54–61

*Host and locality.*—Kibinago, *Spratelloides gracilis* (Temminck and Schlegel) (Clupeidae), Kochi, Kochi Prefecture, Shikoku, Japan, 20 Dec 1984 (hosts not examined by us).

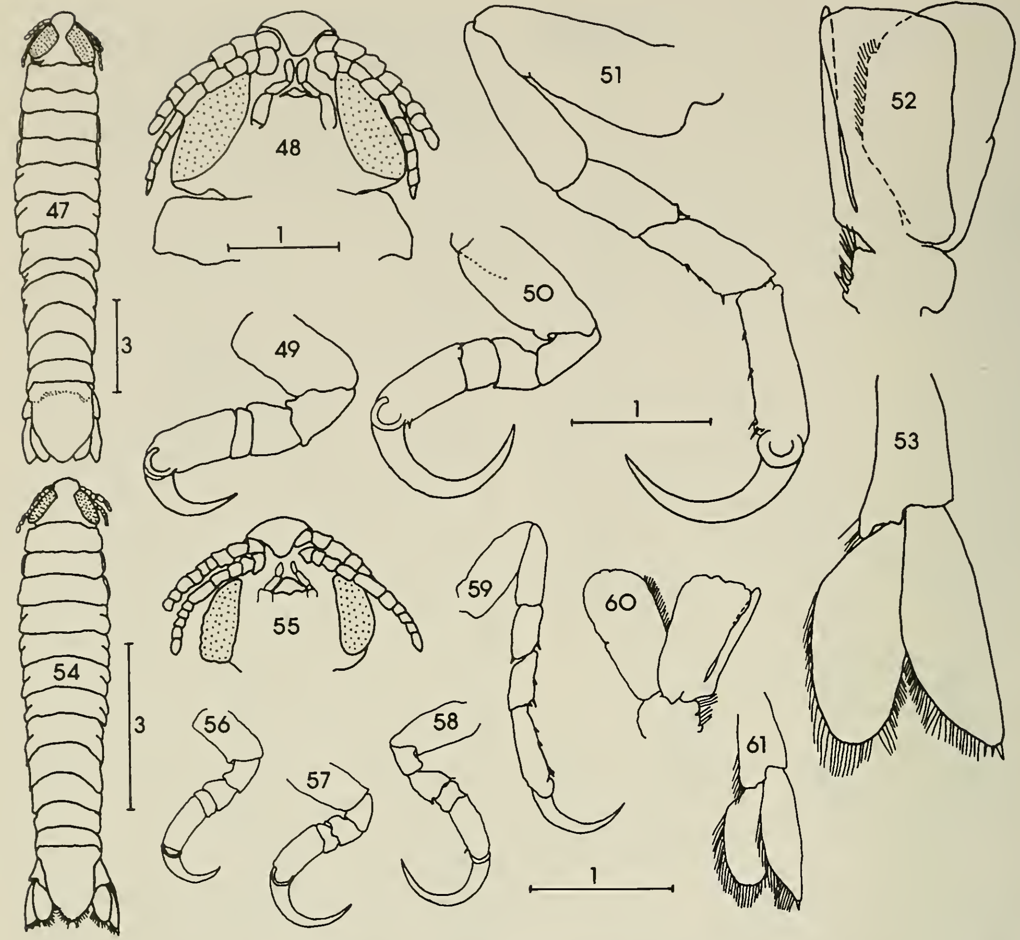
*Male* (N = 2).—USNM 231061, total length 8.9 and 9.1, maximum width 1.6 and 1.7. Antennae 1 8-merous, antennae 2 10-merous. Penes lobes not discernable. Appendix masculina of pleopod 2 linear with unmodified apex, as long as endopod. Pigment spots scattered over dorsal surface. Attached on the lateral dorsal surface behind head of host.

*Remarks.*—The two *Anilocra* sp. seem to represent males of two different species, because the smaller ones (9.0) are well pigmented while the larger (14.2) lack pigment. They may represent one or both of the males of *Anilocra prionuri* or *A. clupei,* the only *Anilocra* species known from this general geographic area. We are unable definitely to match either male with the females of the new species.

The *Spratelloides gracilis* and *Engraulis*



Figs. 32–45. *Anilocra clupei,* 32–36. Female holotype with oostegites; 37–45. Female paratype with oostegites: 32, Dorsal view; 33, Lateral view; 34, Head, ventral view; 35, Head, lateral view; 36, Posterior end, dorsal view; 37, Apex of maxilla 1; 38, Maxilla 1; 39, Apex of maxillipedal palp; 40, Maxilliped; 41, Distal lobes of maxilla 2; 42, Maxilla 2; 43, Incisor process of mandible; 44, Mandible and palp; 45, Apex of distal segment of mandibular palp. (Scale for 38, 40, 42, 44 equal; scale bars in mm.)



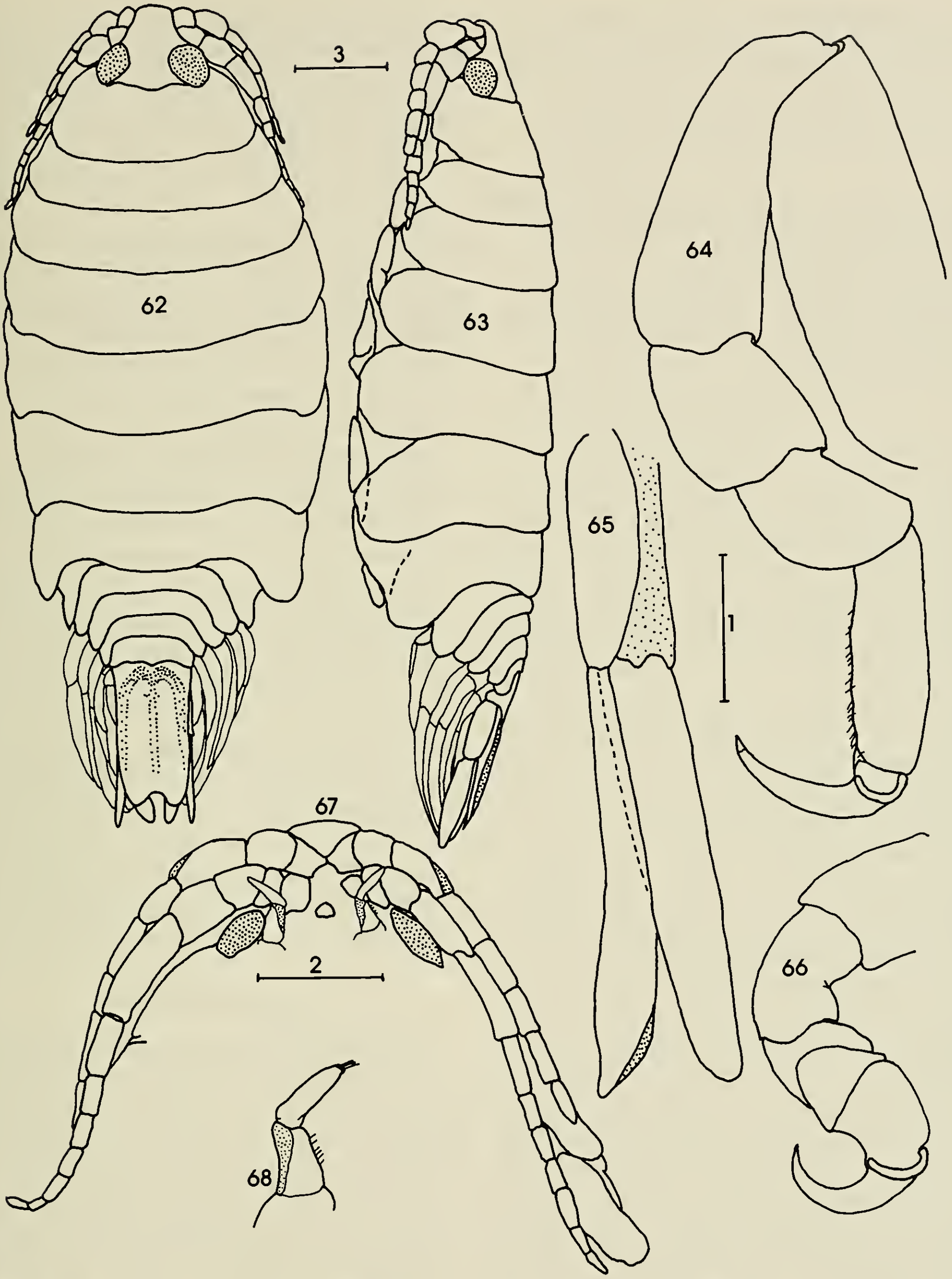
Figs. 47–53. *Anilocra* sp. from *Engraulis japonicus*: 47, Dorsal view; 48, Head, ventral view; 49, Pereopod 1; 50, Pereopod 3; 51, Pereopod 7; 52, Pleopod 2; 53, Uropod. (Scale for 49–53 equal; scale bar in mm.)

Figs. 54–61. *Anilocra* sp. from *Spratelloides gracilis*: 54, Dorsal view; 55, Head, ventral view; 56, Pereopod 1; 57, Pereopod 3; 58, Pereopod 4; 59, Pereopod 7; 60, Pleopod 2; 61, Uropod. (Scale for 55–61 equal; scale bars in mm.)

*japonicus* may be serving as intermediate hosts for these *Anilocra* sp. Williams (1984) demonstrated a life cycle involving intermediate hosts (Cardinalfishes—Apogonidae) with similar small males (micromales) and *Chromis* sp. (Pomacentridae) as final hosts.

The specimens of *Anilocra* sp. from *Engraulis japonicus* were together in a vial with specimens of *Nerocila phaiopleura* Bleeker (Cymothoidae). If this is a representative subsample, then *N. phaiopleura* occurred much more frequently on the *E. japonicus* collected in Kagoshima Bay than did the *Anilocra* sp. Whether both isopods occurred on the same specimen of host was not clear, as the species of isopods were not distinguished by collectors.

Dr. Kazuo Ogawa (pers. comm.) observed large numbers of *Spratelloides gracilis* off Kochi. He estimated 1–2% were infected with an isopod on the dorsal side



Figs. 62–68. *Pleopodias superatus,* female holotype with oostegites: 62, Dorsal view; 63, Lateral view; 64, Pereopod 7; 65, Uropod; 66, Pereopod 1; 67, Head, ventral view; 68, Mandibular palp. (Scale for 64–66 equal; scale bars in mm.)

behind the head, and collected two specimens of *Anilocra* sp.

### *Pleopodias superatus*, new species

Figs. 62–68

*Type locality.*—Yui, Shizuoka Prefecture, Honshu, Japan, 50°06.1'N, 138°33.7'E, 11 Apr 1969 (Host unknown).

*Specimens studied.*—1 gravid female.

*Type specimen.*—Holotype (female), USNM 231069.

*Description.*—Body oval, 26.5 long and 10.4 in maximum width, length-width ratio 2.5. Antennae 1 compressed, extending onto pereonite 2, bases touching, 8-merous. Antennae 2 extending to middle of pereonite 3, 12-merous. Anterior margin of head truncate, flexed and produced into triangular lobe overlapping bases of antennae 1. Head constricted anterior of eyes. Head width-length ratio 1.3. Distance between eyes 33% of head width. Mouthparts not removed to avoid damaging buccal region of single specimen. Setae on outer margin of maxillipedal palp, 3 simple setae on distal segment. Labrum small. Pereonite 5 longest, 4 and 6 equal in length; pereonite 1 longer than 2, 3, or 7. Posteroventral angle of pereonite 6 slightly produced posteriorly, of pereonite 7 produced posteriorly. Pereonite 7 extending over dorsal surface of pleonite 1 and onto pleonite 2. Coxae of pereonites 2–4 extending across entire lateral margins of their segments, coxae of 5 extending ⅔ length of margin, 6 half margin, and 7 one-third length of margin. Pereopods 7 abruptly longer than other pereopods. Pleotelson length-width ratio 1.8. Lateral margins and proximal base of pleotelson curled-up to form "scoop-shape." Median ridge from anterior margin to ¾ length of pleotelson, posterior margin deeply emarginate. Uropods elongate, extending beyond posterior ends of pleotelson and pleopods, rami subequal. Pleopods extending only slightly beyond posterior end of pleotelson.

*Etymology.*—The specific name *superatus* (Latin) refers to pereonite 7 overlying pleonite 1 and part of 2.

*Japanese standard common name.*—Shinkai-yadori-mushi (shin-shô) = parasitic deep-sea isopod.

*Remarks.*—Antennae, pereopods, and uropods were not detached from the holotype to avoid damaging the single specimen.

*Pleopodias superatus* differs from *P. elongatus* Richardson by having pereonite 7 extending over pleonite 1 and part of 2, instead of not extending over any pleonites; antennae 1 extending onto pereonite 2 instead of to middle of pereonite 1; antennae 2 extending to middle of pereonite 3, instead of middle of pereonite 2; pereonite 5 longer than 4, and 1 and 6 longer than 2 and 3, instead of 4 longer than 5, and 1 and 6 approximately equal with 2 and 3; pleotelson with a median ridge and a deep notch on posterior margin, instead of uniform surface and rounded posterior margin; pleopods extend beyond posterior margin of pleotelson but not to posterior ends of uropods, instead of extending well beyond both.

The genus *Pleopodias* is in need of revision. However, Dr. N. L. Bruce (pers. comm.) is describing additional species in the genus, and a revision would be more comprehensive with all available species.

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# DISCOVERY AND SIGNIFICANCE OF ALBANY HANCOCK'S MICROSCOPE PREPARATIONS OF EXCAVATING SPONGES (PORIFERA: HADROMERIDA: CLIONIDAE)

Klaus Rützler and Shirley M. Stone

*Abstract.*—A collection of 91 identified microscope slide preparations of clionid sponge species discovered at The Hancock Museum, Newcastle-upon-Tyne, U.K., is re-examined for the first time in over 100 years. The slides document the material described by Albany Hancock in two papers on "excavating sponges" (Hancock 1849, 1867). Except for *Cliona celata* Grant (seven slides) the collection can be considered type material for 27 species of *Cliona* and two species of *Thoosa* named by Hancock. This valuable discovery will be the basis for species revisions within the Clionidae henceforth.

Albany Hancock (1806–1873) trained as a lawyer but after two years in practice left (1833) to follow his first love, the study of natural history for which he had developed a distinct flair. During his 67 years, he wrote or co-authored over 70 papers on a wide range of animals.

Albany was a self-taught naturalist, developing a remarkable capacity for minute and accurate observation. He became an accomplished artist and a gifted anatomist showing meticulous skill in dissection. He distinguished himself in the field of malacology, where his studies culminated in the celebrated Ray Society "Monograph of the British Nudibranchiate Mollusca," published in collaboration with Joshua Alder in 1855. The colored plates, renowned both for their delicate beauty and accurate detail, were nearly all prepared by Hancock.

His studies convinced him that a sound classification depends on a knowledge of the living animal visualized functionally, in order better to appreciate the significance of the gross morphology. This rather advanced view is apparent in his sponge work. As early as 1845 he became interested in the mechanics of burrowing as demonstrated by various invertebrates. He studied molluscs and barnacles before turning his attention to the clionid sponges.

In the course of his study, Hancock (1849) not only developed important theories about the mechanisms by which sponges penetrate their substrate but also discovered that not all excavating sponges belong to one species, *Cliona celata* Grant, as had been assumed by his contemporaries. In fact, Hancock claimed to have "determined upwards of fifty species" of clionids, but he only described 25 in his first paper (Hancock 1849), including two belonging to his new genus *Thoosa*. "Twelve" of these species came from the British coasts, the rest from other parts of the world which were not always clearly stated, presumably because the mollusk shells studied lacked detailed data.

Hancock's (1849) descriptions were unusually detailed being based not only on the shape and size of spicules, but also on pattern and dimensions of papillary perforations and subsurface excavations, and on color of the live (when known) or dry specimens. Spicules of all species were drawn to the same scale and several excavation patterns were also illustrated. Unfortunately, Hancock overlooked most of the microscleres in his original temporary microscope

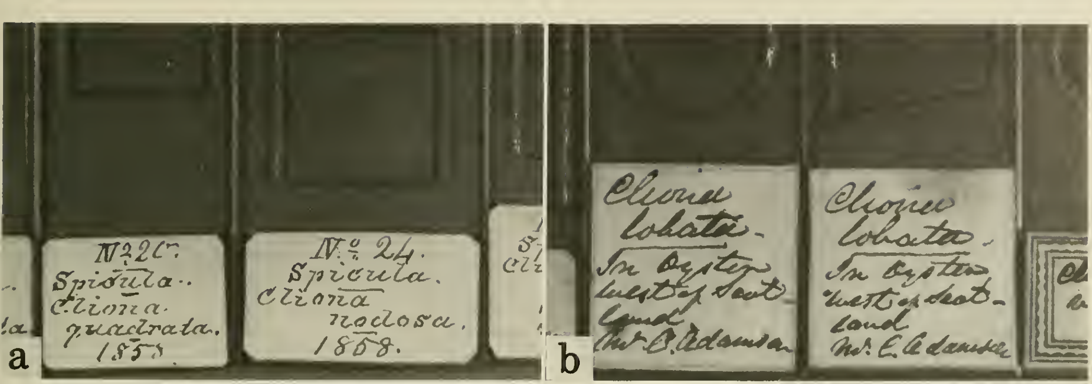

Fig. 1. A. Hancock slides, styles of handwriting: a, Style 1 by J. Alder; b, Style 2 by A. Hancock.

preparations. These taxonomically important spicules were not noted until about a decade later when Hancock re-examined his material and made permanent mounts of spicules and some tissue in Canada balsam. This renewed study was prompted by Hancock's continued curiosity about the excavation technique used by clionid sponges, thought to be mechanical and leaving visible traces in the form of substrate chips, and led to a follow-up publication (Hancock 1867). In this work the earlier diagnoses of nine British *Cliona* species were amended by description and illustration of their microscleres and four foreign species of *Cliona* were named and described. Another purpose of Hancock's (1867) paper was to defend his views on excavation powers and species diversity in clionids, both heavily criticised by his contemporary Bowerbank (1866).

As far as we know, neither Bowerbank nor other critics of Hancock's (1849, 1867) species concept, such as Topsent (1888, 1891) and Vosmaer (1933), examined the type preparations at the Newcastle Museum, as it was then known. When more recent attempts to reevaluate Hancock's work failed because neither Hancock's excavated shells nor his slides could be located, it was assumed that the entire collection was lost during the chaos of World War II.

However, after a visit by one of us (SMS) to The Hancock Museum late in 1970, three sets of Hancock's microscope slides (165 slides in all but not all identified) were discovered after a determined search by one of the resident curators. Of these, 91 named slides (excluding *C. celata* of Grant), representing all 27 *Cliona* species and the two *Thoosa* species described by Hancock (1849, 1867) have now been examined by us and, where possible, an opinion is given about the validity of the species. We regard all 91 slides as primary type material of Albany Hancock (holotypes by monotypy, or syntypes).

Many of the slides bear a number, written in the hand of the labeller, which we assume to be Hancock's coded number for the species because never more than one number is ever cited for a multi-specimen species. In the numbering sequence 1–46, five numbers (1, 19, 28, 29, 35) are not represented by slides at the present time. Slide labels are written in two different styles of handwriting. The first (style 1, Fig. 1a) is associated with "1858" when this date appears on the label, and the second (style 2, Fig. 1b) with the date "1867." Comparisons with labels of known origin in The Hancock Museum demonstrate that style 1 is by the hand of Joshua Alder, Hancock's friend and collaborator; style 2 is the handwriting of Albany Hancock himself (P. Davis, pers. comm.).

Catalog (registration) numbers in this text are those of The Hancock Museum, Newcastle-upon-Tyne.

## Annotated List of New Species Described by A. Hancock

In the following account Hancock's (1849, 1867) species are listed in alphabetical order. Comments on spicule types and shape and measurements of spicules are based on our own examination of the microscope slides. Spicule dimensions given by us are averaged total length × width of the most abundant size class for each type (for tylostyles, maximum shaft width, not head diameter, was taken). Measurements by the original author of the "full developed spiculum" (Hancock 1849:332) were converted from inches to micrometers and added with Hancock's initials (A.H.) in parentheses for comparison.

### *Cliona* Grant

### *Cliona alderi* Hancock

Fig. 2a

*Cliona Alderi* Hancock, 1849:337, pl. XV, fig. 9; 1867:239.

*Material examined.*—5 slides (3 tissue squash, 2 acid cleaned), from at least two specimens (A.H. no. 4); four dated 1858, one dated 1867.

*Syntypes.*—4.15.01–4.15.04.

*Additional material.*—4.15.05.

*Type locality.*—Isle of Man, Great Britain.

*Spicules.*—(a) Tylostyles with inconspicuous subterminal heads, 240 × 7 μm (A.H.: 219 μm). (b) Styles, 250 × 7 μm.

*Remarks.*—Spicules vary strongly in size and proportion of tylostyles: styles between preparations. Hancock considered the styles to be slightly shorter than the tylostyles. This species was synonymized with *Cliona celata* Grant by Bowerbank (1866:212). However, strong differences in tylostyle size and shape exist between this species and typical specimens of *Cliona celata* Grant described by Hancock (1849:332). These differences, as well as the occurrence of styles (and transition forms) suggest that *Cliona alderi* should be considered a valid species pending the discovery of more material.

### *Cliona angulata* Hancock

Fig. 2b

*Cliona angulata* Hancock, 1849:343, pl. XV, fig. 13.

*Material examined.*—1 slide (acid cleaned), containing only few and mostly broken spicules; A.H. no. 16, dated 1858.

*Syntype.*—4.15.06.

*Type locality.*—Mediterranean Sea.

*Spicules.*—Tylostyles with inconspicuous irregular and often ill-defined subterminal heads, some with one step near the point, some styloid forms, 210 × 5 μm (A.H.: 217 μm).

*Remarks.*—Considered a synonym of *Cliona celata* Grant by Topsent (1900:32). The existing preparation is insufficient for upholding this species.

### *Cliona canadensis* Hancock

Fig. 6e, f

*Cliona Canadensis* Hancock, 1849:340, pl. XIV, fig. 10.

*Material examined.*—4 slides (acid cleaned) from one specimen; only three of the slides conform with description of the species; A.H. no. 3, dated 1858.

*Holotype* (by monotypy).—4.15.07–4.15.09.

*Type locality.*—Not stated (substrate: "*Ostrea Canadense*").

*Spicules.*—(a) Tylostyles, many with subterminal heads, 190 × 5 μm (A.H.: 180 μm); a second, larger type (260 × 7 μm) with elongate, inconspicuous terminal head is probably foreign. (b) Oxea, microspined, many with centrotyl swelling, 120 × 5 μm. (c) Microrhabds, spiny, many centrotyl, 12 × 2 μm.

*Remarks.*—Vosmaer (1933:403, 411) tentatively synonymized this species with *Cliona vastifica* Hancock, suspecting that microrhabds ("spinispirae") may have been overlooked during the original description. The type slides indeed contain microrhabds. A fourth slide 4.15.10 with the same inscription as the two above contains spicules of an entirely different *Cliona* (very thin tylostyles with subterminal head, 200 × 2 μm; spiny microrhabds and amphiasters, 10 × 2 μm).

### *Cliona carpenteri* Hancock
Fig. 4a, b

*Cliona Carpenteri* Hancock, 1867:241, pl. VIII, fig. 4.

*Material examined.*—2 slides (acid cleaned) from one specimen (without A.H. no.); labelled by Hancock (style 2), dated 1867.

*Holotype* (by monotypy).—4.15.11, 4.15.12.

*Type locality.*—Mazatlan (Pacific Mexico).

*Spicules.*—(a) Tylostyles with rounded heads, 250 × 5 μm (A.H.: 254 μm). (b) Oxea, two size classes, 130 × 10 μm (A.H.: 127 μm; smaller category not mentioned and probably not considered "full developed"), and 63 × 4 μm; both with rough surface (difficult to detect in regular transmitted light) and including many centrotyi forms. (c) Microrhabds, straight and spiny, 13 × 3 μm (A.H.: 13 μm).

*Remarks.*—Topsent (1888:77; 1891:566) treats this as a good species, particularly pointing out the straight fusiform shape of the microscleres to distinguish it from *Cliona vastifica* Hancock. The two size classes of oxea have not been noted before.

### *Cliona cervina* Hancock
Fig. 6h

*Cliona cervina* Hancock, 1849:339, pl. XV, fig. 8.

*Material examined.*—1 slide (acid cleaned), A.H. no. 9, dated 1858.

*Syntype.*—4.15.19.

*Type locality.*—Not stated (substrate: "*Meleagrina albina*?").

*Spicules.*—(a) Tylostyles with flattened head, 250 × 5 μm (A.H.: 254 μm). (b) Oxea, tuberculated, 55 × 5 μm (A.H.: 64 μm); as shown by Hancock's figure they have a large range of lengths (40–80 μm). (c) Microrhabds bearing microspine clusters, straight, twisted or spiral, 20 × 4 μm and 7 × 2 μm.

*Remarks.*—As suspected by Vosmaer (1933:411) Hancock overlooked the microscleres in this sponge. However, the shape and size range of the oxea and the size range and variety of microrhabds and spirasters do not suggest identity with *Cliona vastifica* Hancock.

### *Cliona corallinoides* Hancock
Fig. 5a, b

*Cliona corallinoides* Hancock, 1849:337, pl. XV, figs. 1 & 2; 1867:238, pl. VII, fig. 3.

*Material examined.*—5 slides; two dated 1858 and labelled in style 1 (acid cleaned, A.H. no. 8); two in style 2 handwriting, dated 1867, labelled "In *Pecten maximus,* Jersey, Mr. H. T. Mennell" (squash preparation) and "In *Tapes virginia,* M. H. T. Mennell" (acid cleaned); one with style 2 label but without information other than the queried species name (acid cleaned).

*Syntypes.*—4.15.20, 4.15.21

*Additional material.*—4.15.22–4.15.24.

*Type locality.*—Britain.

*Spicules.*—(a) Tylostyles with knobbed or subterminal heads, 300 × 4 μm (maximum length 350 μm; A.H.: 363 μm) (b) Oxea, microspined, 100 × 2.5 μm (A.H.: 73 μm/121 μm): (c) microrhabds, spiny, 11 × 12 μm (A.H.: 13 μm), straight, S-shaped, W-shaped and spiralled. The H. T. Mennell slides (4.15.22, 4.15.23) contain identical spicules except that the tylostyles are smaller (230 × 3 μm).

*Remarks.*—This species is generally considered a junior synonym of *Cliona vastifica* Hancock (Topsent 1891:558, 564; Vosmaer 1933:402, 407).

### *Cliona dendritica* Hancock
Fig. 4c, d

*Cliona dendritica* Hancock, 1849:340, pl. XII, fig. 5; pl. XV, fig. 4.

*Material examined.*—1 slide (tissue squash); A.H. no. 7, dated 1858.

*Syntype.*—4.15.25.

*Type locality.*—Not stated (substrate: "*Patella Mexicana*").

*Spicules.*—(a) Tylostyles small with rounded or ovate heads, 160 × 4 μm (A.H.: 145 μm). (b) Oxea, microspined, 70 × 2.5 μm. (c) Microrhabds, spiny, seemingly two size classes: stout, 14 × 3 μm, pointed on both ends or rounded at one, many centrotyl; slender, 14 × 1 μm.

*Remarks.*—The microrhabds were not noted by the original author. Vosmaer (1933: 41), suspecting this oversight, considers this species a synonym of *Cliona vastifica* Hancock.

### *Cliona fryeri* Hancock
Fig. 5g, h

*Cliona Fryeri* Hancock, 1849:338, pl. XIV, figs. 2–4 & 9.

*Material examined.*—2 slides (acid cleaned) of the same specimen; both contain only very few spicules; A.H. no. 41, dated 1858.

*Syntypes.*—4.15.26, 4.15.27.

*Type locality.*—Not stated (substrate: "*Placuna placenta*").

*Spicules.*—(a) Tylostyles, with oval heads, 200 × 4.5 μm (A.H.: 219 μm). (b) Oxea, microspined, very rare, 75 × 3 μm. (c) Microrhabds, spiny, W-shaped or spiral, with up to five bends, 10–15 × 2 μm.

*Remarks.*–No microrhabds were originally described. Vosmaer (1933:411) considers this species identical with *Cliona vastifica* Hancock.

### *Cliona globulifera* Hancock
Fig. 2c

*Cliona globulifera* Hancock, 1867:240, pl. VIII, fig. 3.

*Material examined.*—1 slide (acid cleaned); without A.H. no., labelled in style 2, dated 1867.

*Holotype* (by monotypy).—4.15.28.

*Type locality.*—Mediterranean Sea.

*Spicules.*—Tylostyles only, with subterminal heads, 320 × 6 μm. Most heads are 10–25 μm removed from the rounded end; there are also multiple swellings.

*Remarks.*—Lendenfeld (1896:100) synonymized this species with *Papillella suberea* (*Cliona celata* Grant).

### *Cliona gorgonioides* Hancock
Fig. 2d

*Cliona gorgonioides* Hancock, 1849:333, pl. XIV, figs. 1 & 6; 1867:237.

*Material examined.*—6 slides (acid cleaned); all without A.H. nos., labelled in style 1 and dated 1858.

*Syntypes.*—4.15.29–4.15.34.

*Type localities.*—Northumberland (England) and Prestonpans (Scotland).

*Spicules.*—Tylostyles only, with subterminal heads, 270 × 7 μm (A.H.: 270 μm).

*Remarks.*—Already Hancock (1867:237) considered this species "probably a mere variety of *C. celata*"; several subsequent authors agreed (Vosmaer 1933:349, 361).

### *Cliona gracilis* Hancock
Fig. 5c, d

*Cliona gracilis* Hancock, 1849:334, pl. XIV, fig. 7; 1867:238, pl. VII, fig. 4.

*Material examined.*—2 slides (1 acid cleaned, A.H. no. 39, labelled in style 1, dated 1858; 1 squash without A.H. no., labelled in style 2, dated 1867 but denoted "From original specimen").

*Holotype* (by monotypy).—4.15.35, 4.15.36.

*Type locality.*—"Probably from Orkney," northern Scotland.

*Spicules.*—(a) Tylostyles, with rounded heads, 330 × 5 μm (A.H.: 330 μm). (b) Oxea, microspined, 110 × 3 μm (A.H.: 10 μm).

(c) Microrhabds, spiny, zigzagged, 18 × 2 μm (A.H.: 17 μm).

*Remarks.*—Topsent (1891:565) considers this species to be a synonym of *Cliona vastifica* Hancock, a view also maintained by Vosmaer (1933:402, 406).

### *Cliona howsei* Hancock

Fig. 3a, b

*Cliona Howsei* Hancock, 1849:336, pl. XIV, fig. 8; 1867:238, pl. VII, fig. 5.

*Material examined.*—3 slides (acid cleaned); A.H. no. 36 (2 slides), all dated 1858.

*Syntypes.*—4.15.37–4.15.39.

*Type localities.*—Northeastern and south coasts of England.

*Spicules.*—(a) Tylostyles, with subterminal heads, 220 × 3 μm (A.H.: 254 μm); a second category (?) of tylostyles is 10–20% longer than the first and has a second swelling about 80 μm down the shaft, or has only this mid-shaft swelling and none at the rounded end. (b) Microrhabds, strongly spined, with spines having blunt ends, straight, bent or angulated, 35 × 3 μm (A.H.: 42 μm), with a range of 15–55 μm in length, 2–4 μm in width.

*Remarks.*—Topsent (1891:569) synonymized this species with *Cliona lobata* Hancock.

### *Cliona insidiosa* Hancock

Fig. 2e

*Cliona insidiosa* Hancock, 1849:333, pl. XV, fig. 5.

*Material examined.*—5 slides (acid cleaned); A.H. no. 25, all dated 1858.

*Syntypes.*—4.15.40–4.15.44.

*Type locality.*—Not stated (substrate: "*Tridacna gigas*").

*Spicules.*—Tylostyles only, robust, with rounded heads, many heads distally flattened, 250 × 10 μm (A.H.: 217 μm).

*Remarks.*—Two other kinds of spicules are present on some of the slides but are here regarded as contaminants because they are not consistently and closely associated with the tylostyle clusters: abundant smooth oxea, 120 × 6 μm, resembling the spicules of *Cliona labyrinthica* Hancock; and rare spiny microrhabds, 55 × 2.5 μm, resembling those occurring in *Cliona lobata* Hancock.

### *Cliona labyrinthica* Hancock

Fig. 7c

*Cliona labyrinthica* Hancock, 1849:345, pl. XV, fig. 7.

*Material examined.*—4 slides (acid cleaned); A.H. no. 30, all dated 1858.

*Syntypes.*—4.15.45–4.15.48.

*Type locality.*—Not stated (substrate: "*Tridacna gigas*").

*Spicule.*—Oxeas only, 2 size classes, 120 × 10 μm and 110 × 5 μm (A.H.: 109 μm). The larger category has a characteristic shape, stout and curved, with mucronate tips.

*Remarks.*—Laubenfels (1936:155) transferred this species to his genus *Aka,* a new name for the preoccupied *Acca* Johnson. Indeed, shape and size of the characteristic oxea on Hancock's slides (unfortunately, there is no tissue mount) agree well with figures and descriptions of *Acca* species (Johnson 1899:461–462, figs. 1–4). On the other hand, they are also in close agreement with observations on *Siphonodictyon* species, *S. obruta* in particular, described by Rützler (1971). We therefore conclude that *Acca* (to be replaced by *Aka*) is a senior synonym of *Siphonodictyon.*

### *Cliona lobata* Hancock

Fig. 3c, d

*Cliona lobata* Hancock, 1849:341, pl. XII, figs. 4 & 8; 1867:239, pl. VII, fig. 6.

*Material examined.*—4 slides (3 acid-treated squash preparations, 1 tissue squash). Only one slide (acid treated squash) bears Hancock's no. 5; the other three were later provided by Mr. Charles Adamson from Scotland (Hancock 1867:239) and are so designated.

*Syntypes.*—4.16.01.

*Additional material.*—4.16.02–4.16.04.

*Type locality.*—Guernsey, English Channel.

*Spicules.*—(a) Tylostyles, most with subterminal heads, 200 × 5 μm (A.H.: 254 μm). (b) Microrhabds, spiny and zigzagged, obtuse-ended, apparently in two size classes; 50 × 4 μm (A.H.: 51 μm) and 15 × 3 μm.

*Remarks.*—The tylostyles on the holotype slide are much shorter than noted by Hancock who measured "1/100th of an inch" (Hancock 1849:342); on the other slides these spicules are even shorter (180 × 5 μm). Despite some suggestions to synonymize this species with *Cliona celata* Grant (Bowerbank 1866:12; Vosmaer 1933: 349, 362) most authors treat it as good species, readily distinguishable from the latter (Topsent 1900:70; Hartman 1958:19).

### *Cliona mazatlanensis* Hancock

Fig. 6a, b

*Cliona mazatlanensis* Hancock, 1867:240, pl. VIII, fig. 1.

*Material examined.*—2 slides (acid cleaned), from one specimen (without A.H. no., but both dated 1867).

*Holotype* (by monotypy).—4.16.05, 4.16.06.

*Type locality.*—Mazatlan, Pacific Mexico.

*Spicules.*—(a) Tylostyles with rounded heads, 200 × 5 μm (A.H.: 145 μm). (b) Oxea, microspined, 100 × 3 μm (A.H: "half the length of the former"). (c) Microrhabds, microspined, straight to wavy with 2–3 bends, 10 × 2 μm (A.H: 20 μm).

*Remarks.*—Spicule measurements in the original publication are obviously in error, except that the oxea are indeed "half the length" of the tylostyles. This species was synonymized with *Cliona vastifica* Hancock (Topsent 1891:565).

### *Cliona millepunctata* Hancock

Fig. 2f

*Cliona millepunctata* Hancock, 1849:341, pl. XII, fig. 9.

*Material examined.*—2 slides (acid cleaned), from one specimen; A.H. no. 15, dated 1858.

*Holotype* (by monotypy).—4.16.07, 4.16.08.

*Type locality.*—Not stated (substrate: "*Cassis tuberosa*").

*Spicule.*—Tylostyles only, very weakly silicified, 210 × 2 μm (A.H.: 181 μm).

*Remarks.*—There are only few intact spicules on the slides. This species has been all but ignored by subsequent authors.

### *Cliona muscoides* Hancock

Fig. 6g

*Cliona muscoides* Hancock, 1849:335, pl. XV, fig. 11.

*Material examined.*—2 slides (acid cleaned) from one specimen; A.H. no. 11, both dated 1858.

*Holotype* (by monotypy).—4.16.09, 4.16.10.

*Type locality.*—Not stated (substrate: "*Monoceros fusoides*").

*Spicules.*—(a) Tylostyles, 180 × 4 μm (A.H.: 181 μm); the majority with one terminal head and a second swelling about 20 μm below the first; a few have a third swelling further down the shaft, others have only one swelling which is subterminal. (b) Oxea, microspined, with a sharp central bend and almost all centrotylote, 110 × 4 μm. (c) Microrhabds, microspined and centrotylote, 13 × 1.5 μm.

*Remarks.*—The fact that Hancock missed the microrhabds was already suspected by Vosmaer (1933:403, 411), who tentatively synonymized the species with *Cliona vastifica* Hancock. The consistent presence of tylote swellings in all spicules, even the microrhabds, is certainly remarkable.

### *Cliona nodosa* Hancock
Fig. 7d

*Cliona nodosa* Hancock, 1849:344, pl. XV, fig. 10.

*Material examined.*—4 slides (acid cleaned); three bear a single number (A.H. no. 24), the fourth, unusually, bears three numbers (A.H. nos. 24, 26, 31); all are dated 1858.

*Syntypes.*—4.16.11–4.16.14.

*Type locality.*—Not stated (substrate: "*Tridacna gigas*").

*Spicules.*—Oxeas only, 2 size classes, 170 × 9 μm and 150 × 5 μm (A.H.: 145 μm); oxeas are bent rather sharply in the center.

*Remarks.*—This species was transferred to *Aka* by Laubenfels (1936:155); the same comments apply that were given above for *Cliona labyrinthica* Hancock. A fourth slide in the series (4.16.14) contains a mixture of styles, tylotes, oxeas, tylostyles, *Thoosa*-type amphiasters, sigmas, and toxas; it is useless for the characterization of *Cliona nodosa* Hancock.

### *Cliona northumbrica* Hancock
Fig. 5e, f

*Cliona northumbrica* Hancock, 1849:336, pl. XIV, fig. 5; 1867:237, pl. VII, fig. 1.

*Material examined.*—9 slides; three from the original specimen (2 acid cleaned, 1 tissue squash) bear Hancock's number (A.H. no. 17), and are dated 1858; three from additional specimens without A.H. nos. (2 acid cleaned, dated 1858, 1 squash, dated 1867) collected later "from oysters" from Scotland(?) (Hancock 1867:237); one labelled like the original preparation but obviously incorrectly.

*Syntypes.*—4.16.15–4.16.17.

*Additional material.*—4.16.18–4.16.23.

*Type locality.*—Cullercoats' haddock grounds, off the northeast coast of England.

*Spicules.*—(a) Tylostyles, straight with large round heads, 330 × 7 μm (A.H.: 330 μm). (b) Oxea, microspined, regular or sharply bent in the center, 110 × 5 μm (A.H.: 82 μm). (c) Microrhabds, microspined, wavy, 14 × 3 μm (A.H.: 14 μm); most of these microscleres have 4–5 bends, but some have only slight bend, others are S- or W-shaped.

*Remarks.*—The label of one slide of the series (4.16.23) has been crossed out in pencil and, indeed, the spicules do not agree with the species description (only tylostyles are present, 450 × 9 μm, which resemble those of typical *Cliona celata* Grant). Topsent (1888:46) puts *Cliona northumbrica* into synonymy with *C. vastifica* Hancock.

### *Cliona purpurea* Hancock
Fig. 7e, f

*Cliona purpurea* Hancock, 1849:343, pl. XII, fig. 6.

*Material examined.*—2 slides (acid cleaned); A.H. no. 21, both dated 1858.

*Syntypes.*—4.16.24, 4.16.25

*Type locality.*—Not stated (substrate: "*Tridacna gigas*").

*Spicules.*—(a) Tylotes, with unpronounced terminal swellings, spined at both ends, 260 × 5 μm (A.H.: 254 μm). (b) Acanthotornotes, 120 × 5 μm (A.H.: 127 μm); their lengths having a considerable range (60–170 μm). (c) Isocheles, palmate, 18 μm. (d) Toxa, all broken, 75 μm estimated length, about 1 μm thick.

*Remarks.*—Hancock, in the original description, did not note the microscleres. Kirkpatrick (1900:353) subsequently studied the type, also overlooked the microscleres, and thus transferred the species to his new genus *Dyscliona*; he did, however, confirm the boring habit of this sponge. Topsent (1907), primarily interested in the purple pigmentation of *Cliona purpurea,* obtained a fragment of the type and described and illustrated the entire spicule complement, including isocheles and toxa

(Topsent 1907:XIX); he determined that *Dyscliona* was not the appropriate genus to receive *purpurea.* Hallman (1920:772), finally, established *Paracornulum* for *Cornulum dubium* Hentschel and transferred *Cliona pupurea* to this genus.

### *Cliona quadrata* Hancock
Fig. 3g, h

*Cliona quadrata* Hancock, 1849:344, pl. XV, fig. 6.

*Material examined.*—2 slides (acid cleaned); A.H. no. 20, both dated 1858.

*Syntypes.*—4.16.26, 4.16.27.

*Type locality.*—Not stated (substrate: "*Tridacna gigas*").

*Spicules.*—(a) Tylostyles, fusiform, with round head well set off from the shaft, 380 × 25 μm (A.H.: 363 μm). (b) Amphiasters, most with 5–7 rays delicately branched at the ends, 25 μm in total length.

*Remarks.*—Several authors misinterpreted this species because no microscleres were known (Vosmaer 1933:345, 356, 382, 383). This reexamination, revealing the characteristic amphiasters, places *Cliona quadrata* clearly into the genus *Cliothosa* Topsent.

### *Cliona radiata* Hancock
Fig. 2g, h

*Cliona radiata* Hancock, 1849:334, pl. XV, fig. 3.

*Material examined.*—2 slides (acid cleaned); A.H. no. 6.

*Syntypes.*—4.16.28, 4.16.29.

*Type locality.*—Not stated (substrate: "*Triton variegatus*").

*Spicule.*—(a) Tylostyles, consistently with subterminal heads, 290 × 8 μm (A.H.: 289 μm). (b) Raphids, ca. 100 μm in length (mostly broken).

*Remarks.*—Raphids were not noted in the original description. This species is generally considered a synonym of *Cliona celata* Grant (Vosmaer 1933:361, 362).

### *Cliona rhombea* Hancock
Fig. 4e, f

*Cliona rhombea* Hancock, 1849:342, pl. XII, fig. 7.

*Material examined.*—2 slides (acid cleaned); A.H. no. 27, one dated 1858, the other undated.

*Syntypes.*—4.16.30, 4.16.31.

*Type locality.*—Not stated (substrate: "*Tridacna gigas*").

*Spicules.*—(a) Tylostyles, straight, with rounded heads, 300 × 7 μm (A.H.: 292). (b) Oxea, microspined, bent in the center, 130 × 5 μm (A.H.: 146 μm). (c) Microrhabds, microspined, spindle shaped, straight or slightly curved, 12 × 2 μm.

*Remarks.*—The microrhabds were not noted in the original description. Vosmaer (1933:411), suspecting this oversight, synonymized the species with *Cliona vastifica* Hancock.

### *Cliona spinosa* Hancock
Fig. 4g, h

*Cliona spinosa* Hancock, 1849:339, pl. XIII, figs. 5–7.

*Material examined.*—4 slides (acid cleaned), all labelled as [A.H.] no. 10 and dated 1858; one "from *Perna*" (4.16.32) was used for the original figures (Hancock 1849: 339).

*Syntypes.*—4.16.32–4.16.35.

*Type locality.*—Not stated (substrates: "*Perna femoralis*" and "*Placuna sella*").

*Spicules.*—(a) Tylostyles, straight, with round heads, 290 × 5 μm (A.H.: 292 μm). (b) Oxea, microspined, bent in the center, 120 × 5 μm (A.H.: 97 μm). (c) Microrhabds, microspined, 17 × 2 μm.

*Remarks.*—The microrhabds were not described originally. Again, Vosmaer (1933: 411) concluded that they were overlooked and synonymized *Cliona spinosa* with *C. vastifica* Hancock.

### *Cliona vastifica* Hancock
Fig. 6c, d

*Cliona vastifica* Hancock, 1849:342, pl. XV, fig. 2; 1867:237, pl. VII, fig. 2.

*Material examined.*—4 slides (acid cleaned tissue squash, as well as spicule spreads), presumably of material teased from a number of different specimens, but certainly all from the same species. All without A.H. nos. and date, labelled in style 2.

*Syntypes.*—4.16.36–4.16.39.

*Type locality.*—Prestonpans?, Firth of Forth, Scotland.

*Spicules.*—(a) Tylostyles, straight with round heads, 300 × 5 μm (A.H.: 292 μm). (b) Oxea, microspined, slightly bent, 100 × 3 μm (A.H.: 97 μm). (c) Microrhabds, microspined, straight spindleshaped, or S- or W-shaped, 12 × 3 μm (A.H.: 12 μm).

*Remarks.*—Though the slides lack date and original number they all agree closely in spiculation and accord well with Hancock's description. This species has been generally accepted as valid (refer to Hartman 1958).

### *Cliona vermifera Hancock*
Fig. 3e, f

*Cliona vermifera* Hancock, 1867:239, pl. VIII, fig. 2.

*Material examined.*—3 slides (acid cleaned); two from "*Chama* no. 2," one from "*Chama* no. 3." All dated 1867, labelled in style 2.

*Syntypes.*—4.16.40–4.16.42.

*Type locality.*—Not stated (substrate: "*Chama*").

*Spicules.*—(a) Tylostyles, robust with mainly subterminal heads, two size classes, 300 × 7.5 μm and 220 × 11 μm (A.H.: 254 μm). (b) Rhabds, smooth, spiralled or undulated, with 3–5 bends and obtuse extremities, 60 × 4 μm (A.H.: 64 μm).

*Remarks.*—Generally considered a good species with constant spicule characteristics.

### *Thoosa* Hancock
### *Thoosa bulbosa* Hancock
Fig. 7a

*Thoosa bulbosa* Hancock, 1849:346, pl. XII, figs. 10 & 11; pl. XIII, fig. 8.

*Material examined.*—10 slides (7 acid cleaned and 3 tissue squashes); A.H. nos. 22a & 22b, and unnumbered from "*Chama*" and "*Tridacna*" (7 dated 1858, labelled style 1; 3 undated, labelled style 2).

*Syntypes.*—4.16.43–4.16.48, 4.17.01–4.17.04.

*Type locality.*—Not stated (substrates: "*Tridacna gigas,*" mentioned in description, and "*Chama,*" noted on some labels).

*Spicules.*—All slides have at least the amphiasters in common. (a) Amphiasters of six-rayed type, with 14 microspined nodules, 25 × 17 μm. (b) Oxyasters, smooth or microspined, reduced to biradiate ("bird wings"), triradiate, or tetraradiate forms; ray dimensions 70 × 2.5 μm (A.H.: 86 μm). (c) Oxyasters (can be rare or absent), microspined, with lanceolate ray tips; ray dimensions 25 × 2 μm. (d) Oxeas, centrotyle (150 × 2.5 μm) or regular (200 × 8 μm); not necessarily proper to the species.

*Remarks.*—Topsent (1888:81) and Volz (1939:30) both commented on the great variety of spicules encountered in sponges of this genus.

### *Thoosa cactoides* Hancock
Fig. 7b

*Thoosa cactoides* Hancock, 1849:345, pl. XIII, figs. 1 & 2.

*Material examined.*—2 slides (acid cleaned) from one specimen; without A.H. no., dated 1858.

*Holotype* (by monotypy).—4.17.05, 4.17.06.

*Type locality.*—Not stated (substrate: "*Meleagrina margaritifera*").

*Spicules.*—Amphiasters are the only preserved type; they are smaller and stouter than in the previous species, 23 × 15 $\mu$m (A.H.: 145 × 109 $\mu$m).

Remarks.—Hancock's spicule measurements ("1/175th of an inch long and 1/234th of an inch broad") are obviously in error. This species is the type of the genus. It is regrettable that no other spicule types were described or preserved but the amphiasters.

## Conclusions

Examination of the Hancock material sheds considerable new light on spicule details preserved in this pioneering collection but, unfortunately, it does not solve species problems in clionid sponges. We should, however, highlight some of our findings to provide basic information for those who might plan experimental ecological work involving this group.

Species containing tylostyles only are particularly difficult to interpret. Traditionally, but in many cases without justification, these have been synonymized with *Cliona celata* Grant. They include *Cliona alderi, C. angulata, C. globulifera, C. gorgonioides, C. insidiosa, C. millepunctata,* and *C. radiata.* The latter species seems to contain raphids in addition to tylostyles, a characteristic not unusual for some populations of bona fide *C. celata* (Volz 1939) but also confirmed for another species, *C. amplicavata* Rützler (1974).

Tylostyles accompanied by spiny rhabds or spirasters are found in *Cliona howsei* and *C. lobata.* Tylostyles are very similar in both but spiny rhabds are shorter and rather straight in the former, longer and undulating in the latter. Tylostyles and smooth wavy rhabds are present in *C. vermifera,* one of the few species almost never doubted in the literature. Tylostyles joined by amphiasters are characteristic of *C. quadrata* and allows us to transfer this species to the genus *Cliothosa.* Finally, knobby amphiasters without the company of tylostyles (albeit presence of several other spicule types) confirm the validity of the curious genus *Thoosa,* with species *T. bulbosa* and *T. cactoides,* most likely distinct from each other.

By far the largest species complex in the collections is represented by specimens containing three spicule types: tylostyles, microspined oxeas, and microspined microrhabds. Hancock described 14 species with this spicule combination although he recognized the microrhabds in only six. Subsequent authors maintained only two of these species as valid, *Cliona carpenteri* with straight fusiform microrhabds, and *C. vastifica* with angulated microrhabds; all other species were placed in synonymy with *C. vastifica.*

If one examines the spicules of species in the *Cliona vastifica* complex one finds great variability among all types but very little correlation between characters, such as relative sizes, position of swelling on the tylostyles, and spination and shape of oxea and microrhabds. Using spicule characteristics alone one can group the following: (1) *C. carpenteri, C. dendritica, C. rhombea,* and *C. spinosa* (straight spindle-shaped microrhabds); species described much later, such as *C. robusta* Old (1941:9), *C. truitti* Old (1941:10), and *C. lampa* Laubenfels (1950:110) could be adjoined here. (2) *C. corallinoides, C. gracilis, C. northumbrica,* and *C. fryeri* (with zigzagged microrhabds of commonly 3–5 bends); *C. spirilla* Old (1941:10) belongs here as well. (3) *C. mazatlanensis* and *C. vastifica* (with angulated microrhabds of 2–3 bends). (4) *C. canadensis* and *C. muscoides* (with centrotyl microrhabds, centrotyl oxea, and tylostyles with multiple swellings); *C. robusta* Old (1941: 9) also fits this group. (5) *C. cervina* (with two size classes of microrhabds and coarse tuberculation—microspine clusters—on both microrhabds and oxea).

Unfortunately, many transitions in size and shape of spicules are present and no

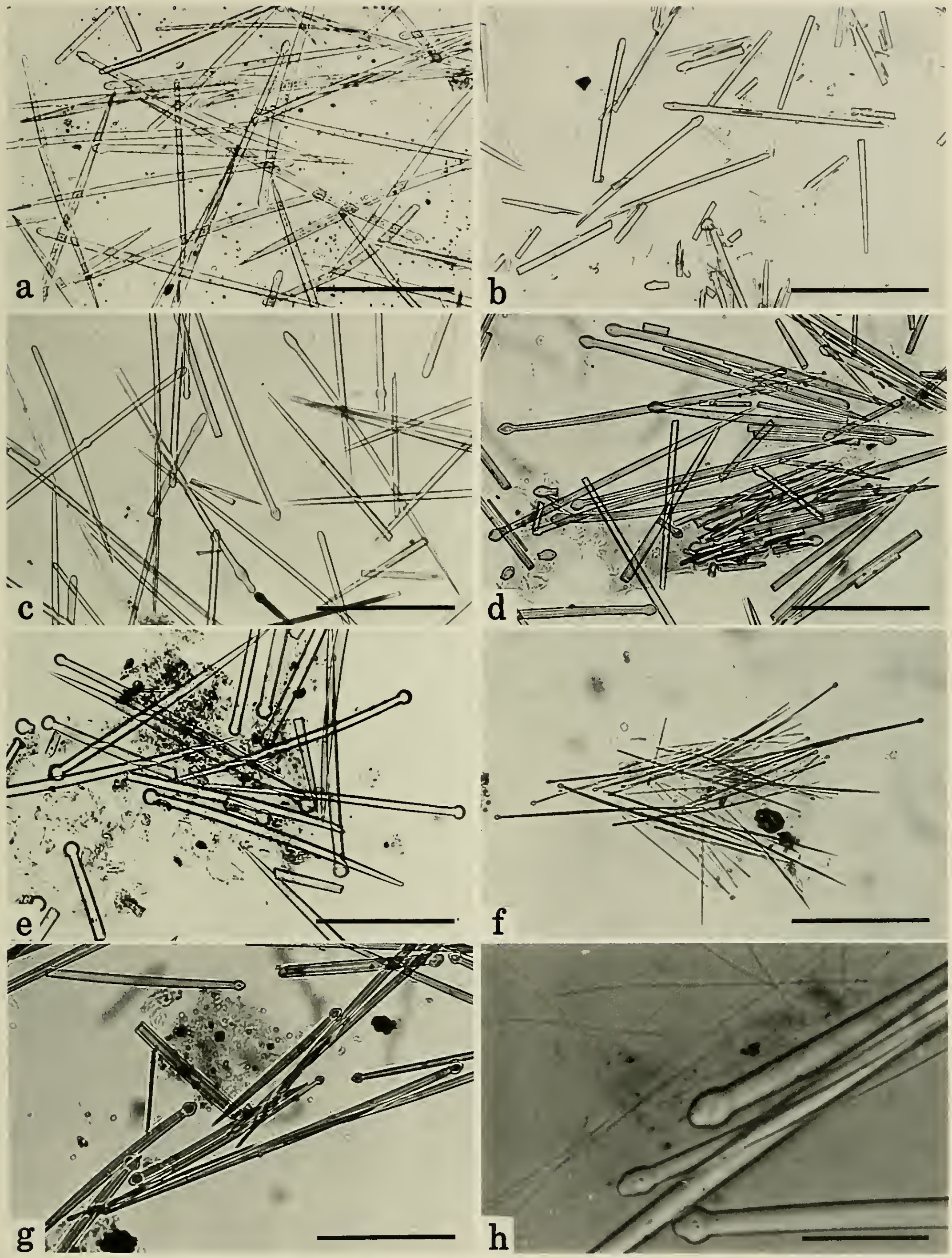

Fig. 2. Photomicrographs of spicules: a, *Cliona alderi,* tylostyles; b, *C. angulata,* tylostyles; c, *C. globulifera,* tylostyles; d, *C. gorgonioides,* tylostyles; e, *C. insidiosa,* tylostyles; f, *C. millepunctata,* tylostyles; g, *C. radiata,* tylostyles; h, *C. radiata,* tylostyle heads and raphides. Scales: a–g, 100 μm; h, 25 μm.

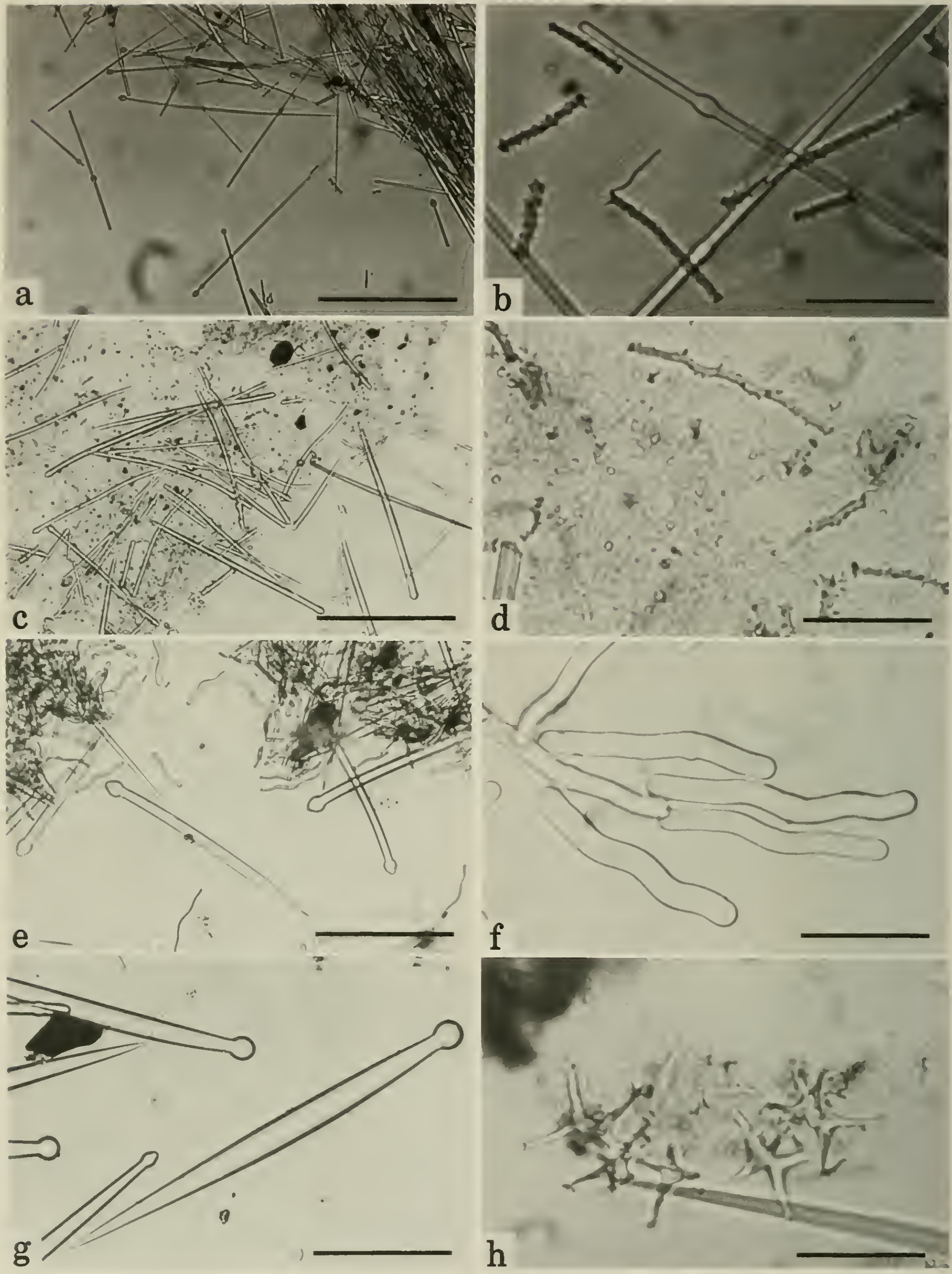

Fig. 3. Photomicrographs of spicules: a, *Cliona howsei*, tylostyles; b, *C. howsei*, spined microrhabds; c, *C. lobata*, tylostyles; d, *C. lobata*, spiny microrhabds; e, *C. vermifera*, tylostyles; f, *C. vermifera*, smooth spiralled rhabds; g, *C.* (=*Cliothosa*) *quadrata*, tylostyles; h, *C.* (=*Cliothosa*) *quadrata*, amphiasters. Scales: a, c, e, g, 100 μm; b, d, f, h, 25 μm.

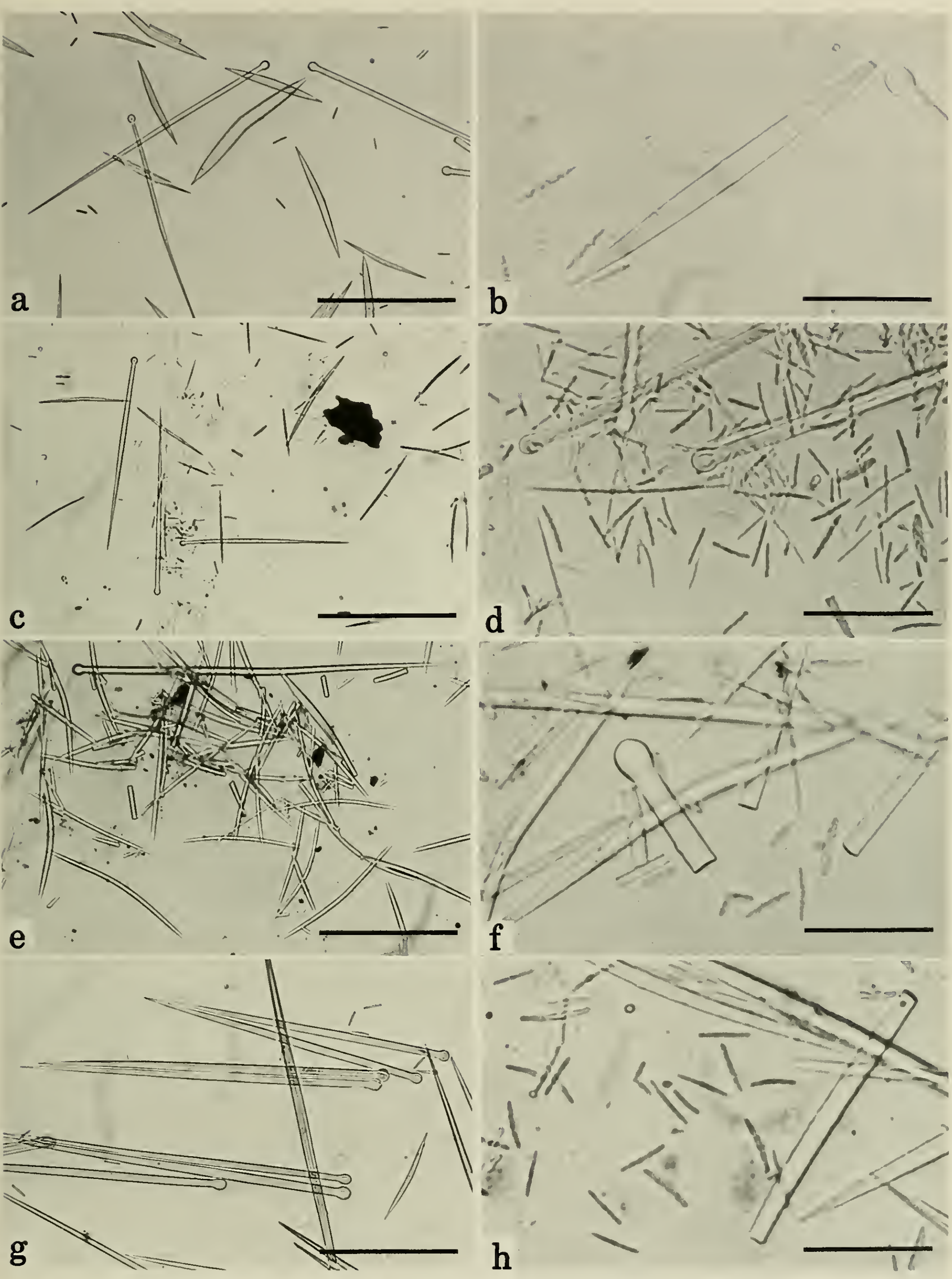

Fig. 4. Photomicrographs of spicules: a, *Cliona carpenteri,* tylostyles and microscleres; b, *C. carpenteri,* microspined oxea and microrhabds; c, *C. dendritica,* tylostyles and microscleres; d, *C. dendritica,* tylostyle heads, microspined oxeas and microrhabds; e, *C. rhombea,* tylostyle and microscleres; f, *C. rhombea,* tylostyle head, microspined oxeas, and microrhabds; g, *C. spinosa,* tylostyles and microscleres; h, *C. spinosa,* microspined oxeas and microrhabds. Scales: a, c, e, g, 100 μm; b, d, f, h, 25 μm.

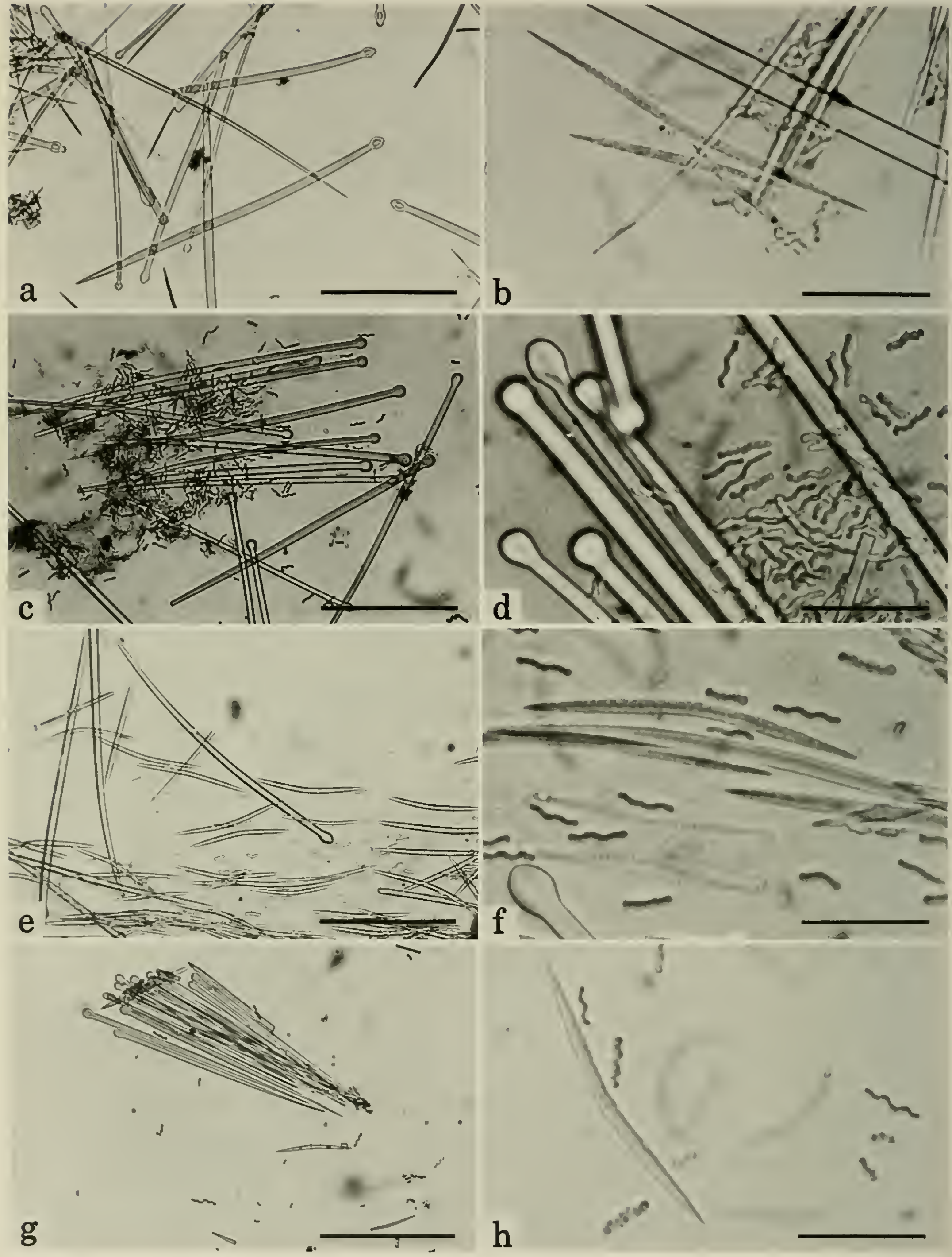

Fig. 5. Photomicrographs of spicules: a, *Cliona corallinoides,* tylostyles; b, *C. corallinoides,* microspined oxeas and microrhabds; c, *C. gracilis,* tylostyles and microscleres; d, *C. gracilis,* tylostyle heads and microspined microrhabds; e, *C. northumbrica,* tylostyles and microscleres; f, *C. northumbrica,* microspined oxeas and microrhabds; g, *C. fryeri,* tylostyles and microscleres; h, *C. fryeri,* microspined oxea and microrhabds. Scales: a, c, e, g, 100 μm; b, d, f, h, 25 μm.

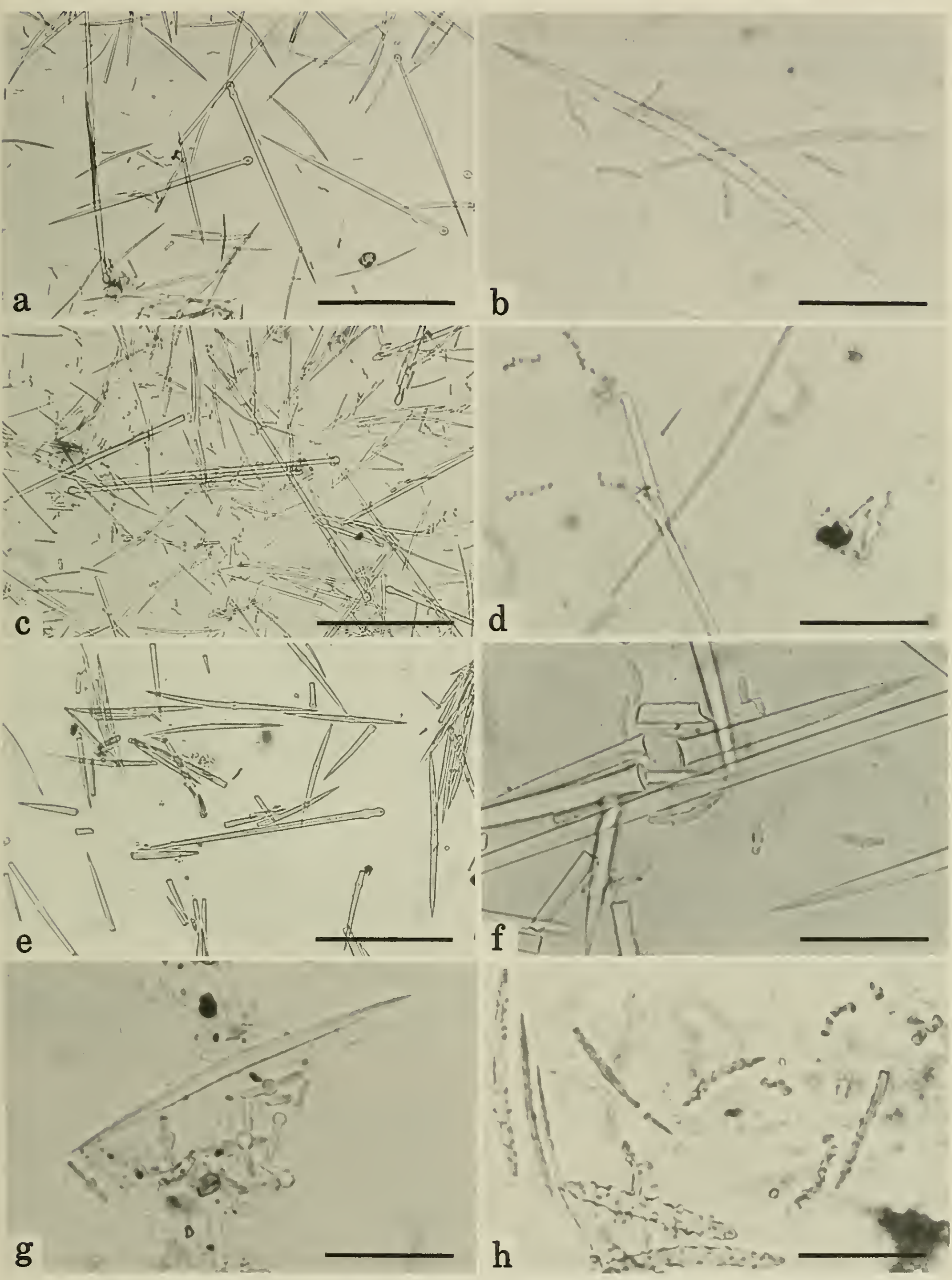

Fig. 6. Photomicrographs of spicules: a, *Cliona mazatlanensis,* tylostyles and microscleres; b, *C. mazatlanensis,* microspined oxeas and microrhabds; c, *C. vastifica,* tylostyles and microscleres; d, *C. vastifica,* microspined oxeas and microrhabds; e, *C. canadensis,* tylostyles and microscleres; f, *C. canadensis,* microspined oxeas and microrhabds; g, *C. muscoides,* microspined oxea and centrotylote microrhabds; h, *C. cervina,* tuberculated oxea and microrhabds bearing microspine clusters. Scales: a, c, e, 100 μm; b, d, f–h, 25 μm.

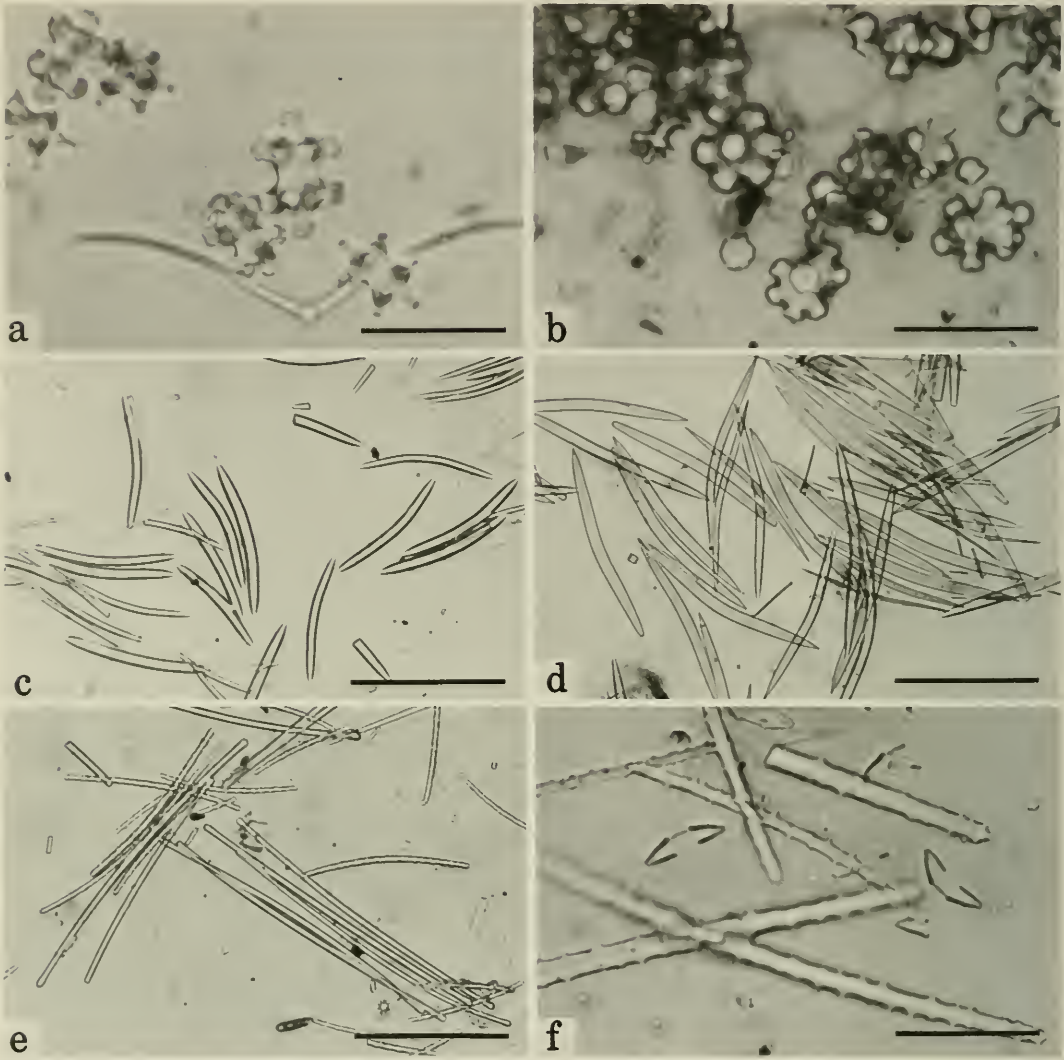

Fig. 7. Photomicrographs of spicules: a, *Thoosa bulbosa,* amphiasters and reduced oxyaster ("bird wing"); b, *T. cactoides,* amphiasters; c, *Cliona* (=*Aka*) *labyrinthica,* oxeas; d, *C.* (=*Aka*) *nodosa,* oxea; e, *C.* (=*Paracornulum*) *purpurea,* tylotes and acanthotornotes; f, *C.* (=*Paracornulum*) *purpurea,* acanthotornotes and palmate isocheles. Scales: a, b, f, 25 μm; c, d, e, 100 μm.

final conclusions can be drawn without study of fresh and complete material, entire populations, and knowledge of environmental parameters. Topsent (1932:558) already had evidence that environmental conditions, such as salinity, can modify the spiculation of *Cliona vastifica.* Availability of dissolved silicic acid is another important factor known to influence spicule shape and size (Simpson 1981). On the other hand, populations of *Cliona lampa* (group (1), above) studied in Bermuda (Rützler 1974) display very stable spicule characteristics but turn out to represent two distinct species distinguishable by color, spicule size, and growth habit, as confirmed by long term observations and field experiments (Rützler, in prep.).

Excavating sponges described by Hancock but not belonging to the *Clionidae* are

*Cliona labyrinthica* and *C. pupurea.* The former, transferred to *Aka,* is now viewed by us as a member of the Oceanapiidae (Haplosclerida), and the latter, transferred to *Paracornulum,* may belong to the Coelosphaeridae (Poecilosclerida).

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# NEWLY ESTABLISHED FAMILIES OF THE ORDER BRANCHIOBDELLIDA (ANNELIDA: CLITELLATA) WITH A SYNOPSIS OF THE GENERA

Perry C. Holt

*Abstract.*—General remarks and a brief survey of the branchiobdellid literature are followed by a review of the group's taxonomic characters, methods of study and speculations as to its origins. A key to newly recognized families and eighteen genera is given. The order is divided into five families: Branchiobdellidae, Bdellodrilidae, Xironodrilidae, Caridinophilidae, Cambarincolidae. A synopsis of the genera is included with the familial diagnoses.

The annelid worms of the order Branchiobdellida are currently attracting a modest degree of attention. Since 1950, nine of the eighteen genera and more than eighty of their 132 included species have been diagnosed. The opinion once held that the branchiobdellidans are a homogeneous group (Stephenson 1930:796) has long since been abandoned; their former association with either the Hirudinea or Oligochaeta has been dissolved (Holt 1965b).

This proliferation of taxa and the recognition of the structural diversity expressed thereby now make it appropriate to segregate the genera of this previously monotypic order into families and to present a synopsis of the included genera. A brief summary of branchiobdellidan natural history will be followed by a review of selected literature devoted to them, a consideration of the methods and anatomical characters that have been used in taxonomic studies of them and a discussion of the group's origin and distribution. This introduction is followed by keys to the families and genera and diagnoses of these taxa with illustrations, literature citations, number of included species and geographical range. It is to be emphasized that these efforts should be considered as provisional and transitional in nature: probably much less than half of the world fauna of the worms is known.

The branchiobdellidans are obligate symbionts of Holarctic (with limited excursions into the borders of the Neotropical and Oriental regions in Central America and China) freshwater crustaceans (crayfish, crabs, shrimps and isopods) that move in a leech-like fashion over the bodies of their hosts and feed on a variety of substances: the host's blood, eggs and (?) young, other external symbionts and, most often, the bacterial and algal gloea that often covers the host's body. Among those found on astacoidean crayfishes, different species tend to occur on different regions of the host animal and their feeding habits may reflect their occupancy of these microhabitats.

Nearly all astacoideans carry these symbionts. Although there is no known species-to-species host specificity, some branchiobdellidans, e.g., the isopod egg-eating *Cambarincola aliena* Holt, 1963, may be restricted to a single species of host because of such feeding adaptations. Branchiobdellidans have been rather diffidently reported as living away from any host (Holt 1973a: 152–159), but there is no record of them depositing cocoons except on the host's body. The first report of branchiobdellidans from other than astacoidean hosts (Hobbs and Villalobos 1958) was followed by the additions of several such instances: freshwater crabs in Central America, Mexico and

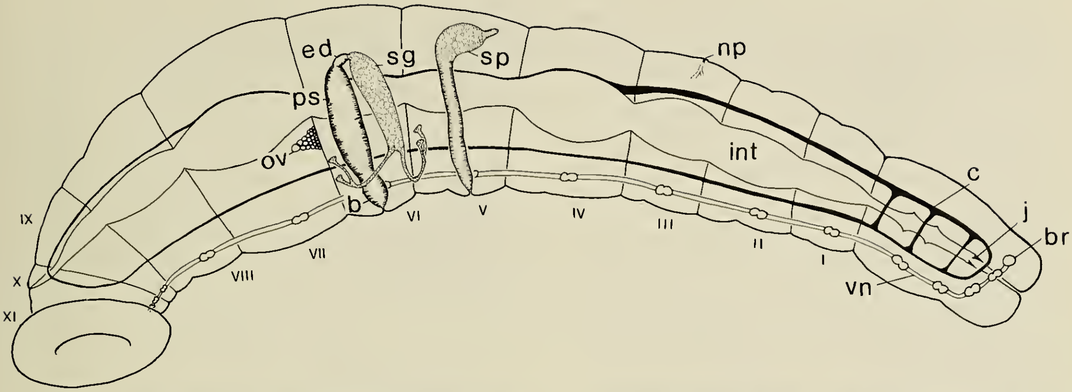

Fig. 1. Generalized branchiobdellid. Abbreviations: I–XI, trunk segments; b, bursa; br, brain; c, circulatory system; ed, ejaculatory duct; int, intestine; j, jaws; np, nephridiopore; ov, ovary; ps, penial sheath; sg, spermiducal gland; sp, spermatheca; vn, ventral nerve cord (from Holt 1969).

Louisiana; troglobitic isopods from Tennessee and Mexico; pseudothelphusid crabs from Central America and Mexico; freshwater shrimps from China. These instances seem to be from unusual habitats (caves) or from regions at the periphery, or beyond (Nicaragua and Costa Rica), of the range of the usual hosts. Little is known of other aspects of the life history, ecology, and physiology of these worms. Some studies of their natural history are marred by improper or inadequate taxonomic determinations.

The taxonomy of the group is incomplete and in some ways unsatisfactory simply because a large proportion of the branchiobdellidan fauna is undescribed: many new forms are known to await diagnosis in the collections of the National Museum of Natural History of the Smithsonian Institution.

*A brief history of studies of the branchiobdellidans.*—Only the major taxonomic works are considered herein; other references may be found in them.

In Europe, the number of nominal species of the genus *Branchiobdella* Odier, 1823, had reached forty-three when Pop (1965) reduced it to four species, one with three subspecies. This is almost surely an extreme example of "lumping," but there are probably only a few species of branchiobdellidans in Europe.

The Japanese and Korean branchiobdellidan fauna was studied by Yamaguchi (1934). A few species have been recognized by Chinese workers (Liang 1963; Liu 1964, 1984; Liu and Chang 1964; Liu and Zhang 1983). The Asiatic fauna, as now known, consists of 32 species assigned to six genera (two of these genera are new ones to be proposed by Gelder and Liu (pers. comm.) and one is the North American genus *Cambarincola* represented by the introduced *C. okadai* Yamaguchi, 1933).

The principal homeland of the branchiobdellidans is North America. Important early contributions to a knowledge of these worms were made by Moore (1895b) in his anatomical study of *Bdellodrilus illuminatus,* which has served as a model for all subsequent such studies, and the recognition of new forms (Moore 1894, 1895a). Ellis (1912, 1918, 1919) diagnosed the genera *Cambarincola* (1912), *Xironodrilus* (1918), and *Xironogiton* (1919) and recognized a total of seven new species in these and other genera. Hall (1914) raised the family Branchiobdellidae to the status of a superfamily and erected the genus *Ceratodrilus.* Goodnight (1940) assembled these works and others, divided the Branchiobdellidae into two subfamilies and added some generic diagnoses and species descrip-

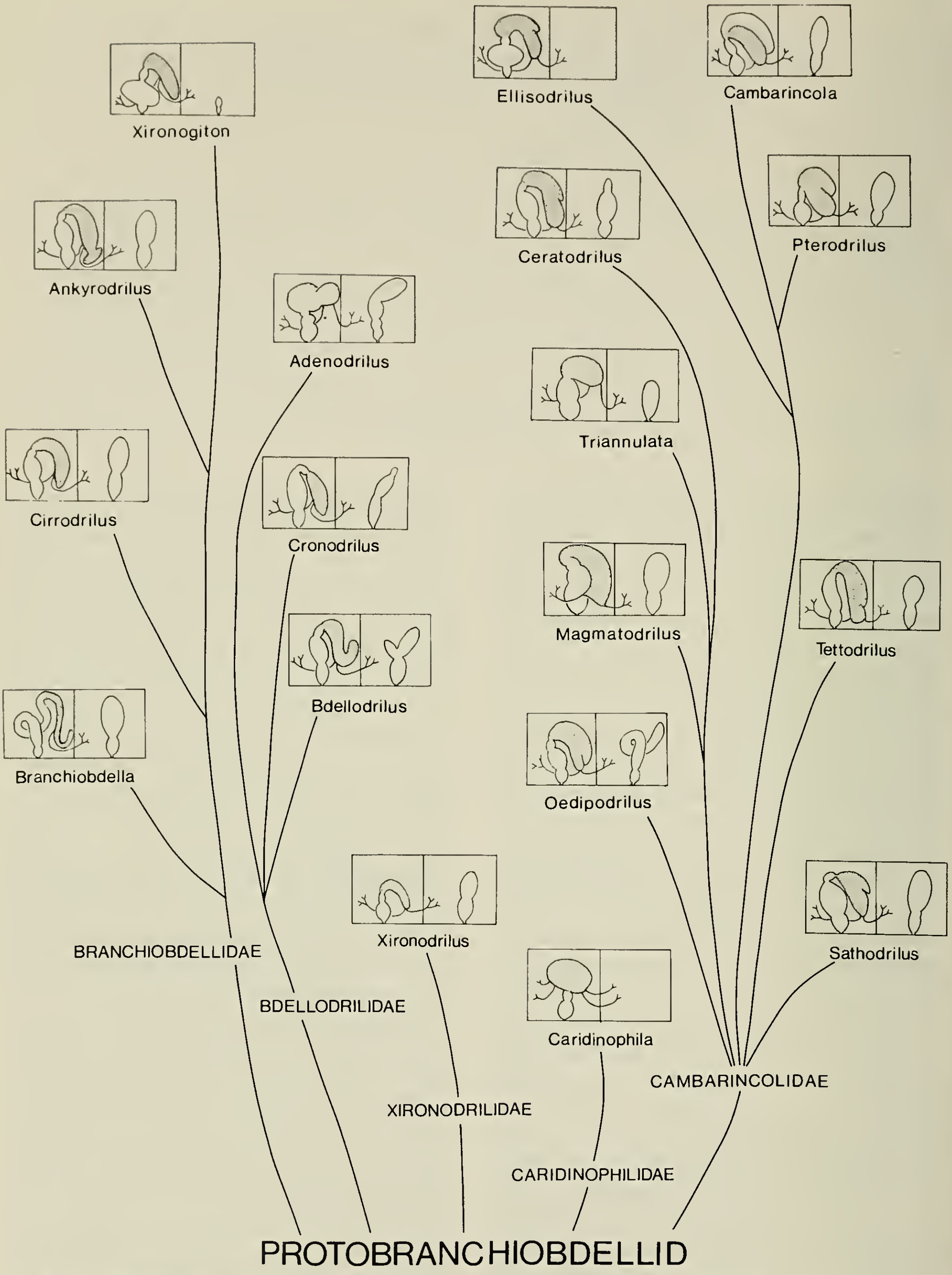

Fig. 2. Suggested relationships of the genera and families of the order Branchiobdellida.

tions. Hoffman (1963) treated 21 species, 12 of them new, in his monograph of the genus *Cambarincola* which also contains important reflections on taxonomic characters. Holt (1949) demonstrated the importance of the reproductive systems as a source of taxonomically important characters. Since then, he has described 55 new species and erected eight new genera (Holt 1960b, 1965a, 1967a, b, 1968b, 1977b) and published monographs of the genera *Pterodrilus* (Holt 1968c) and *Xironogiton* (Holt 1974b). The argument for raising the family Branchiobdellidae to ordinal rank (Holt 1965b) was followed by a review that is semipopular in style (1968a) and zoogeographic treatments (Hobbs et al. 1967, Holt 1969), among other studies.

*Methods of collection, preservation and preparation for study.*—An inhibiting factor in the study of the branchiobdellidans is the difficulty of doing anatomical studies of them. The worms range from about one to six millimeters in length (when contracted) and are opaque unless special methods are used. The preparation of serial sections is often hampered by the presence of diatoms in the gut, but it is essential that beginning students familiarize themselves with the basic anatomy of the animals by studies of such sections and of dissections. The preparation of stained whole mounts of the animals requires live specimens to be relaxed (? with 1–5% magnesium chloride), fixed and stained. The more usual method is to dehydrate specimens in ethanol, clear in clove oil and mount unstained in Canada balsam. Microscopic study of specimens so treated requires the use of an objective for the microscope that is adjusted to an unusually long working distance (approximately 1.5 mm) that enables the student to see through the total thickness of the worm or to turn over the slide on which it is mounted in order to view it from both sides.

Another nuisance occurs because much of the material presented to the student has been taken from the sediment at the bottom of jars in which crayfish have been collected. The students of crayfish usually preserve their animals in 70% ethanol and jam all the crayfish they can find into a collecting jar. The result is rotten worms often totally useless for serious study. For the best results, using the method described above, the branchiobdellidans should be preserved in 5% formalin in 70% ethanol and the collecting jars should not be overcrowded.

*Taxonomic characters.*—The students of the branchiobdellidans have used a number of features as taxonomic characters. To evaluate these usages a brief description of a generalized branchiobdellidan (Fig. 1) is required. The body consists of 15 segments of which four constitute a head and the remainder a trunk with a terminal sucker. Only the post-cephalic body segments have traditionally been numbered.

The prostomium is absent and the first cephalic segment, the peristomium, is usually divided into upper and lower lips which may be further subdivided into lobes; occasionally lateral lobes are present. The upper lip in some forms may be furnished with digitate projections or tentacles. The body segments are indicated externally by intersegmental furrows and are usually subdivided by a circular groove which produces a secondary annulus. The anterior annulus of some segments in some species is greater in diameter than the secondary annulus: there are "dorsal ridges." The dorsal ridges may carry fan-like or finger-like projections. The greater diameter of the anterior annuli in these cases is produced by the insertion of slips of the longitudinal segmental muscles into the outer body wall posterior to the intersegmental furrows and into the secondary furrow that delimits the posterior, secondary annulus, or sometimes in front of this furrow (Holt 1960b:fig. 7). The body outline is said to be smooth if the dorsal ridges are absent. The anterior nephridia open on segment III through two dorsolateral pores or by a median dorsal pore. The anus opens dorsally on what apparently is always segment X. The posterior sucker (the peristomium forms an anterior one) is formed from the eleventh segment with, apparently, in some cases portions of segment X included. Both suckers are aided in their function by glandular secretions (Weigl 1980). Three otherwise dissimilar genera are characterized by a dorsoventral flattening of some of the mid-body segments.

The nervous and circulatory systems are annelidan, apparently invariant, and rarely mentioned in taxonomic works. The digestive system likewise presents few features of taxonomic interest: the gut is expanded much more noticeably in some segments of dorsoventrally flattened forms, the pharynx has one or more expansions (pharyngeal sulci); and all branchiobdellidans possess, dorsally and ventrally, pharyngeal placoids (jaws) that normally bear teeth and that vary in shape, size and number of teeth. Oral papillae, thought to be sensory in function, surround the mouth opening in several forms. However, it is possible that these small structures are present in most branchiobdellidans and because of their size have been simply overlooked in the descriptions of many species.

There are two pairs of nephridia. An anterior pair lies asymmetrically alongside the gut in segments I–IV, and discharges to the exterior on segment III. Variation in the position of anterior nephridia may exist among members of a species or between species (Moore 1897:329–330), but this possibility has not been further investigated. The posterior pair lie, one on each side, in segment VIII (Moore 1897:332) and open on the anterior lateral surface of segment IX (Freeman 1963).

The female reproductive system consists of paired ovaries, placed laterally on the posterior face of septum 6/7 and a spermatheca in segment V. There are no oviducts; eggs are expelled through a pair of ventrolateral pores in the body wall of segment VII. The spermatheca opens by a median pore on the venter of segment V and is a blindly ending sac that may be variously modified along its length. The epidermis of segments VI and VII is provided with glands forming a mucus-secreting clitellum.

The male system is more complex. Two pairs of testes located on the posterior faces of septa 4/5 and 5/6 break up at maturity into morulae that release spermatozoa into the body cavity. Paired male funnels in the posteroventral quadrats of the testicular segments open into thin ducts, the vasa efferentia, that unite to form vasa deferentia. The latter fuse to form a glandular organ, the spermiducal gland, which may have a diverticulum of greater or lesser distinctiveness, the prostate. In most forms a muscular tube joins the spermiducal gland to the penial sheath, the ental part of the bursa, which encloses the penis. The latter projects into a cavity, the bursal atrium, which opens mid-ventrally on segment VI. The penis takes several forms: in some genera it is eversible, consisting of a cuticular tube with or without hooks and with or without strands (presumably muscular) that attach it to the inner wall of the penial sheath. In other forms it is clearly muscular and is protruded by the eversion of the wall of the atrium as a cone-shaped mass. In some species this mass is narrowed and similar in composition and apparent eversibility to those of species in which a clearly eversible penis has strands connecting it to the inner wall of the penial sheath (Holt 1982:254–255).

There are numerous permutations of the elements of the reproductive systems, of the variations of the jaws and their teeth and of the features of the body surface. Most of the variations in structure shown by the branchiobdellidans are stable and discontinuous and no instance is now known with certainty of North American species that gradually vary in space. Consequently no subspecies of these have been recognized (but cf. *Cambarincola osceolai* Hoffman, 1963:331).

Some variations in body form are obvious adaptations to a particular way of life, but nothing can be said about the significance of most of the differences in structures that are used in the taxonomy of the group.

Members of a genus usually present a common facies, although interspecies differences are common in some external features (for example, the presence or absence of peristomial tentacles or dorsal ridges which occur within the confines of a single genus). Two of the three dorsoventrally flattened genera and several terete ones cannot be separated on the basis of external appearance and recourse must be had to features of the male reproductive system to do so. The same is true of the jaws: although members of a genus share a basic plan of jaw structure, one type of jaw may be shared by several genera. The number of anterior nephridiopores (one or two) are of necessity shared by several genera. Supraspecific taxa must, perforce, be based on modifications of the male reproductive system.

There have been other discussions of taxonomic characters used in studies of the branchiobdellidans (Hoffman 1963; Holt 1953, 1960a, 1965a, 1968a, b, 1973c; Holt and Hoffman 1959, inter alia) and suppositions expressed as to "primitive" as opposed to "advanced" characters (cf. Holt 1973c:3). These efforts, however, have been directed to features diagnostic of both genera and species. Herein attention will be directed to features that characterize genera and suprageneric taxa and many features used in the diagnosis of species ignored. Their usage may be derived from the taxonomic works cited above.

Of the somatic (non-genitalic) characters, only one is important in the present context. (The shape of the jaws has not been carefully considered, though Ellis (1919:241–243) laid the basis for a system utilizing the jaws). The ancestral branchiobdellidans probably were provided with separate openings of the anterior nephridia: five genera are so characterized; the remaining genera have a common opening (one anterior nephridiopore). In all cases, these openings, whether one or two, are obscure pores on the dorsum, or latero-dorsum, of segment III. In two of these five genera the middle segments are dorsoventrally depressed, but there is no reason to believe that there is any phylogenetic relationship between the presence of two anterior nephridiopores and a depressed body form (segment III of all branchiobdellidans is terete).

There is no way of knowing, except by uncertain inferences, the anatomical shapes and relationships of the components of the reproductive systems of the ancestors of the branchiobdellidans. Among living forms, the female system is relatively invariant. The spermatheca may be absent, reduced to vestigialness or "bifid" (having a lateral branch). Otherwise the variations in the presence or absence of an ental bulb, the shape of the spermathecal bulb (the sperm-storing part of the organ) and of the ectal spermathecal duct and bursa are only uncertainly, and in not all cases, associated with groups of species forming genera.

This is not true of the male system. The testes may consist of one or two pairs. The vasa deferentia may enter the spermiducal gland ectad to its inner end or entally and there may or may not be a prostate or rudiment thereof associated with it. The penis is variable in its structure. The composition of its wall ranges from a cuticular tube, with or without hooks, to a dense cone-shaped mass of muscle: the former type is eversible; the latter protrusible.

There are left, then, relatively few features whose states may serve to characterize suprageneric groupings and presumptively "primitive" characters (Holt 1968a:83–84) are found in more than one of any possible groupings of genera. Whether there are one or two nephridiopores; the number of pairs of testes and their location; the nature of the junction of the vasa deferentia with the spermiducal gland; the presence or absence of a prostate associated with the spermi-

Table 1.—Data matrix for some major characters.

| | Caridinophilidae | Cambarincolidae | Xironodrilidae | Bdellodrilidae | Branchiobdellidae |
|---|---|---|---|---|---|
| Spermiducal gland: globose → elongate | globose | elongate | elongate | elongate | elongate |
| Vasa deferentia enter spermiducal gland: terminally → subterminally | — | terminally | terminally | subterminally | subterminally |
| Spermatheca: present → absent | absent | absent-present | present | present | present |
| Mid-body depression: present → absent | absent | absent | present | absent | absent-present |
| Anterior nephridiopores: 2 → 1 | 1 | 1 | 2 | 1 | 2 |
| Prostate: absent → present | absent | absent-present | absent | absent | absent |
| Testes 2 pairs → 1 pair | 2 | 2 | 2 | 2 | 1 or 2 |
| Penis: eversible → protrusible | ? | eversible-protrusible | protrusible | eversible | eversible |

ducal gland and its degree of development; and the composition of the penis and its eversibility or protrusibility seem to be the totality of such characters. One would need to know in detail the phylogenetic history of the members of the order, and there are no clear clues to this history offered by the study of the anatomy of the worms or their present distribution, in order to assert that any of these features are primitive (Table 1).

*Origins and distributions.*—It is probably futile to seek the ancestral stock of the branchiobdellidans among the other clitellates. Stephenson (1930:704–705) regarded them as oligochaetes and derived them from the Lumbriculidae. Holt (1965b) showed that they are not oligochaetes, but said nothing as to their origins. Brinkhurst (in Brinkhurst and Jamieson 1971:169–172, fig. 4.2) argued for the primitive position of the lumbriculids and in his schema of phylogenetic relationships (Brinkhurst and Jamieson 1971:191, fig. 4.4) places the branchiobdellidans next to the former, but otherwise does not mention them. The branchiobdellidans are derived from an ancient stock of the Ur-oligochaetes, possibly quite different from any living form. The problem cries for restudy with the use of modern techniques, including cyto-chemistry and electron microscopy (see Weigl 1980).

Nonetheless, some speculations as to the origins and historical wanderings of the order and its members deserve, if for no other reason than refutation, brief mention.

The distribution of the families and genera of the branchiobdellidans is not congruent with that of the astacoideans (Holt 1968a:85–86). Holt's speculations therein antedate the general acceptance of the geological theories of plate tectonics and may now be regarded as an example of the efforts of earlier historical zoogeographers to explain the distribution of animals. More credible is Hobbs' (1974:2; 1981:52) belief that the unusual distribution of the families of the Astacoidea is the result of separate invasions of freshwaters by different ancestral marine stocks.

But the branchiobdellidans originated in freshwater: no saline-tolerant branchiobdellidans are known.

The uncertainties of the consequences of floating and colliding continental land masses (and fragments, "terranes," thereof) and the utter lack of a fossil record preclude any conclusions as to the times of origin prior to the Cretaceous and the subsequent migrations of the branchiobdellidans. They arose in the nothern regions of Pangaea that today are incorporated into the two Holarctic lands.

The branchiobdellidans are an independent group, evolving in response to a myriad of environmental factors, only a few of which are determined by their means of transport. They were most likely adapted to symbiosis with unknown freshwater animals (? crustaceans) when the various stocks of the astacoideans came in out of the sea. They can, thus, hardly be expected to bear the burden of explaining the evolutionary vagaries of their hosts. This is not to deny that plausible theories correlating the distribution of both worms and hosts that now occupy a common area cannot be devised (Hobbs et al. 1967; Holt 1968c, 1969, 1973c, 1974b, inter alia).

*Problems of classification.*—Any attempt at grouping the genera of the branchiobdellidans into families is not only faced with the usual difficulties of such efforts, but is complicated by an unusual number of apparent convergences. Two such cases are of particular relevance: the penis appears to have evolved from a cuticular eversible tube into a muscular organ that may be either eversible or protrusible in more than one lineage or the opposite; the prostate is of variable development or absent in what otherwise are clearly related groups. These inconsistencies defy all attempts at organization. Two salient features of members of the order are used to derive the arrangement which follows: the number of anterior nephridiopores and the points of entry of the vasa deferentia into the spermiducal gland. The problem of the variations in the structure of the penis and the apparent convergencies presented by these differences may well be solved by more careful studies of the nature of the muscular penes in several genera. (The problem has received little attention and has only recently been broached by Holt (1978a:479; 1982:254).) And the muscular penes of such genera as *Ankyrodrilus* Holt, 1965; *Xironogiton* Ellis, 1919; and *Adenodrilus* Holt, 1977, among others, are different from and may not be homologous with those of the much better known ones of *Cambarincola* Ellis, 1912. If this should prove to be the case, the arrangement presented herein is basically sound (Fig. 2).

One other unrelated difficulty exists: Liu and Zhang (1983) described a Chinese species that they assigned to *Branchiobdella* as *B. heterorchis* with only one pair of testes in segment VI. If there is only one pair of testes in this segment in this species it possibly should be placed in a separate family. Stuart R. Gelder and Liu Si-Cheng (pers. comm.) are considering this in a forthcoming review of east Asian branchiobdellidans. The species will not be further referred to herein. But it is conceivable that work yet to come on the Eurasian fauna will justify the creation of suborders on the basis of the number and location of pairs of testes. For now the characters discussed herein do not clearly require this, though neither do they negate such a classification.

The following, then, is proposed as a suprageneric classification of the branchiobdellidans.

Class Clitellata

Order Branchiobdellida
Family Branchiobdellidae
Bdellodrilidae
Xironodrilidae
Caridinophilidae
Cambarincolidae

## Key to the Families and Genera of the Order Branchiobdellida Holt

A key to the then known branchiobdellidan genera of North America was provided by Holt (1978b:292–295) for Pennak's (1978) *Freshwater Invertebrates of the*

*United States,* but no comprehensive one for all the genera of the order has been published since Goodnight's (1940:28–30) now outdated one. The one presented below is followed by familial and generic synonymies, diagnoses, location of types, ranges, number of species and literature references.

1. Vasa efferentia enter spermiducal gland separately; no vasa deferentia; spermiducal gland globose. Family Caridinophilidae ............................. *Caridinophila*
– Vasa efferentia unite to form vasa deferentia; spermiducal gland elongate ...................... 2
2. (1) Vasa deferentia enter ental end of spermiducal gland ........... 3
– Vasa deferentia enter ectad to ental end of spermiducal gland ....... 12
3. (2) Some body segments flattened; two anterior nephridiopores. Family Xironodrilidae ..... *Xironodrilus*
– Terete; one anterior nephridiopore. Family Cambarincolidae .. 4
4. (3) Penis eversible cuticular tube ...................... *Oedipodrilus*
– Penis ectally a muscular epithelial tube, or connected by strands to inner wall of penial sheath, or densely muscular .............. 5
5. (4) Ectal end of penis cellular epithelial tube enclosing eversible cuticular tube; prostate arises entad to junction of spermiducal gland and ejaculatory duct ............................ *Tettodrilus*
– Penis variously muscular ....... 6
6. (5) Penis eversible, connected to inner wall of penial sheath by strands ...................... 7
– Penis densely muscular ........ 8
7. (6) Body ornamented with peristomial tentacles and dorsal projections ................. *Ceratodrilus*
– Both without tentacles or dorsal projections ............ *Sathodrilus*
8. (6) Spermiducal gland without a prostate ...................... 9
– Prostate or prostatic rudiment associated with spermiducal gland 10
9. (8) Penis composed of muscular, eversible ejaculatory duct ............................ *Triannulata*
– Bursa long, muscular; retracted penis short, eversible; spermiducal gland long, slender .. *Magmatodrilus*
10. (8) Spermatheca absent; penis composed of atrial fold. .*Ellisodrilus*
– Spermatheca present; penis protrusible muscular cone ......... 11
11. (10) Prostate incompletely divided from spermiducal gland .. *Pterodrilus*
– Prostate arises at junction of spermiducal gland and ejaculatory duct ..................... *Cambarincola*
12. (2) One anterior nephridiopore. Family Bdellodrilidae .......... 13
– Two anterior nephridiopores. Family Branchiobdellidae ...... 15
13. (12) Penis cuticular tube lying free in elongated penial sheath ............................ *Cronodrilus*
– Penis muscular ................ 14
14. (13) Penis and penial sheath eversible; ejaculatory duct short, dilated; bursa with pair of glands; spermatheca bifid .......... *Bdellodrilus*
– Penis densely muscular; ejaculatory duct short, with three layers of muscle; no bursal glands; spermatheca without lateral branches ........................ *Adenodrilus*
15. (12) Penis cuticular tube; one pair of testes in segment V ......... .................... *Branchiobdella*
– Penis membraneous or muscular 16
16. (15) Penis membraneous, eversible, attached to inner wall of penial sheath by thin strands ... *Cirrodrilus*
– Penis muscular ................ 17
17. (16) Penial sheath eversible; ejaculatory duct short, ectal tip forming protruded penis; ental end of spermiducal gland bifurcated ....... ....................... *Ankyrodrilus*
– Bursa asymmetrically spherical enclosing protrusible muscular pe-

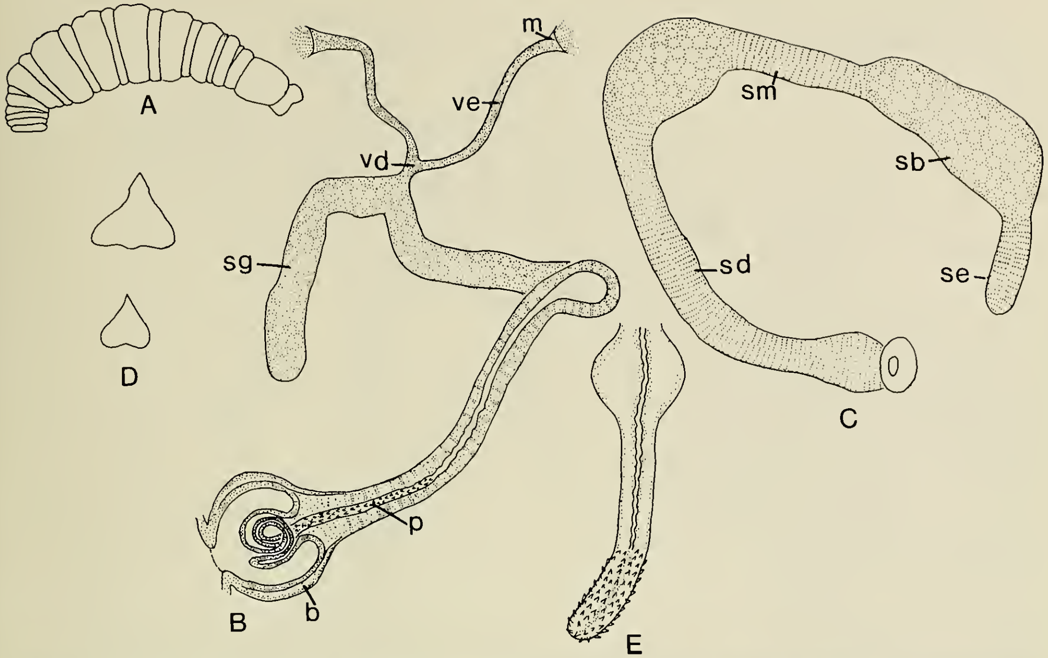

Fig. 3. *Branchiobdella astaci*: A, Lateral view of animal; B, Male efferent apparatus; C, Spermatheca; D, Jaws; E, Tip of everted penis. Abbreviations: b, bursa; m, male funnels; p, penis; sb, spermathecal bulb; sd, ectal duct of spermatheca; se, ental process of spermatheca; sg, spermiducal gland; sm, median duct of spermatheca; ve, vas efferens; vd, vas deferens. (A, B, after Pop 1965:22; C, D, E, after Dorner 1864: plate 37.)

nis; spermatheca vestigial ......
........................ *Xironogiton*

### Order Branchiobdellida

Clitellate annelids with constant number of segments (15); without setae or prostomium; peristomium forming anterior sucker; with posterior sucker; dorsal and ventral pharyngeal dental placoids; body divided into head of 4 segments, trunk of 11; anus dorsal, subterminal; 2 pairs of nephridia, asymmetrical pair in trunk segments I–IV, symmetrical pair in trunk segments VIII–IX; muscles non-syncytial, composed of cells with outer contractile and inner undifferentiated cytoplasm; testes in trunk segments V and VI or one of these segments only; paired male funnels and ducts in each testicular segment; male efferent apparatus opening through single pore on venter of trunk segment VI; a pair of ovaries and ovipores without oviducts and funnels in trunk segment VII; unpaired spermatheca, if present, in trunk segment V; clitellum on trunk segments VI and VII; Holarctic symbionts of freshwater crustaceans (modified from Holt 1965b:30–31).

### Family Branchiobdellidae

Branchiobdellinae Goodnight, 1940:27 (in part).

*Diagnosis.*—Two anterior nephridiopores; vasa deferentia enter spermiducal gland ectad to latter's ental end; no prostate.

### Genus *Branchiobdella*
Fig. 3

*Branchiobdella* Odier, 1823. [Type species, by subsequent designation (Goodnight 1940:28), *Branchiobdella astaci* Odier 1823:75. Gender; feminine.]

*Deposition of type specimens.*—Unknown, presumably never designated.

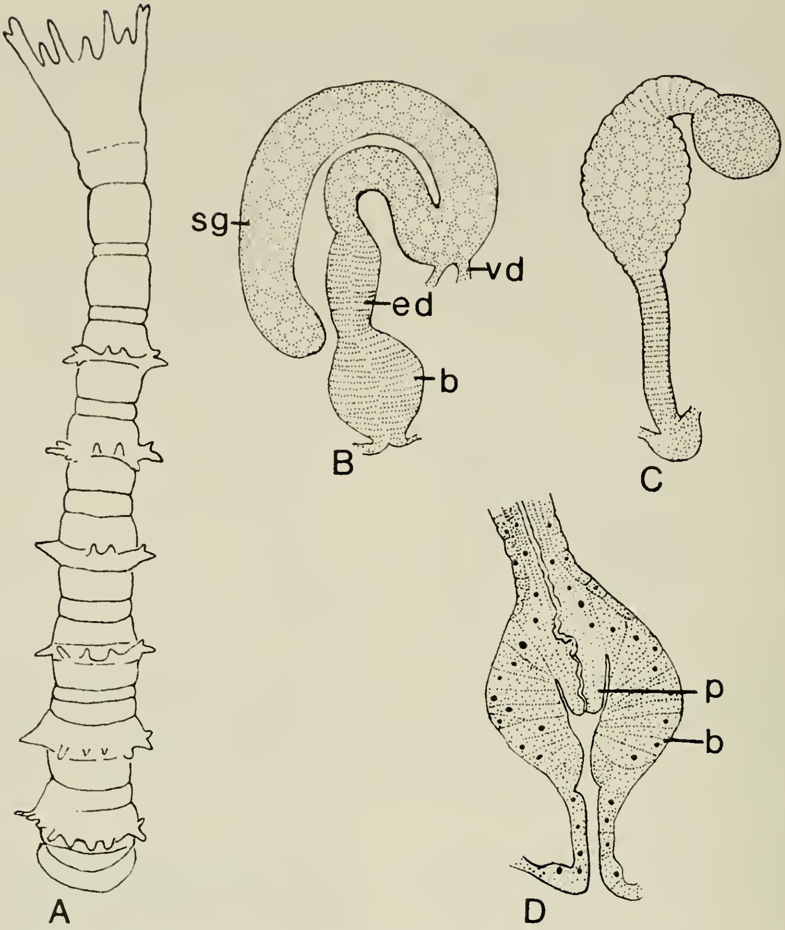

Fig. 4. *Cirrodrilus cirratus*: A, Dorsal view; B, Male efferent apparatus; C, Spermatheca; D, Longitudinal section through bursa and penis. Abbreviations: ed, ejaculatory duct; others as for Fig. 3 (after Yamaguchi 1934, figs. 4, 5).

*Diagnosis.*—One pair of testes in segment V; penis eversible, cuticular tube.

*Range.*—Europe; Asia: China, Korea, Japan.

*Number of species.*—Pop (1965) recognized four species, one with three subspecies; Karaman (1970), six species, two with a subspecies each in Europe; seven east Asian species are accepted as valid by Gelder and Liu (in ms.).

*References.*—Pierantoni 1906a, 1912; Stephenson 1930; Yamaguchi 1934; Goodnight 1940; Georgevitch 1955, 1957; Pop 1965; Karaman 1970; Gelder and Liu (ms.).

*Note.*—The literature pertaining to the genus *Branchiobdella* is confusing. The species currently assigned to it in both Europe and Asia may well include more than one genus in both regions.

### Genus *Cirrodrilus*
Fig. 4

*Cirrodrilus* Pierantoni, 1905:2. [Type species, by subsequent designation (Goodnight 1940:63), *Cirrodrilus cirratus* Pierantoni, 1905:1. Gender: masculine.]

*Ceratodrilus* Yamaguchi, 1932a:361, 366.

*Carcinodrilus* Yamaguchi, 1932b:62.

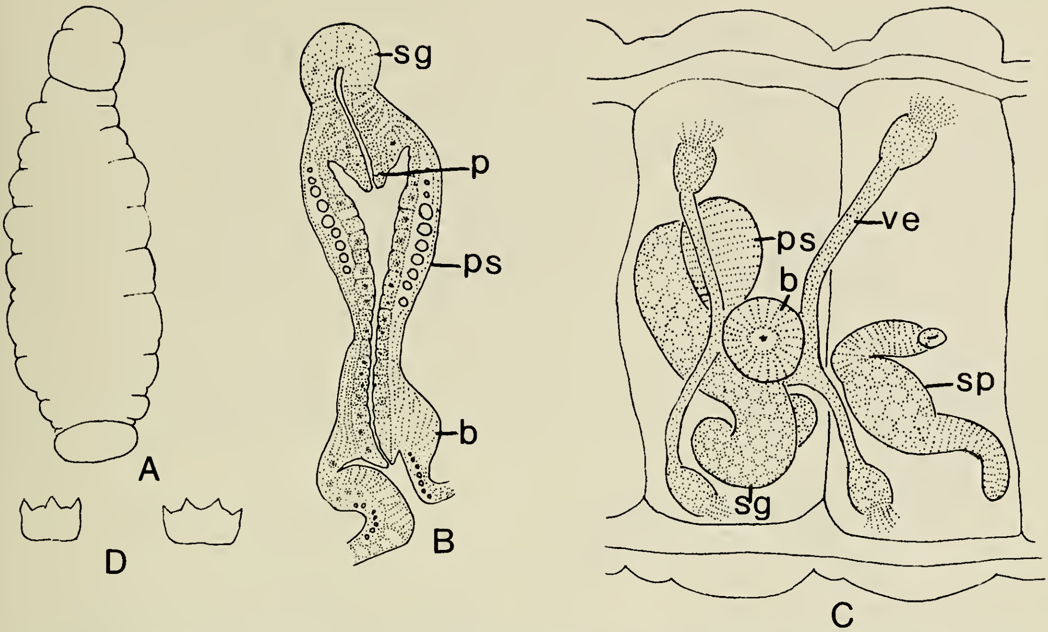

Fig. 5. *Ankyrodrilus koronaeus*: A, Dorsal view; B, Longitudinal section through bursa and penis; C, Ventral view, reproductive systems; D, Jaws, upper to left. Abbreviations: sp, spermatheca; others as above (after Holt 1965a, figs. 6, 9, 1, 4, 5).

*Stephanodrilus* (*Stephanodrilus*) Yamaguchi, 1934:191–192.
*Stephanodrilus* (*Ceratodrilus*) Yamaguchi, 1934:191–192.
*Cirrodrilus* Goodnight, 1940:63; Holt, 1960a:54–57, 1967b:3.

*Disposition of type specimens.*—Unknown; some of Pierantoni's material is deposited in the Zoologische Museum at Hamburg (Holt 1967b:5).

*Diagnosis.*—Two pairs of testes in segments V and VI; penis membraneous, eversible, attached by strands to inner wall of penial sheath. [This genus is heterogeneous and should be subdivided. See Yamaguchi 1934:199–200.]

*Range.*—Asia: Japan, Korea, China.

*Number of species.*—Twenty-one species are accepted by Gelder and Liu (23, with the removal of *C. truncatus* (Liang, 1963) to a new genus, are proposed in ms. by these authors); other names are available.

*References.*—Pierantoni 1905, 1906b, 1912; Yamaguchi 1932a, b, 1934; Goodnight 1940; Holt 1960a, 1967b.

### Genus *Ankyrodilus*
Fig. 5

*Ankyrodrilus* Holt, 1965a:10. [Type species, by original designation, *Ankyrodrilus koronaeus* Holt, 1965a:10. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1965a:11).

*Diagnosis.*—Two pairs of testes; ental end of spermiducal gland bifurcated; penis muscular, penial sheath eversible; ejaculatory duct absent; mid-portion of body depressed.

*Range.*—Eastern North America: southwest Virginia to middle Tennessee.

*Number of species.*—Two.

*References.*—Holt 1965a, Hobbs et al. 1967.

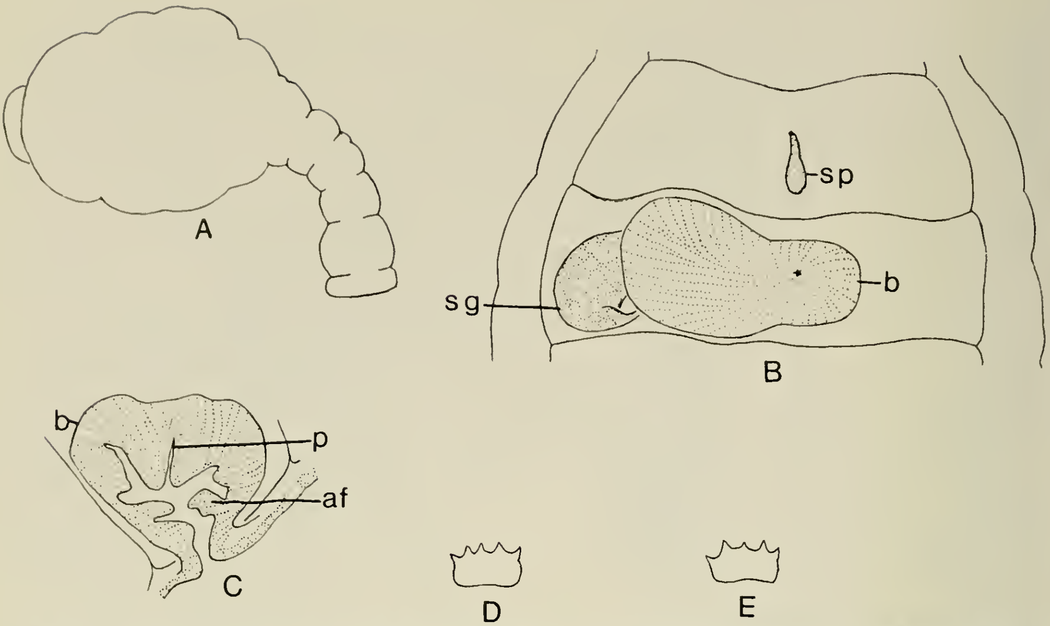

Fig. 6. *Xironogiton instabilis*: A, Dorsal view; B, Ventral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Upper jaw; E, Lower jaw. Abbreviations: af, atrial fold; others as above (after Holt 1974b; fig. 2).

### Genus *Xironogiton*
Fig. 6

*Xironogiton* Ellis, 1919:247. [Type species, by original designation, *Xironogiton oregonensis* Ellis, 1919:248. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Ellis 1919:249).

*Diagnosis.*—Two pairs of testes; penis, muscular, protrusible; bursa large, spherical to asymmetrical; spermiducal gland not bifurcated entally; spermatheca small; midportion of body depressed.

*Range.*—North America: higher elevations of Appalachian uplands; north portion of Pacific versant.

*Number of species.*—Five.

*References.*—Ellis 1919; Goodnight 1940; Holt 1949, 1974b.

## Family Bdellodrilidae

*Cambarincolinae* Goodnight, 1940:53 (in part).

*Diagnosis.*—One anterior nephridiopore; vasa deferentia enter spermiducal gland ectad to its ental end; no prostate.

### Genus *Bdellodrilus*
Fig. 7

*Bdellodrilus* Moore, 1895b:498. [Type species, by subsequent designation (Goodnight 1940:53) *Brachiobdella illuminata* Moore, 1894:421. Gender: masculine.]

*Disposition of type specimens.*—Uncertain; Moore's collections are now in those of the National Museum of Natural History, Smithsonian Institution.

*Diagnosis.*—Penis eversible, epithelial (Moore 1895b:591, figs. 19, 20); bursa provided with 2 lateral glands enclosed in its muscular wall; spermatheca with lateral process; body wall thin, glandular.

*Range.*—North America: eastern United States, Mexico.

*Number of species.*—One.

*References.*—Moore 1895b, Hobbs et al. 1967; Holt 1973c.

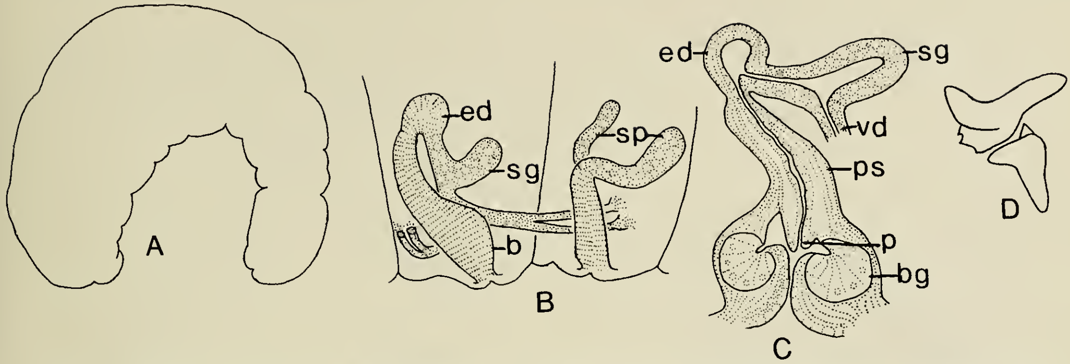

Fig. 7. *Bdellodrilus illuminatus*: A, Lateral view; B, Lateral view, reproductive systems; C, Lateral view of part of male efferent apparatus; D, Jaws. Abbreviations: bg, bursal gland; others as above (B, C, after Moore 1885b, figs. 19, 20; A, D, after Hobbs et al. 1967, fig. 13).

### Genus *Cronodrilus*
Fig. 8

*Cronodrilus* Holt, 1968a:308. [Type species, by original designation, *Cronodrilus ogygius* Holt, 1968a:308. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1968a:308).

*Diagnosis.*—Penis eversible, cuticular; penial sheath very long; ejaculatory duct short.

*Range.*—North America: Georgia.

*Number of species.*—One.

*Reference.*—Holt 1968a.

### Genus *Adenodrilus*
Fig. 9

*Adenodrilus* Holt, 1977b:727. [Type species, by original designation, *Adenodrilus hemophagus* Holt, 1977b:727.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1977b:727).

*Diagnosis.*—Penis muscular, (?) eversible; ejaculatory duct composed of 3 layers

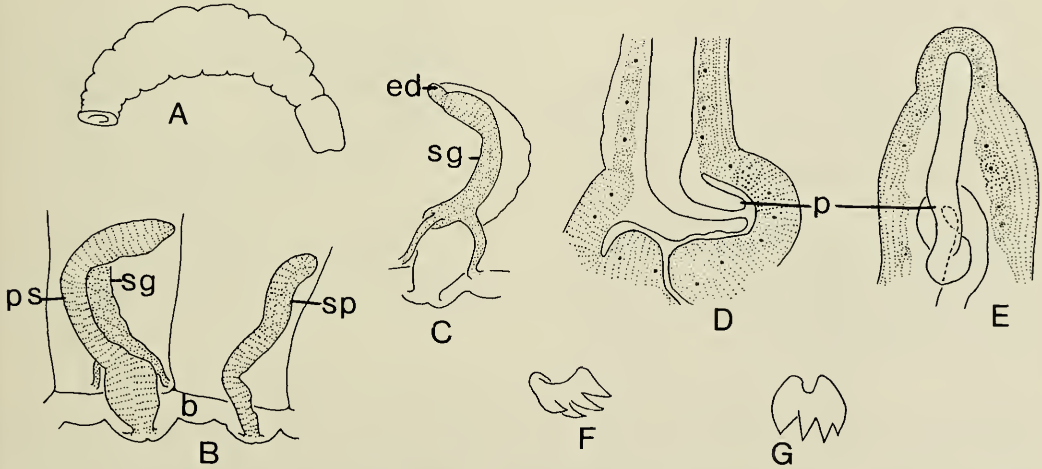

Fig. 8. *Cronodrilus ogygius*: A, Lateral view; B, Lateral view, reproductive systems; C, Lateral view, spermiducal gland; D, Ectal end of penis; E, Ental end of penis; F, Oblique view, upper jaw; G, Oblique view, lower jaw. Abbreviations: as above (after Holt 1968b, figs. 7, 8).

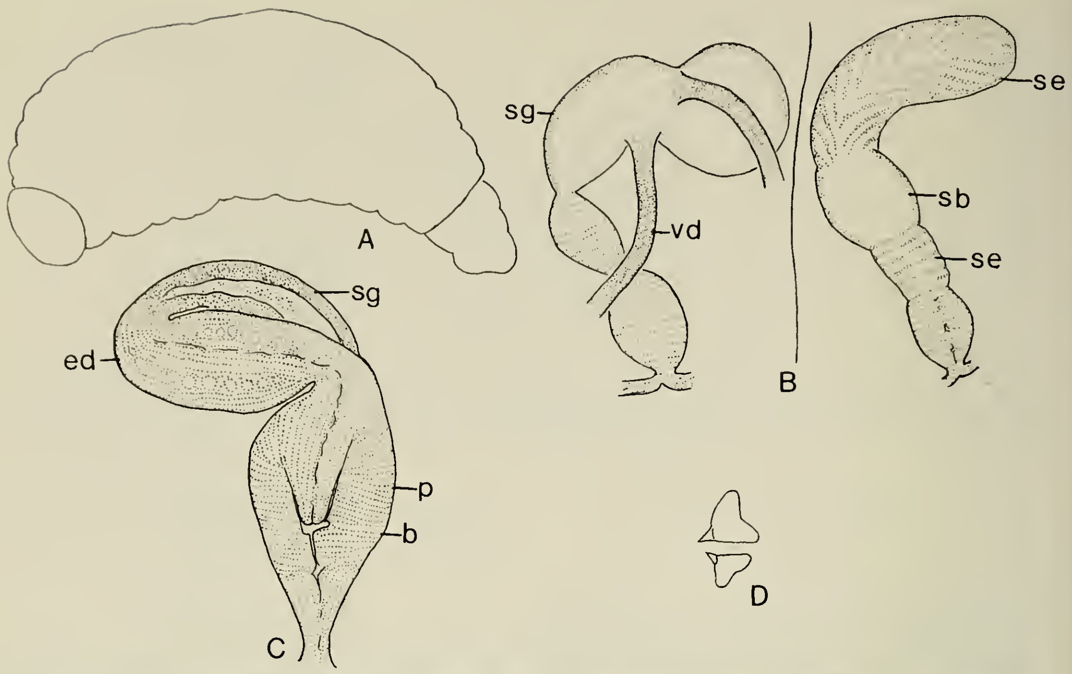

Fig. 9. *Adenodrilus hemophagus*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and ejaculatory duct; D, Jaws. Abbreviations: as above (after Holt 1977b, figs. 1, 3, 5, 2).

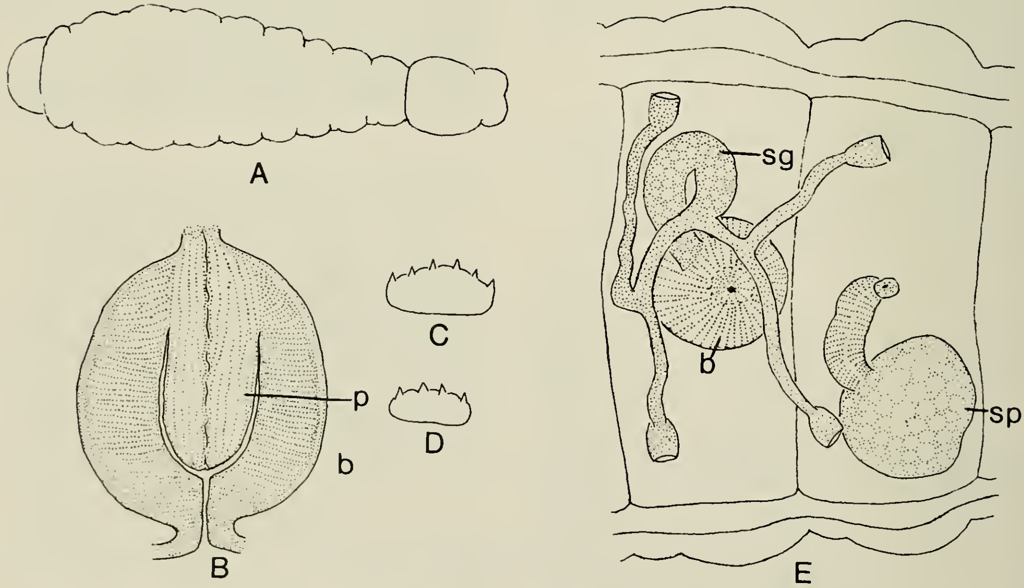

Fig. 10. *Xironodrilus formosus*: A, Dorsal view; B, Longitudinal section through bursa and penis; C, Upper jaw; D, Lower jaw; E, Ventral view, reproductive systems. Abbreviations: as above (original).

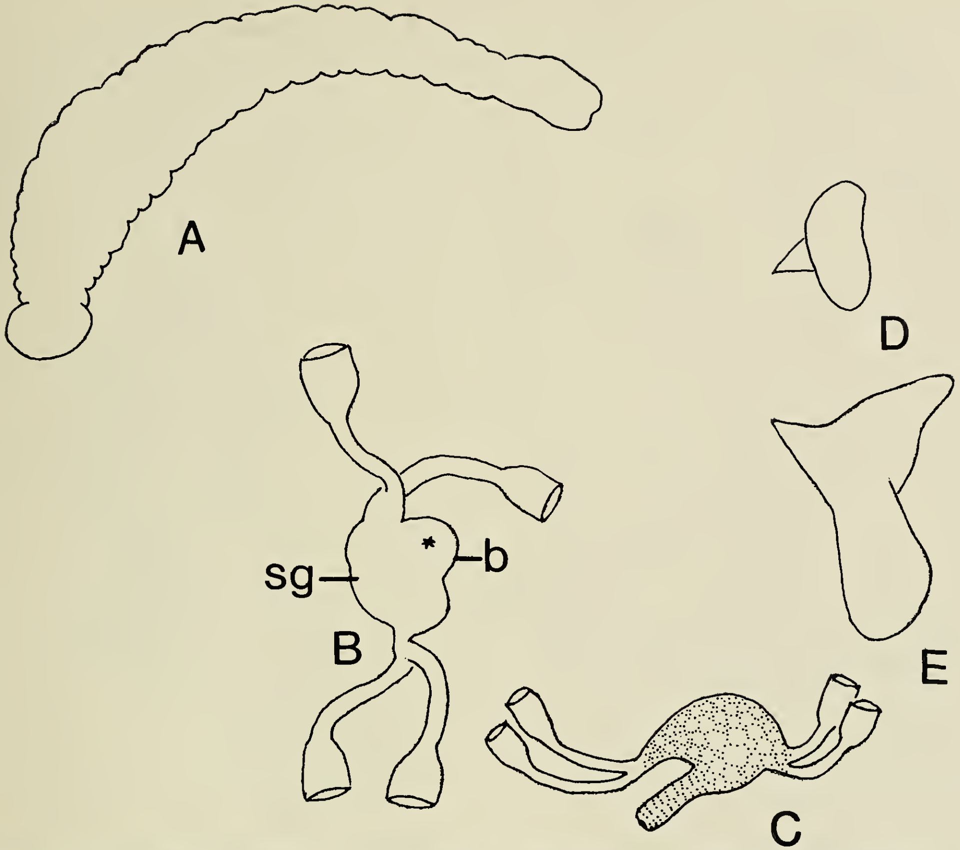

Fig. 11. *Caridinophila unidens*: A, Lateral view; B, Ventrolateral view, male efferent apparatus; C, Same, lateral view, diagrammatic; D, Upper Jaw; E, Lower jaw. Abbreviations: as above (after Liang 1963, fig. 3A, F, I, C, D).

of muscles; spermiducal gland constricted at junction with vasa deferentia; body wall thin, glandular.

*Range.*—North America: Oregon.

*Number of species.*—One.

*Reference.*—Holt 1977b.

## Family Xironodrilidae

Cambarincolinae Goodnight, 1940:48 (in part).

*Diagnosis.*—Two anterior nephridiopores; two pairs of testes; vasa deferentia enter ental end of spermiducal gland; no prostate; penis muscular, protrusible.

## Genus *Xironodrilus*

Fig. 10

*Xironodrilus* Ellis, 1918:49. [Type species, by subsequent designation (Ellis 1919: 244), *Xironodrilus formosus.* Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Ellis 1919:244).

*Diagnosis.*—As for the family; mid-portion of body depressed.

*Range.*—North America: Michigan southeast to the Piedmont of North Carolina.

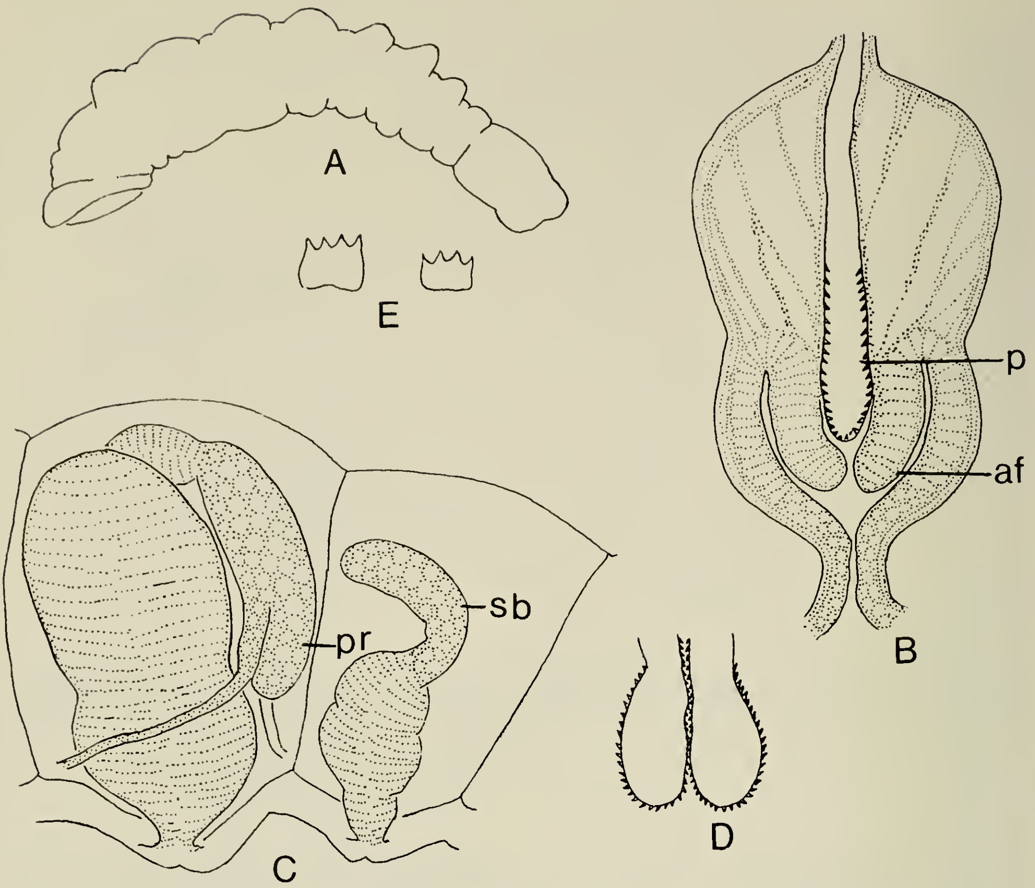

Fig. 12. *Oedipodrilus oedipus*: A, Lateral view; B, Longitudinal section through bursa and penis; C, Lateral view, reproductive systems; D, Tip of partially everted penis; E, Jaws, upper to left. Abbreviations: pr, prostate; others as above (A, C, E, after Holt 1967a; figs. 1, 4, 2, 3; B, D, after Holt 1984a, fig. 3).

*Number of species.*—Five.

*References.*—Moore 1894; Ellis 1919; Goodnight 1940, 1943; Holt and Weigl 1979.

### Family Caridinophilidae

*Diagnosis.*—One anterior nephridiopore; 2 pairs of testes; vasa efferentia enter subspherical spermiducal gland separately (no vasa deferentia); no prostate; no spermatheca.

### Genus *Caridinophila*
Fig. 11

*Caridinophila* Liang, 1963:565, 569. [Type species, by original designation, *Caridinophila unidens* Liang, 1963:565. Gender: feminine.]

*Disposition of type specimens.*—Unknown.

*Diagnosis.*—As for the family.

*Range.*—Asia: Yunnan Province, China.

*Number of species.*—One.

*Reference.*—Liang 1963.

### Family Cambarincolidae

Cambarincolinae, Goodnight, 1940 (in part).

*Diagnosis.*—One anterior nephridiopore; 2 pairs of testes; vasa deferentia enter ental end of spermiducal gland.

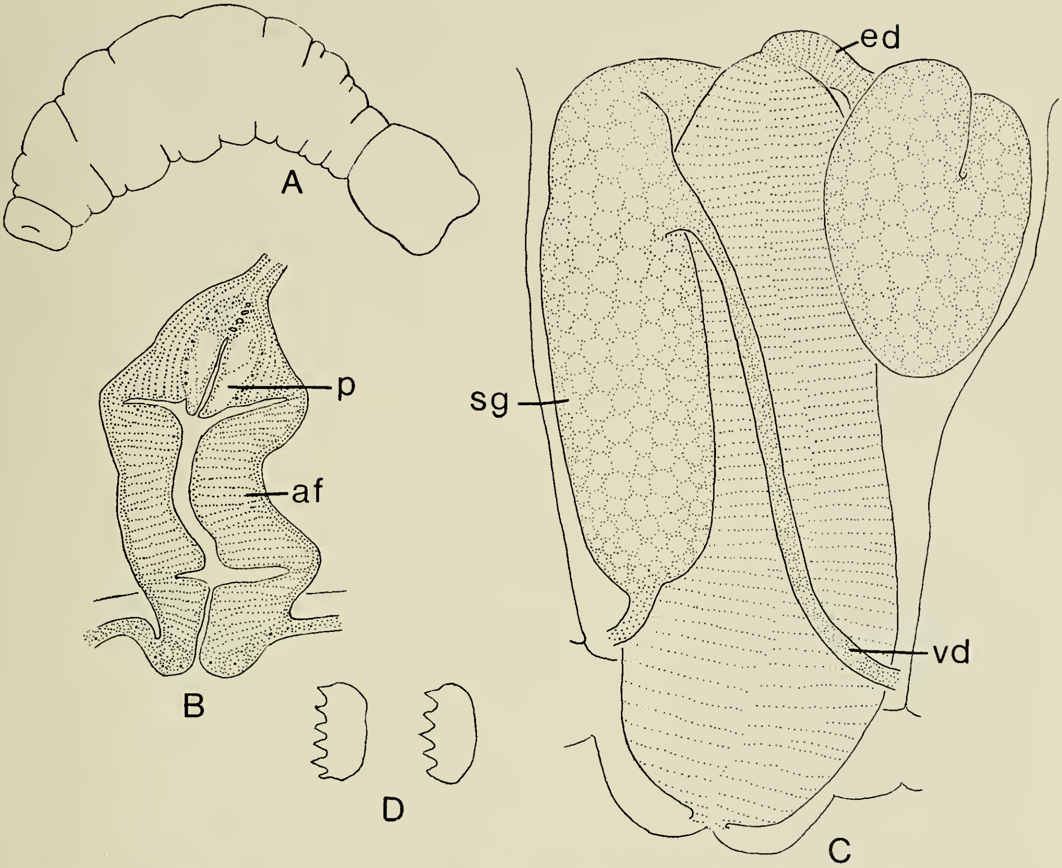

Fig. 13. *Magmatodrilus obscurus*: A, Lateral view; B, Longitudinal section through bursa and penis; C, Lateral view, male efferent apparatus; D, Jaws, upper to left. Abbreviations: as above (A, C, D, after Holt 1967b, figs. 3, 4, 1, 2; B, after Holt 1974a, fig. 4).

### Genus *Oedipodrilus*
Fig. 12

*Oedipodrilus* Holt, 1967a:58. [Type species, by original designation, *Oedipodrilus oedipus* Holt, 1967a:58. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1967a:58).

*Diagnosis.*—Penis eversible, cuticular, provided with many small recurved hooks; prostate rudimentary to well developed lobe of ental portion of spermiducal gland.

*Range.*—North America: Kentucky, Tennessee, Mexico.

*Number of species.*—Three.

*References.*—Holt 1967a, 1984a.

### Genus *Magmatodrilus*
Fig. 13

*Magmatodrilus* Holt, 1967b:3. [Type species, by original designation (Holt 1967b:3), *Stephanodrilus obscurus* Goodnight, 1940:55. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1967b:3).

*Diagnosis.*—No prostate, penis short, eversible; bursa large, atrial region elongated; spermiducal gland long.

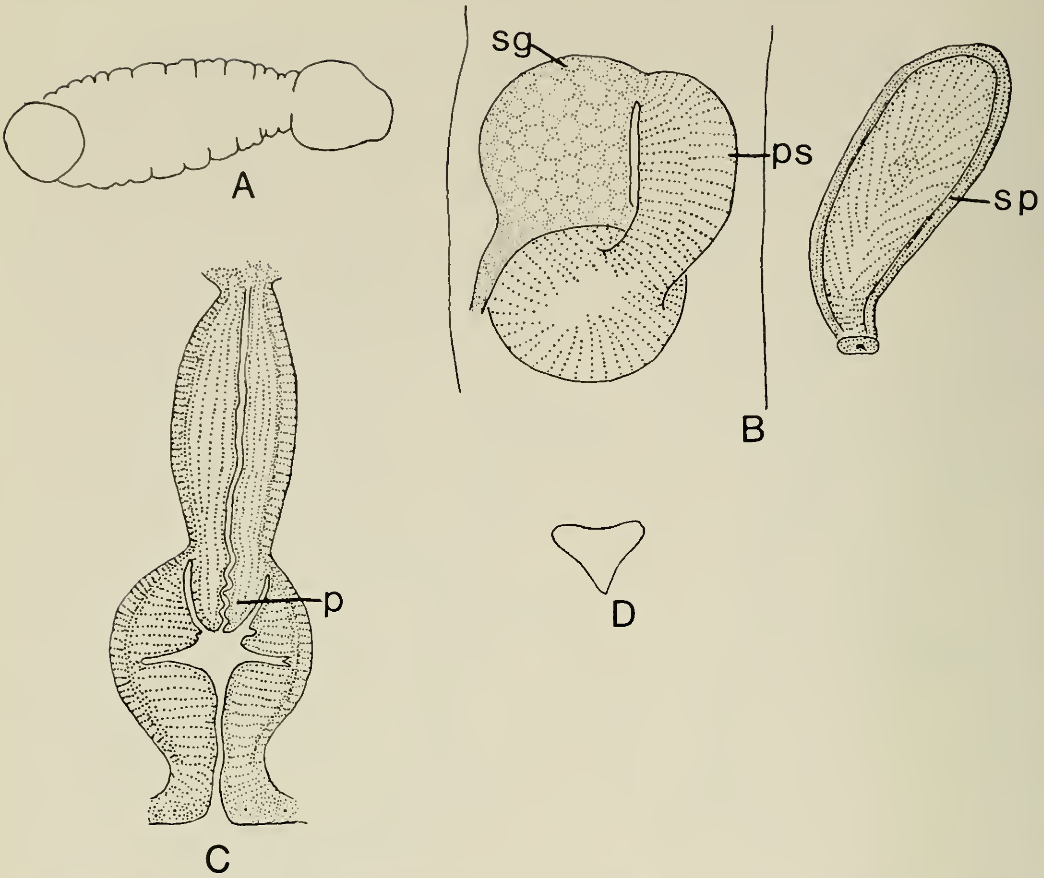

Fig. 14. *Triannulata magna*: A, Lateral view; B, Laterodorsal view, reproductive systems; C, Longitudinal section through bursa and penis; D, Ventral jaw. Abbreviations: as above (after Holt 1974a, figs. 1, 2, 3).

*Range.*—North America: California.

*Number of species.*—One.

*References.*—Goodnight 1940; Holt 1967b, 1974a.

### Genus *Triannulata*
Fig. 14

*Triannulata* Goodnight, 1940:56. [Type species, by original designation, *Triannulata magna* Goodnight, 1940:56. Gender: feminine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Goodnight 1940:57).

*Diagnosis.*—No prostate; no ejaculatory duct; penis long, muscular, eversible; atrial portion of bursa spherical; spermiducal gland short, subspherical; spermatheca short, muscular.

*Range.*—North America: Oregon, Washington.

*Number of species.*—One.

*References.*—Goodnight 1940, Holt 1974a.

### Genus *Ceratodrilus*
Fig. 15

*Ceratodrilus* Hall, 1914:191. [Type species, by original designation, *Ceratodrilus thysanosomus* Hall, 1914:191. Gender: masculine.]

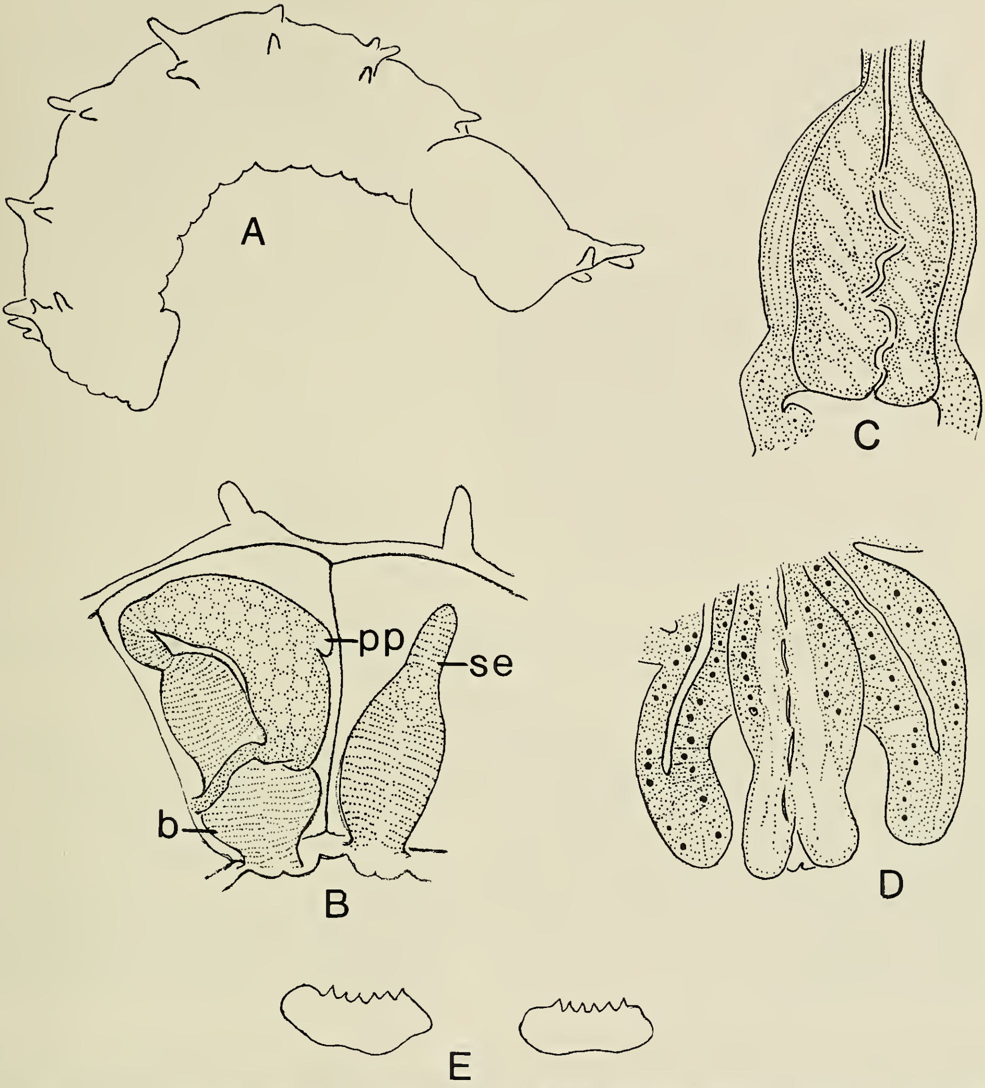

Fig. 15. *Ceratodrilus thysanosomus*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through penial sheath and penis; D, Everted penis; E, Jaws, upper to left. Abbreviations: pp, prostatic protuberance; others as above (after Holt 1960a, figs. 11, 12, 6, 7, 15, 16).

*Stephanodrilus (Ceratodrilus)* Yamaguchi, 1934:192. [Type species, by subsequent designation (Goodnight 1940:55), *Stephanodrilus sapporensis* Pierantoni, 1906b:3.]

*Cirrodrilus* Pierantoni, 1905:2. [Type species, by subsequent designation (Goodnight 1940:63), *Cirrodrilus cirratus* Pierantoni, 1905:2.]

*Ceratodrilus* (Holt, 1960a:53–73).

*Disposition of type specimens.*—"U.S.N.M. (Bureau of Animal Industry Helminthological Collection" (Hall 1914: 191).

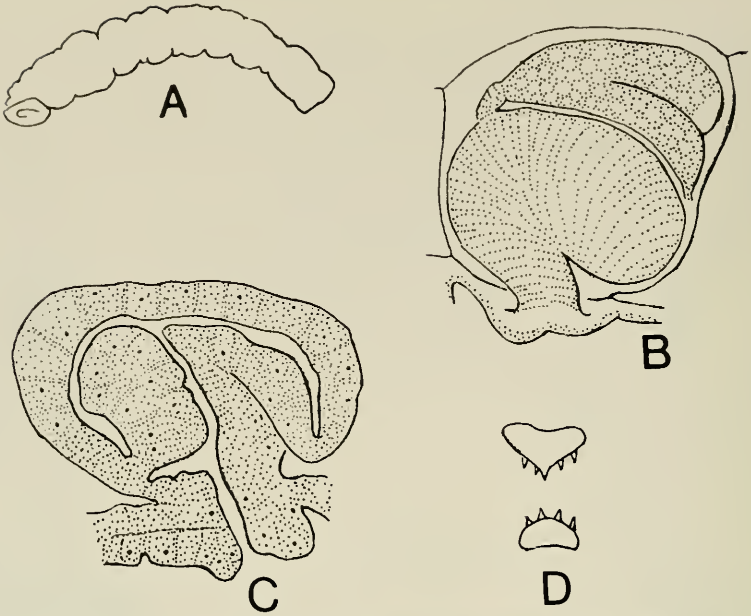

Fig. 16. *Ellisodrilus clitellatus*: A, Lateral view; B, Male efferent apparatus; C, Longitudinal section through bursa; D, Jaws (after Holt 1960b, figs. 1, 2, 3, 4).

*Diagnosis.*—Digitate projections on dorsum of segments II–VII; peristomium tentaculated; prostatic bulb near ental end of spermiducal gland; penis membraneous, eversible, attached by strands to inner wall of penial sheath; bursa elongate.

*Range.*—North America: Utah, Idaho, Oregon, Wyoming.

*Number of species.*—Two.

*References.*—Hall 1914; Yamaguchi 1934; Goodnight 1940; Holt 1960a.

### Genus *Ellisodrilus*
Fig. 16

*Ellisodrilus* Holt, 1960b:170. [Type species, by original designation, *Ellisodrilus clitellatus* Holt, 1960a:170. Gender: masculine.]

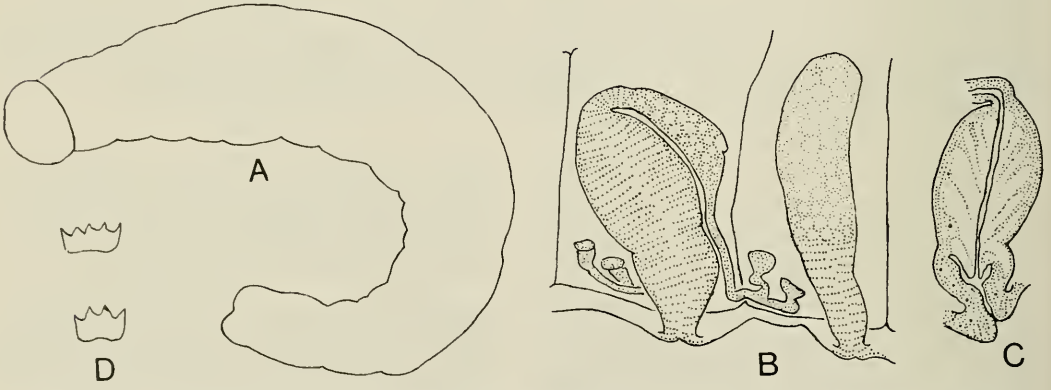

Fig. 17. *Sathodrilus carolinensis*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Jaws (after Holt 1968b, figs. 2, 1).

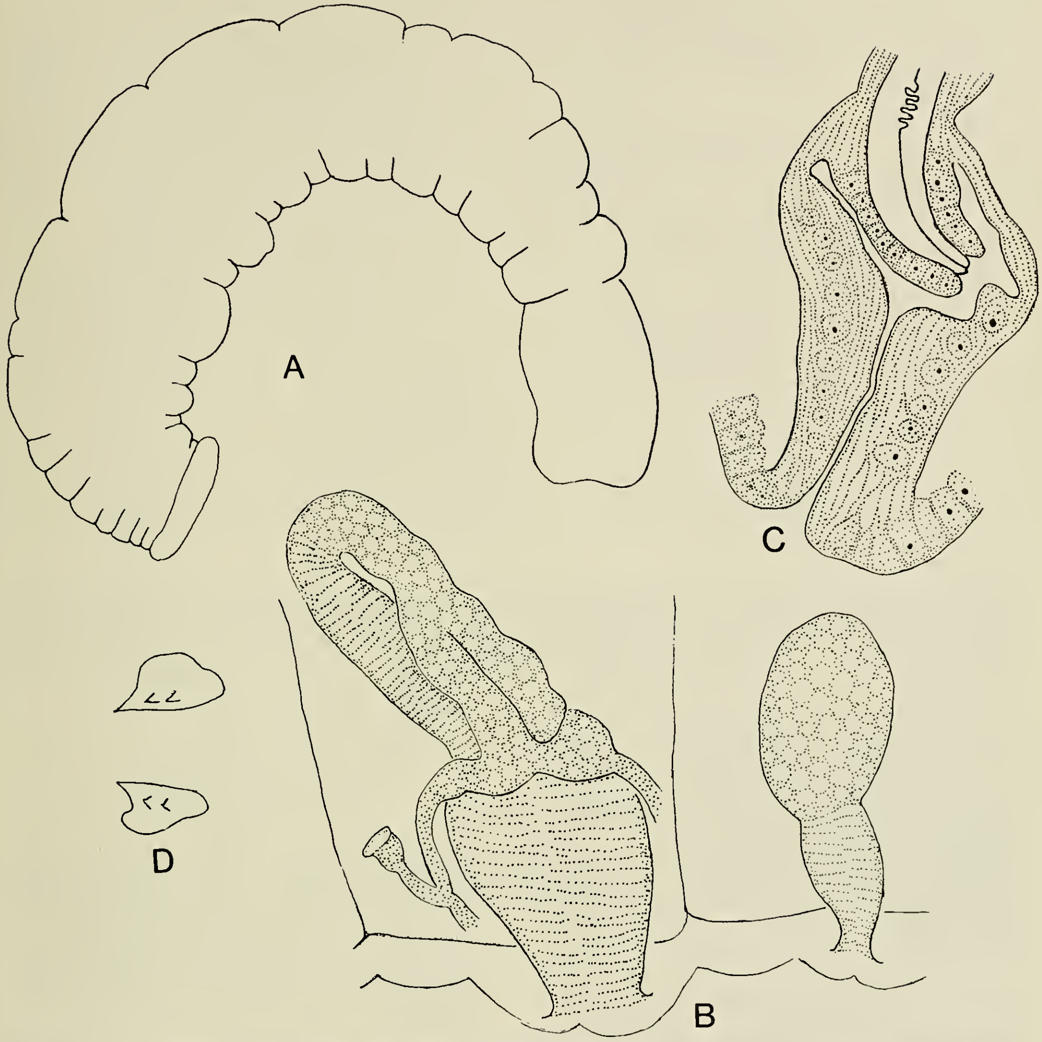

Fig. 18. *Tettodrilus friaufi*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Jaws (after Holt 1968b, fig. 9).

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1960b:170).

*Diagnosis.*—Prostate arises from mid-portion of spermiducal gland; penis reduced to pore on ectal surface of penial sheath; bursa asymmetrically subspherical; no spermatheca.

*Range.*—North America: Kentucky, Indiana, Michigan.

*Number of species.*—Two.

*Reference.*—Holt 1960b.

## Genus *Sathodrilus*

Fig. 17

*Sathodrilus* Holt, 1968b:294. [Type species, by original designation, *Sathodrilus carolinensis* Holt, 1968b:294. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1968b:294).

*Diagnosis.*—Prostatic protuberance, or prostate arising along mid-portion of sper-

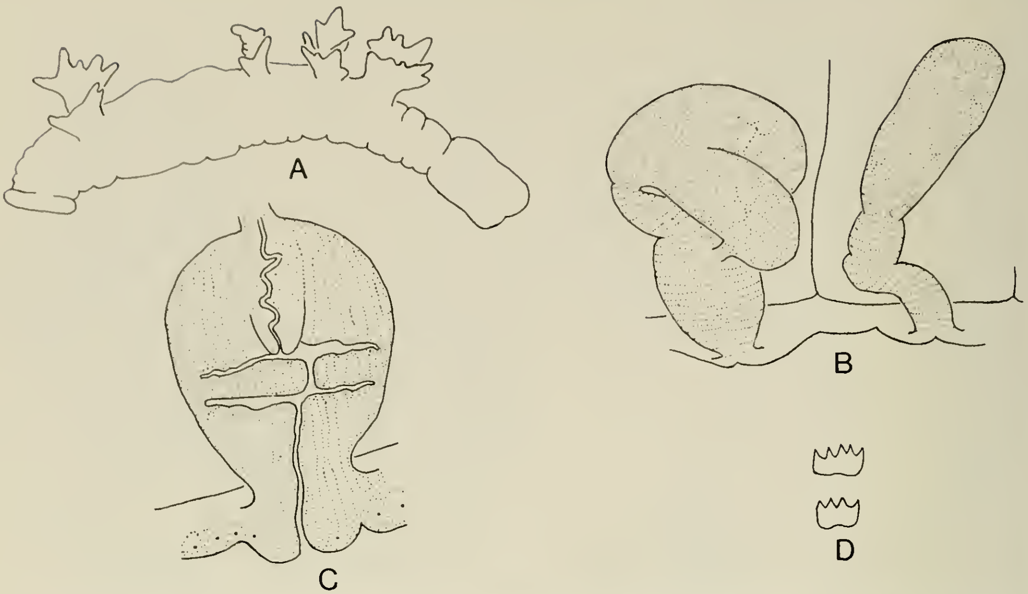

Fig. 19. *Pterodrilus alcicornus*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Jaws (A, B, from Holt 1968c, fig. 7; C, D, original).

midual gland or absent; penis membraneous, attached by strands to inner wall of penial sheath; bursa usually elongate; dorsal body surface without digitate projections.

*Range.*—North America.

*Number of species.*—Fifteen.

*References.*—Holt 1968b, 1973b, 1977a, 1978a, 1981b.

### Genus *Tettodrilus*
Fig. 18

*Tettodrilus* Holt, 1968b:312. [Type species, by original designation, *Tettodrilus friaufi* Holt, 1968b:314. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Holt 1968b:312).

*Diagnosis.*—Penis eversible, cuticular; ejaculatory duct projects as epithelio-muscular tube into atrium of bursa, enclosing ectal (when retracted) portion of penis; prostate arises at mid-portion of slender spermiducal gland.

*Range.*—North America: Tennessee.

*Number of species.*—One.

*Reference.*—Holt 1968b.

### Genus *Pterodrilus*
Fig. 19

*Pterodrilus* Moore, 1895a:449. [Type species, by subsequent designation (Goodnight 1940:58), *Pterodrilus alcicornus* Moore, 1895a:449. Gender: masculine.]

*Disposition of type specimens.*—(?) Lost (Holt 1968c:6).

*Diagnosis.*—Anterior annulus of segment VIII with elevated dorsal ridge, those of other segments often so, some or all such ridges often with fan-like digitate projections; small worms; prostate arising at mid-portion of short spermiducal gland; penis muscular, protrusible; bursa ovoid to pyriform.

*Range.*—North America: eastern United States.

*Number of species.*—Eight.

*References.*—Moore 1895a; Ellis 1919; Goodnight 1940; Holt 1968c, 1973c.

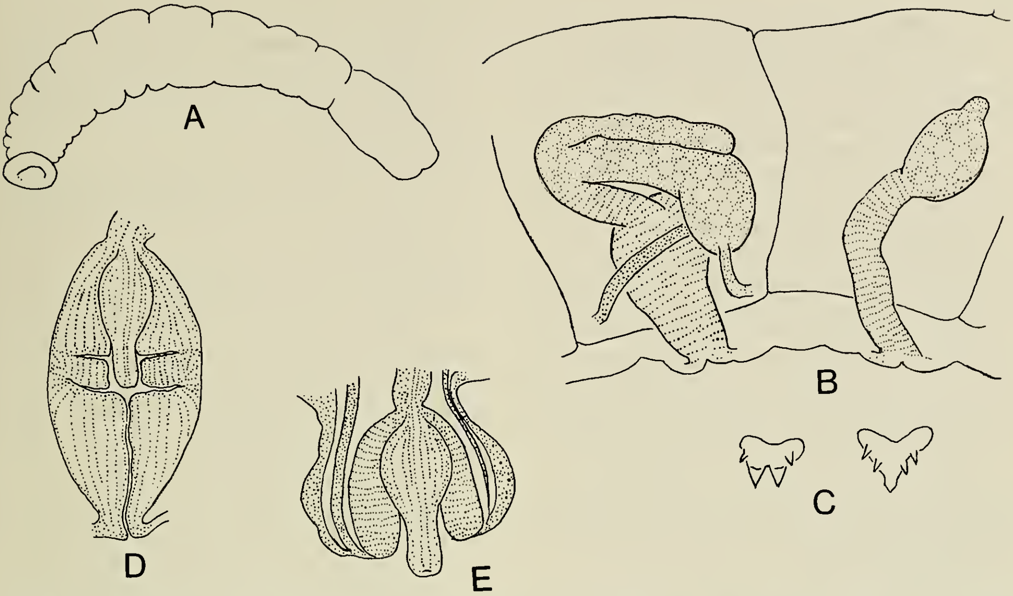

Fig. 20. *Cambarincola macrodontus*: A, Lateral view; B, Lateral view, reproductive systems; C, Jaws (after Holt and Hoffman 1959, figs. 1, 2, 4, 3). *Cambarincola illinoisensis*: D, Longitudinal section through bursa and penis; E, Everted bursa, protruded penis (after Holt 1982, fig. 1D, E).

### Genus *Cambarincola*
Fig. 20

*Cambarincola* Ellis, 1912:481. [Type species, by original designation, *Cambarincola macrodontus* Ellis, 1912:481. Gender: masculine.]

*Disposition of type specimens.*—National Museum of Natural History, Smithsonian Institution (Ellis 1912:451).

*Diagnosis.*—Prostate arising at ectal end (junction with ejaculatory duct) of spermiducal gland; penis muscular, protrusible; body segments often with raised anterior annuli (dorsal ridges), never with fan-like or digitate projections.

*Range.*—North America; introduced into Japan.

*Number of species.*—Forty-seven.

*References.*—Ellis 1912, 1919; Goodnight 1940; Hoffman 1963; Holt 1949, 1954, 1963, 1964, 1973b, c, d, e, 1974a, 1978a, 1981a, 1982, 1984a, b; Leidy 1851.

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# OCCURRENCE OF LARVAL *ILLEX ILLECEBROSUS* AND OTHER YOUNG CEPHALOPODS IN THE SLOPE WATER/GULF STREAM INTERFACE

Michael Vecchione and Clyde F. E. Roper

*Abstract.*—Specimens and data suggest that larval short-finned squid, *Illex illecebrosus,* may concentrate in water where density ($\sigma_t$) is approximately 26.7, indicating that spawning occurs in the subsurface interface where Slope Water mixes with the Gulf Stream. Because these water masses occur year-round within the range of *I. illecebrosus,* spawning may be a prolonged or progressive process along the shoreward edge of the Gulf Stream. The distribution of other species indicates mesoscale spatial separation of young cephalopods in the vicinity of the Gulf Stream.

Among many unanswered questions in cephalopod ecology, two currently are receiving much attention: (1) what are the season and site(s) of spawning for the commercially important species *Illex illecebrosus* and (2) what factors in the early life history of the species are crucial to its survival and recruitment to the fishery?

A multinational effort was organized by Canada, Japan, and the United States to attempt to answer these questions. Intensive directed sampling for the early stages of *I. illecebrosus* was conducted during February and March 1982 on cruise 8201 of the Japanese Research Vessel *Kaiyo-Maru.* Personnel from all three sponsoring nations participated in the two-part cruise.

The area sampled was centered on the Gulf Stream east of New England and south of Nova Scotia. During the second leg of the cruise, from which our specimens were obtained, the Gulf Stream was meandering through the sampling area. Thus, the 40 stations for which we have data include water masses characteristic of Boreal Slope Water, the Gulf Stream, and the Sargasso Sea.

## Materials and Methods

Sampling was done primarily with oblique tows. A model 1271 open bongo-net system with 61 cm diameter mouth opening and 0.5 mm mesh was used to sample between the surface and 200 m depth. Sampling between the surface and 1000 m depth was done with an open midwater trawl (KMT; 100 m long, 18 mm mesh cod-end), and a rectangular midwater trawl (KYMT; 3 × 3 m mouth opening, 17 m long, 1.7 mm mesh cod-end). Data on hydrographic conditions were collected using expendable bathythermographs and multiple bottle casts for conductivity, temperature, and dissolved oxygen.

The biological samples were sorted at sea and field identifications were attempted for larval and juvenile *Illex,* sometimes under rather severe weather conditions. Preserved specimens then were divided among the representatives of the participating countries: 50% to the Japanese, 25% to the Canadian, and 25% to the U.S. participants.

## Results

The material available for analysis consisted of 66 specimens that were identified to 18 taxa. Young *Illex* (we believe *I. illecebrosus*; see Vecchione 1979) was the most abundant cephalopod collected (Table 1). The material also included several other taxa for which our current knowledge of early

Table 1.—Ranking by abundance of cephalopod specimens from Leg II of *Kaiyo-Maru* cruise 8201.*

| Taxon | No. of specimens | Rank | Mantle length (mm) Min. | Median | Max. |
|---|---|---|---|---|---|
| *Illex* sp. (cf. *illecebrosus*) | 16 | 1 | 3.0 | 4.0 | 10.7 |
| Octopodidae | 6 | 3 | 3.7 | 4.0 | 6.1 |
| *Gonatus fabricii* | 6 | 3 | 2.7 | 7.0 | 13.3 |
| *Ommastrephes* sp. | 6 | 3 | 2.1 | 3.8 | 8.1 |
| *Leachia* sp. | 4 | 5.5 | 14.7 | 17.9 | 28.0 |
| *Pterygioteuthis* sp. | 4 | 5.5 | 3.1 | 4.6 | 10.0 |
| *Abralia* sp. | 3 | 8 | 2.8 | 4.3 | 4.7 |
| *Octopoteuthis* sp. | 3 | 8 | 3.1 | 6.3 | 6.8 |
| *Teuthowenia megalops* | 3 | 8 | 4.3 | 5.0 | 5.7 |
| *Pyroteuthis margaretifera* | 2 | 12.5 | 2.7 | 3.3 | 3.9 |
| *Onychoteuthis banksii* | 2 | 12.5 | 3.8 | 4.8 | 5.8 |
| *Onykia carribaea* | 2 | 12.5 | 6.7 | 7.0 | 7.3 |
| *Ctenopteryx sicula* | 2 | 12.5 | 2.8 | 3.0 | 3.1 |
| *Brachioteuthis* sp. | 2 | 12.5 | 2.1 | 2.5 | 2.8 |
| unid. oegopsid | 2 | 12.5 | 2.3 | 2.7 | 3.1 |
| *Abraliopsis* sp. | 1 | 16 | 8.2 | 8.2 | 8.2 |
| *Histioteuthis* sp. | 1 | 16 | 2.7 | 2.7 | 2.7 |
| *Ornithoteuthis antillarum* (?) | 1 | 16 | 2.6 | 2.6 | 2.6 |
| Total | 66 specimens | 18 taxa | | | |

* Represents 25% of total collected; see text.

life history is even more limited. These taxa include young *Gonatus fabricii,* as well as several other ommastrephids, onychoteuthids, enoploteuthids, cranchiids, and octopodids.

Station locations and isotherms at the surface and at 200 m depth are shown in Fig. 1. These depths were selected because they represent the sampling envelope of the oblique bongo tows. The temperature structure shows the turbulent nature of the current in the sampling area, as is typical of the transition zone between the Gulf Stream and the North Atlantic Drift. It also shows the substantial variability in thermal structure within the sampled depth range. Distribution of the five most abundant taxa is shown also in Fig. 1. Based on this limited subset of the complete set of data, we see indications of mesoscale spatial segregation among these taxa. Whereas *Gonatus fabricii* was collected only along the Slope-Water edge of the system, *Illex illecebrosus* and the unidentified octopods were concentrated along the central axis of the system, and *Leachia* sp. and *Ommastrephes* sp. appeared to be concentrated on the Sargasso Sea side of the system.

The six stations at which *Illex* were collected included a broad range of surface temperatures (Fig. 2A). Inferences on the distribution of young *Illex* based only on surface conditions where oblique tows collected specimens would indicate eurytopic habitat requirements, from 8°C to nearly 20°C. However, based on our earlier work with sampling programs from shelf and slope waters of the western North Atlantic (Roper and Lu 1979, Vecchione 1979), we have reason to believe that larval *I. illecebrosus* are concentrated deeper in the water column. At approximately 100 m depth all of the temperature sections begin to converge and by 150 m the temperatures concentrate around 13°–18°C. If we assume, based on earlier studies, that this is close to the depth at which most of the *Illex* were collected, then we have reason to point out strong similarities among all of these stations.

The temperatures and salinities of these

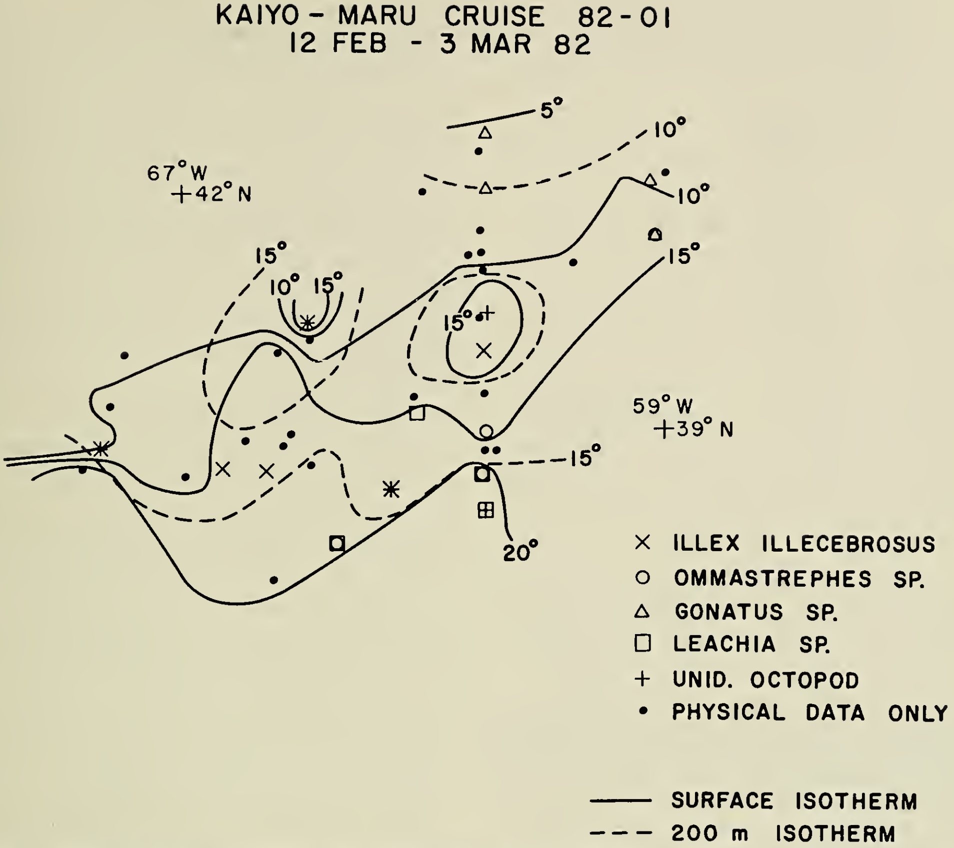

Fig. 1. Study area showing station locations, surface and 200 m isotherms, and occurrence of the five most abundant cephalopod taxa (*Kaiyo-Maru* cruise 8201, Feb–Mar 1982).

stations at 150 and 200 m depths are shown in Fig. 2B. These waters are approximately isopycnal at $\sigma_t$ of about 26.7, an indication of subsurface mixing. The isopycnal mixing extends between what Wright and Parker (1976) refer to as the "slope-water thermostad" and the Gulf Stream. Some captures are in the discrete water types and some are in the intermediate water; the aggregate of the captures is what would be expected in subsurface mixing between two water types because it extends along isopycnal lines. Based on these indications, we believe that hatching probably occurs in subsurface waters at the interface between the Slope Water and the Gulf Stream. Since both of these water masses occur within the distributional range of *I. illecebrosus* throughout the year, these data may also indicate a prolonged spawning season along the shoreward edge of the Gulf Stream over a very extensive latitudinal range.

## Discussion and Recommendations

Prior to O'Dor and Durward's (1979) demonstration that *Illex illecebrosus* spawns pelagic egg masses, it was assumed that *Illex* probably spawned demersally on the continental slope (Roper and Lu 1979, Vecchione 1979). The concept that an obligate relationship exists between the Gulf Stream and the early life history of *Illex* is now gaining support (Coelhó 1985, O'Dor and

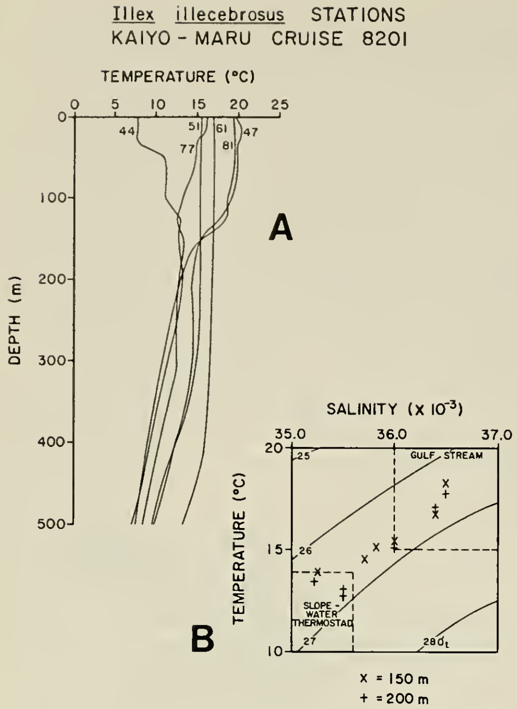

Fig. 2. A, Temperature profiles at *Kaiyo-Maru* stations where *Illex illecebrosus* larvae were captured (station numbers indicated); B, T-S diagram of *Kaiyo-Maru* stations where *Illex illecebrosus* larvae were captured with notation of water-mass type (cruise 8201, Feb–Mar 1982).

Balch 1985, Rowell et al. 1985, Hatanaka et al. 1985). Additionally, our data from this cruise and unpublished observations from other cruises (Vecchione et al. 1986) indicate that similar relationships may exist for other cephalopod species.

Hypotheses are now being proposed to explain this relationship for *I. illecebrosus,* but conclusive tests of these hypotheses are very difficult because of problems with sampling and taxonomy. Not only has it so far been impossible to collect *Illex* eggs in the field (O'Dor and Balch 1985) and difficult to collect planktonic young, but specific identification of the young must be inferred from adult distributions. South of Cape Hatteras such identifications are confounded by the presence of a complex of three species (*I. illecebrosus, I. coindetii,* and *I. oxygonius*) which even as adults are very similar morphologically. Thus, distributional patterns of larvae collected on cruises in or near the area of species overlap (e.g., Rowell et al. 1985) may result from spawning by one or more of these species.

Often, inferences on larval ecology have been based on surface conditions at stations where the larvae have been collected in oblique subsurface tows. This practice is particularly faulty for a species like *Illex illecebrosus* for which data on vertical distribution are extremely limited. For instance, assumptions like that of Rowell et al. (1985) that "it is likely that the majority [of *Illex* larvae] were taken in the upper 50 m" of oblique tows between the surface and 200–300 m depth are not supported by data. Observations on *I. illecebrosus* egg masses by O'Dor and Balch (1985) indicate that the egg masses in nature are probably suspended in midwater at about the depth of the pycnocline (about 150 m in our samples). Furthermore, O'Dor et al. (1986) have shown that laboratory-hatched *I. illecebrosus* larvae avoid the surface but are capable of diel vertical migration from mesopelagic depths. This is consistent with the very limited observations by Hatanaka et al. (1985) of a diel shift in the depth of maximum abundance of larval *Illex.*

An analysis of the distribution of *Illex illecebrosus* collected off Nova Scotia during *Kaiyo-Maru* cruise 8201 has been compiled by Hatanaka et al. (1985). This report presumably was based on field-log entries of identifications for all specimens, since several specimens remained in our possession as a result of subdividing the catch upon completion of the cruise. During the first leg of the cruise, discrete-depth bongo tows were attempted at four stations. These attempts were successful at only one station in collecting a complete set of samples (from several depth strata between the surface and 200 m depth). Subsequently, discrete-depth sampling was abandoned. Inferences by Hatanaka et al. (1985) on *Illex* larval distribution were therefore based on physical conditions in the 0–100 m depth range at oblique-tow stations (however, their very limited discrete-depth data indicated that larval *Illex* may be concentrated at 100 m or greater depth during the daytime). Inferences by Hatanaka et al. (1985) about the relationship between *Illex* larval distribution and the boundary between the Gulf Stream and Slope Water do not contradict our impressions which are based on reexamination of a subset of the collections, but we do feel, however, that some deficiencies in the data must be pointed out so that similar problems can be avoided in the future.

Although we are able to speculate about the larval occurrence and distribution of *I. illecebrosus* and other species, a more precisely defined sampling program probably would have provided sufficient data to test our hypothesis. To achieve this, we recommend several changes in future sampling programs. First, once the general area and season of larval abundance have been determined for the target species, discrete-depth sampling should be considered a requirement for the study of early life history. Such a sampling regime can be accomplished either with bongo systems or with multiple opening/closing systems such as the MOCNESS Multiple Opening-Closing Net and Environmental Sensing System (Weibe et al. 1976). If time and funding constraints are imposed on the number of samples that can be collected and processed, then the number of stations occupied should be reduced to ensure that discrete-depth sampling can be accomplished. Second, definitive sorting and verification of species-level identifications should not be attempted at sea. Our cross-checks of the field logs against subsequent laboratory identifications indicate that several of the field identifications were incorrect. Even under the best of conditions use of a microscope at sea is difficult. Hatchlings of only about 2 mm or less in length are easily overlooked sloshing about in a petri dish of plankton; furthermore, the minute taxonomic characters required for identification are difficult to distinguish, let alone confirm. Thus, we cannot be confident enough in the shared, complete set of field-log entries of identifications to infer distribution and abundance based on all specimens collected but subdivided prior to verification of identifications.

A complete set of samples from this cruise, examined by a specialist in cephalopod systematics, would have been of considerable value in fulfilling the goals of this study. An additional benefit of onshore examination of all specimens by a single specialist is that the distribution of non-target species, such as *Gonatus fabricii*, could confidently be assessed along with the distribution of larval *Illex*.

We very strongly support international collaborative studies and coauthorship as an effective, efficient means of helping to answer many of the important questions we face in biological oceanography, fisheries biology, and systematics. To help achieve these ends, we recommend that future collections be identified and analyzed at one institution, prior to dividing the material among participating organizations. This will ensure consistency of analysis and interpretation without diminishing the collaborative effort.

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# *ASTYANAX SCOLOGASTER,* A NEW CHARACID (PISCES: OSTARIOPHYSI) FROM THE RÍO NEGRO, SOUTH AMERICA

Marilyn J. Weitzman and Richard P. Vari

*Abstract.*—*Astyanax scologaster* is described from a series of localities in the middle and upper Río Negro of Venezuela and Brazil. The presence of exserted anterior spines of the pelvic bones serve to define a subunit of *Astyanax* consisting of the relatively small-sized species *A. scologaster, A. essequibensis, A. mucronatus,* and *A. zonatus.* The extensive development of the exserted pelvic spine, large eye diameter, branched anal-fin ray count, number of pored lateral-line scales, and pigmentation pattern of *Astyanax scologaster* delimit that species within this assemblage.

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The presence of exserted strong spine-like pelvic bones which project anteriorly from the anteroventral body wall was first noted for characids by Eigenmann (1911:180, and Fig. 2) in his description of *Deuterodon acanthogaster.* In that species account Eigenmann noted a similar condition for *Astyanax mucronatus* Eigenmann, although no mention of the modification had been made in the original description (Eigenmann 1909: 19–20) and subsequent treatments of that species until 1921. In that year, Eigenmann (p. 280) inserted "... *innominate bones protruding as spines in front*" in his redescription of *Astyanax mucronatus.* Recent collecting efforts in the Río Negro basin of Venezuela and Brazil have revealed the presence of an undescribed *Astyanax* species with very well developed anteriorly exserted pelvic bones. Comparative studies associated with the description of the new species have uncovered the presence of comparable spines in individuals of three additional *Astyanax* species and in a second *Deuterodon* species.

*Materials and methods.*—Counts and measurements in the description follow the methods outlined in Fink and Weitzman (1974). All measurements are given as percentages of standard length (SL) except for subunits of the head which are presented as percentages of head length (HL). Vertebral counts were taken from radiographs and cleared and counterstained specimens. This number includes the four vertebrae incorporated into the Weberian apparatus and considers the fused $PU_1 + U_1$ as a single element. In the meristic values detailed, the range of the holotype and measured paratypes is presented first, with the value for the holotype indicated in brackets.

The following abbreviations are used for institutions: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; MBUCV, Museo de Biologia, Instituto de Zoologia Tropical, Universidad Central de Venezuela, Caracas; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

### *Astyanax scologaster,* new species
Figs. 1 and 3, Table 1

*Holotype.*—MBUCV V-15249, 37.5 mm SL, Venezuela, Territorio Federal Amazonas, Departamento Río Negro, lower por-

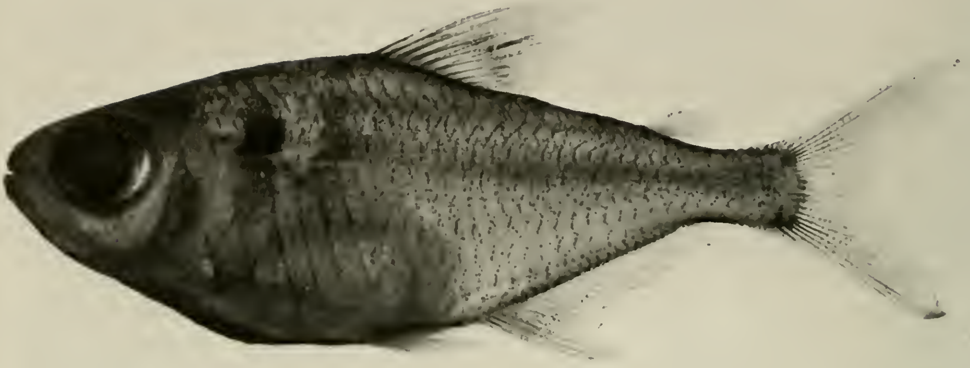

Fig. 1. *Astyanax scologaster*, new species, holotype, MBUCV V-15249, 37.5 mm SL, Venezuela, Caño Manu.

tion of Caño Manu, which drains into the Río Casiquiare about 250 m upstream of Solano (approx. 02°00'N, 66°57'W); coll. R. P. Vari, C. J. Ferraris, Jr., O. Castillo, and J. Fernandez, 7 Dec 1984.

*Paratypes.*—(All from Venezuela, Territorio Federal Amazonas, Departamento Río Negro, unless noted otherwise): MBUCV V-15250, 5, 28.8–37.2 mm SL; USNM 272612, 8, 24.5–36.2 mm SL (4, cleared and counterstained for bone and cartilage); AMNH 56173, 3, 27.5–30.0 mm SL; ANSP 157596, 3, 26.7–28.6 mm SL; BMNH 1985.10.14:1–3, 3, 26.9–30.0 mm SL; CAS 57471, 3, 24.9–35.0 mm SL; FMNH 96616, 3, 26.5–29.6 mm SL; MZUSP 36288, 3, 24.7–29.9 mm SL; taken with the holotype.—AMNH 56174, 5, 38.7–40.7 mm SL; USNM 276503, 5, 39.6–42.0 mm SL; MBUCV V-15251, 5, 38.0–40.6 mm SL, Río Negro at San Carlos de Río Negro, 2 Feb 1984.—USNM 272609, 4, 35.3–36.0 mm SL, Caño Chola, where crossed by road from San Carlos de Río Negro to Solano (01°58'N, 67°00'W), 5 Dec 1984.—USNM 272611, 5, 29.6–33.0 mm SL, Río Negro, one-half hour upstream of San Carlos de Río Negro, 4 Dec 1984.—USNM 272610, 5, 32.2–36.0 mm SL, San Carlos de Río Negro, Río Negro margin upstream of town landing, 3 Dec 1984.—MZUSP 30252, 6, 31.8–38.9 mm SL; USNM 276505, 6, 37.0–41.4 mm SL, Brazil, Amazonas, Rio Negro, Massarabi, sandy beach just above Barcelos (approx. 00°57'S, 62°56'W), 18 Oct 1979.—MZUSP 30247, 6, 32.7–37.3 mm SL; USNM 276504, 5, 35.7–39.8 mm SL, Brazil, Amazonas, Rio Negro, beach, Ilha Tamaquaré just downstream from Tapurucuara (approx. 00°25'S, 64°55'W), 10 Oct 1979.

The following non-type specimens were also examined: USNM 276502, 14; MBUCV V-15253, 24; Río Negro, one-half hour upstream of San Carlos de Río Negro.—USNM 276501, 15, San Carlos de Río Negro, Río Negro margin, upstream of town landing.—AMNH 56175, 33; MBUCV V-15252, 20, Río Negro at San Carlos de Río Negro.

*Diagnosis.*—The presence of prominent anteriorly divergent pelvic bones that are exserted in most individuals of *Astyanax scologaster* distinguishes the species from other characids with the exception of *A. mucronatus* Eigenmann, *A. essequibensis* Eigenmann, *A. zonatus* Eigenmann, *Deuterodon pinnatus* Eigenmann and *D.*

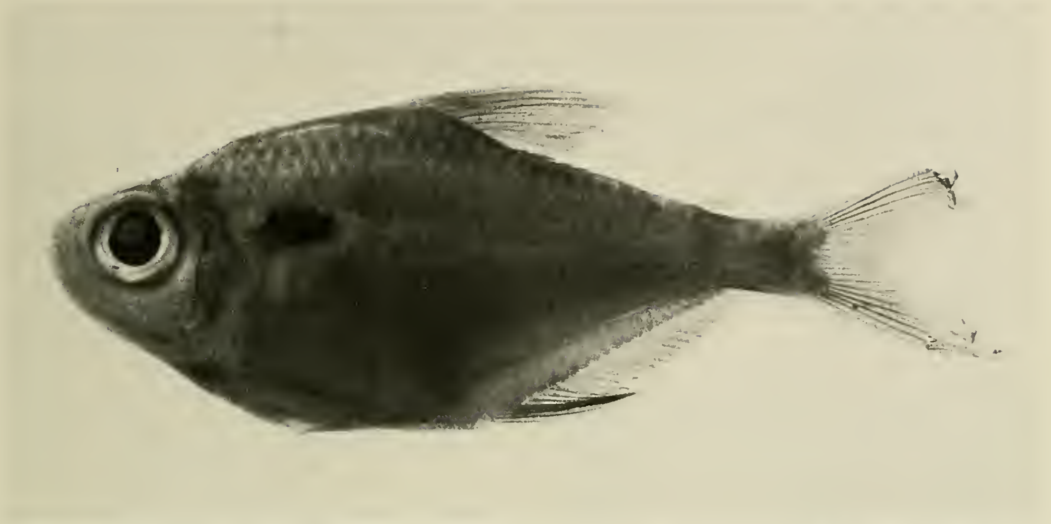

Fig. 2. *Astyanax mucronatus* Eigenmann, cotype, FMNH 53521, 54.6 mm SL, Guyana, Potaro River, Tukeit.

*acanthogaster* Eigenmann. *Astyanax scologaster,* as other *Astyanax* species, has strong central cusps on all teeth and an abrupt change in the size of the teeth on the dentary which distinguishes the new species from all *Deuterodon* species which have flattened teeth without strong central cusps, and dentary teeth in a graduated size series. *Astyanax scologaster* has 21 or 22 branched anal-fin rays compared with 24 or 25 in *A. mucronatus,* 19 or 20 in *A. essequibensis,* and 25 to 29 in *A. zonatus. Astyanax scologaster* has 33 to 35 scales in the lateral series versus 40 to 45 for *Astyanax zonatus.* Although the pigmentation patterns of *Astyanax scologaster* and *A. mucronatus* are similar, the anterior humeral spot of *A. scologaster* is narrower and more vertically elongate than the horizontal wedge-shaped humeral spot of *A. mucronatus* (compare Figs. 1 and 2). The relatively large eye of *Astyanax scologaster* (42.2–48.8% of HL) distinguishes that species from *A. zonatus* (37.7–40.6% of HL) and *A. essequibensis* (38.5–44.0% of HL). *Astyanax scologaster* is not as deep bodied as *A. mucronatus* (34.9–42.1 vs. 36.9–45.4% of SL; compare also Figs. 1 and 2), but deeper bodied than *A. essequibensis* (30.7–36.8% of SL) or *A. zonatus* (31.8–35.9% of SL).

*Description.*—Table 1 gives morphometrics of holotype and measured paratypes. No evidence of sexual dimorphism in meristics or morphometrics was found. Body moderately deep, somewhat compressed, broadest in region of exsertion of pelvic spines in both sexes. Greatest body depth between origins of dorsal and pelvic fins, except in population from Massarabi in which greatest depth is in region of pelvic-spine exsertion, about midway between origins of pectoral and pelvic fins. Origin of dorsal fin closer to tip of snout than to hypural joint and often anterior to vertical line through origin of pelvic fin. Distance from snout to pelvic-fin origin ($\bar{x}$ = 50.9% of SL) usually greater than distance from snout to dorsal-fin origin ($\bar{x}$ = 49.2% of SL). Dorsal profile of head and body slightly convex from dorsal to orbit to dorsal-fin origin. Dorsal profile of body along dorsal-fin base nearly straight, posteroventrally oriented, nearly straight to slightly convex between dorsal and adipose fins. Caudal peduncle slender, compressed, rather short. Ventral profile of body slightly convex from sym-

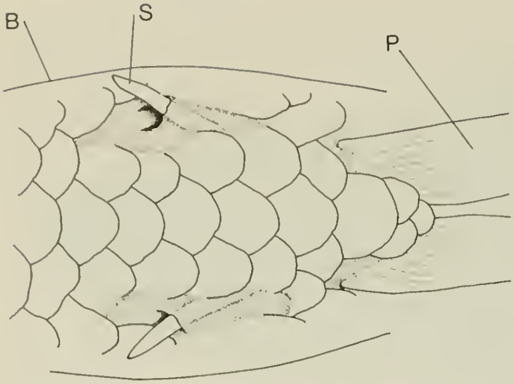

Fig. 3. *Astyanax scologaster,* new species, USNM 276503, 42.0 mm SL. Ventral view of pelvic-fin insertion and anteriorly proximate portion of body showing anteriorly divergent, exserted pelvic bones. Area in stipple pattern is without scales. S, pelvic spine. P, pelvic fin. B, body profile.

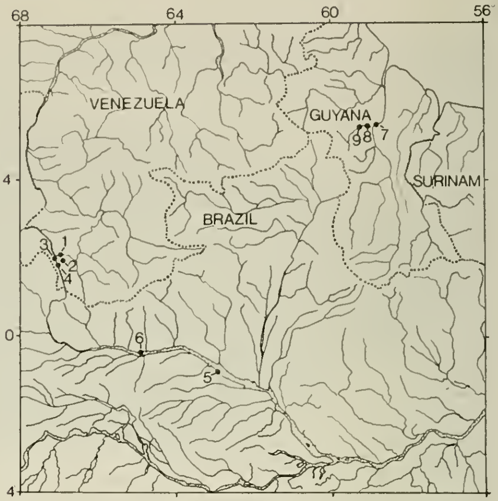

Fig. 4. Map of portion of northern South America showing collecting localities of specimens of *Astyanax scologaster,* new species, *A. mucronatus* Eigenmann and *A. essequibensis* Eigenmann reported on in this paper (dotted lines depict international boundaries). Localities 1 to 6 are collection sites of *A. scologaster*: 1, Caño Manu; 2, Caño Chola; 3, upstream of San Carlos de Río Negro; 4, San Carlos de Río Negro; 5, Massarabi; 6, Ilha Tamaquaré. See listing of holotype, paratypes, and non-type specimens examined for detailed locality and collection information. Localities 7 to 9 are collection sites of *A. mucronatus* and *A. essequibensis*: 7, Crab Falls; 8, Tumatumari; 9, Tukeit. See listing of "Comparative Material Examined" for more detailed locality information.

physis of lower jaw to origin of pelvic fin, sometimes with sharp angle at point of pelvic-spine exsertion from body; body transversely rounded anterior to this fin. Profile nearly straight between pelvic and anal fins (or nearly straight between pelvic-spine exsertion and anal-fin origin as in Fig. 1); straight and posteroventrally oriented along base of anal fin. Ventral profile of caudal peduncle slightly concave.

Head length moderate, slightly more than one-quarter of standard length, snout rounded in profile, moderate in length, jaws equal and mouth terminal, or lower jaw slightly shorter and mouth barely subterminal. Mouth nearly horizontal or slightly posteroventrally slanted; gape moderate, wider than snout length. Eye large. Interorbital width moderate, flat to slightly rounded transversely, but narrower than upper jaw width. Maxilla long, slightly lobed posteriorly; reaching slightly posterior to vertical line through anterior border of eye, and ventral to horizontal line through ventral border of eye.

Maxilla with 3 to 5 very small compressed teeth; usually with 4 cusps, but with 5 cusps in some populations, third cusp longest. Premaxillary teeth in two series. Outer series usually in rather uneven row of 4 teeth of differing forms; third tooth from symphysis narrower, rather round in cross section, and with 3 cusps. Remaining teeth of outer premaxillary series broader, more ovoid in cross section, with at least a very small additional pair of cusps for a total of 5. Inner series of premaxillary teeth consisting of 5 broad teeth extending across gape. Each tooth with prominent central cusp flanked by two or, more usually, three pairs of cusps of decreasing size arranged in semicircle progressing around anterior border of tooth. Lateralmost premaxillary tooth smaller, semi-compressed, sometimes almost indistinguishable in form from dorsalmost maxillary tooth. Dentary with 5 large teeth along anterodorsal margin of

Table 1.—Morphometrics of *Astyanax scologaster,* new species. Standard length is expressed in mm; measurements 1 to 12 are percentages of standard length; 13 to 16 are percentages of head length.

| | | Paratypes (59) | |
|---|---|---|---|
| | Holotype | Range | Average |
| Standard length | 37.5 | 28.8–42.0 | |
| 1. Greatest body depth | 38.9 | 34.9–42.1 | 38.2 |
| 2. Snout to pelvic-fin origin | 50.1 | 48.3–53.2 | 50.9 |
| 3. Snout to dorsal-fin origin | 48.3 | 47.3–52.0 | 49.2 |
| 4. Dorsal-fin origin to caudal base | 56.0 | 53.6–57.6 | 55.6 |
| 5. Snout to anal-fin origin | 64.3 | 61.9–67.4 | 64.1 |
| 6. Caudal peduncle length | 12.3 | 11.2–13.6 | 12.5 |
| 7. Caudal peduncle depth | 9.9 | 8.8–10.6 | 9.7 |
| 8. Pelvic-fin length | 16.8 | 15.1–18.3 | 17.0 |
| 9. Length pelvic bone | 10.9 | 10.0–12.6 | 11.5 |
| 10. Distance between exserted tips of pelvic bones | 8.3 | 5.3–14.2 | 9.4 |
| 11. Snout to pectoral-fin origin | 28.5 | 26.5–30.3 | 28.6 |
| 12. Bony head length | 28.8 | 27.7–31.2 | 29.6 |
| 13. Horizontal eye diameter | 46.3 | 42.2–48.8 | 45.9 |
| 14. Snout length | 29.6 | 23.6–31.1 | 27.4 |
| 15. Upper jaw length | 42.6 | 38.4–44.0 | 41.4 |
| 16. Bony interorbital width | 29.6 | 26.7–34.2 | 30.6 |

bone. Large dentary teeth similar in form to inner premaxillary teeth, fitting closely behind latter when mouth closed. Central cusp long and strong; usually flanked by two pairs of smaller cusps. Larger dentary teeth followed posteriorly by 6 to 8 very small teeth with 1 to 3 uneven cusps.

Infraorbital series complete, all elements relatively small, ventral and posterior infraorbitals not contacting sensory tube of preopercle. Frontoparietal fontanel extending into posterior portion of ethmoid; parietals completely separated; frontals in contact only at epiphyseal bar. Fontanel gradually widening posteriorly, extending onto dorsomedial portion of supraoccipital. Supraoccipital spine moderately developed. Adipose eyelid (a thick band of clear connective tissue) extending posteriorly from nostrils over lateral surface of head and anterior midlateral portion of body to anterior humeral spot; with large, almost circular opening over eye.

Dorsal-fin rays ii,8,i or ii,9 [ii,9]; second unbranched ray usually rather short, less than one-half length of longest fin-ray; longest rays are first and/or second branched rays. Dorsal fin length moderate. Pectoral-fin rays i,11 to i,14 [i,13]. Pectoral fin length moderate, usually not extending posteriorly to vertical through pelvic-fin origin. Cleithrum large, anterodorsal border approaches posterior border of preopercle. Posterolateral tips of coracoid bones widely separated. Pelvic-fin rays i,7 in all specimens. Fin moderate in length, tips usually extending to near anal-fin origin. No hooks present on fin rays. Overall shape of pelvic bone modified anteriorly into strong spine. Anterior tips of two pelvic bones diverging widely and usually exserted from body wall. Length of pelvic bone measured from insertion of fin rays to tip of exserted spine 10.0–12.6% of SL, $\bar{x}$ = 11.5 [10.9], up to nearly half of length of bone exserted; distance between anterior tips of spines 5.3–14.2% of SL, $\bar{x}$ = 9.4 [8.3].

Anal fin with 2 or 3 unbranched anterior rays (first ray very small in many specimens examined, suggesting that very small first ray typically present but not always visible) [2], followed by 20 to 23 branched rays, $\bar{x} = 21.6$ [23]. Last ray divided to base and counted as two rays in most individuals, but in many specimens from Massarabi and Tamaquaré posterior portion of ray unbranched and not included in branched-ray count. Anal-fin margin concave with longer anterior rays forming small anterior lobe; following rays abruptly shorter; fin shape similar in both sexes. No hooks present on anal-fin rays, but absence of hooks on anal- and pelvic-fin rays may be seasonal. Basal sheath of scales on anal fin short, consisting of 5 to 7 scales along anterior portion of fin base. Caudal-fin rays i,9/8,i in all specimens examined. Caudal fin moderate in length, rather narrow, deeply forked, ventral lobe usually slightly larger than dorsal. Adipose fin of moderate size.

Scales in lateral series 33 to 36 [35]. Scale rows in vertical series between dorsal- and pelvic-fin origins usually 7/5 [7/5].

Vertebrae of holotype and 25 paratypes: 33 (1), 34 (20), 35 (5).

*Color in life.*—Overall coloration of head and body bright silver.

*Color in alcohol.*—Color description based on holotype (Fig. 1). Scales lacking guanine, ground color pale yellowish tan, slightly darker dorsally. Head with small to medium dark brown chromatophores dorsally and anteriorly. Few large brownish chromatophores ventrally near maxilla and on first infraorbital bones; larger, darker chromatophores on opercle and preopercle. Dark blackish chromatophores extending along base of dorsal fin and posteriorly to dorsal caudal-fin rays. Dark chromatophores present along base of anal fin. Scattered fine dark chromatophores along borders of scales of median predorsal scale row, horizontal scale rows 1 to 3 on region anterior to dorsal fin, and scales of most of body posterior to dorsal fin. Anteroventral portions of body pale except for few chromatophores along scale borders and ventral portions of humeral spots.

Two humeral spots present. Anterior a dusky vertical bar darkest on third and fourth scales of sixth horizontal scale row. Bar extending dorsally into third horizontal scale row and ventrally into ninth scale row; somewhat paler ventral to lateral line. Posterior humeral spot about two scales behind anterior spot. On holotype two humeral spots about same length but posterior spot narrower dorsally and much lighter. Most other specimens with posterior humeral spot smaller. Light dusky midlateral band of widely scattered small dark chromatophores extending from posterior border of posterior humeral spot to caudal-fin base, widening on caudal peduncle to form pale, indistinct caudal spot terminating posteriorly at caudal-fin base. Few large brown chromatophores proximally on membranes of middle caudal-fin rays. Dusky patches on dorsal and ventral lobes of caudal fin aligned with dorsal and ventral corners of caudal peduncle spot.

Dorsal-fin membranes with patch of small black chromatophores forming indistinct horizontal band across middle of fin. Anal fin with band of dusky chromatophores along middle of fin and basal dusky spot anteriorly. Median portion of pectoral fin dusky. Dorsal border of adipose fin with several black chromatophores. Pelvic and pectoral fins almost clear.

*Etymology.*—The specific epithet, *scologaster* from the Greek *skolos,* thorn or pointed object, and *gaster,* stomach, refers to the exserted spinous pelvic bones on the ventral surface of the body of this species.

*Relationships.*—The common possession of an exserted pelvic bone and *Astyanax*-type dentition (see "Diagnosis") unites *Astyanax scologaster, A. mucronatus, A. essequibensis,* and *A. zonatus.* The exact relationships of the species within this grouping remain unresolved.

*Ecology.*—*Astyanax scologaster* is an inhabitant of the black-water main river channels and tributary streams over much of the Río Negro basin. The species has been captured both along the margins of the swiftly flowing main channel of the Río Negro and in slowly flowing terra-firma tributary streams. Comparative daytime and nighttime sampling with nets at two localities on the upper Río Negro has shown that the species is active at night, but absent during the daylight hours (RPV, pers. obs.).

*Comparative material examined.—Astyanax mucronatus* Eigenmann: FMNH 53520, holotype; Guyana, Essequibo, Potaro River, Tumatumari Cataract.—FMNH 53521, 5 cotypes; CAS 39347, 4 cotypes; MCZ 29963, 1 cotype; Guyana, Essequibo, Potaro River, sandbank at Tukeit.

*Astyanax essequibensis* Eigenmann: FMNH 53519, holotype; CAS 39144, 24 paratypes; SU 21956, 5 paratypes; Guyana, Essequibo, Potaro River, Tumatumari Cataract.—FMNH 52962, 11 cotypes; MCZ 29958, 2 cotypes; CAS 39146, 23 cotypes; Guyana, Essequibo, Essequibo River, Crab Falls.

*Astyanax zonatus* Eigenmann: MCZ 20768, 1 syntype; MCZ 20766a, 1 syntype; MCZ 20753, 2 syntypes; Brazil, Amazonas, Rio Solimões, Tabatinga.

*Deuterodon pinnatus* Eigenmann: FMNH 53525, holotype; FMNH 53526, 3 paratypes; MCZ 29952, 2 paratypes; Guyana, Essequibo, Potaro River, Amatuk Cataract.—MCZ 29951, 2 cotypes; Guyana, Essequibo, Essequibo River, Warraputa Cataract.

*Deuterodon acanthogaster* Eigenmann: FMNH 54748, holotype; Brazil, Mato Grosso do Sul, Corumbá.—FMNH 54750, 5 cotypes; Brazil; Mato Grosso do Sul, Rio Jaurú, SW of São Luis de Caceres.—USNM 232385, 3; Paraguay, Amambay, Río Aquidaban, Parque Nacional Cerro Cora.—MZUSP 30868, 5; Brazil, Para, Rio Itacainos, Serra dos Carajás.—MZUSP 30543, 5; Brazil, Para, Rio Tapajos between Jacaré-a-Canga and Itaituba.

*Remarks.*—Eigenmann (1911:180, Fig. 2) in his original description of *Deuterodon acanthogaster* noted that the species was characterized by protruding innominate bones (= pelvic bones) but did not comment on the presence of the structures in any other members of the genus. Comparative studies associated with this study have disclosed comparable spines in *Deuterodon pinnatus* Eigenmann.

*Resumen.—Astyanax scologaster* es descrita provenientes de varias localidades del medio y alto Río Negro de Venezuela y Brasil. Esta especie se caracteriza por poseer la sección anterior de los huesos pélvicos modificados en unas espinas lateralmente divergentes, las cuales se extienden a través de la piel en la mayoría de los individuos. Una modificación similar ha sido observada en *Astyanax essequibensis, A. mucronatus, A. zonatus, Deuterodon pinnatus,* y *D. acanthogaster.* Las tres especies de *Astyanax* con los huesos pélvicos prominentes pueden ser distinguidas de las especies de *Deuterodon,* por una serie caracteres dentales. *Astyanax scologaster* se diferencia de sus congéneres por poseer 21 ó 22 radios anales bifurcados, comparado con 24 ó 25 en *A. mucronatus,* 19 ó 20 en *A. essequibensis* y 25–29 in *A. zonatus.* Los patrones de coloración y diferencias morfométricas y merísticas, distinguen aún más a *A. scologaster* del resto de las especies.

## Acknowledgments

The specimens that served as the basis for this study were collected by a joint MBUCV-USNM expedition to the upper Río Negro, and as a corollary to AMNH collecting efforts associated with the expedition to Cerro de la Neblina National Park organized by La Fundacion para el desarrollo de Las Ciencias Fisicas, Matematicas y Naturales. We thank Dr. Antonio Machado-Allison (MBUCV) for his efforts in organizing the MBUCV-USNM expedition. He, along with Mr. Carl J. Ferraris, Jr., Lic. Justa M. Fernandez, Lic. Otto Castillo, and Sr. Ramiro Royero assisted in collecting the specimens. Specimens from the Brazilian portions of the Rio Negro were collected in

1979 by Dr. Michael Goulding, then of the Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil. That material, subsequently sorted and housed at the Museu Paraense Emilio Goeldi, Belém, Pará, Brazil, and now deposited at MZUSP, was loaned for this study by Dr. Naércio A. Menezes. Mr. Andrew G. Gerberich, Mr. Kurt A. Bruwelheide and Ms. Ann M. Williams provided technical assistance at USNM. Figures 1 and 2 were prepared by Mr. Theophilus Britt Griswald. The Spanish translation of the "Resumen" was provided by Dr. Antonio Machado-Allison. Participation by one of us (RPV) in collecting efforts on the upper Río Negro was made possible by a grant from the Scholarly Studies Program of the Smithsonian Institution. Research associated with this study was supported in part by the I.E.S.P. Neotropical Lowland Research Program of the Smithsonian Institution. This paper was improved by the comments and suggestions of Dr. Stanley H. Weitzman and Dr. Wayne C. Starnes.

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# BARNACLES (CIRRIPEDIA: BALANIDAE) FROM THE LOWER PLEISTOCENE JAMES CITY FORMATION, NORTH CAROLINA COASTAL PLAIN, WITH THE DESCRIPTION OF A NEW SPECIES OF *BALANUS* DA COSTA

Victor A. Zullo and William Miller, III

*Abstract.*—Numerous specimens of *Balanus neusensis*, new species, and *B. improvisus* Darwin, and a few specimens of *B. calidus* Pilsbry occur in association with a *Crepidula fornicata* (Linnaeus) biostrome in the lower Pleistocene James City Formation at Johnson Point, Neuse River, Craven County. *Balanus improvisus* and *B. neusensis* also are reported from an isolated James City outcrop at Dam Creek on the Neuse River and from a tidal inlet deposit of presumed equivalent age at Woodside, Pender County. The extant tropical American and Carolinian species *B. calidus* is common in inner shelf deposits of early Pleistocene age in the Carolinas, whereas the extant North Atlantic species *B. improvisus* is more typically found in younger Pleistocene marginal marine deposits of the region. *Balanus neusensis* appears to be the youngest surviving species of the *B. pacificus* Pilsbry group in the western Atlantic, and a descendent of the Pliocene species *B. oppidieboraci* Ross.

Bulk sediment samples from two localities in the lower Pleistocene James City Formation on the Neuse River, Craven County, North Carolina yielded remains of three species of barnacles (Fig. 1). The samples were taken and processed by Miller as part of a paleoecologic study of the James City fauna (Miller and DuBar, in prep.). The majority of barnacle specimens were associated with a *Crepidula fornicata* (Linnaeus) biostrome at Johnson Point in the type area of the formation (UNCW locality Z-807). The second locality (UNCW locality Z-808) near Dam Creek, is an isolated outcrop of James City sediments that yielded relatively few barnacle remains. The abundance of barnacles at the Johnson Point locality is related to the numerous attachment sites for sessile, epibenthic organisms provided by the large, tabular accumulation of the sedentary epifaunal gastropod *Crepidula fornicata*. Two of the Johnson Point barnacles, *Balanus improvisus* Darwin and *B. calidus* Pilsbry, are extant species with Pleistocene fossil records on the Atlantic coast. The third and most abundant barnacle is a new species that bears considerable superficial resemblance to the extant estuarine Atlantic Coast species *B. eburneus* Gould, but is, rather, related to the *Balanus pacificus* Pilsbry group. Extant members of the *B. pacificus* group are known only from the Pacific basin, but Neogene representatives are known from the Atlantic Coast Pliocene, and *Balanus oppidieboraci* Ross, a likely precursor of the new species, occurs in the Pliocene Yorktown Formation of Virginia.

Only a few specimens of the new species and of *B. improvisus* were identified at the Dam Creek locality. As discussed in the section on paleoenvironments and paleoecology, differences in abundances of barnacle remains at the two sites are related to the location of the two sites within the James City embayment and to concomitant differences in depositional environment. The Johnson Point biostrome accumulated in a relatively high energy, shallow water envi-

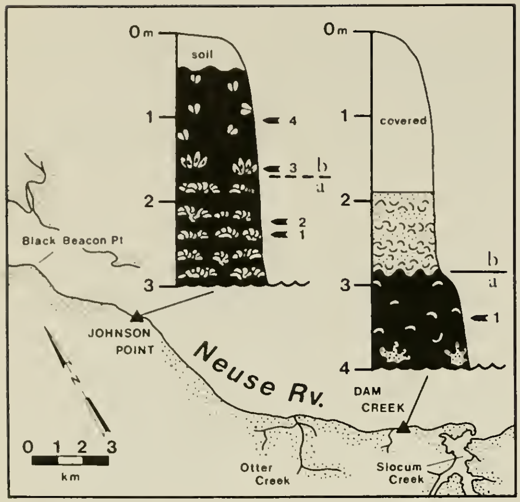


Fig. 1. Location of James City Formation collecting sites on the Neuse River, Craven County, North Carolina.

ronment where sedimentation rates were low. Barnacles, in addition to requiring the hard substrata for settlement provided by the *Crepidula fornicata* biostrome, are filter feeders that thrive in higher energy sites with little sedimentation. The Dam Creek site, by comparison, represents a deeper water, bay-center deposit where very fine-grained sediments were being deposited and few hard substrata were available. It is likely that the barnacle remains preserved at the Dam Creek locality are allochthonous.

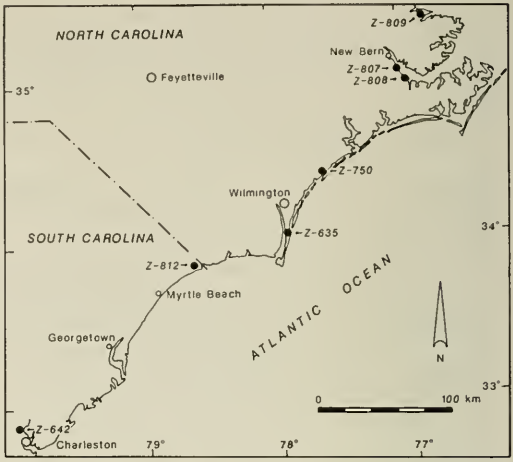


Fig. 2. Location of North and South Carolina Pleistocene sites discussed in text.

A few, worn, disarticulated specimens of the new species and some juvenile, but well preserved entire individuals of *B. improvisus* were obtained from a tidal inlet deposit of presumed equivalent age at Woodside, Pender County, North Carolina (UNCW locality Z-750; Fig. 2). This is the only other known occurrence of the new species. *Balanus improvisus,* however, is common in later Pleistocene, marginal-marine deposits both in North and South Carolina and is presently found to range from the nearshore subtidal up through the mid-intertidal zone, primarily in marginal-marine environments. To the north of Cape Hatteras, *B. improvisus* is essentially restricted to estuaries (oligohaline through polyhaline), but to the south this species can be abundant in polyhaline and coastal euhaline waters.

*Balanus calidus* is probably the most commonly encountered barnacle in lower Pleistocene deposits of the Carolinas. Pleistocene examples are usually found in great numbers on shells of *Ostrea sculpturata* Conrad from localities that have been interpreted as representing open water environments or embayments with unrestricted circulation (e.g., Lee Creek Mine, Beaufort County, North Carolina). Extant populations are found in marine waters at subtidal depths and are best developed on the inner and middle shelf.

## Stratigraphic Setting

Three lithostratigraphic units crop out along the Neuse River east of New Bern (DuBar and Solliday 1963, Mixon and Pilkey 1976, Miller 1985). These are, in ascending order: 1) lower Pleistocene James City Formation, exposed for the most part along the south shore from Black Beacon Point downstream to Johnson Point; 2) middle Pleistocene Flanner Beach Formation, in bluffs along both sides of the river extending from Johnson Point to the Suffolk (or Grantsboro) Scarp; and 3) upper Pleistocene Core Creek sand, which is poorly exposed downstream from the Suffolk Scarp (Fig. 1). All three units were deposited during glacio-eustatic high stands that occurred at 1,000,000–800,000 yr, 200,000 yr, and 100,000 yr B.P., respectively (McCartan et al. 1982, Cronin et al. 1984).

The oldest Pleistocene depositional cycle is represented by fine-grained, fossiliferous, nearshore marine beds of the James City Formation (DuBar and Solliday 1963, DuBar and Howard 1969, DuBar et al. 1974). The Johnson Point exposure consists of a bluish gray to olive gray, shelly mudstone to siltstone, broadly divisible into a lower bed made up of discontinuous, thin layers of *Crepidula fornicata* shells in life position (stacks of adhering shells) and an upper bed characterized by varied, abundant fossil bivalves, especially *Anadara aequicostata* Conrad, *Ostrea sculpturata* Conrad and *Noetia limula* Conrad. At Dam Creek, slightly over one meter of the James City Formation is overlain disconformably by the Flanner Beach Formation. Here, the James City is a bluish-gray, moderately fossiliferous mudstone to claystone containing valves of the small bivalve *Nuculana acuta* (Conrad). Near the base of the outcrop, heads of the ahermatypic coral *Septastrea* occur in apparent life position (Miller 1985:120).

The James City beds, both at Johnson Point and Dam Creek, were deposited as muddy, more or less shelly sediments within a protected, subtropical marine embayment. Johnson Point appears to be part of a regressive sequence, with deeper subtidal deposits containing the *Crepidula* bank fauna succeeded in the section by shallower subtidal deposits containing a great variety of mollusks and other organisms. Dam Creek seems to be a deeper, bay-center deposit that accumulated basinward of the Johnson Point sequence.

Presumably contemporaneous, sandy, open marine beds are exposed 40 km north of the Neuse River in the Lee Creek Mine at Aurora (referred to as "Croatan Formation" by many workers; see contributions in Ray 1983). The exact temporal and paleogeographic relationships between the James City Formation in the Neuse River Valley area and the Waccamaw Formation in southeastern North Carolina and northeastern South Carolina, traditionally regarded as coeval units, are far from being clear. A recent interpretation based on multiple lines of evidence suggests that the James City Formation may be a little younger than most of the Waccamaw (Cronin et al. 1984).

## Paleoenvironments and Paleocommunities

Table 1 lists the most abundant autochthonous invertebrate fossils in samples collected from Johnson Point and Dam Creek. This list gives a general sense of the benthic paleocommunity contexts for balanids living in James City depositional environments. A part of this ecosystem-level context at Johnson Point included long-term community replacement resulting from sustained, unidirectional habitat alteration in subevolutionary time (Miller 1986). The faunal transition at Johnson Point involved the fairly abrupt decline of the biostrome and its replacement by a more diverse, level-bottom community with many infaunal, suspension-feeding bivalves, carnivorous and scavenging gastropods, and occasional clumps of oysters.

Little is known about the conditions conducive to extensive buildups of *C. fornicata* into banks the size of the Johnson Point biostrome, which is estimated to have covered up to 15,000 m$^2$ of sea floor during maximum development (Miller and DuBar, in prep.). A long period of low turbidity, consistent currents carrying food supplies, and near-normal marine salinity probably were key factors (see Johnson 1972, DuBar et al. 1974:111, Hoagland 1979). Changes in currents, probable shallowing in the Johnson Point area, and a shift in local disturbance regime (seasonality, frequency, intensity, and geographic extent of physical disturbance; see Sousa 1985, Connell and

Table 1.—Most important components of fossil associations from the James City Formation in the Neuse valley. Only organisms with individuals making up ≥0.5% of the association are listed. Format includes taxon, relative abundance, followed by organism type/substrate niche + feeding category. All abbreviations explained at foot of table; sample numbers refer to Fig. 1.

| | | |
|---|---|---|
| I. *Crepidula* biostrome association (Johnson Point, samples 1 and 2) | | |
| *Crepidula fornicata** | 43.2% | Ga/EPSF |
| *Boonea seminuda* | 29.5 | Ga/EPPA |
| *Balanus* spp. | 8.6 | Ci/EPSF |
| *Nuculana acuta* | 4.8 | Bi/INDF |
| *Ostrea sculpturata* | 4.3 | Bi/EPSF |
| *Anadara aequicostata* | 2.3 | Bi/INSF |
| *Anachis lafresnayi* var. | 1.5 | Ga/VAGC |
| *A. obesa* | 1.5 | Ga/VAGC |
| *Nassarius albus* | 0.8 | Ga/VAGS |
| II. *Ostrea* clump association (Johnson Point, sample 3) | | |
| *Crepidula fornicata* | 30.2% | Ga/EPSF |
| *Boonea seminuda* | 27.9 | Ga/EPPA |
| *Balanus* spp. | 10.8 | Ci/EPSF |
| *Nuculana acuta* | 7.4 | Bi/INDF |
| *Ostrea sculpturata** | 6.7 | Bi/EPSF |
| *Anadara aequicostata* | 2.7 | Bi/INSF |
| *Mulinia lateralis* | 1.2 | Bi/INSF |
| *Turbonilla* (*Chemnitzia*) sp. | 1.1 | Ga/EPPA |
| *Sphenia* sp. | 1.1 | Bi/INSF? |
| *Boonea impressa* | 1.1 | Ga/EPPA |
| *Anachis obesa* | 1.0 | Ga/VAGC |
| *A. lafresnayi* var. | 0.9 | Ga/VAGC |
| *Mercenaria* sp. cf. *M. permagna* | 0.7 | Bi/INSF |
| *Abra aequalis* | 0.7 | Ga/VAGC |
| *Urosalpinx perrugata* | 0.7 | Ga/VAGS |
| *Busycon* sp. | 0.6 | Ga/VAGS |
| *Nassarius albus* | 0.6 | Ga/VAGS |
| brachyurans | 0.5 | Ma/VAGS |
| III. *Anadara-Noetia* association (Johnson Point, sample 4) | | |
| *Crepidula fornicata* | 17.8% | Ga/EPSF |
| *Boonea seminuda* | 17.2 | Ga/EPPA |
| *Ostrea sculpturata* | 11.9 | Bi/EPSF |
| *Nuculana acuta* | 11.4 | Bi/INDF |
| *Balanus* spp. | 8.7 | Ci/EPSF |
| *Anadara aequicostata** | 8.0 | Bi/INSF |
| *Abra aequalis* | 4.4 | Bi/INDF |
| *Sphenia* sp. | 2.1 | Bi/INSF? |
| brachyurans | 1.5 | Ma/VAGS |
| *Anachis lafresnayi* | 1.5 | Ga/VAGS |
| *Boonea impressa* | 1.4 | Ga/EPPA |
| *Cumingia tellinoides* | 1.1 | Bi/INSF |
| *Mercenaria* sp. cf. *M. permagna* | 1.1 | Bi/INSF |
| *Mulinia lateralis* | 0.9 | Bi/INSF |
| *Turbonilla* (*Pyrgiscus*) sp. | 0.9 | Ga/EPPA |
| *Anachis obesa* | 0.8 | Ga/VAGC |
| *Turbonilla* (*Chemnitzia*) sp. | 0.7 | Ga/EPPA |
| *Melanella conoidea* | 0.7 | Ga/VAGU |
| *Urosalpinx perrugata* | 0.7 | Ga/VAGC |
| *Nucula proxima* | 0.6 | Bi/INDF |
| *Nassarius albus* | 0.6 | Ga/VAGS |
| *Polinices* sp. | 0.5 | Ga/VAGC |
| *Prunum* sp. | 0.5 | Ga/VAGU |
| *Noetia limula** | 0.5 | Bi/INSF |
| *Vermicularia* sp. cf. *V. knorri* | 0.5 | Ga/EPSF? |
| IV. *Nuculana* association (Dam Creek) | | |
| *Nuculana acuta** | 61.3% | Bi/INDF |
| *Mulinia lateralis* | 24.2 | Bi/INSF |
| *Parvilucina multilineata* | 4.0 | Bi/INSF |
| *Abra aequalis* | 2.1 | Bi/INDF |
| *Anadara aequicostata* | 1.1 | Bi/INSF |
| *Crassinella lunulata* | 1.1 | Bi/INSF |
| *Ensis* sp. | 1.0 | Bi/INSF |
| *Balanus* spp. | 1.0 | Ci/EPSF |
| *Prunum* sp. | 0.7 | Ga/VAGU |
| *Vermicularis* sp. cf. *V. knorri* | 0.5 | Ga/EPSF? |
| *Ostrea* sp. | 0.5 | Bi/EPSF |
| *Gemma gemma* | 0.5 | Bi/INSF |

Symbols used in table: *—dominant organism in terms of biovolume; lends name to association. Organism type: Bi—bivalve mollusk, Ga—gastropod mollusk, Ci—cirriped crustacean, Ma—malacostracan crustacean. Substrate niche + feeding category: INSF—infaunal suspension-feeder, INDF—infaunal deposit-feeder, EPSF—epifaunal suspension-feeder, EPPA—epifaunal parasite, VAGC—vagrant carnivore, VAGS—vagrant scavenger, U—unknown.

Keough 1985) led to disruption of the *Crepidula*-dominated community and establishment of the community represented by the *Ostrea* clump and *Anadara-Noetia* fossil associations (Table 1). In terms of changing spatial patterns, laterally extensive blankets of *Crepidula* stacks gave way to a much patchier and consequently more diverse community with only a few isolated *Crepidula* aggregations persisting in the area. Although barnacles are abundant throughout the transition sequence, they are more numerous in shelly beds within the biostrome probably because of widespread availability of hard substrata in the form of exposed *Crepidula* shells.

By comparison, balanids are uncommon at Dam Creek (Table 1) in a fossil association dominated by the infaunal, deposit-feeding bivalve *Nuculana acuta.* This association was derived from a deeper subtidal community inhabiting a very fine-grained, soft to possibly thixotropic bottom, offshore from the *Crepidula* biostrome and *Anadara-Noetia-Ostrea* paleocommunities (see Parker 1976).

## Locality Descriptions

University of North Carolina at Wilmington (UNCW):

Z-635 Cape Fear coquina, south side of Snows Cut, 650 m west of U.S. Highway 421 bridge over Atlantic Intracoastal Waterway, southern New Hanover County, North Carolina. V. Zullo, coll., 5 Sep 1980.

Z-642 Upper Pleistocene shell bed in borrow pit (since reclaimed) for construction of Mark Clark Expressway, on north side of Ashley Hall Road, 1370 m east of intersection with State Highway 61 (Ashley River Road) and west of Ashley River, Charleston County, South Carolina. V. Zullo, coll., 7 Feb 1981.

Z-750 Waccamaw Formation, quarry at seaward edge of +7.6 m terrace, southeast of U.S. Highway 17 at Woodside, Pender County, North Carolina. V. Zullo, coll., 26 Jun 1985.

Z-807 James City Formation, north side of Johnson Point in steep-sided bank, 500 m upstream (northwest) from tip of point and 400 m downstream (southeast) from pier at Veterans of Foreign Wars building, south shore of Neuse River, Craven County, North Carolina. W. Miller, coll., Aug 1982.

Z-808 James City Formation, basal bed in low bank 3.8 km upstream (northwest) from mouth of Slocum Creek and 700 m downstream (southeast) from mouth of Dam Creek, south shore of Neuse River, Craven County, North Carolina. W. Miller, coll., Aug 1982.

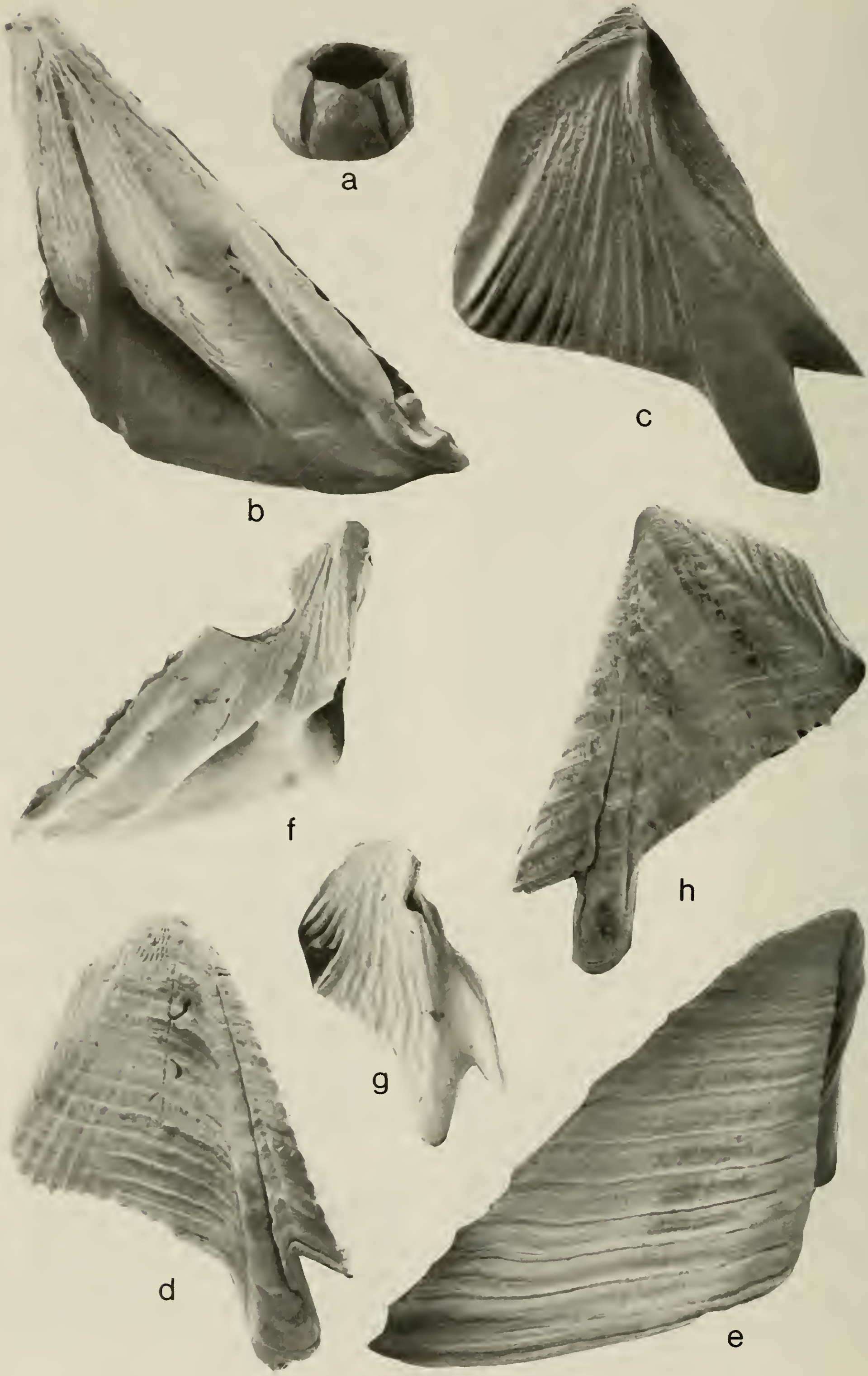
Z-809 "Croatan Sand," Lee Creek Mine, south shore of the Pamlico River, Richland Township, north of Aurora, Beaufort County, North Carolina. Aura Baker, coll., date unknown.

Z-812 Waccamaw Formation, Cedar Creek Village quarry, southeast side of U.S. Highway 17, Little River, Horry County, South Carolina. V. Zullo and W. B. Harris, coll., 1977.

## Systematic Paleontology

Suborder Balanomorpha Pilsbry, 1916
Superfamily Balanoidea Leach, sensu Newman and Ross, 1976
Family Balanidae Leach, sensu Newman and Ross, 1976
Subfamily Balaninae Leach, sensu Newman, 1980
Genus *Balanus* Da Costa, 1778
*Balanus improvisus* Darwin, 1854
Fig. 3

*Balanus improvisus* Darwin, 1854:250, pl. 6, fig. 1a–c; Pilsbry, 1916:84, text fig. 16a, pl. 24, figs. 3–3b, 5–5d; Henry and McLaughlin, 1975:68, text fig. 16, pl. 5, figs. a–f, g, h–j (see for complete synonymy).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*Material examined.*—Johnson Point, Neuse River, UNCW locality Z-807: 16 complete shells, over 200 compartmental plates, over 50 opercular plates.—Dam Creek, Neuse River, UNCW locality Z-808: 18 compartmental plates, 1 scutum.—Woodside, Pender County, UNCW locality Z-750: 6 shells, some with opercular plates, 8 isolated scuta, 3 isolated terga.—Snows Cut, New Hanover County, UNCW locality Z-635: 7 shells, 3 scuta, 5 terga.—Charleston County, South Carolina, UNCW locality Z-642: 9 compartmental plates, 1 tergum.

*Disposition of specimens.*—Figured hypotypes USNM 405359 through 405365 are in the collection of the Department of Paleobiology, National Museum of Natural History, Washington, D.C. Remaining specimens are in the collection of the Department of Earth Sciences, University of North Carolina at Wilmington.

*Geologic and geographic range.*—Recent: Scotland and Baltic Sea to West Africa; Mediterranean, Black, Caspian and Red seas; Nova Scotia to Patagonia; Oregon to Peru; Japan; Australia (Henry and McLaughlin 1975). Documented fossil occurrences: Pleistocene, North and South Carolina.

*Discussion.*—*Balanus improvisus* is a common element of estuarine faunas of the North Atlantic basin, and has been introduced to various localities throughout the world by ships. Fossils of this species have not been reported previously from the East Coast of North America. Kolosváry (1955, 1959, 1961a, b) cited *B. improvisus* from the Miocene (Burdigalian and Tortonian) of Hungary and the USSR without accompanying descriptions or illustrations of the specimens. Because of the antiquity of this extant species suggested by these records, and because of the distance of these localities from the known natural range of *B. improvisus,* Kolosváry's identifications are in doubt.

The specimens from the James City Formation and from Woodside are typical for the species, which is identified by: (1) its narrow radii with nonseptate sutural edges; (2) its scutum which lacks external radial striae and bears a well-developed adductor ridge; and (3) its tergum with its long, very narrow tergal spur and partially infolded spur furrow. *Balanus improvisus* is also known from late Pleistocene deposits in the Carolinas, including the Cape Fear "coquina" in southern New Hanover County, North Carolina (UNCW locality Z-635) and an upper Pleistocene shell bed northwest of Charleston, South Carolina (UNCW locality Z-642; Zullo 1986).

### *Balanus neusensis,* new species

Figs. 4a–e, 5, 6

*Holotype.*—Shell with opercular plates, USNM 405366.

*Type locality.*—*Crepidula fornicata* biostrome, UNCW locality Z-807, James City Formation, Johnson Point, Neuse River, Craven County, North Carolina.

*Diagnosis.*—Smooth to irregularly plicate, high conic shell with moderately-toothed, subtriangular orifice and broad radii with oblique, crenate summits; parietal tubes open throughout; basis porous, pores not septate; scutum very narrow, with prominent radial striae, markedly denticu-

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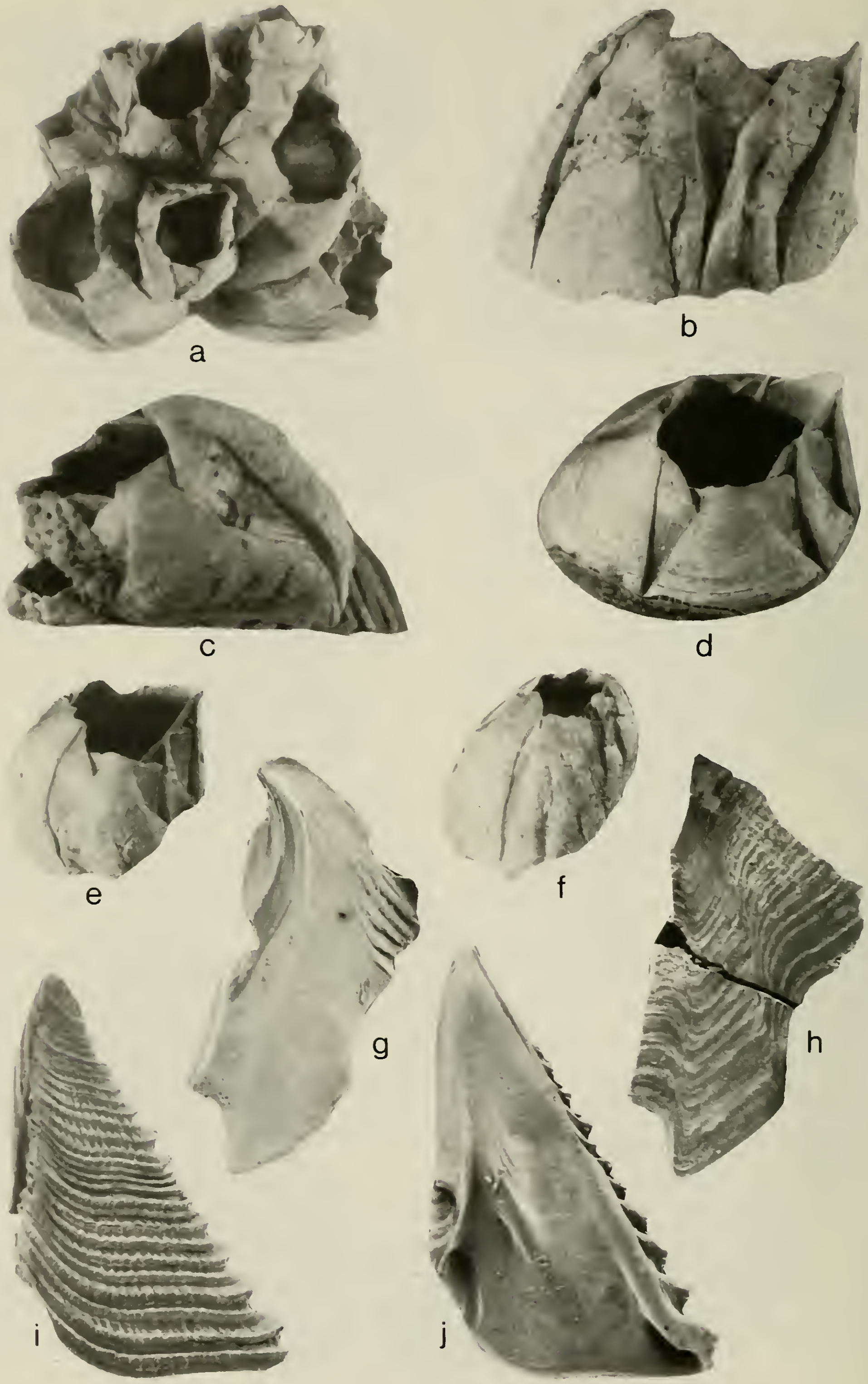
Fig. 3. *Balanus improvisus*: a, Side view of shell, hypotype USNM 405359, ×3; b, Interior of scutum, hypotype USNM 405360, ×18; c, Interior of tergum, hypotype USNM 405361, ×21; d, Exterior of tergum, hypotype USNM 405362, ×21; e, Exterior of scutum, hypotype USNM 405363, ×25; f, g, Interiors of scutum and tergum, hypotype USNM 405364, ×37; h, Exterior of tergum, hypotype USNM 405365, ×33. Figures a–e, UNCW locality Z-807, Johnson Point; f, g, UNCW locality Z-750, Woodside; h, UNCW locality Z-642, Charleston.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late occludent margin, prominent, high adductor ridge extending nearly from apex to basal margin and separated from erect articular ridge by deep, narrow cleft; tergum relatively narrow, with infolded, partially closed spur furrow and short, narrow spur placed its own width from basiscutal angle; basal margin of tergum not embayed on carinal side.

*Description.*—Shell (Figs. 4a–e, 5d–g) of moderate size (largest 2.4 cm in height and 2 cm in greatest basal diameter), high conic to subcylindric, with large, moderately-toothed, subtriangular orifice; parietes smooth or irregularly plicate, plications reflecting irregularities of substratum; radii thick, solid, moderately broad, glossy, horizontally striate, with roughly crenulated summits sloping about 30° from horizontal; sutural edges of radii septate, with prominent denticulae on lower sides of septa; edges of parietes receiving sutural edges of radii also septate, with denticulae on upper sides of septa; alae thick, broad, short, with moderately convex summits and finely-septate sutural edges; sheath solid, short, confined to upper third of interior of shell; basal margin of sheath thin, dependent, forming deep, narrow, non-vesiculate cavity between edge of sheath and interior of parietes; interior of parietes strongly and regularly ribbed near base, ribs fading towards base of sheath; internal ribs conforming to parietal septa; parietal tubes numerous, round to oval, moderately large, open from apex to base; occasional, single, fine, secondary septa extending into parietal tubes from external lamella; basis porous, thin at center, thickening at margin; basal tubes small, non-septate.

Scutum (Figs. 5c, d, g, 6a–c) nearly flat, very narrow, thick; narrow strip of tergal margin sharply reflexed inward at 90°; exterior ornamented by prominent growth ridges (best developed on lower half of plate) that are broken into nodes where they are crossed by deeply incised radial striae on central third of plate; striate central third of plate noticeably sulcate; reflexed tergal margin and narrow strip of plate adjacent to occludent margin without radial striae; major growth ridges extending onto occludent margin to form large, obliquely-inclined occludent teeth; apex and basioccludent angle acute, basitergal angle truncate at about 45°; occludent margin straight; tergal margin straight to slightly convex; basal margin sinuous, with central third convex, reflecting central, external sulcus of plate; length of basal margin no more than one-half length of occludent margin; articular ridge prominent, erect, with broad, flat upper surface, and extending from just below apex of plate to just beyond midpoint of plate; articular furrow moderately broad, deep, crossed by 2 or 3, low, sharp, nearly vertical growth ridges; adductor ridge prominent, highest in center, inclined toward articular ridge, very long, extending from just below upper end of articular ridge nearly to basal margin; adductor ridge not confluent with articular ridge, leaving deep, narrow cleft between ridges extending nearly to apex of plate; adductor muscle pit large, usually deep, oval, located near midpoint of plate between adductor ridge and occludent margin; 2 short, low, thin, nearly equally-spaced, vertical ridges occurring on lower third of interior of scutum between adductor ridge and basitergal angle; ridge closest to truncate basi-

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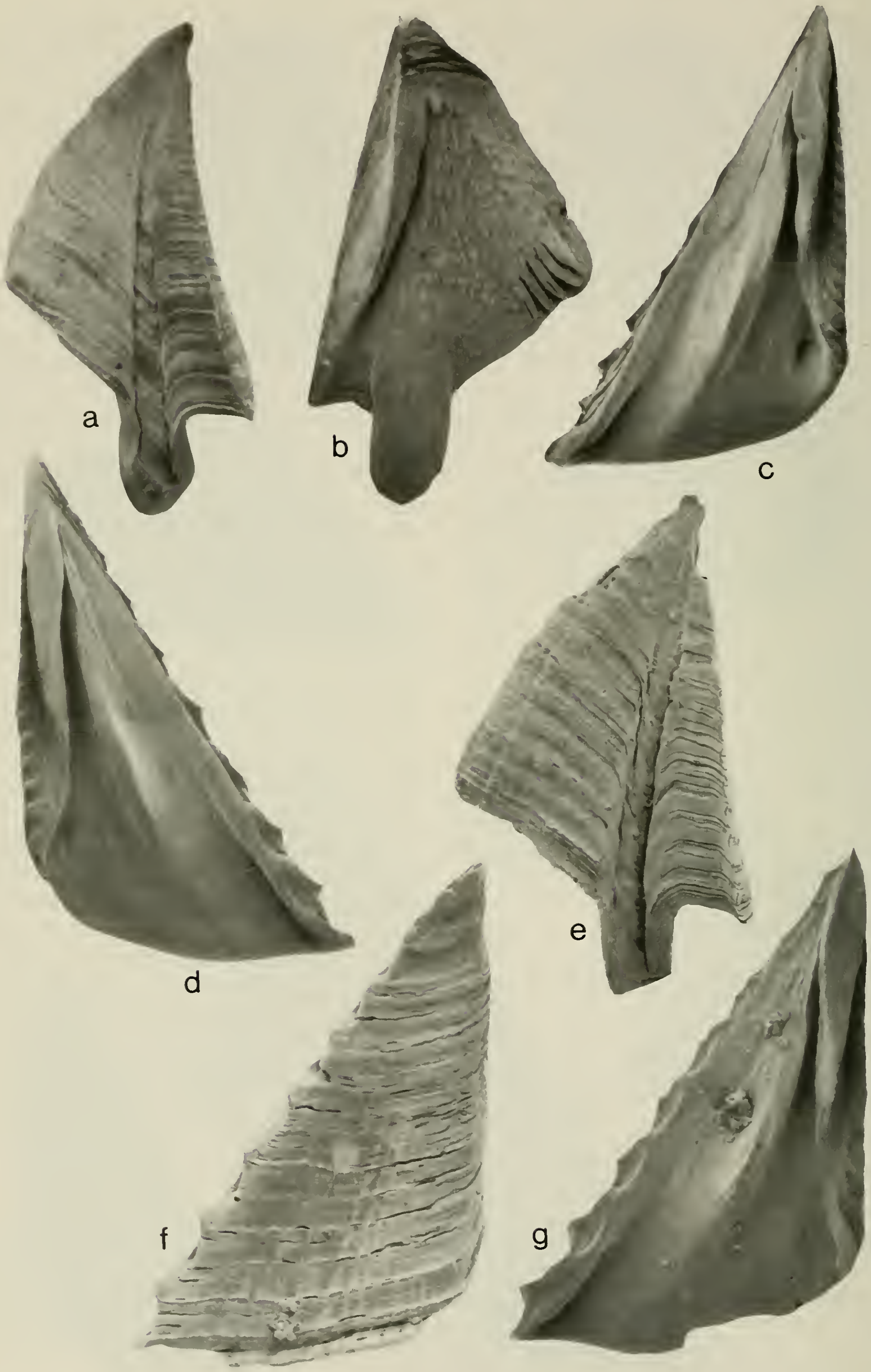
Fig. 4. a–e, *Balanus neusensis,* UNCW locality Z-807, Johnson Point: a, Shell clump, including holotype USNM 405366 (lower center) and paratype lot USNM 405367, ×2; b, Side view of shell, paratype USNM 405368, ×2.4; c, Rostrocarinally elongate shell growing on scutum, paratype USNM 405369, ×6.5; d, Oblique view of shell with convex basis, previously attached to interior of *Crepidula* shell, paratype USNM 405370, ×2.4; e, Oblique view of subcylindric shell, paratype USNM 405371, ×2.4; f–j, *Balanus calidus,* hypotype USNM 405372, UNCW locality Z-807, Johnson Point: f, Oblique view of shell, ×6.5; g, Interior of tergum, ×32; h, Exterior of broken tergum, ×32; i, Exterior of scutum, ×33; j, Interior of scutum, ×33.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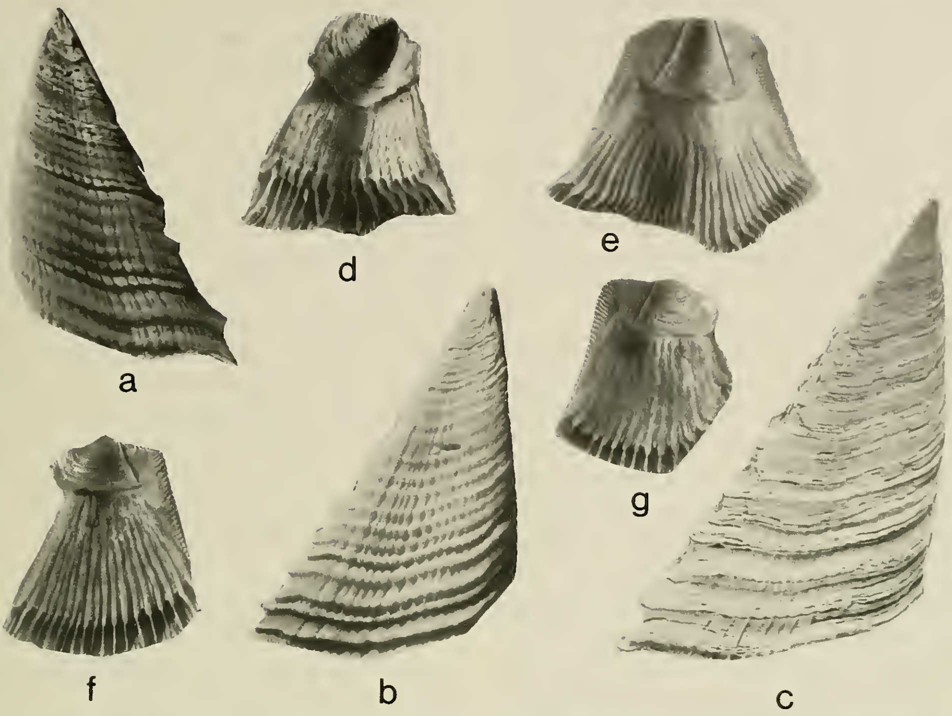

Fig. 6. *Balanus neusensis,* UNCW locality Z-807, Johnson Point. a–c, Exteriors of scuta showing range in development of external radial striae: a, paratype USNM 405377, ×6; b, paratype USNM 405378, ×6; c, paratype 405379, ×12; d, Interior of carina, paratype USNM 405380, ×2.5; e, Interior of rostral plate, paratype USNM 405381, ×2.5; f, Interior of lateral plate, paratype USNM 405382, ×2.5; g, Interior of lateral plate, paratype USNM 405383, ×2.5.

tergal angle forming lateral border of large, deeply impressed, ovoid to triangular, lateral depressor muscle pit situated next to basitergal angle; rostral depressor muscle pit long, narrow; upper part of interior of plate between adductor ridge and occludent border markedly ridged or papillate especially in larger specimens; basal margin of larger specimens nodose, nodes reflecting external radial striae.

Tergum (Figs. 5a–c, e) relatively thin, narrow, with acute apex, slightly concave scutal margin and gently convex carinal margin; basal margin broadly V-shaped; exterior ornamented by low growth ridges crossed by faint radial striae; tergal furrow partially infolded, but open from apex to base of spur; tergal spur narrow, relatively short, straight to slightly arched toward scutum, with parallel sides and gently rounded base; width of spur between one-fifth and one-fourth width of basal margin; distance of spur from basiscutal angle approximately equal to its width; length of spur about one-fifth length of tergum; articular ridge prominent, sharp, arcuate, nearly erect, highest in upper third

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Fig. 5. *Balanus neusensis,* UNCW locality Z-807, Johnson Point: a, Exterior of scutum, paratype USNM 405373, ×13; b, Interior of tergum, paratype USNM 405374, ×13; c, Interior of scutum, paratype USNM 405375, ×12; d, Interior of scutum, paratype USNM 405376, ×14; e–g, Tergum exterior, scutum exterior, scutum interior, holotype USNM 405366, ×18.

of plate, and extending from apex to, or nearly to, basiscutal angle; articular furrow broad, shallow, crossed by 2 or 3 low, sharp, steeply oblique growth ridges; depressor muscle crests well developed, short, increasing in length toward carinal margin, up to 6 in number; interior of tergum between articular ridge and carinal margin markedly rugose, rugosities fading toward basal margin; interior surface of apex marked by sharp, closely-spaced growth ridges.

*Material examined.*—Johnson Point, Neuse River, UNCW locality 807: 37 complete shells, one with opercular plates; over 1000 compartmental plates, over 500 opercular plates. Dam Creek, Neuse River, UNCW locality 808: 12 compartmental plates, 1 scutum. Woodside, Pender County, UNCW locality Z-750: three worn scuta.

*Disposition of types.*—Holotype USNM 405366, paratypes USNM 405368–405371 and 405373–405383, and paratype lot 405367 are in the collection of the Department of Paleobiology, National Museum of Natural History, Washington, D.C.

*Geologic and geographic distribution.*—Early Pleistocene, North Carolina.

*Etymology.*—The specific name is taken from the Neuse River, which is adjacent to the type locality at Johnson Point, Craven County.

*Discussion.*—*Balanus neusensis* is typically a robust, thick-walled, conic barnacle. There are, however, some rather odd specimens from the Johnson Point locality that are small (up to 5 mm in greatest basal diameter), laterally asymmetric, and tear-drop shaped, being widest at the rostral, and narrowest at the carinal end (Fig. 4c). These specimens are attached to scuta of *B. neusensis,* and their shape is governed by the form of that plate. Because of the consistency in asymmetry and shell alignment, it is probable that these small barnacles were growing on scuta of living adults.

The shell of *B. neusensis,* in external aspect, bears considerable resemblance to that of the extant western Atlantic species *B. eburneus* Gould, but is readily distinguished by the lack of transverse septa in the parietal and basal tubes, and the solid, rather than vesicular sheath. The scutum of *B. neusensis* also resembles that of *B. eburneus* in bearing prominent external radial striae, but is otherwise quite distinct, being considerably narrower, and in having a much longer and more prominent adductor ridge which is not confluent with the base of the articular ridge. The deep, narrow cleft formed between the adductor and articular ridges is a very distinctive feature of *B. neusensis.* The tergum is very unlike that of *B. eburneus,* having a well-defined, partially infolded spur furrow, and lacking any indication of an embayment on the carinal side of the basal margin.

The shell and opercular plates of *B. neusensis* most closely resemble those of *B. oppidieboraci* Ross from the Pliocene Yorktown Formation of Virginia and its equivalents in the Carolinas (see Ross 1964, Zullo 1986). The shells of the two species are virtually identical in form, but can be distinguished by the summits of the radii. Although Ross (1964:490) described the summits of the radii of *B. oppidieboraci* as varying from 45° to subhorizontal, examination of nearly 100 specimens from the Yorktown Formation of Virginia indicates that oblique radii are very rare in this species and are confined to individual plates of specimens with otherwise subhorizontal summits. The summits of the radii of *B. neusensis,* on the other hand, are always oblique and are, additionally, crenate, whereas those of *B. oppidieboraci* are smooth. The scutum of *B. oppidieboraci* bears finer, more numerous radial striae over almost the entire external surface of the plate, is not sulcate longitudinally, and the growth ridges are not broken into prominent nodes. The articular ridge is reflexed over the articular furrow, and its upper surface is not flattened. The tergum is broader, the tergal spur is broader and longer, and the tergal furrow, although open throughout its length, is narrower as a result of infolding from the sides.

*Balanus neusensis* and *B. oppidieboraci* appear to be related to species of the *B. amphitrite* Darwin complex and, especially, to the *B. pacificus* Pilsbry group, which is represented in the Virginia Pliocene fauna by *B. pacificus prebrevicalcar* Ross. The *B. pacificus* group is not known in the extant Atlantic fauna, surviving only in the eastern Pacific. It is possible that *B. neusensis* is a derivative of *B. oppidieboraci* and the last survivor of the *B. pacificus* group in the North Atlantic basin.

### *Balanus calidus* Pilsbry, 1916
Fig. 4f–j

*Balanus spongicola* var. Darwin, 1854:225, pl. 4, fig. 1d.

*Balanus calidus* Pilsbry, 1916:118, pl. 25, figs. 1–1c, text fig. 32a–f.—Zullo, 1966: 235.—Newman and Ross, 1976:65 (see for complete synonymy).

*Material examined.*—Johnson Point, Neuse River, UNCW locality Z-807; 2 complete shells (one with opercular plates), 4 compartmental plates.—Lee Creek Mine, Beaufort County, UNCW locality Z-809: over 200 shells on *Ostrea sculpturata,* many with opercular plates.—Waccamaw Fm., Little River, South Carolina, UNCW locality Z-812: over 500 shells on *Ostrea sculpturata,* many with opercular plates.

*Disposition of specimens.*—Figured hypotype USNM 405372 is in the collection of the Department of Paleobiology, National Museum of Natural History, Washington, D.C. Remaining specimens are in the collection of the Department of Earth Sciences, University of North Carolina at Wilmington.

*Geologic and geographic range.*—Recent: North Carolina south to the West Indies and the Gulf of Mexico. Pleistocene: North and South Carolina (Wells and Richards 1962; and reported herein); (?) northern Colombia (Nilsson-Cantell 1939). (?) Miocene (Tortonian), Bulgaria (Kolosváry 1962).

*Discussion.*—*Balanus calidus* was the most common balanoid barnacle on the continental shelf of the Carolinas (Zullo 1966), but in recent years has been replaced by the related tropicopolitan species *B. trigonus* Darwin. There is some suggestion that *B. trigonus* is a recent introduction to the Atlantic coast of the United States (see Wells 1966:84), a suggestion that is supported by the Pleistocene fossil record. *Balanus calidus* is abundant in lower Pleistocene marine deposits of the Carolinas, whereas no specimen of *B. trigonus* has yet been identified positively from the region (see Ross 1965: 273). The Pleistocene shells from the James City Formation have the small orifice, relatively narrow radii and ribbed parietes characteristic of *B. calidus.* The externally striate scutum is rather thick and narrow, and bears a rather short and indistinct adductor ridge. The tergum is distinguished by its broad, basally truncate spur.

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# THE SYNONYMY OF *CIROLANA TUBERCULATA* (RICHARDSON, 1910) (ISOPODA: FLABELLIFERA: CIROLANIDAE)

Paul M. Delaney

*Abstract.*—The syntypes of *Alcirona tuberculata* Richardson, 1910 (Corallanidae) were examined and determined to be more appropriately placed in the genus *Cirolana* Leach, 1818 (Cirolanidae). The species is redescribed here as *Cirolana tuberculata.*

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### *Cirolana* Leach, 1818

*Diagnosis.*—Rostral process minute or absent. Frontal lamina flat. Antennular peduncle 2- or 3-articulate; articles 1 and 2 of antennule not forming right angles to one another (as in *Eurydice*). Antenna peduncle 5-articulate. Mandible with broad tridentate incisor; lacinia mobilis and molar process well-developed. Maxilliped usually with 1–3 coupling hooks (occasionally more) on endite. Pereopod dactyls with small secondary ungues. Pleonite 1 often concealed by pereonite VII; pleonite 5 narrower than 1–4, with lateral margins covered by pleonite 4. Pleopods 1 and 2 similar to each other; endopod of pleopod 5 without setae. Appendix masculinum arising basally from endopod of pleopod 2. Inner angle of uropod peduncle strongly produced; uropod rami with or without plumose marginal setae. (Modified after Brusca and Iverson 1985.)

### *Cirolana tuberculata* (Richardson, 1910)
Figs. 1, 2

*Alcirona tuberculata*Richardson, 1910:8, figs. 7a,b.

*Material examined.*—Philippine Islands; U.S. Bureau of Fisheries Steamer *Albatross,* sta 5141, Jolo Light, 5.5 mi. S 17 E, (6°09′00″N, 120°58′00″E) 53 m, “in coral and sand” USNM No. 40910, syntypes 1 male, 7.5 mm 1 female, 8.0 mm. 15 Feb 1908.

*Description of male.*—Cephalon without tubercles; eyes lateral (Fig. 1a). Antennular peduncle 2-articulate, flagellum 14-articulate, with simple setae and aesthetascs (Fig. 2c); extending to midlength of pereonite I (Fig. 1a). Antennal peduncle 5-articulate, 4–5 elongate; flagellum 20-articulate (Fig. 2a), extending to midlength of pereonite III (Fig. 1c). Frontal lamina flat, pentagonal; clypeus short, broad; labrum short, broad, quadrangular (Fig. 2b). Mandible incisor broad; lacinia mobilis lobular, rounded, with simple setae and 3 distal spines; molar process triangular, with 12 spines and many simple setae; 3-articulate palp arising from middle of mandible, middle article with simple marginal setae, distal article with simple and comb-like setae (Fig. 2d). Maxillule, lateral lobe with 10 apical spines, medial lobe with 3 large plumose spines (Fig. 2g). Maxilla, lateral lobes with 4 and 9 simple setae; medial lobe with 6 simple and 6 plumose setae (Fig. 2e). Maxillipedal palp with simple, bifid and comb-like setae as figured; endite extending to second palp article, with 1 coupling hook, apex with 2 plumose and 1 simple setae (Fig. 2f).

Pereon length 5 times pleon length; pereon widest at pereonite V; pereon without dorsal tubercles or setae. Coxal plates large, increasing in size and acuteness posteriorly;

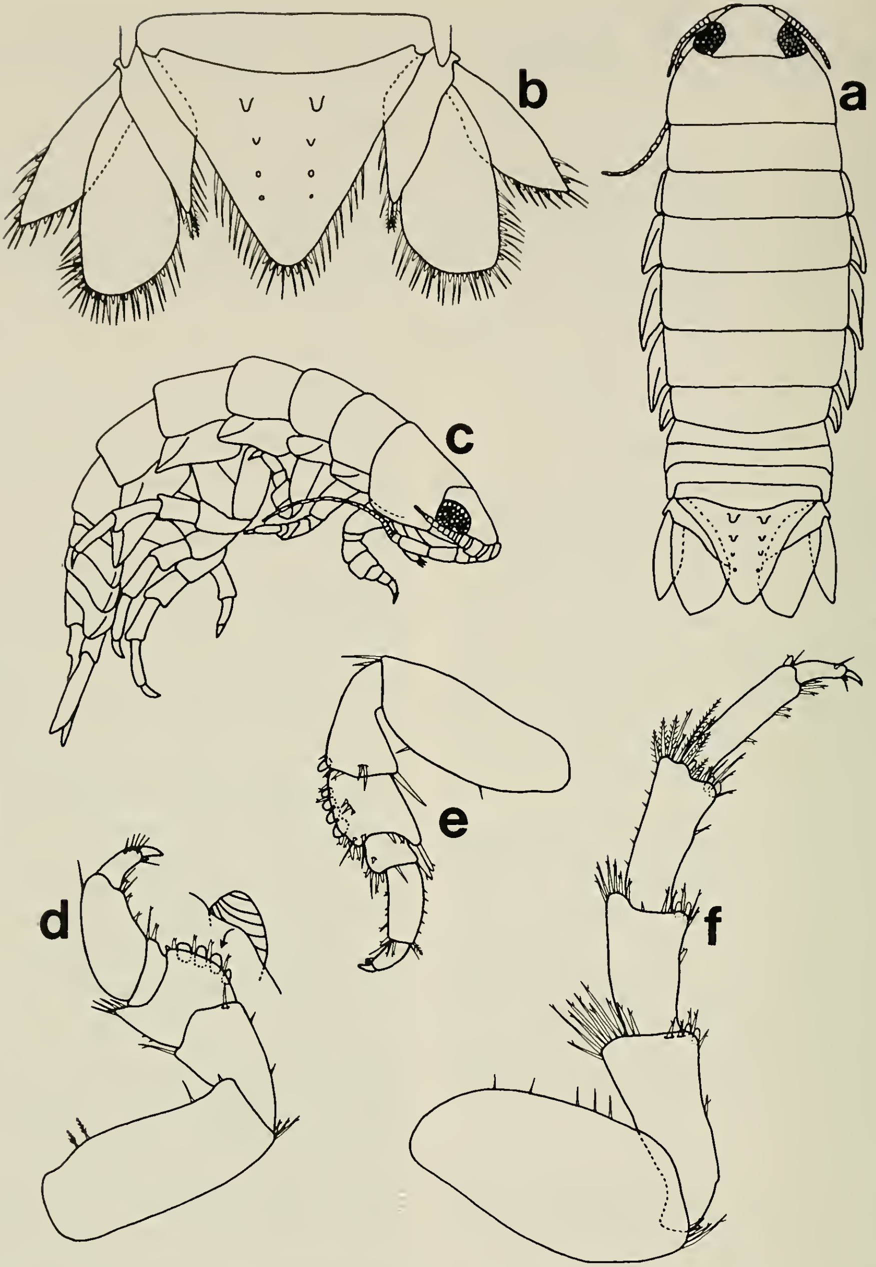

Fig. 1. *Cirolana tuberculata*: a, Dorsal view, pleotelson and uropod setae and spines not shown; b, Pleotelson and uropods; c, Lateral view; d, Pereopod I; e, Pereopod III; f, Pereopod VII.

coxae IV–VII extending beyond posterior margins of their respective pereonites; coxae VII extending to midlength of pleonite 2; coxae II–VII with single oblique carina, no spines or setae (Fig. 1c). Pereopods I–III prehensile, dactyl with small secondary unguis, merus with 4–5 short, blunt spines on medial margin; simple, bifid and plumose

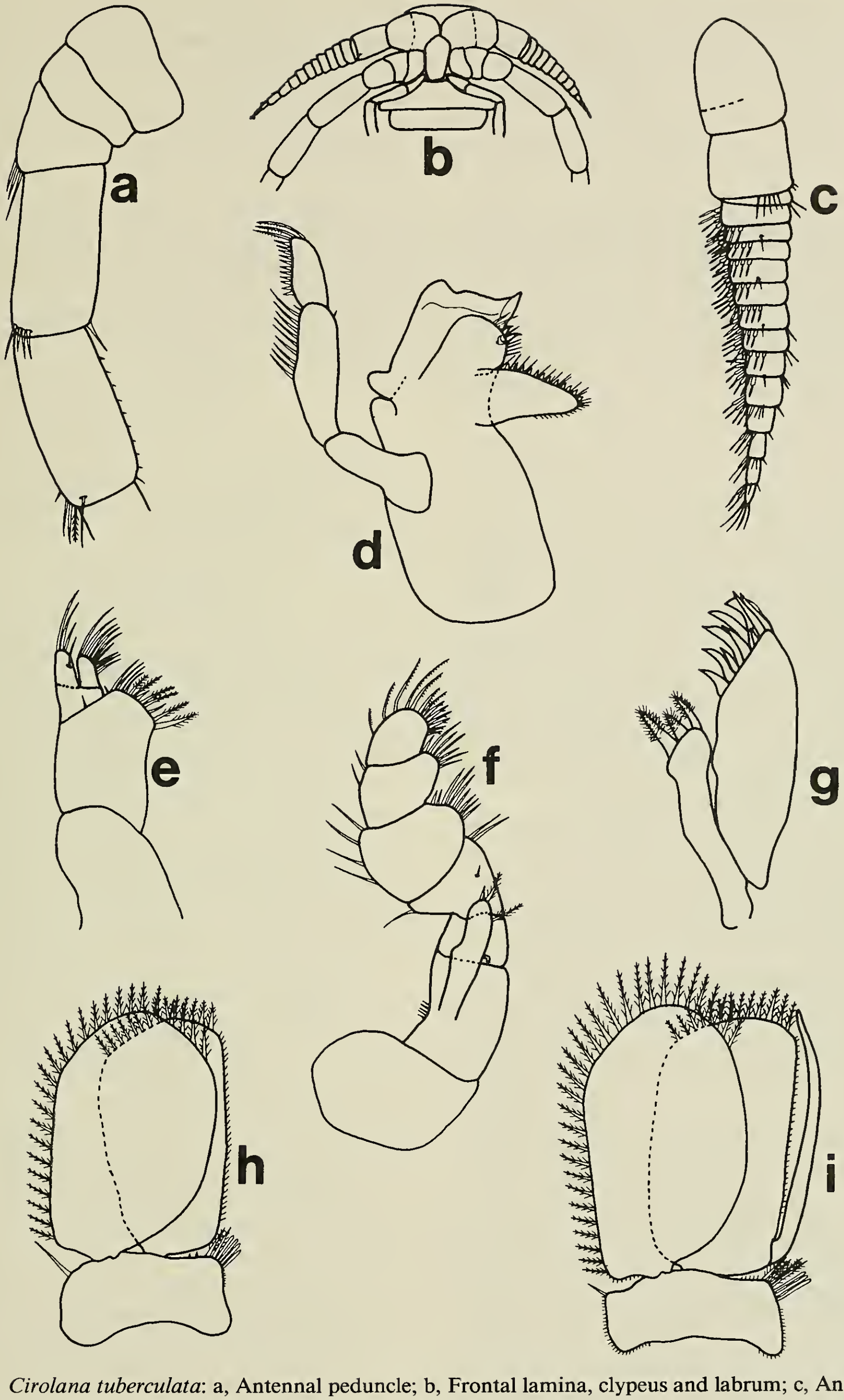

Fig. 2. *Cirolana tuberculata*: a, Antennal peduncle; b, Frontal lamina, clypeus and labrum; c, Antennule; d, Mandible; e, Maxilla; f, Maxilliped; g, Maxillule; h, Pleopod 1; i, Pleopod 2.

setae as figured (Fig. 1d, e). Pereopods IV–VII with small secondary unguis, and short blunt spines on medial margins; simple, bifid and plumose setae as figured (Fig. 1f).

Pleon widest at pleonites 3–4; pleonite 1 covered by pereonite VII; lateral margins of pleonite 5 overlapped by pleonite 4; pleonites 1–5 without dorsal setae or tubercles. Pleopods with plumose marginal setae (except endopod of pleopod 5), peduncles with 3 coupling spines and 2–4 plumose setae on medial margins (Fig. 2h, i). Male pleopod 2 with rodlike appendix masculinum arising from proximal medial margin of endopod (Fig. 2i). Pleotelson triangular, lateral margins slightly concave; apex with simple setae and 7 spines. Pleotelson dorsum with two parallel rows of 4 tubercles, decreasing in size posteriorly (Fig. 1b). Uropods extending well beyond posterior margin of pleotelson; exopod one-half width of endopod; apex acute, margins with setae and 7–8 spines; endopod broadly rounded, margins with setae and 11 spines. Uropodal peduncle, inner margin with 3–5 simple and 2 plumose marginal setae (Fig. 1b).

*Female.*—Similar to male but with less distinct tuberculation on pleotelson.

*Remarks.*—Richardson (1910) described this species as *Alcirona tuberculata* from two specimens collected in the Philippines, but figured only the posterior portion of the body and pereopod I of the male. The genus *Alcirona* Hansen, 1890, is distinguished from other genera in the family Corallanidae primarily by mouthpart morphology, including characters of the maxillule (lateral lobe with 2 large recurved spines, and occasionally 1–3 smaller spines between the 2 large ones), maxilla (short rounded lobe), and maxilliped (palp articles of approximately equal length, endite absent). For a key to the genera of Tridentellidae and Corallanidae see Delaney and Brusca (1985). The mouthparts of this species (Fig. 2d–g) show that it clearly does not belong in *Alcirona* but to *Cirolana* (Cirolanidae).

The linear pattern of pleotelson tuberculation in *Cirolana tuberculata* closely resembles that of *C. pleonastica* Stebbing, (1900:629, pl. LXVIIa) from New Britain in the southwest Pacific. *Cirolana tuberculata* differs from that species in number of pleotelson tubercles (4 pairs in *C. tuberculata,* 5 pairs in *C. pleonastica*), lack of dorsal pleotelson setae, lack of pereonal and pleonal tuberculation, number of coupling spines on peduncles of pleopods 1–2 (3 in *C. tuberculata,* 4 in *C. pleonastica*) and shape of labrum and maxilliped.

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# NOTES ON THE CRAYFISH *PROCAMBARUS* (*ORTMANNICUS*) *XILITLAE* (DECAPODA: CAMBARIDAE)

Horton H. Hobbs, Jr. and Andrew G. Grubbs

*Abstract.*—With the acquisition of the exuviae of a first form male revealing the structure of the secondary sexual features (described and illustrated herein), the affinities of the troglobitic crayfish *Procambarus (Ortmannicus) xilitlae* are reassessed. Its tentative assignment to the subgenus *Scapulicambarus* by Hobbs and Grubbs (1982) was found to be in error when it was discovered that a shoulder was lacking on the cephalic surface of the first pleopod of the first form ("adult") male.

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*Procambarus (Scapulicambarus) xilitlae* Hobbs and Grubbs, 1982, was described from Hoya de las Guaguas, near the town of Xilitla, San Luis Potosí, Mexico. The authors based their description on a second form male and two females, and they tentatively assigned the crayfish to the subgenus *Scapulicambarus,* making the statement that "The availability of a first form male of this new crayfish would greatly strengthen our confidence in the inferences that we have made in assessing its relationship to other crayfishes." While they were confident that it is a member of the genus *Procambarus,* they were ". . . less certain as to which of the subgenera it should be assigned, *Ortmannicus* or *Scapulicambarus*" (Hobbs and Grubbs 1982:49).

The only feature that serves consistently to separate the members of these two subgenera is the presence of a strong, usually angular shoulder on the cephalic surface of the left first pleopod of the male; the shoulder on the right pleopod is folded caudomesially and pressed against the mesial face of the appendage. Ignoring the shoulder, the two subgenera seem clearly to merge through forms like *Procambarus* (*O.*) *evermanni* (Faxon, 1890), *P.* (*O.*) *xilitlae, P.* (*S.*) *paeninsulanus* (Faxon, 1914), and *P.* (*S.*) *strenthi* Hobbs (1977). A shoulder is present in the second form male of all members of *Scapulicambarus,* but it is often much weaker than that of first form individuals (see figs. 280 to 284 in Hobbs 1974). The small bulge on the cephalic surface of the pleopod of the holotypic male, form II, of *P. (O.) xilitlae* (see fig. 1b in Hobbs and Grubbs 1982) appeared to represent such a shoulder, thus prompting the original assignment of this crayfish to the subgenus *Scapulicambarus.*

With the rearing of a second form male in the laboratory by one of us (AGG) and preserving its exuviae, one of which was shed when molting from form I to form II (see below), we discovered that the first pleopod lacks a shoulder. thus the species must be transferred to the subgenus *Ortmannicus.*

The absence of pigment from the body and eyes, the non-faceted cornea, the presence on the first pleopod of the first form male of a well developed caudal process, and the absence of an adventitious process will serve to distinguish this crayfish from all others. A description and illustrations of the secondary sexual and certain other features of the first form exuviae of this topotypic male are offered to complete the basic description of this crayfish.

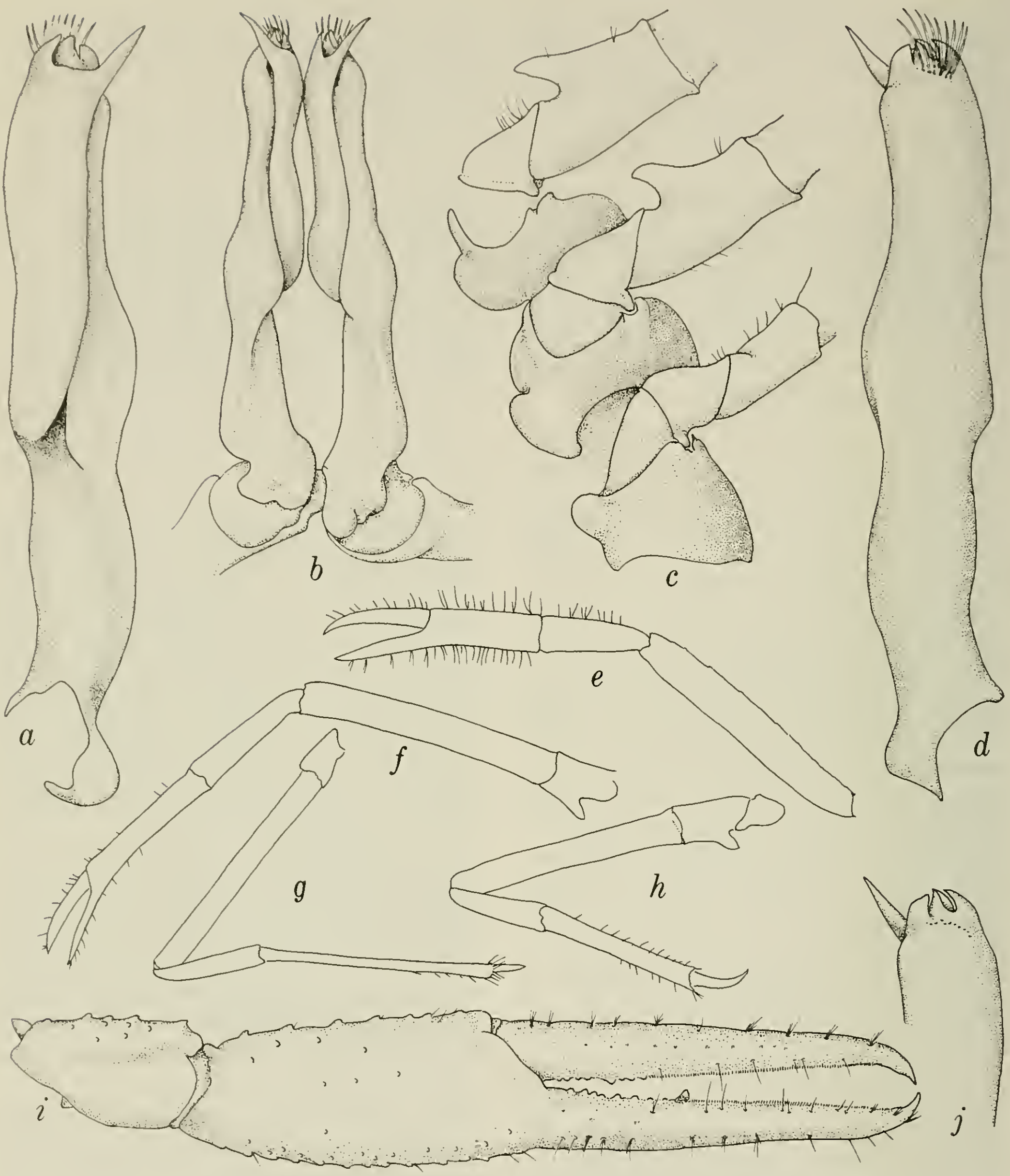

Fig. 1. *Procambarus* (*Ortmannicus*) *xilitlae* (all from exuviae of first form male): a, Mesial view of first pleopod; b, Caudal view of first pleopods (proximal parts probably shrunken, but asymmetry real); c, Proximal podomeres of third, fourth, and fifth pereiopods; d, Lateral view of first pleopod; e, Distal podomeres of second pereiopod; f, Same of third pereiopod; g, Same of fifth pereiopod; h, Same of fourth pereiopod; i, Same of first pereiopod; j, Lateral view of distal part of first pleopod without subapical setae.

### *Procambarus* (*Ortmannicus*) *xilitlae*

Fig. 1

*Procambarus* (*Scapulicambarus*) *xilitlae* Hobbs and Grubbs, 1982:45–50, 1 fig.

*Male, Form I.*—Chela (Fig. 1i) differing from that of holotype in following respects: mesial margin of palm with row of 7 small tubercles; opposable margin of fixed finger with row of 8 small corneous teeth along proximal third; larger, more ventrally situated one as in holotype; fifth tubercle from base largest of 8 present on proximal third of opposable margin of dactyl. Ischia of third and fourth pereiopods with simple hooks (Fig. 1c), that on third overreaching basioischial suture; neither opposed by tubercle on basis.

First pleopods (Fig. 1a, b, d, j) reaching coxae of third pereiopods, distinctly asymmetrical but contiguous basally; cephalic surface lacking shoulder; distal extremity bearing large slender tapering mesial process directed distolaterally; cephalic process short, with corneous acute apex, curved caudodistally parallel to short, corneous, acute, beaklike central projection; caudal process corneous, short, wedgelike, its distal margin sloping cephalodistally to angle, apex of which directed toward tip of central projection. Cephalic process and central projection overreaching apex of caudal process but falling short of that of mesial process. Sockets of distally directed subapical setae forming arc on lateral surface just proximal to bases of terminal elements.

*Relationships.*—As pointed out in the introductory remarks, this crayfish is allied to those species that appear to bridge the gap between the subgenera *Ortmannicus* and *Scapulicambarus.* Seemingly it is rather distantly related to the other troglobitic members of *Ortmannicus* which populate much of the peninsula and eastern part of the panhandle of Florida even though the annulus ventralis is much like those of *P.* (*O.*) *horsti* Hobbs and Means (1972) and *P.* (*O.*) *orcinus* Hobbs and Means (1972). Among the Mexican crayfishes, it shares more in common with *P.* (*O.*) *caballeroi* Villalobos (1944), *P.* (*O.*) *acutus cuevachicae* (Hobbs, 1941), *P.* (*S.*) *strenthi,* and *P.* (*Pennides*) *roberti* Villalobos and Hobbs (1974) than with any others.

*Remarks.*—The topotypic specimen from which the exuviae of the first form was obtained was collected on 26 November 1981, and, when brought into the laboratory, had a carapace length of 26.8 (postorbital carapace length, 21.7) mm. It underwent three molts, remaining in the second form, without any increase in the total length of the carapace. The dates on which the first two exuviae were removed from the aquarium were not recorded, but the third was found on 5 November 1982. Another test was discovered in the aquarium on 23 February 1983 in which the corresponding lengths of the carapace were 27.8 and 22.0 mm. The next was removed on 29 July 1983, but it was so torn that accurate measurements could not be made. Presumably it was at this molt that the transformation to form I was accomplished, for the next exuviae, found on 12 December 1983, furnished the models for the illustrations depicted herein. The corresponding lengths of the carapace were 29.2 and 23.1 mm. The crayfish, found dead on 6 November 1984, had reached a stage of decomposition such that measurements of the carapace could not be made. All of these exuviae and the partly decomposed remains, in form II, are in the collection of the Smithsonian Institution.

To our knowledge, other than the type series and the specimen cited above, only five specimens of *P. (O.) xilitlae* have been collected. These were obtained at the type locality by R. Rhorer and AGG on 4 August 1982 and deposited in the Smithsonian Institution (1 ♂II, 1 j♂, 1 j♀) and the Texas Memorial Museum (1 ♀, 1 j♂).

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# A NEW SPECIES OF *ELACHOCHARAX* (TELEOSTEI: CHARACIDAE) FROM THE RÍO NEGRO REGION OF VENEZUELA AND BRAZIL

Stanley H. Weitzman

*Abstract.—Elachocharax mitopterus* is described as a new species of the characid fish subfamily Characidiinae from the Río Negro system of Venezuela and Brazil. The new species is distintuished from *Elachocharax pulcher* Myers, *E. junki* (Géry), and *E. geryi* Weitzman and Kanazawa by a variety of color pattern, morphometric, and meristic characters outlined in the key and text. *Elachocharax pulcher* is the sister group of the other three species which form an unresolved trichotomy. Although some of these species have seemingly allopatric distributions, it is probable that their geographic ranges broadly overlap.

The three previously known species of *Elachocharax* Myers (1927:114) were treated most recently by Weitzman and Kanazawa (1978) and Weitzman and Géry (1981). The phylogeny of *Elachocharax* was discussed and a cladogram of the relationships of the recognized species was presented by Weitzman and Géry (1981:898–910). The genus is not confined to the Amazon region as stated by Géry (1984:356) since two species, *Elachocharax pulcher* Myers (1927: 115) and *Elachocharax geryi* Weitzman and Kanazawa (1978:173), previously were reported from both the Orinoco and Amazon basins. *Elachocharax junki* (Géry, 1971: 154) and the new species, *Elachocharax mitopterus,* are so far known only from Amazon drainages, but both species occur in the Río Negro (the new one in the upper portion of that system) and may be expected to be found at least in black water streams of the upper portions of the Río Orinoco.

## Methods and Materials

Counts and measurements are recorded as described by Fink and Weitzman (1974: 1–2). Body depth is measured vertically from dorsal-fin origin. All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of head which, unless otherwise stated, are recorded as a percentage of head length. Total vertebral counts, taken from radiographs and from one cleared, Alizarin and Alcian blue stained specimen, include all vertebrae of Weberian apparatus and with fused PU + U of caudal skeleton counted as a single vertebra. In text and table, count or morphometric character given first is of holotype unless otherwise noted; next series of figures is range of all specimens (given in parentheses in text). This is followed by mean ($\bar{x}$) of all specimens. Specimens examined for this study are deposited in Museo de Biologia, Instituto de Zoologia Tropical, Universidad Central de Venezuela (MBUCV-V), Museu de Zoologia da Universidade de São Paulo (MZUSP), and National Museum of Natural History, Smithsonian Institution (USNM).

## Artificial Key to the Species of *Elachocharax* Myers

1. Premaxillary teeth tricuspid anteriorly followed by a few bicuspid and/or unicuspid teeth. Dentary with tricuspid teeth anteriorly followed by none, one, or a few bicus-

Fig. 1. *Elachocharax mitopterus*, new species, holotype MBUCV-V-15270, SL 13.9 mm, Caño Chola, Departamento Río Negro, Territorio Federal Amazonas, Venezuela, 5 Dec 1984.

pid teeth and then several unicuspid teeth lateroposteriorly. Adipose fin present ........ *Elachocharax pulcher*

– Premaxillary teeth and dentary teeth all unicuspid. Adipose fin absent 2

2\. Total dorsal-fin rays 17 or 18, usually 18. Scales in lateral series to hypural joint 24 or 25. Branchiostegal rays 5. Horizontal scale rows between dorsal- and pelvic-fin origins 7. Total vertebrae 29 ........................ *Elachocharax mitopterus*

– Total dorsal-fin rays 19 to 22, usually 21 or 22. Scales in lateral series 27 to 33, usually 28 to 32. Branchiostegal rays 4. Horizontal scale rows between dorsal- and pelvic-fin origins 8. Total vertebrae 31 to 33, usually 31 or 32 ................ 3

3\. Caudal fin without obvious vertical dark bars. Teeth on ectopterygoid 8 to 13. Inner row dentary teeth 19 to 20. Upper limb gill rakers 5 to 6. Anterior anal-fin origin in advance of a vertical line drawn through dorsal-fin base. Snout length about 5.4 to 6.1% of SL. Caudal peduncle length about 19.0 to 22.0% of SL ............. *Elachocharax junki*

– Caudal fin with 13 or 14 narrow vertical dark bars. Teeth on ectopterygoid 4 or 5. Inner row dentary teeth 13 to 16. Upper limb gill rakers 3. Anal-fin origin at or slightly posterior to a vertical line drawn through posterior termination of dorsal-fin base. Snout length about 6.0 to 8.0% of SL. Caudal peduncle length about 16.0 to 19.0% SL. .*Elachocharax geryi*

*Elachocharax mitopterus*, new species
Figs. 1–3, Table 1

*Holotype.*—MBUCV-V-15270, SL 13.9 mm, Venezuela, Territorio Federal Amazonas, Departmento Río Negro, Caño Chola, where crossed by road from San Carlos de Río Negro to Solano, about 01°58′N, 67°00′W, 5 Dec 1984, R. P. Vari, A. Machado-Allison, C. Ferraris, O. Castillo, J. M. Fernandez.

*Paratypes.*—1, MBUCV-V-15271, SL 13.8 mm.—2, USNM 270147, SL 12.3–12.7 mm (jaws and opercle of right side of one specimen cleared and stained).—1, cleared and stained, USNM 274101, SL 12.6 mm. All preceding paratypes with same collection data as holotype.—3, MZUSP 29871,

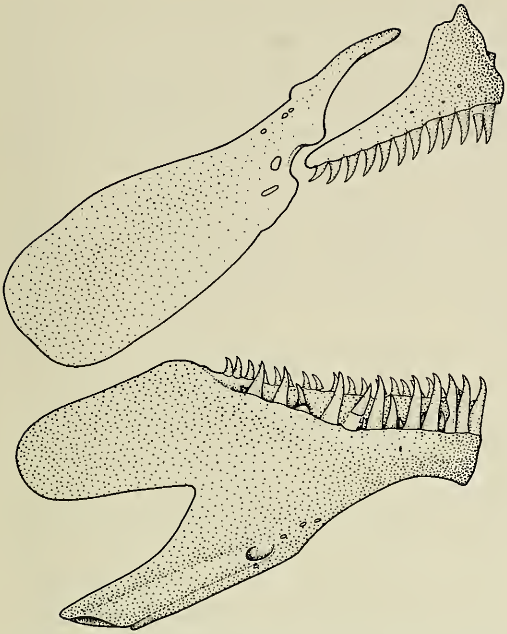

Fig. 2. *Elachocharax mitopterus,* new species, from a paratype, USNM 274101, SL 12.6 mm, Caño Chola, Departamento Río Negro, Territorio Federal Amazonas, Venezuela, 5 Dec 1984. Lateral view of premaxilla, maxilla, and dentary of right side; anterior to right. Outer dentary tooth row lies in a deep groove. Replacement teeth of this row develop within groove. Inner-row dentary teeth present posterior to or near visible dorsal border of ridge seen internal to outer-row dentary teeth. Note that third dentary tooth from midline partly eroded away and its replacement tooth (to its left) easily visible posterior and interior to it. Anterior to right.

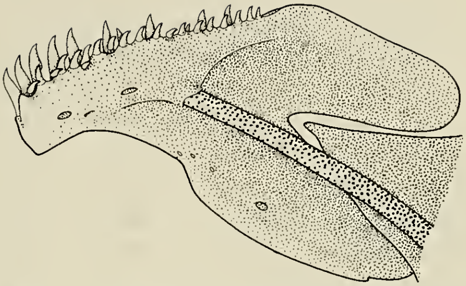

Fig. 3. *Elachocharax mitopterus,* new species, from a paratype, USNM 274101, SL 12.6 mm, Caño Chola, Departamento Río Negro, Territorio Federal Amazonas, Venezuela, 5 Dec 1984. Medial view of right dentary. Seventeen fully-developed inner-row teeth visible on dentary ridge. Five replacement teeth present interior to inner-row teeth. These teeth point inwards and not fully or not at all attached to dentary ridge. Full complement of inner-row teeth about 19, counting in-place fully-developed teeth and their replacement teeth as one. Anterior to left.

SL 11.7–13.2 mm, Brazil, Amazonas, igarapé Tarumãzinho, about 45 km north of Manaus on road between Manaus, Amazonas and Caracarai, Roraima, about 2°42′S, 60°02′W, 25 Sep 1976, Ivanzier Vieira.—2, USNM 274100, SL 12.7–13.3 mm (jaws and opercle of right side of one specimen cleared and stained), with same collection data as MZUSP 29871.

*Diagnosis.*—Distinguished from all other species of *Elachocharax* by having 29 instead of 30 to 33 vertebrae, 7 instead of 8 scale rows between anterior base of dorsal fin and pelvic fin, and 24 to 26 scales in lateral series instead of 27 to 33. This species, *E. geryi,* and *E. junki* are distinguished from *E. pulcher* by having only conic teeth in jaws (no tricuspid or bicuspid teeth). *Elachocharax mitopterus* is similar to *E. geryi* and especially *E. pulcher* but unlike *E. junki* in having two strong black pigment bars on anal fin and one on pelvic fin. *Elachocharax mitopterus* has only five narrow dark bars on base of caudal fin rather than 13 to 14 of these bars as in *E. geryi.* As in *E. geryi,* anal fin of *E. mitopterus* originates at or near imaginary vertical line drawn through posterior basal termination of dorsal fin rather than anterior to such a line as in *E. junki* or slightly posterior to one as in *E. pulcher.*

*Description.*—See Table 1 for morphometric values. Body relatively short, as in other species of *Elachocharax*; greatest depth at dorsal-fin origin. Profile of head and back from snout tip to dorsal-fin origin gently convex. Dorsal-fin origin in advance of imaginary vertical line drawn through pelvic-fin origin. Anal-fin origin at or near imaginary vertical line drawn through posterior termination of dorsal-fin base. Profile of ventral surface of head somewhat convex. Belly slightly convex or nearly flat from

Table 1.—Morphometrics of two population samples of *Elachocharax mitopterus*. Standard length expressed in mm. Other measurements are percentages of standard length except for eye diameter, snout length, and interorbital width which are percentages of head length.

| | Venezuela, Caño Chola | | | Brazil, igarapé Tarumãzinho | |
|---|---|---|---|---|---|
| | Holotype | Range, n = 5 | $\bar{x}$ | Range, n = 5 | $\bar{x}$ |
| Standard length | 13.9 | 12.3–13.9 | | 11.7–13.3 | |
| Depth at dorsal-fin origin | 30.2 | 29.7–30.9 | 30.4 | 29.5–30.8 | 30.4 |
| Snout to dorsal-fin origin | 53.2 | 52.2–54.3 | 53.1 | 52.0–53.1 | 52.7 |
| Snout to pelvic-fin origin | 57.6 | 55.8–58.3 | 57.2 | 56.3–59.0 | 57.1 |
| Snout to anal-fin origin | 79.1 | 78.3–79.1 | 78.8 | 78.0–79.7 | 78.7 |
| Caudal peduncle depth | 14.1 | 13.8–15.4 | 14.7 | 15.2–16.5 | 16.0 |
| Caudal peduncle length | 15.1 | 15.1–17.1 | 16.2 | 14.2–16.7 | 15.0 |
| Pectoral-fin length | 32.4 | 32.4–37.8 | 34.7 | 32.3–36.7 | 34.9 |
| Pelvic-fin length | 26.6 | 23.2–26.8 | 25.3 | 21.2–23.6 | 22.8 |
| Bony head length | 31.7 | 31.2–33.9 | 32.2 | 31.4–33.8 | 32.2 |
| Horizontal eye diameter | 33.0 | 31.4–33.0 | 32.5 | 32.2–35.1 | 34.0 |
| Snout length | 18.2 | 15.2–18.2 | 16.8 | 17.9–20.0 | 18.8 |
| Least width interorbital | 34.1 | 27.9–34.1 | 31.2 | 30.5–33.8 | 30.5 |

region of isthmus to pelvic-fin origin. Profile of body between pelvic-fin origin and anal-fin origin gently convex to nearly straight. Caudal peduncle short, deep. Both dorsal and ventral profiles of caudal peduncle slightly concave.

Head moderately long. Mouth terminal. Snout relatively blunt; eyes large, horizontal diameter exceeds snout length.

Teeth on dentary in two rows (Figs. 2, 3). Outer row with 11 (12–13) conic teeth. Inner row uncounted in holotype (18–19, 3 Alizarin preparations) conic teeth, Figs. 3, 4. Premaxilla with single row of 9 (12–12, 3 Alizarin preparations) conic teeth. Maxilla toothless. Ectopterygoid teeth uncounted in holotype (4–9, 3 Alizarin preparations) conic teeth in single row.

Branchiostegal rays uncounted in holotype (5 in 3 Alizarin preparations); two slender anterior rays attached to anterior part of ceratohyal followed by broad ray attached to posterior part of ceratohyal; fourth broad ray attached to epihyal. Gill rakers 4 (3–4) on dorsal limb and 8 (7–8) on ventral limb. Range of gill raker counts based on 3 Alizarin preparations. Frontal-parietal foramen greatly reduced. A narrow antorbital bone present dorsal and posterolateral to posterior and dorsal portion of anterior (first) infraorbital. First infraorbital with laterosensory canal and anterior process extending dorsal and anterior to anterior dorsal slender process of maxillary bone. Second infraorbital bone primarily a laterosensory tube but some laminar bone present. Other infraorbital bones absent.

Scales cycloid, usually 4–5 radii on exposed field. Lateral line with 5 (5–6, $\bar{x}$ = 5.1, n = 10) perforated scales. Scales in lateral series 26 (24–26, $\bar{x}$ = 25.2, n = 10). Horizontal scale rows between dorsal and pelvic fins 7 (7, n = 10). Horizontal scale rows around caudal peduncle 10 (10, n = 5 in specimens from type locality; 12–14, $\bar{x}$ = 12.8, n = 5 in specimens from igarapé Tarumãzinho). (See section on population variation.) Predorsal scales 8 (8–9, $\bar{x}$ = 8.3, n = 10).

Dorsal-fin rays ii, 16 (ii,15, n = 2, ii,16, n = 8); total dorsal-fin rays 18 (17–18, $\bar{x}$ = 17.8, n = 10). Last dorsal-fin ray not split to its base. Adipose fin absent. Externally visible anal-fin rays ii,16 in all specimens. Extremely small, but not externally visible, third anterior unbranched ray revealed in 9 of 10 radiographed and cleared and stained specimens. Posterior anal-fin ray split to its base. Pectoral fin elongate, reaching to or beyond midlength of pelvic fin when both fins are laid against body. Pectoral-fin rays usually undivided, sometimes rays three and/or four with some division. Total rays 6 (6–7, $\bar{x} = 6.5$, n = 10). Pelvic fin i,7 in all specimens. Pelvic fins reach somewhat posterior to anal-fin origin, reaching level of second or third anal-fin rays. Caudal fin forked, principal ray count 10/9 in all specimens.

Total number of vertebrae including Weberian apparatus 29, n = 10.

*Color in alcohol.*—Background body color pale yellowish-brown. About ten irregular, rather indefinite dark vertical bars present on body; see Fig. 1 of holotype. These nearly absent on somewhat faded paratype from igarapé Tarumãzinho, Amazonas. *Elachocharax mitopterus* also shows variability in body pigment noted by Weitzman and Géry (1981:898) for other three species of *Elachocharax.* Approximately ten dark vertical body bars of *E. mitopterus* similar to those of *E. pulcher* (8–10) and *E. geryi* (10–12) rather than those found in *E. junki* (16 to 18). Dark bars on body of *E. mitopterus* more distinct posteriorly than anteriorly and continuous with dark pigment of pelvic and anal fins. Belly with same color pattern as body sides.

Top of head pale brown to very dark brown. A dark bar from dorsoposterior border of eye to near nape present as in other species of *Elachocharax.* Snout pale to dark brown dorsally, a prominent dark stripe extends from oral border of premaxilla and anterior part of maxilla to anterior border of eye. Stripe complete in holotype (Fig. 1) but in some specimens stripe does not extend over premaxilla to snout tip although mottled dark pigment is present in this region. Anterior tip of lower jaw dark brown. Dark brown chromatophores ventral to eye organized into one broad or two more or less distinct, short vertical bars. Opercle with scattered dark chromatophores which may be expanded and coalesced into variable blotches. As on body, pigment of head varies according to expansion or contraction of dark brown chromatophores. Ventral surface of head also pale to dark, depending on chromatophore expansion. Caudal fin with none (faded?) to as many as five narrow vertical bars. Bars occur on basal area of fin and are absent distally. Pigment of these bars occurs on rays or at least along ray borders. Posterior border of three large terminal scales over base of caudal fin usually broadly covered with dark pigment (Fig. 1), producing a heavy, irregular vertical bar in addition to five or so narrow vertical bars on fin rays. Intraradial membranes of caudal fin nearly without pigment except immediately adjacent to fin rays. Dorsal fin with two prominent horizontal pigment rows in unfaded specimens. As in other species of *Elachocharax,* a dark horizontal band is present along length of dorsal fin near its base. More distal band also well developed in unfaded specimens of *E. mitopterus* but dark chromatophores less concentrated. In both bands, dark chromatophores occur both on rays and membranes between them. Distal one-fourth of dorsal fin appears free of dark chromatophores. Anal and pelvic fins with two broad dark vertical bars (Fig. 1). Pectoral fins dusky in unfaded specimens, pigment concentrated along ray borders. Dark band present at basal region of pectoral fin.

*Relationships.*—In this cladistic analysis, outgroup information is the same as that derived in Weitzman and Géry (1981:898–905). Outgroup analysis for additional characters is presented here. The reasons for placing the new species in *Elachocharax* are quite clear. These are the high number of dorsal-fin rays, 17 or 18 in this species, and the position of the origin of the anal fin at or near an imaginary vertical line drawn through the posterior termination of the dorsal fin. These features agree with characters one and two used as synapomorphies for *Elachocharax* by Weitzman and Géry (1981:898–901). Within *Elachocharax, E.*

*mitopterus* belongs to the group containing *E. junki* and *E. geryi* and consistently having unicuspid jaw teeth and no adipose fin.

Weitzman and Géry (1981:902) also used a reduction (from 5 to 4) of branchiostegal rays to diagnose *E. junki* and *E. geryi* as a group. *Elachocharax mitopterus* has five branchiostegal rays and would not fit a group diagnosed by four branchiostegal rays as a synapomorphy. Weitzman and Géry (1981: 902) note that the sample size of *E. junki* and *E. geryi* is small and that in characidiine outgroups there is variation in this character within genera and species and occasionally between the two sides of the head of a single specimen. If the character is at all useful as a synapomorphy within *Elachocharax* it would now allow recognition of *E. junki* and *E. geryi* as a sister group of *E. mitopterus*. This hypothesis is weakly supported by a synapomorphy consisting of an increased number of dorsal-fin rays, 19 to 21 in *E. junki* and 20 to 22 in *E. geryi*. *Elachocharax mitopterus* has 17 or 18 dorsal-fin rays, a number more nearly approaching that of most outgroup species in the Characidiinae, 11 to 14 rays. However, *E. pulcher*, the nearest outgroup to *E. mitopterus*, *E. junki*, and *E. geryi*, has 17 to 20 dorsal-fin rays, variously overlapping in full, or in part, the ranges of the rays of the other species of *Elachocharax*. With this much overlap and such small samples at hand it seems premature to suggest that a decreased number of branchiostegal rays and an increased number of dorsal-fin rays constitute synapomorphous evidence of a group formed by *E. junki* and *E. geryi*.

Regarding autapomorphies six and seven, the number and width of vertical body bars, in Weitzman and Géry (1981:903, 904), *E. mitopterus* has about 10 narrow, relatively uninterrupted vertical body bars. Thus the high number (16 or 17) and also the interrupted nature of each of the vertical body bars of *E. junki* appear to be autapomorphies for that species. *Elachocharax pulcher* has about 8 to 10 wide vertical body bars. *Elachocharax geryi* and *E. mitopterus* share 9 to 12 narrow body bars. The narrow nature and number of the bars in *E. geryi* and *E. mitopterus* appear to be plesiomorphic, more like the vertical bar pattern in outgroup genera such as *Characidium* Reinhardt and *Klausewitzia* Géry than the autapomorphous wide bars in *E. pulcher* or the relatively derived high number of interrupted autapomorphous bars in *E. junki*.

Characters nine to twelve in Weitzman and Géry (1981:904) are autapomorphies for *E. geryi*. Two of these, numbers nine and eleven (number of inner-row dentary teeth and number of caudal-fin bars) remain clearly autapomorphous for that species. *Elachocharax mitopterus* has 18 or 19 teeth in the inner dentary row; *E. pulcher* has 20 to 24 and *E. junki* 19 to 20. *Elachocharax geryi* has a reduced number of 13 to 16. Similarly, *E. mitopterus*, *E. pulcher*, and *E. junki* have 0 to 5 caudal-fin bars. *Elachocharax geryi* has an increased number of 13 or 14. The remaining two characters, ten and twelve (number of ectopterygoid teeth and number of epibranchial gill rakers) are no longer clearly autapomorphous for *E. geryi* since *E. mitopterus* demonstrates character overlap. The number of ectopterygoid teeth in *E. pulcher* is 7 to 10, in *E. junki*, 8 to 12, in *E. mitopterus*, 4 to 9, and in *E. geryi* it is 4 or 5. Similarly, the number of epibranchial gill rakers in *E. pulcher* is 4 or 5, in *E. junki*, 5 or 6, in *E. mitopterus*, 3 or 4, and in *E. geryi* it is 3. There might be a synapomorphous "trend" towards reduction in these two characters shared by *E. mitopterus* and *E. geryi*. However, such "trends" are poor indicators of synapomorphy because of overlap and, especially in this case, because they are based on so few cleared and Alizarin stained or partly dissected samples, 3 in *E. mitopterus*, 2 in *E. junki*, 2 in *E. geryi*, and 10 in *E. pulcher*. Since the discovery of an additional taxon shows that these two characters are not as distinct as when utilized by Weitzman and Géry (1981:904), it now seems premature to use them as synapomorphies or autapomorphies for these species.

*Elachocharax mitopterus* has several unique characters appearing to be autapomorphies, such as 29 vertebrae versus 30 to 33 in other species of *Elachocharax,* 24 to 26 scales in lateral series versus 26 to 33, 7 scale rows between the dorsal-fin origin and the pelvic-fin origin versus 8, and a tendency to have fewer scale rows around the caudal peduncle, 10 to 14 versus always 14 in the other species of *Elachocharax.* These unique reductions in meristic values in *E. mitopterus* make it unlikely that this species is a hybrid between other known species of *Elachocharax,* or that any one of them could be a hybrid between *E. mitopterus* and one of the other species. Also, these counts are low compared to most species in other genera of the Characidiinae with at least two exceptions. *Ammocryptocharax elegans* Weitzman and Kanazawa (1976:335) and *Klausewitzia aphanes* Weitzman and Kanazawa (1977:151) have 12 scale rows around the caudal peduncle. The most parsimonious cladogram of character distribution among characidiine taxa indicates that this similarity is homoplaseous.

Based on the above analysis, it seems that *E. pulcher* is the sister group of the other three species of *Elachocharax,* all characterized by two synapomorphies, unicuspid jaw teeth and loss of an adipose fin. Except for a reduced number of branchiostegal rays and perhaps a reduced number of dorsal-fin rays in *E. geryi* and *E. junki,* the only apomorphies that so far seem clear and distinct for *E. junki, E. geryi,* and *E. mitopterus* are a series of autapomorphies for each. As discussed above, two putative synapomorphies that might diagnose *E. junki* and *E. geryi* as a group seem somewhat dubious, especially the dorsal-fin ray count. Therefore *E. junki, E. geryi,* and *E. mitopterus* are currently considered to form an unresolved trichotomy.

*Population variation.*—Only small numbers, five each, of two population samples are available, making population variation study nearly impossible. However, one striking difference is present in the two samples. Specimens from near San Carlos, Venezuela always had 10 horizontal scale rows around the caudal peduncle, a very reduced number compared to the other species. The sample from igarapé Tarumãzinho, Brazil had 12 to 14, $\bar{x} = 12.8$. This appears to be an absolute difference in the two population samples of *E. mitopterus.* However, the samples are small and the possible magnitude of the variation is unknown. That variation of this sort occurs at all is surprising. Usually in *Elachocharax* the caudal peduncle scale row count is a constant 14. I would expect a count of 10 to be constant in *E. mitopterus,* as it appears to be in the San Carlos sample. The variation in the count in the igarapé Tarumãzinho sample does not appear to be due to hybridization with other species of *Elachocharax* because this sample is like the San Carlos sample in having the other low meristic values characteristic for this species. An analysis of the caudal row scale count variation in *E. mitopterus* must await collection of larger samples. At this time it would seem premature to recognize the two samples at hand as representing separate taxa.

*Ecological notes.*—The specimens from Caño Chola were taken in a black water forest stream with a temperature of 28.0°C. The stream flow was slow to moderate and the depth of the water was to 1.5 meters. The bottom was sand and logs. Other forest detritus was present as well as filamentous algae and emergent aquatic vegetation. No field notes accompany the specimens from igarapé Tarumãzinho but when I visited the stream at this locality in January 1976 I found it to be a clear, slightly brown, terra firmae stream surrounded by forest. It was similar to the description here for Caño Chola except the water was less dark.

*Etymology.*—The specific name *mitopterus* is from the Greek *mitos* meaning thread and *pteron* meaning wing, hence fin. The name is given in reference to the long thread like rays of the pectoral fin.

## Additional Locality Records for Other Species of *Elachocharax*

Weitzman and Géry (1981:890) reported a few locality records for *E. pulcher* additional to those recorded by Weitzman and Kanazawa (1978:162–164). Since then a few new locality records have come to hand. One specimen of *E. pulcher,* USNM 270142, SL 14.8 mm was found in the same collection as the type locality of *E. mitopterus,* Caño Chola, between San Carlos de Río Negro and Solano, Departamento Río Negro, Territorio Federal Amazonas, Venezuela. A short distance away, four specimens of *E. geryi,* USNM 270146, SL 10.7–13.8 mm, were taken from Caño Manu, a tributary of the Casiquiare Canal, about 250 meters upstream of Solano, at about 02°00'N, 60°59'W. These were taken on 7 Dec 1984 by Richard P. Vari and Antonio Machado-Allison. This locality was a blackwater forest stream. The water temperature was about 27.5°C and the water was moving very slowly. The bottom was sand and forest detritus, the water depth to about 0.5 meter at the capture site. It seems very likely that *E. pulcher, E. geryi, E. mitopterus,* and probably *E. junki,* are sympatric in at least part of their range. All four species are known to live in black acid waters of terra firmae and all have locality records near the Rio Negro, Amazonas, see Weitzman and Kanazawa (1978:162–164, 173) and Weitzman and Géry (1981:890).

In addition, nine specimens of *Elachocharax pulcher,* Naturhistoriska Riksmuseet, Stockholm (NHM SOK) 1984312.3974, SL 9.7–14.7 mm, were collected from Peru, Departamento Loreto, Río Yavari (Javari) system, a quebrada tributary to Río Gálvez, about 25 minutes upstream from Colonia Angamos, about 05°16'S, 73°00'W, by Sven O. Kullander, A. Urteaga C., N. Buendía Y., and A. Hogeborn-Kullander on 31 Jul 1984. This population sample has some specimens with lateral tooth cusps on jaw teeth reduced in size, making them difficult to see except in stained examples. An adipose fin is present in all specimens.

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# NEW SPECIES OF *CUMMINGSIA* FERRIS (MALLOPHAGA: TRIMENOPONIDAE) FROM PERU AND VENEZUELA

Roger D. Price and K. C. Emerson

*Abstract.*—Descriptions and illustrations are given for two new species of *Cummingsia*: *C. barkleyae* off a probable new species of *Thomasomys* Coues from Peru and *C. gardneri* off *Marmosa impavida* (Tschudi) from Venezuela.

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In a recent review of the mallophagan genus *Cummingsia* Ferris (Trimenoponidae), Timm and Price (1985) recognized a total of six species, with five of these in the nominate subgenus and the sixth in the subgenus *Acanthomenopon* Harrison. We have recently obtained two series of *Cummingsia*, each representing a new species; it is our intent here to describe and illustrate these new species.

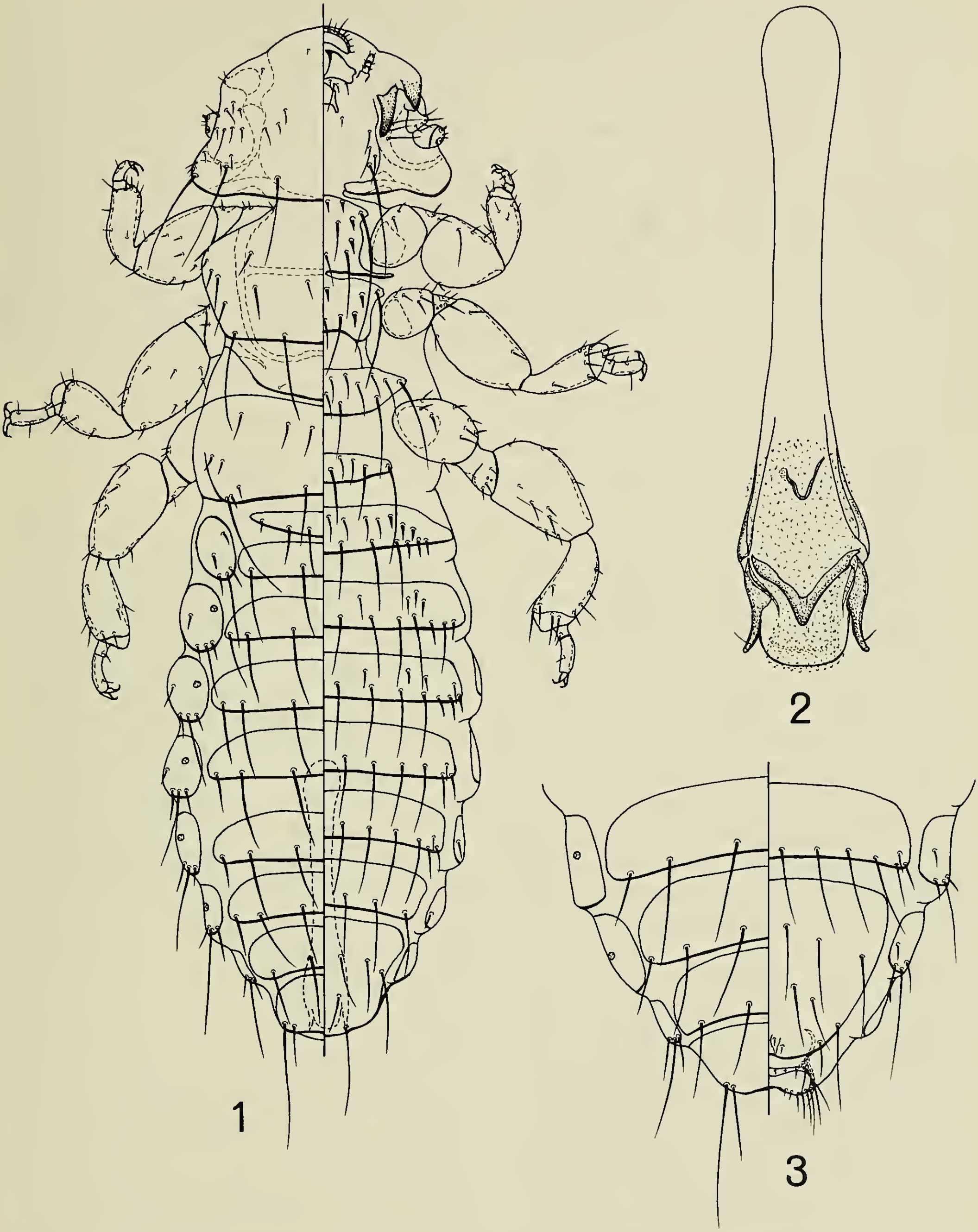
For brevity, the generic and subgeneric characters are as given by Timm and Price (1985) and will not be repeated here. All measurements are in millimeters.

### *Cummingsia* (*Cummingsia*) *barkleyae*, new species
Figs. 1–3

*Type host.*—*Thomasomys* species, probably new [Rodentia: Cricetidae].

*Male.*—As in Fig. 1. Dorsal head chaetotaxy as shown, without any heavier spiniform setae. Both ventral spinous head processes on each side blunt, close together. With well-developed heavily pigmented carina across posterior head margin and lacking medioposterior protrusion. Pronotum with median setae only slightly shorter than pair of lateral setae on each side near end of transverse thickening; metanotum with anterior setae all of essentially similar size. Prosternal plate with 7 long, 7 short stout setae; mesosternal plate with 5 long, 5 short stout setae; metasternal plate with 16–21 short to long setae. Tergal setae: I, 6 (with outermost very short, other 4 subequally long); II, 4–5; III–VII, 6; VIII, 4; IX, 1 very long, 1 medium on each side. Pleura II–VIII each with 3 marginal setae, with middle seta much longer than those adjacent to it. Anterior pleural setae on II, 2; III, 0–1; IV, 1–2; V–VI, 1; VII, 0–1; VIII, 0. Marginal sternal setae: I, 9–11; II, 24–27; III, 21–25; IV, 15–21; V, 12–15; VI, 11–12; VII, 6. Anterior sternal setae: I, 4–6; II, 13–16; III, 5–11; IV, 1–7; V, 0–1; VI–VII, 0. Subgenital plate (fused VIII–IX) with 10 setae. Dimensions: preocular width (POW), 0.27–0.30; temple width (TW), 0.34–0.38; head length (HL), 0.23–0.25; prothorax width (PW), 0.31–0.34; metathorax width (MW), 0.38–0.42; abdomen width at segment V (AW), 0.43–0.47; total length (TL), 1.27–1.41. Genitalia as in Fig. 2, with genital plate broadly tapered, with sac sclerite thin, "U"- to "V"-shaped, and with tip of paramere with subapical seta well removed from end; genitalia width (GW), 0.07–0.08; genital plate width (GPW), 0.05–0.06; genital plate length (GPL), 0.04–0.05.

*Female.*—Much as for male, except as follows. Prosternal plate with 7–9 short stout setae; mesosternal plate with 4–5 long setae. Anterior pleural setae: II, 2–3; III, 1–2; VIII, 0–1. Marginal sternal setae: I, 10–13; II, 27–31; III, 22–27; IV, 19–23; V, 14–18; VI, 13–15; VII (fused with VIII), 6–7. Anterior sternal setae: II, 15–19; III, 7–13; IV, 5–9; V, 1–4; VI, 1–2. Terminalia as in Fig. 3. Subgenital plate (fused VIII–IX) with 11–12 setae, including 4 minute medioposterior



Figs. 1–3. *Cummingsia barkleyae*: 1, Dorsal-ventral male; 2, Male genitalia; 3, Dorsal-ventral female terminalia.

setae. Anus oval, with 26–29 minute to medium setae. Dimensions: POW, 0.29–0.32; TW, 0.39–0.42; PW, 0.35–0.39; MW, 0.46–0.49; AW, 0.57–0.65; TL, 1.62–1.70.

*Remarks.*—By having no abdominal tergites with more than six setae, *C. barkleyae* is allied with *C. albujai* Timm and Price and would be identified with the latter in couplet 2 of the key provided by Timm and Price (1985). However, *C. barkleyae* may be readily distinguished by its having (1) no dorsal head spiniform setae, (2) only four to five setae on tergite II, (3) consistently more marginal sternal setae on II–VI, with ranges well separated especially on II–IV, (4) more anterior sternal setae on II–IV, and (5) all abdominal pleurites with three marginal setae, instead of only two on most pleurites of *C. albujai.*

The chaetotaxy of the abdominal pleurites and dorsal thorax is similar for *C. barkleyae, C. inopinata* Mendez (the only other species known from *Thomasomys*), and *C. perezi* Timm and Price. Both *C. inopinata* and *C. perezi* have more than six setae on at least five abdominal tergites; *C. inopinata* has distinctly fewer metasternal setae and marginal and anterior sternal setae on II–III; and *C. perezi* has distinctively different dorsal head and female subgenital plate chaetotaxy, as well as being larger in most widths and the male genitalia dimensions.

*Etymology.*—This new species is named in honor of Linda J. Barkley, Los Angeles County Museum of Natural History, in recognition of her interest in ectoparasites and for collecting the hosts bearing these lice.

*Holotype.*—Adult ♂, ex *Thomasomys* species, probably new, Peru, Dpto. Huanuco, Unchog, NNW Acomayo, 3450 m, 3 Aug 1984, coll. L. J. Barkley (LJB field catalog number 2438); in collection of U.S. National Museum of Natural History.

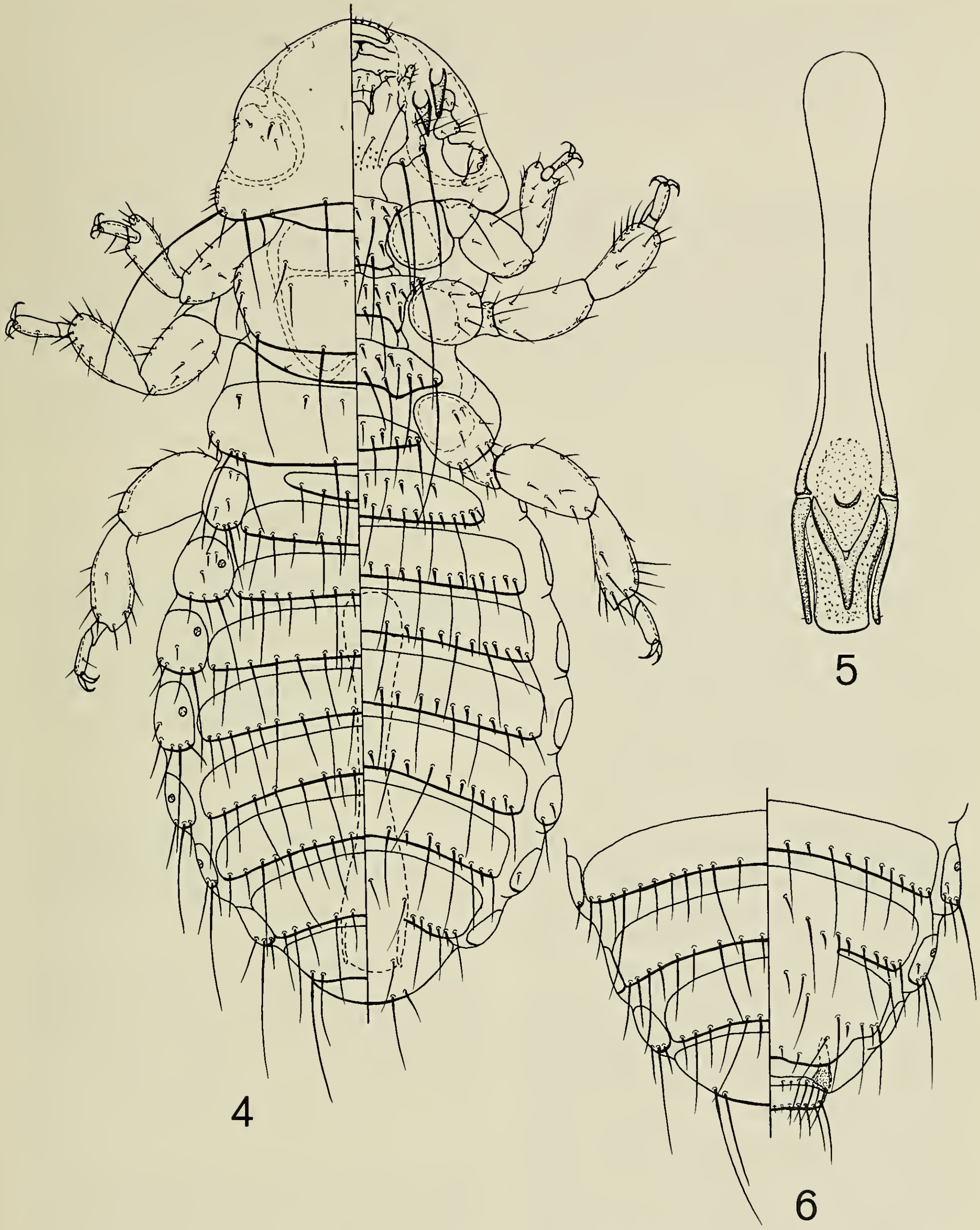
*Paratypes.*—Ex *Thomasomys* species, probably new: 34 ♂♂, 46 ♀♀, same locality and collector data as holotype, 18 Jul–5 Aug 1984 (off 17 host individuals with the following LJB field catalog numbers: 2340, 2341, 2342, 2366, 2376, 2389, 2390, 2391, 2412, 2426, 2432, 2434, 2438, 2439, 2440, 2443, 2449). Paratypes will be distributed among the University of Minnesota, Oklahoma State University, U.S. National Museum of Natural History, and Field Museum of Natural History. Note: Linda J. Barkley informs us that the host is most likely an undescribed species, which will ultimately be described when her studies of the genus *Thomasomys* in Peru are completed.

### *Cummingsia* (*Acanthomenopon*) *gardneri*, new species

Figs. 4–6

*Type host.*—*Marmosa impavida* (Tschudi) [Marsupialia: Didelphidae].

*Male.*—As in Fig. 4. Dorsal head chaetotaxy as shown. Slender pointed ventral inner spinous head process well separated from outer. With reduced carina across posterior head margin and with medioposterior protrusion. Pronotum with median setae very short and fine, with much longer pair of setae on each side near end of transverse thickening; metanotum with anterior setae all of similar length. Prosternal plate with 6 long, 12–15 short stout setae; mesosternal plate with 4 long, 13–15 short stout setae; metasternal plate with 21–22 short to long setae. Tergal setae: I, 6 (shortest outermost, longest innermost); II, 12–14; III, 16–17; IV, 15–19; V–VII, 17–19; VIII, 10; IX, 1 very long, 1 medium on each side. Pleura II and VI each with 4 marginal setae; III–V with 4–5; VII–VIII with 3; all with 1 long among much shorter setae. Anterior pleural setae on II–III, 1–4; IV, 1–2; V–VI, 0–1; VII, 1; VIII, 0. Marginal sternal setae: I, 12–13; II, 29–32; III–VI, 22–24; VII, 18–19. Anterior sternal setae: I, 3; II, 11–12; III–VII, 0. Subgenital plate with 20–21 setae. Dimensions: POW, 0.27–0.28; TW, 0.34–0.37; HL, 0.19–0.22; PW, 0.29–0.32; MW, 0.33–0.34; AW, 0.46–0.49; TL, 1.14–1.17.



Figs. 4–6. *Cummingsia gardneri*: 4, Dorsal-ventral male; 5, Male genitalia; 6, Dorsal-ventral female terminalia.

Genitalia as in Fig. 5, with genital plate elongated, with small semicircular sac sclerite, and with straight to slightly curved parameres each bearing minute seta near tip; GW, 0.07–0.08; GPW, 0.05; GPL, 0.07–0.08.

*Female.*—Much as for male, except as follows. Metasternal plate with 21–24 setae. Tergal setae: I, 8–9; II, 14–16; III, 16–18; IV, 19–20; V, 21–23; VI, 20–22; VII, 16–21; VIII, 12. Pleura III–V each with 5 marginal setae. Anterior pleural setae on II–III, 3–5; V–VI, 1. Marginal sternal setae: I, 13–14; II, 31–34; III–VI, 22–26; VII, 20–22. Anterior sternal setae: I, 4–5; II, 12–14; III, 0–1; IV–VI, 0; VII, 0–2. Terminalia as in Fig. 6. Anus with 25–29 minute to medium setae. Dimensions: POW, 0.28–0.29; PW, 0.31–0.33; MW, 0.37–0.40; AW, 0.52–0.54; TL, 1.25–1.29.

*Remarks.*—Since the subgenus *Acanthomenopon* contains only a single previously-described species, *C. peramydis* Ferris, *C. gardneri* resembles it and keys to it in couplet 1 in Timm and Price (1985), thereby differing grossly from all members of the subgenus *Cummingsia*. The distinguishing features for *C. gardneri* are (1) the consistently smaller size of the female in all dimensions and the male in POW, HL, AW, and TL, (2) the female with more tergal setae on I–III, and (3) the male genitalia smaller in all dimensions, with paramere tips not pronouncedly outwardly curved.

*Etymology.*—This new species is named in honor of A. L. Gardner, U.S. National Museum of Natural History, in recognition of his interest in ectoparasites and his participation in the collection of the hosts bearing these lice.

*Holotype.*—Adult ♂, ex *Marmosa impavida* (Tschudi), Venezuela, T. F. Amazonia, Cerro de la Nebina, 4 Feb 1985, coll. A. L. Gardner and P. J. Spangler (ALG field catalog number 14418); in collection of the U.S. National Museum of Natural History.

*Paratypes.*—Ex *M. impavida*: 6 ♂♂, 8 ♀♀, same locality and collector data as holotype, 3–4 Feb 1985 (off 2 hosts with the following ALG field catalog numbers: 14410, 14418). Paratypes will be distributed among the University of Minnesota, Oklahoma State University, and U.S. National Museum of Natural History.

## Acknowledgments

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PROC. BIOL. SOC. WASH.
99(4), 1986, pp. 753–756

# *PARACYMOTHOA THOLOCEPS*, A NEW FRESHWATER PARASITIC ISOPOD FROM SOUTHERN VENEZUELA (FLABELLIFERA: CYMOTHOIDAE)

Thomas E. Bowman

*Abstract.*—*Paracymothoa tholoceps* is described from a single specimen collected from *Hoplias macrophthalmus* in the Baria River, a tributary of the Orinoco River, in Amazonas State, Venezuela. It differs from the two known species, *P. astyanactis* and *P. parva,* in its larger size, convex anterior margin of the head, convex posterior margin of the telson, longer and more exposed pereonite 7, and less reduced dactyl of pereopod 7. The diagnosis of *Paracymothoa* is emended to accommodate the new species.

The genus *Paracymothoa* was established by Lemos de Castro (1955) for a Brazilian isopod taken from the mouth of *Astyanax bimaculatus.* A second species, *P. parva,* described by Taberner (1976), was found parasitizing *Hyphessobrycon callistus* in Argentina. A third species, from southern Venezuela, is described below.

### *Paracymothoa tholoceps,* new species
Fig. 1

*Material.*—Venezuela, Amazonas territory, Baria River, near base camp of expedition to Cerro de la Neblina, elev. 140 m (ca. 1°45′N, 66°W), ex *Hoplias macrophthalmus* (Pellegrin) (Erythrinidae), leg. Ramiro Ruyero, 26 Feb 1985; 1 ♀ without oostegites, 24.3 mm, holotype USNM 231092.

*Etymology.*—From the Latin "tholus" (dome, rotunda) plus "-ceps" (head), referring to the round anterior margin of the head.

*Diagnosis.*—*Paracymothoa tholoceps* may be distinguished from its two congeners by its greater size, the shape of the head and pleotelson, and the well developed pereonite 7 and dactyl of pereopod 7. The principal differences between the three species are set forth in Table 1.

## Discussion

As defined by Lemos de Castro (1955) and Taberner (1976), *Paracymothoa* differs from its presumed marine ancestor, *Cymothoa* Fabricius, 1793, by the short pereonite 7, almost completely covered by pereonite 6, the short dactyl of pereopod 7, much shorter than the dactyls of the other pereopods, and the weak carinae on the bases of pereropods 4–6, lacking in pereopod 7. *Paracymothoa tholoceps* is closer to *Cymothoa* than *P. astyanaxi* and *P. parva.* Pereonite 7 and the dactyl of pereopod 7 are less reduced, and pereopods 5–6 have well developed carinae on the basis.

The mandible was extremely difficult to remove, and appeared to be firmly attached to the labium. When finally extracted, it had an extraordinary form (Fig. 1f). Brusca (1981) has stated that some authors (including Bowman 1960: fig. 1h) have illustrated a mandible with one lobe of the paragnath attached to it and erroneously considered part of the mandible. Perhaps this explains the unusual form of the mandible in Fig. 1f, yet when removed the labium appeared to be undamaged (Fig. 1g). The labium itself is unusual; the lateral lobes are rather slender and the anterior apices

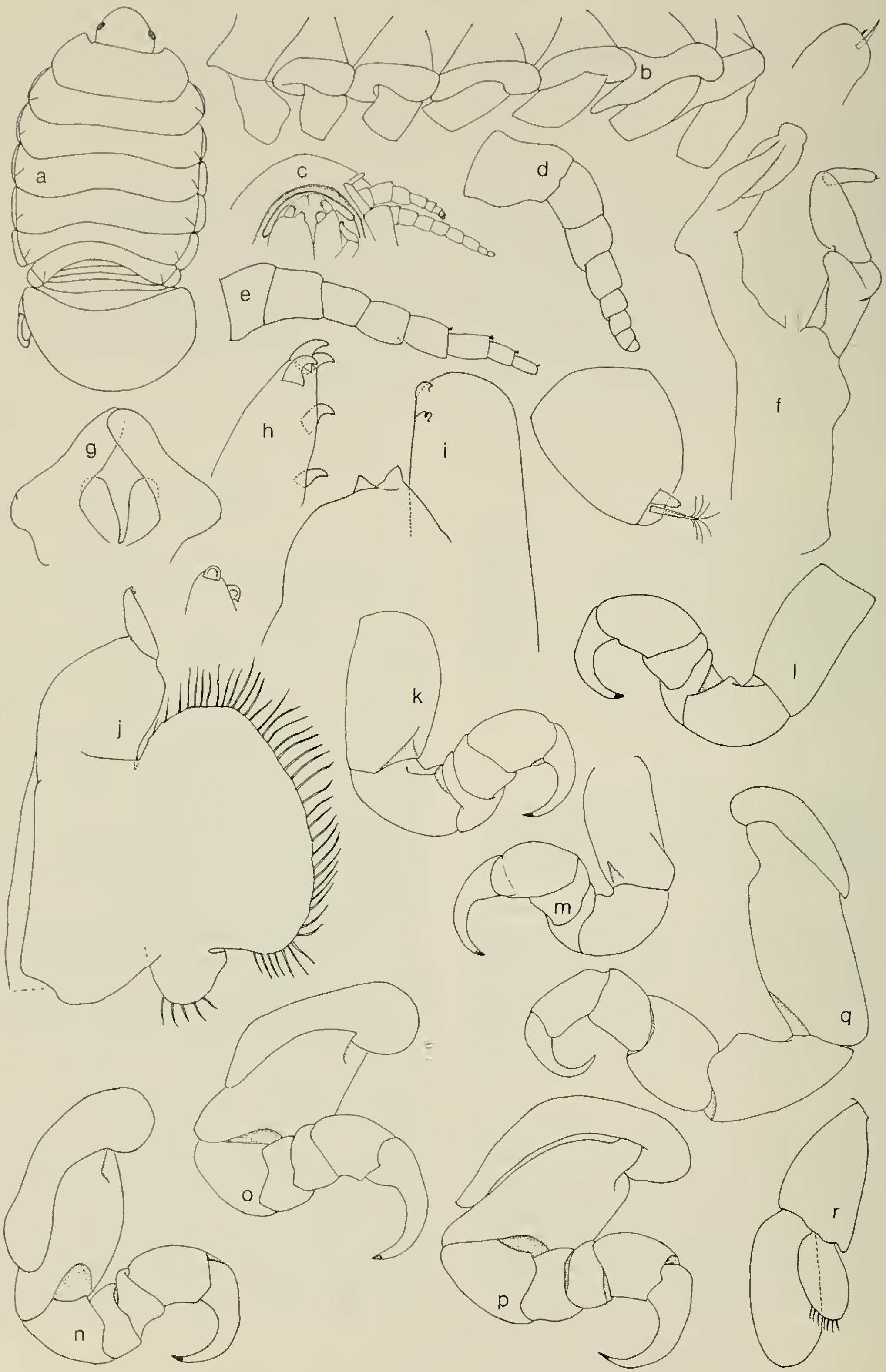
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Table 1.—Characteristics of the species of *Paracymothoa.*

| Character | *P. astyanactis*[1] | *P. parva* | *P. tholoceps* |
|---|---|---|---|
| Length × width (mm) | 10.5 × 5 | 4.2 × 2 | 24.3 × 12.2 |
| Widest pereonite | 6 | 4 | 5 |
| Anterior margin of head | Nearly straight | Nearly straight | Convex |
| Pleotelson width/length | 2.5 | 2 | 2 |
| Pleotelson posterior margin | Emarginate | Nearly straight | Convex |
| Pereonite 7 | Nearly covered by pereonite 6 | Nearly covered by pereonite 6 | Only slightly covered by pereonite 6 |
| Antenna 1 segments | 6 | 7 | 8 |
| Antenna 2 segments | 8 | 8 | 8 |
| Maxilla 1 apical spines | Much larger than subapical spines | Subequal to subapical spines | Subequal to subapical spines |
| Pereopods 4–5, propus | Naked | With row of spines | Naked |
| Pereopod 7, carpus and propus | With row of spines | With row of spines | Naked |
| Propus with distal corner spine | Pereopod 7 | Pereopods 2–7 | None |
| Pereopods 5–6 basis | Not expanded | Not expanded | Expanded |
| Pereopod 7 dactyl | Much shorter than propus | Much shorter than propus | Nearly as long as propus |
| Uropods | Rami subequal, reaching posterior margin of telson | Rami subequal, reaching posterior margin of telson | Outer ramus longer, reaching ca. mid-length of telson |
| Distribution | Rio de Janeiro and Minas Gerais states, Brazil | Corrientes Province, Argentina | Amazonas State, Venezuela |
| Host | *Astyanax bimaculatus* (L.) | *Hyphessobrycon callistus* (Boulanger) | *Hoplias macrophthalmus* (Pellegrin) |

[1] George C. Steyskal has kindly pointed out to me that *astyanaxi* is an incorrect genitive of the host genus and must be corrected to *astyanactis* [(ICZN 32(d)(ii))].

overlap, and the short medial lobes are separated by a deep cleft. Unfortunately the single specimen is insufficient for a thorough study of the mandible and labrum and their relationships.

Since *Paracymothoa tholoceps* does not fit in some respects the definitions of *Paracymothoa* given by Lemos de Castro (1955) and Taberner (1976), an emended definition is given.

## *Paracymothoa* Lemos de Castro, 1955

*Diagnosis* (emended).—Body oval. Head not deeply immersed in pereonite 1; anterior margin broad and almost straight, or convex; not curved ventrally. Antennae short, antennae 1 widely separated at base. Pereonite 1 with short anterolateral angles. Pereonite 7 shorter than other pereonites, sometimes almost completely covered by pereonite 6. Pleon deeply immersed in pereon and much narrower than pereon. Pereopods relatively short; pereopods 1–3 somewhat smaller than pereopods 4–6. Carina of basipod weakly developed in pereopods 4–6 or moderately developed in pereopods 5–6. Pereopod 7 slender, without carina, with dactyl reduced compared to other pereopods. Parasites of freshwater fishes.

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Fig. 1. *Paracymothoa tholoceps*, holotype: a, Habitus, dorsal; b, Pereon, lateral, showing coxae and bases; c, Head, ventral; d, Antenna 1; e, Antenna 2; f, Left mandible; g, Labium; h, Left maxilla 1, apex; i, Left maxilla 2; j, Left maxilliped; k–q, Pereopods 1–7; r, Left uropod.

## Acknowledgments

The expedition to Cerro de la Neblina was organized and led by Dr. Charles Brewer-Carías of the Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales de Venezuela. Principal support for the expedition came from the National Science Foundation, National Geographic Society, Smithsonian Institution, and the American Museum of Natural History. The isopod was given to me by Guido Pereira, Universidad Central de Venezuela, to whom I offer my sincere thanks.

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Taberner, R. 1976. Un nuevo isópodo de la familia Cymothoidae, *Paracymothoa parva* sp. nov. parasito de *Hyphessobrycon callistus* (Boulanger 1900) Eigenmann 1910 (Pisces, Characidae).—Physis (B) 35 (91):163–169.

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# INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

c/o British Museum (Natural History)
Cromwell Road
London SW7 5BD

14 July 1986

The following Opinions, rulings of the International Commission on Zoological Nomenclature, have been published in volume 43, part 2, of the *Bulletin of Zoological Nomenclature* (9 July 1986).

*Opinion No.*
1383 (p. 121) *Apis pilipes* Fabricius, 1775 (Insecta, Hymenoptera): designated as type species of *Megilla* Fabricius, 1805.
1384 (p. 123) *Dromophis* Peters, 1869 (Reptilia, Serpentes): conserved.
1385 (p. 125) *Anolis carolinensis* Voigt, 1832 designated as type species of *Anolis* Daudin, 1802 (Reptilia, Sauria).
1386 (p. 128) *Papilio erato* Linnaeus, 1758 (Insecta, Lepidoptera): neotype designated.
1387 (p. 130) *Curculio picirostris* Fabricius, 1787 and *Tychius stephensi* Schönherr, 1836 (Insecta, Coleoptera, Curculionidae): conserved.
1388 (p. 132) *Callionymus sagitta* Pallas, 1770 (Osteichthyes, Callionymidae): neotype designated.
1389 (p. 134) *Phascolosoma cumanense* Keferstein, 1867 (Sipunculida): given precedence over *Lumbricus edulis* Pallas, 1774.
1390 (p. 136) *Pellonula bahiensis* Steindachner, 1879 (Osteichthyes): replacement lectotype designated.
1391 (p. 138) *Zygaena anthyllidis* Boisduval, [1828] (Insecta, Lepidoptera): conserved.
1392 (p. 140) *Reptomultisparsa* d'Orbigny, 1853 (Bryozoa, Cyclostomata): type species designated.
1393 (p. 142) *Choeropsis* Leidy, 1852 (Mammalia, Artiodactyla): conserved.
1394 (p. 144) *Centrurus limpidus* Karsch, 1879 and *Centruroides ornatus* Pocock, 1902 (Arachnida, Scorpiones): conserved.
1395 (p. 146) *Tomiopsis* Benediktova, 1956 (Brachiopoda, Spiriferida): conserved.
1396 (p. 148) *Byrrhusmurinus* Fabricius, 1794 (Insecta, Coleoptera, Byrrhidae): conserved.
1397 (p. 150) *Rhopalocerus* W. Redtenbacher, 1842 (Insecta, Coleoptera, Colydidae): conserved.
1398 (p. 152) *Capys* Hewitson, [1865] (Lepidoptera, Lycaenidae): conserved.
1399 (p. 154) *Cochliomyia* Townsend, 1915 (Diptera, Calliphoridae): conserved.

The Commission regrets that it cannot supply separates of Opinions.

P. K. TUBBS
Executive Secretary

# INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

c/o British Museum (Natural History)
Cromwell Road
London SW7 5BD

14 July 1986

The following applications have been received by the Commission and have been published in volume 43, part 2, of he *Bulletin of Zoological Nomenclature* (9 July, 1986). Comment or advice on them is welcomed and should be sent c/o The British Museum (Natural History), London, England, Comments will be published in the *Bulletin.*

*Case No.*

1051 *Bubo* Duméril, 1806 and *Surnia* Duméril, 1806 (Aves): proposed confirmation on the Official List.

2463 *Antispila* Hübner, [1825] (Insecta, Lepidoptera): proposed validation of *Antispila stadtmüllerella* [Hübner], 1825 as type species.

2424 *Heteroclonium bicolor* Cope, 1896 (Reptilia, Squamata): proposed conservation by suppression of *Chirotes diglossis* Saenz, 1869.

2493 On the names of two species of the genus *Clytia* Lamouroux, 1812 (Cnidaria, Hydrozoa) common in Western Europe.

2495 *Napomyza* Westwood, 1840 (Insecta, Diptera): proposed conservation by the suppression of *Napomyza* Curtis, 1837.

2397 *Microgaster* Latreille, 1804 (Insecta, Hymenoptera): proposed designation of *Microgaster australis* Thomson, 1895 as type species.

2494 *Sigara scholtzi* Fieber, [1860] (Insecta, Heteroptera): proposed conservation by the suppression of *Sigara scholtzii* Scholtz, 1846.

2519 *Micronecta griseola* Horváth, 1899 (Insecta, Heteroptera, Corixidae): proposed conservation by the suppression of *Sigara minuta* Fabricius, 1794 and *Sigara lemana* Fieber, 1860.

2344 *Calcarina calcer* d'Orbigny, 1839 (Protozoa, Foraminiferida): proposed conservation by the suppression of *Calcarina stellata* de Férussac, 1827.

2395 *Agromyza* Fallén, 1810 (Insecta, Diptera): proposed validation of *Agromyza reptans* Fallén, 1823 as type species.

2537 *Tropiphorus* Schönherr, 1842 (Insecta, Coleoptera): proposed conservation by suppression of *Brius* Dejean, 1821.

2534 *Tetropium* Kirby, 1837 (Insecta, Coleoptera, Cerambycidae): proposed conservation by the suppression of *Isarthron* Dejean, 1835.

2507 *Risomurex* Olsson & McGinty, 1958 (Mollusca, Gastropoda): proposed designation of type species.

2517 *Siphamia* Weber, 1909 and *Siphamia permutata* Klausewitz, 1966 (Osteichthyes, Perciformes): proposed conservation by the suppression of *Beanea* Steindachner, 1902 and *Beanea trivittata* Steindachner, 1902.

2511 *Cyclaxyra* Broun, 1893 (Insecta, Coleoptera): proposed conservation by the suppression of *Melanochroa* Broun, 1882.

1212 SINUITIDAE Dall, 1913, MACLURITIDAE Fischer, 1885 and EUOMPHALIDAE de Koninck, 1881 (Gastropoda, Archaeogastropoda): proposed conservation by suppression of PROTOWARTHIIDAE Ulrich & Schofield, 1897, MACLURAEIDEA Gill, 1817 and SCHIZOSTOMATIDAE Eichwald, 1817.

2408 *Laplysia viridis* Montagu, 1804 (Mollusca, Gastropoda): conservation proposée par la suppression de *Laplisia viridis* Bosc, 1801.

2545 *Orbicula* Cuvier, 1798 (Brachiopoda): proposed suppression.

2546 *Criopus* Poli, 1791 and *Criopoderma* Poli, 1795 (Brachiopoda): proposed suppression.

2551 *Crania tuberculata* Nilsson, 1826 (Brachiopoda): proposed conservation by suppression of *Craniolites brattenburgicus* Schlotheim, 1820.

245 *Trichomonas* Donné, 1836 (Protozoa, Mastigophora): proposed confirmation of spelling.

P. K. TUBBS
Executive Secretary

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99(4), 1986, pp. 760–761

# BIOLOGICAL SOCIETY OF WASHINGTON PROCEEDINGS

## 113th Annual Meeting, 9 May 1986

The 1986 Annual Meeting of the Biological Society of Washington was called to order at 11:00 a.m. on 9 May 1986 in the Waldo Schmitt Room of the National Museum of Natural History. Twenty-four members were present. The Editor, Brian Kensley, was in Aldabra and was represented by Steve Cairns.

Treasurer Don Wilson reviewed the financial status of the Society, noting first that it was solvent and that the Auditing Committee (Drs. Pawson and Ferrari) promised their report later in the month. He further discussed the computer that has been purchased and is being used for billing and record-keeping. With reference to page-charges, Wilson suggested that a slight increase (about $5.00) would allow shipping charges to be prepaid and thus afford the Society some financial benefits. A motion to that effect was made by Bruce Collett, seconded by Tom Bowman, and passed. It was noted that, compared with 1984, the Society's financial status looked weak, but that it was not so. The problem resulted from five issues being paid for in calendar year 1985, leaving a comparatively meagre balance at the end of the year. Wilson asked that the Council approve subscription increases as follows:

General subscriptions
  Domestic $25.00
  Foreign $30.00
Membership
  Domestic $15.00 (no change)
  Foreign $20.00

The motion was made by Collett, seconded by Williams, and passed.

The opinion was expressed that returns on publication of Society data in the Allen Press list of publications did not justify the expenditure, and that the practice should be discontinued. A motion to that effect was made by Olsen, seconded by Collett, and passed.

Steve Cairns presented the Editor's report for Brian Kensley, saying that Volume 97 (1985 Proceedings) contained 1066 pages representing 106 papers. Some 60+ pages per part (256 pages for the year) were subsidized by the Society. Steve pointed out that four papers were botanical, representing an increase over previous years, and that the time between acceptance and publication remained unchanged from 1984.

There followed a short discussion of a volume commemorating the 100th anniversary of the Proceedings. Paul Spangler indicated that he had a rough draft of an index through 1971, that it would not necessitate a great effort to update it, and that it might be suitable to publish it as a Bulletin.

Don Davis then mentioned the results of the recent election of officers: President—Austin B. Williams; President-elect—Kristian Fauchald; Secretary—C. W. Hart, Jr.; Treasurer—Don E. Wilson; Councillors—Stephen D.

Cairns, Mason E. Hale, Robert P. Higgins, Richard P. Vari, Stanley H. Weitzman, and Donald R. Whitehead.

There being no further business to discuss, the meeting was adjourned at 11:45 a.m.

Respectfully submitted
C. W. Hart, Jr.
Secretary

# INFORMATION FOR CONTRIBUTORS

*Content.*—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with 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-163, 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 asked to assume publication costs of page-charges, tabular material, and figures, at the lowest possible rates. Authors are required to pay the charges for figures, tables, changes at proof stage, and reprints. Payment of full costs will facilitate speedy publication.

Costs: Printed page @ $60.00, figures @ $10.00, tabular material $3.00 per printed inch. One ms. page = approx. 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. Manuscripts in dot-matrix will not be accepted. 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.

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