PROCEEDINGS

of the

Biological Society of Washington

VOLUME 103
1990

Vol. 103(1) published 21 March 1990
Vol. 103(2) published 28 June 1990
Vol. 103(3) published 25 September 1990
Vol. 103(4) published 19 December 1990

WASHINGTON
PRINTED FOR THE SOCIETY

All correspondence should be addressed to the
Biological Society of Washington, Smithsonian Institution
Washington, D.C. 20560

ALLEN PRESS INC.
LAWRENCE, KANSAS 66044

OFFICERS AND COUNCIL
of the
BIOLOGICAL SOCIETY OF WASHINGTON
FOR 1990–1991

OFFICERS

President
LESLIE W. KNAPP

President-Elect
STORRS L. OLSON

Secretary
G. DAVID JOHNSON

Treasurer
MICHAEL VECCHIONE

COUNCIL

Elected Members

ROGER F. CRESSEY, JR.
JANET R. GOMON
ROBERT HERSHLER
JANET W. REID
WAYNE C. STARNES
JEFFERY T. WILLIAMS

TABLE OF CONTENTS

Volume 103

INDEX TO NEW TAXA

Volume 103

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

ARTHROPODA

Pycnogonida

Crustacea

Insecta

CHAETOGNATHA

ECHINODERMATA

CHORDATA

Pisces

Amphibia

Reptilia

Aves

Mammalia

PLANTAE

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 103 NUMBER 1
21 MARCH 1990
ISSN 0006-324X

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

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

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

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

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 1-5

THE EXTINCT SLOTH, *MEGALONYX* (MAMMALIA: XENARTHRA), FROM THE UNITED STATES MID-ATLANTIC CONTINENTAL SHELF

H. Gregory McDonald and Clayton E. Ray

Abstract.—A radius of the ground sloth, *Megalonyx,* from off the coast of New Jersey, is the first evidence that ground sloths, along with mastodons and mammoths, inhabited this region during glacial lowering of sea level in the Pleistocene.

During the Pleistocene large areas of the continental shelf were exposed by the lowering of sea level and were inhabited by the terrestrial Pleistocene fauna. Subsequent sea level rise has made recovery and documentation of the species that inhabited this region difficult. Most discoveries of vertebrate remains from the continental shelf are accidental; hence, the currently known diversity of terrestrial vertebrates from this area is low. Evidence of a ground sloth from the continental shelf contributes to our knowledge of the faunal diversity of this area during the Pleistocene.

In July 1966, Ronald Stires of the trawler *Kingfisher* recovered a partial left radius of the ground sloth *Megalonyx* while dredging on the continental shelf off Sandy Hook, New Jersey. Location of the specimen was 40°16.5′N latitude and 73°54.5′W longitude. The specimen was recovered from a bottom depth of 19 meters.

Description of specimen.—The radius (USNM 25175) (Fig. 1) lacks the distal end; the proximal end is eroded. The specimen is dark in color and well permineralized. Breakage of the distal end is angular, with some rounding of the edges of the breaks. Part of the articular surface of the proximal end is preserved but the perimeter of this area has weathered, exposing trabecular bone. There is a slight amount of weathering of the overall surface of the bone. These modifications preclude satisfactory measurements of original dimensions, but the following permit an approximation of the size of the bone: anteroposterior diameter of the proximal articular surface—53 mm, mediolateral diameter of proximal end—51 mm, anteroposterior width of shaft, distally—88 mm. Despite the fragmentary nature of the specimen, enough is preserved to show the distinctive sigmoid curvature of the shaft, characteristic of the radii of megalonychid sloths, in which the distal end is offset anteriorly relative to the proximal end. The distal end of the shaft is compressed mediolaterally relative to the proximal end, which is roughly equidimensional. The medial surface is slightly concave with a complementary convexity on the lateral surface. Preserved on the medial surface are the muscle scars of the *m. pronator quadratus.* Proximal to the offset of the shaft the bone is circular in cross section. The radial tuberosity is large and well developed and offset medially on the posterior edge. There is no indication of an epiphyseal line on the proximal end, which, along with the general massiveness of the bone and rugosity of the muscle scars, suggest that it is probably from an adult.

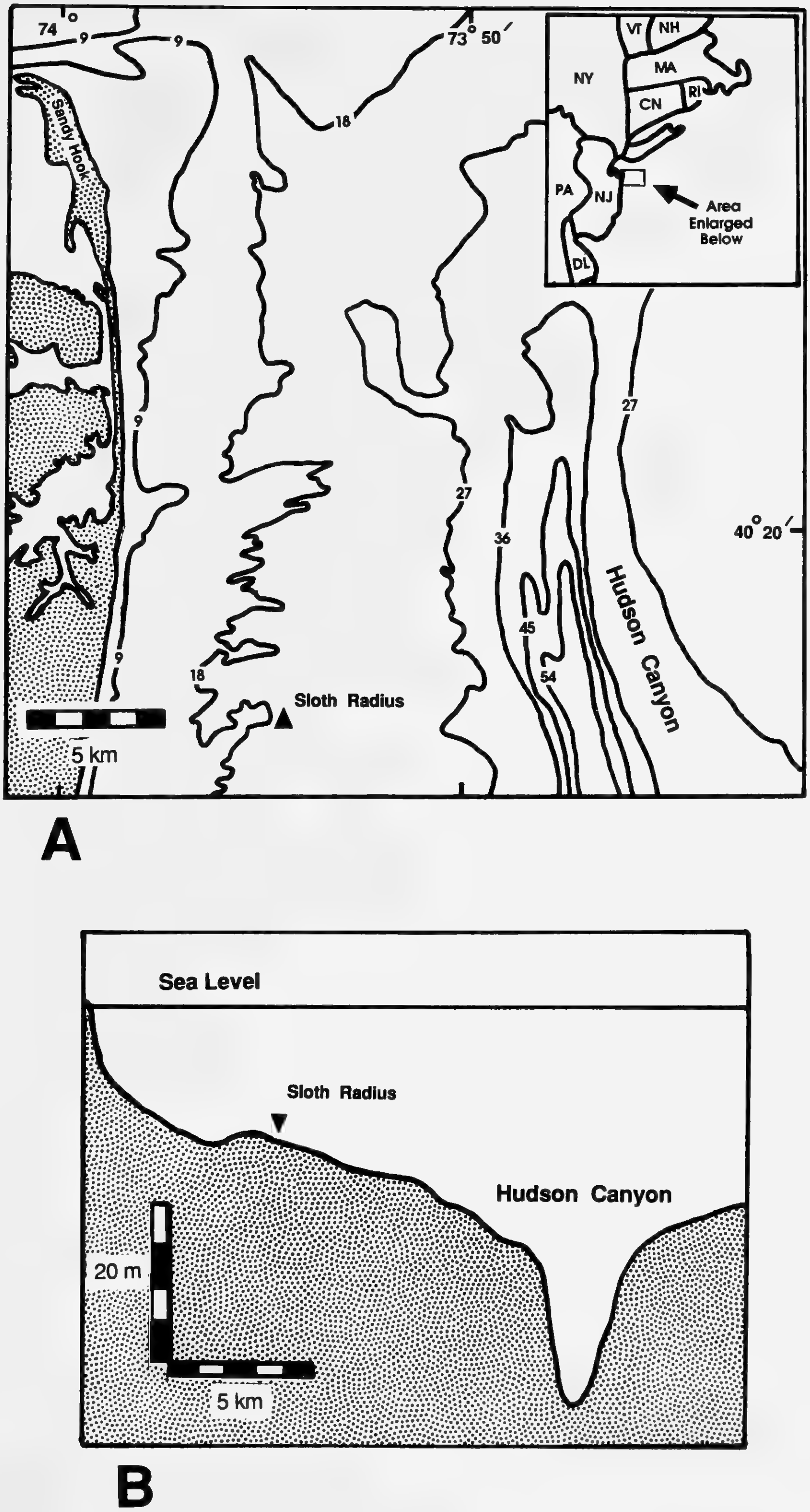
Biogeography.—Whitmore et al. (1967), Oldale et al. (1987) and Gallagher et al. (1989) have documented the distribution of mammoths and mastodons on the Atlantic

Fig. 1. *Megalonyx* cf. *jeffersonii,* partial left radius, USNM 25175. A. Lateral view. B. Medial view.

continental shelf of North America. Although ground sloths have been mentioned as part of the fauna recovered from the continental shelf, no genus or species has ever been given. The specimen described here definitely can be referred to the genus *Megalonyx,* and is probably *M. jeffersonii* although, given the fragmentary nature of the specimen, identification to species is tenuous. *Megalonyx jeffersonii* is the only late

→

Fig. 2. A. Approximate locality at which *Megalonyx* radius was recovered. Depth in meters. B. Cross section along 40°6.5′N latitude showing relationship of location of *Megalonyx* radius to shore and the submarine Hudson Canyon. Map modified from Veatch and Smith (1939). (Original depths for map and cross section from Veatch and Smith [1939] were in feet and fathoms.)


74°
73° 50′
40° 20′
9
18
27
36
45
54
Sandy Hook
Sloth Radius
Hudson Canyon
5 km
VT
NH
NY
MA
CN
RI
PA
NJ
DL
Area Enlarged Below
A
Sea Level
Sloth Radius
Hudson Canyon
20 m
5 km
B

Pleistocene species of the genus (McDonald 1977), and the size of the specimen is within the range of that species.

Megalonyx is the most widespread of the North American ground sloth genera and was present in the northeastern United States at least as early as the Irvingtonian (Middle Pleistocene). Late Pleistocene records for the genus in this region are not uncommon (Parris 1983), so it is not unexpected that it would be among the megafauna migrating onto the continental shelf exposed by the lowering of sea level.

The ecology of *Megalonyx* commonly has been interpreted as that of a forest edge browser (Stock 1925). Utilization of gallery forests along rivers also has been postulated (McDonald & Anderson 1983), although the pattern could be biased by the fact that vertebrate remains are more readily buried and recovered along rivers than in upland habitats. As sea level lowered and rivers extended onto the continental shelf *Megalonyx* may have utilized the expanding gallery forests if this was indeed its preferred habitat. The proximity of the location of the specimen described here to the Hudson River and its canyon on the continental shelf (Fig. 2) fits this pattern. As noted by Dillon & Oldale (1978), outflow of glacial meltwater in the Hudson River Channel eroded a broad valley across the continental shelf until about 12,000 years B.P.

The fragmentary and abraded nature of the specimen does suggest the alternative interpretation that the specimen does not represent primary burial of an individual inhabiting and dying on the exposed continental shelf. The proximity of the specimen to the mouth of the Hudson River and nearness to shore make secondary transport of the specimen a factor to consider.

Because of the permineralization of the specimen no absolute date is possible. However if the specimen represents primary deposition on the continental shelf and not secondary transport, then some inferences regarding the time of its presence on the continental shelf can be made. Although *Megalonyx* was the only genus of ground sloth to range as far north as Alaska (Stock 1942), this was probably during an interglacial phase and does not necessarily indicate that the genus was capable of better thermoregulation than other ground sloths (McNab 1985). Bloom (1983) states that the Atlantic Coastal Plain from lower New York Harbor eastward and northward was glaciated north of latitude 40°30′N. The proximity of the location of this specimen (40°16.5′N longitude) to Bloom's boundary would place it rather close to the edge of the continental glacier during glacial maximum. The location of the specimen is probably too close to the ice front at this time for the animal's thermoregulatory capabilities, based on our current understanding of ground sloth physiology. It is more likely that the presence of *Megalonyx* on the continental shelf post-dates the retreat of the continental glacier from the region. Whitmore et al. (1967) provide dates of around 11,000 years for intertidal salt marsh peat deposits on the Atlantic continental shelf, indicating subaerial exposure until this time, so the sloth remains may be as young as 11,000 years. Further confirmation of the presence and timing of ground sloths on the Mid Atlantic Continental Shelf will require the recovery of additional specimens.

Acknowledgments

This discovery would have remained unknown if Ronald Stires had not presented the specimen to the National Museum of Natural History. His generosity is greatly appreciated. We wish to thank William B. Gallagher et al. (1989) for allowing us access to their manuscript when 'in press' and for permission to cite it. The photos for Figure 1 were made by Victor Krantz and the figure prepared by Mary Parrish. Anita Buck kindly read early drafts of the manuscript and made many helpful editorial suggestions. Robert J. Emry and David C. Parris read and improved the penultimate draft.

Literature Cited

Bloom, A. L. 1983. Sea level and coastal morphology of the United States through the Late Wisconsin glacial maximum. Pp. 215–229 *in* H. E. Wright, Jr., ed., Late-Quaternary environments of the United States, Vol. 1. The Late Pleistocene (S. C. Porter, ed.), University of Minnesota Press, Minneapolis, 407 pp.

Dillon, W. P., & R. N. Oldale. 1978. Late Quaternary sea-level curve: Reinterpretation based on glaciotectonic influence.—Geology 6:56–60.

Gallagher, W. B., D. C. Parris, B. S. Grandstaff & C. DeTample. 1989. Quaternary mammals from the continental shelf off New Jersey.—The Mosasaur 4:101–110.

McDonald, H. G. 1977. Description of the osteology of the extinct gravigrade edentate *Megalonyx* with observations on its ontogeny, phylogeny and functional anatomy. Unpublished M.S. Thesis, University of Florida, 328 pp.

———, & D. C. Anderson. 1983. A well-preserved ground sloth (*Megalonyx*) cranium from Turin, Monona County, Iowa.—Proceedings Iowa Academy Science 90(4):134–140.

McNab, B. K. 1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. Pp. 219–236 *in* G. G. Montgomery, ed., The evolution and ecology of armadillos, sloths and vermilinguas, Smithsonian Institution Press, Washington, D.C., 451 pp.

Oldale, R. N., F. C. Whitmore, Jr., & J. R. Grimes. 1987. Elephant teeth from the western Gulf of Maine, and their implications.—National Geographic Research 3(4):439–446.

Parris, D. C. 1983. New and revised records of Pleistocene mammals of New Jersey.—The Mosasaur 1:1–21.

Stock, C. 1925. Cenozoic gravigrade edentates of western North America.—Carnegie Institution of Washington Publication 331: 206 pp.

———. 1942. A ground sloth in Alaska.—Science 95: 552–553.

Veatch, A. C., & P. A. Smith. 1939. Atlantic submarine valleys of the United States and the Congo submarine valley.—Geological Society America Special Paper No. 7: 101 pp.

Whitmore, F. C., Jr., K. O. Emery, H. B. S. Cooke, & D. J. P. Swift. 1967. Elephant teeth from the Atlantic continental shelf.—Science 156(3781): 1477–1481.

(HGM) Cincinnati Museum of Natural History, Cincinnati, Ohio 45202; (CER) Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 6–25

SYSTEMATICS OF THE "GREEN-THROATED SUNANGELS" (AVES: TROCHILIDAE): VALID TAXA OR HYBRIDS?

Gary R. Graves

Abstract.—Four species of hummingbirds, *Heliangelus squamigularis* Gould, 1871, *Heliangelus barrali* Mulsant & Verreaux, 1872, *Heliotrypha speciosa* Salvin, 1891, and *Heliotrypha simoni* Boucard, 1892, were described from 19th century commercial "Bogotá" collections. The systematic status of these taxa, which I collectively refer to as "green-throated sunangels" (GTS), is unresolved, but they have been variously treated as one or more valid species or as hybrids. I examined three systematic hypotheses—that GTS specimens represent (1) one or more valid species; (2) genetic variants of other species; or (3) hybrids. Plumage and mensural characters of GTS (n = 14) suggest they represent hybrids of *Heliangelus amethysticollis* × *Eriocnemis cupreoventris* from the Eastern Cordillera of the Colombian Andes. Alternate hypotheses of hybridity are discussed. Discrimination of hybrids and identifying their parental species depends upon an efficient "hybrid diagnosis." The current method of diagnosing hybridity is often insufficient in that the materials, methods, and results are not properly documented. I address these problems and suggest guidelines for hybrid diagnoses.

Untold thousands of hummingbird skins were exported from northwestern South America in the 19th century for the millinery trade and collectors of natural history specimens. Systematists sorted through some of the massive shipments of "Bogotá" trade skins and described dozens of new species, a few from unique specimens (e.g., Boucard 1892). Most were subsequently verified by the discovery of populations; others were determined to be of hybrid origin (Berlioz & Jouanin 1944). However, the validity of more than a dozen taxa remains indeterminate (Morony et al. 1975). These represent some of the most challenging problems in avian taxonomy. Resolving their systematic status depends on the mechanics of discriminating avian hybrids from valid biological species.

This paper has two aims that are addressed concurrently. I evaluate the systematic status of an enigmatic group of hummingbird taxa known only from a handful of 19th century specimens. Of more general interest, I examine the assumptions, materials, and methods of the hybrid diagnosis in avian taxonomy.

Taxonomy of the "Green-throated Sunangels"

Four species of hummingbirds, that I collectively refer to as "green-throated sunangels" (hereafter abbreviated as GTS), were described from 19th century "Bogotá" collections: *Heliangelus squamigularis* Gould, 1871; *Heliotrypha barrali* Mulsant & Verreaux, 1872; *Heliotrypha speciosa* Salvin, 1891; and *Heliangelus simoni* Boucard, 1892. *Heliotrypha* Gould, 1853 is now considered a junior synonym of *Heliangelus* Gould, 1848.

Taxonomic uncertainty within the group began with Gould (1871), who was initially inclined to consider the type specimen of *H. squamigularis* a sport or variant of some other *Heliangelus* species, but who after further investigation characterized it as a new species related to *Heliangelus exortis* and *H. amethysticollis. H. barrali* and *H. squamigularis* were not compared with one another before being described. Salvin (1892) considered these taxa as identical, but distinct from his newly described *H. speciosa.* In the first review of all four taxa, Boucard (1895) followed Salvin's synonymy of *H. barrali* and *H. squamigularis,* but treated *H. simoni* (Boucard 1892) and *H. speciosa* as valid species, while noting the possibility that both were varieties of *H. squamigularis.* Cory (1918) lumped *H. speciosa* and *H. simoni* and initiated the two-species taxonomy for the group adopted by Simon (1921), Peters (1945), and provisionally by Morony et al. (1975). Hartert (1922), perhaps cued by Boucard (1895), proposed that *H. simoni* and *H. speciosa* were aberrations of a single valid GTS species (=*H. squamigularis*). The possible hybrid origin of GTS was first raised by Berlioz (1936), who suggested that a specimen in Paris, which had previously been identified as *H. simoni* (discussed later), represented a hybrid of *Heliangelus exortis* × *Haplophaedia aureliae.* This opinion was endorsed by Jouanin (1950) and Greenway (1978), but Berlioz & Jouanin (1944) were less conclusive, stating simply that GTS were hybrids between either *H. exortis* or *H. amethysticollis* and some species of *Eriocnemis* (including the closely related genus *Haplophaedia*). Meyer de Schauensee (1949) at first doubted the notion of hybridity but later agreed with Berlioz & Jouanin (1944) and supposed that GTS were hybrids of *Eriocnemis* sp. × *Heliangelus* sp. (Meyer de Schauensee 1966). Hilty & Brown (1986) listed *H. speciosa* and *H. squamigularis* as presumed hybrids without mentioning parental species.

Syntypes of *Heliotrypha simoni*

Boucard's (1892) use of the plural "specimens" in his description of *H. simoni* implied that the description was based on two or more syntypes. Cory (1918) and Lord Rothschild (Hartert 1922) each obtained a syntype of *H. simoni,* presumably from Boucard before his death in 1905. The labels of both specimens (FMNH 46294, AMNH 483683) are marked, "*Heliotrypha simoni,* ♂, Typical specimen, Colombia," in what appears to be Boucard's handwriting (fide Greenway 1978). Simon (1921) stated in a footnote that he could not find the type of *H. simoni* in Boucard's collection, which suggests that only two syntypes existed, both of which were sold or exchanged by Boucard to other museums. Berlioz (1936), however, argued that a specimen in the Boucard Collection labeled "*Heliotrypha speciosa,* ♂, Colombia" (now deposited in MNHN, Paris), was in fact the type and only existing specimen of *H. simoni* (see Berlioz & Jouanin 1944, Jouanin 1950). He apparently based his conclusion on the close resemblance of the specimen to Boucard's description of *H. simoni,* and on the fact that Boucard (1895) did not mention possessing a specimen of *H. speciosa.*

Several explanations are possible for this discrepancy. Assuming that there were originally three examples of *H. simoni,* Boucard may have attached a new label to the remaining syntype after disposing of the other two. Other possibilities are that Boucard (1895) obtained the specimen of *H. speciosa* after the publication of his monograph or that the specimen was labeled by Boucard as *H. speciosa* before he described *H. simoni* and never relabeled afterwards. In any event, only specimens designated by Boucard Museum labels as "*H. simoni*" should be regarded as syntypes.

Materials and Methods

The type specimens of GTS are deposited in three different museums and are not available for loan. This prevented me from comparing all type specimens simultaneously. I examined three type specimens: (1) the type of *Heliotrypha barrali* (AMNH

Fig. 1. Ventral view of "green-throated sunangels" deposited in the American Museum of Natural History (from left to right: 483680, 483681, 483678, 483684, 483682, syntype of "*Heliotrypha simoni*" [483683], type of "*Heliotrypha barrali*" [37655]).

37655) and (2) a syntype of *Heliotrypha simoni* (AMNH 483683) in the American Museum of Natural History (see Hartert 1922, Greenway 1978); and (3) a syntype of *Heliotrypha simoni* (FMNH 46294) in the Field Museum of Natural History. The AMNH types were compared directly with five additional specimens (AMNH 483678, 483680, 483681, 483682, 483684) that have been variously identified as one or more of the GTS taxa (Fig. 1). The FMNH type was compared directly with FMNH 46286 (identified as *H. barrali* on its Boucard Museum label). I examined one additional GTS specimen (ANSP 160344 [formerly AMNH 483679]). These specimens were compared with mensural data and color transparencies of the following specimens: one labeled *H. speciosa* (considered by Berlioz [1936] as a syntype of *H. simoni*) in the Museum National D'Histoire Naturelle (MNHN), Paris; the types of *H. squamigularis* (BM 88.7.25.178) and *H. speciosa* (BM 87.3.22.889), and an unnumbered specimen of *H. barrali* (photographs only) in the British Museum of Natural History (see Appendix). GTS specimens and color transparencies were compared with series of all hummingbird species in the National Museum of Natural History (USNM) and the American Museum of Natural History. In addition to the GTS specimens examined in this study, at least one other specimen exists (Berlioz 1964). Color comparisons of specimens were made under Examolites® (Macbeth Corp.).

Measurements (wing chord, tail from insertion of central rectrices to tip of the outer and innermost rectrices, and culmen from anterior extension of feathers) were taken

Table 1.—Measurements (mm) of "green-throated sunangels."

	Age[a]	Wing chord	Outermost rectrix	Central rectrix	Culmen
Type specimens					
(1) *squamigularis* (BM)	adult	63.5[b]	43.2[b]	33.0[b]	16.6[c]
(2) *barrali* (AMNH)	immature	63.1	42.8	34.5	17.3
(3) *speciosa* (BM)	adult	63.5[b]	40.6[b]	36.8[b]	19.4[c]
(4) *simoni* (AMNH)	immature	60.4	43.4	33.6	18.5
(5) *simoni* (FMNH)	adult	64.5	43.3	34.7	16.9
Other specimens					
(6) "*speciosa*" (MNHN)	adult	64.0[d]	42.5[d]	32.0[d]	19.0[d]
(7) FMNH 46286	immature	64.5	43.9	35.7	16.8
(8) AMNH 483678	adult	64.6	43.9	35.9	17.1
(9) AMNH 483680	immature	64.5	43.8	35.6	15.7
(10) AMNH 483681	adult	63.7	41.4	33.6	16.3
(11) AMNH 483682	adult	56.5	—	—	—
(12) AMNH 483684	adult	62.3	40.8	—	16.8
(13) ANSP 160344	immature	60.5	39.8	33.6	16.8

[a] Immatures have corrugations on the ramphothecum of the upper jaw.
[b] Measurement from Salvin 1892.
[c] Measurement courtesy of J. Becker.
[d] Measurement courtesy of C. Jouanin.

with digital calipers and rounded to the nearest 0.1 mm (Table 1).

I used principal components analysis (PCA) on untransformed variables to reduce the dimensionality of data and to facilitate the analysis of morphology in two dimensions. Unrotated principal components were extracted from correlation matrices (SYSTAT).

Systematic Status of Green-throated Sunangels

Investigations of GTS have engendered a remarkable variety of systematic opinions. If nothing else, this strongly suggests that multiple hypotheses of origin must be addressed. Accordingly, I considered three possibilities. GTS may represent one or more of the following entities: (1) rare genetic variants of other *Heliangelus* species (Gould 1871); (2) hybrids (Berlioz 1936; Berlioz & Jouanin 1944; Meyer de Schauensee 1949, 1966; Jouanin 1950; Greenway 1978; Hilty & Brown 1986), or (3) population samples of one or more valid biological species (Gould 1871, Salvin 1892, Boucard 1895, Cory 1918, Peters 1945, Morony et al. 1975).

Do green-throated sunangels represent rare genetic variants of other species?—Several examples of intra-population variation in plumage are known in *Heliangelus* species. Polymorphism in the number of iridescent gorget feathers in females has been well documented, particularly in *Heliangelus exortis* (Chapman 1917; Zimmer 1951; Bleiweiss 1985a, b), and melanism involving part or the entire plumage is known in a number of Andean genera (Hartert 1922, Greenway 1978, Graves, pers. obs.). Intrasexual color polymorphism, however, does not appear to be significantly correlated with size. GTS closely resemble some species of *Heliangelus* (e.g., *H. exortis*), but differ in body proportions from all species and by having lengthened tibial plumes and a green or silvery-green gorget in combination with brilliantly reflective plumage on the posterior part of the body. These qualitative characters indicate that GTS are not plumage variants of any other species of hummingbird.

Hybrids or species?—As demonstrated by a century of equivocal taxonomy, it is difficult to determine whether GTS are hybrids or valid species. This is due primarily to two factors. GTS specimens were collected in the 19th century and are unaccompanied by ecological, sexual, or locality data. They are believed to have originated from the Andean region of northwestern South America, an area of high species diversity where new species of hummingbirds are still being discovered (e.g., *Eriocnemis mirabilis*). The large number of GTS specimens (n = 15), presumably collected in a biotically diverse but poorly-known region, favors the valid species hypothesis. On the other hand, the plumage color and morphology of GTS are variable and intermediate between sunangels (*Heliangelus*) and pufflegs (*Eriocnemis* and *Haplophaedia*). This suggests that hybridization is involved. As hybrids have no standing in zoological nomenclature, the burden of proof is on taxonomists to reject the hybrid origin of GTS conclusively before conferring species status on them.

The process of discriminating avian hybrids and their parental species can be termed the "hybrid diagnosis." Most taxonomists consider the pathways of hybrid diagnosis to be self-evident and the documentation of methods and diagnostic assumptions to be unnecessary. However, omissions of these crucial data obscure the diagnoses of all but the most obvious cases of hybridity. Beyond calling attention to an "unusual" specimen, a hybrid report based on an incomplete diagnosis is of little value to taxonomists and evolutionary biologists. As a minimum, the following points (not mutually exclusive), should be explicitly addressed in hybrid diagnoses.

1. Potential parental species: What species were considered as possible parental species and why?
2. Diagnostic assumptions of character analysis: What operational assumptions were made concerning the inheritance of plumage and morphological characters of hybrids? How were characters defined and apomorphies identified?
3. Documentation of results: Can the hypothesis of hybridity be rejected? If not, how were the parental species identified to the exclusion of all others? How were alternate hypotheses (e.g., valid taxon; genetic or developmental variant) rejected?

Hybrid Diagnosis

Potential parental species.—For any hybrid of unknown parentage, the pool of potential parental species (species hypothetically or actually available for hybridization) can be defined taxonomically and geographically. Interordinal hybridization is unknown in birds (Gray 1958); interfamilial hybridization has been reported in captivity (e.g., turkey × guinea fowl) but is unknown in nature. Thus, the taxonomic pool can be narrowed considerably if the hybrid can be identified to a particular family-level group (e.g., hummingbird or duck), which is always the case. The taxonomic pool may be further restricted to a subfamily, genus, or a single pair of species when the rationale for doing so can be vigorously supported. For example, Parkes (1984) properly restricted the pool of potential species of a hybrid cuckoo collected in Pennsylvania to the only pair of *Coccyzus* species that occur sympatrically in North America north of the Gulf coast. In the interest of comprehensiveness, however, he could have also addressed the six other species of *Coccyzus* in a few sentences in much the same way a taxonomist would mention other species in the differential diagnosis of a new species.

As suggested by the cuckoo example, the pool of potential parental species can be limited geographically. The degree of limitation depends on knowledge of the migratory habits of the potential parental species and the geographic origin of the hybrid. For instance, the taxonomic pool of potential parental species of a hybrid hummingbird is defined by the family Trochilidae (345+

species). A hybrid hummingbird originating from Arizona could have no more than 20 potential parental species (190 species combinations). On the other hand, a hybrid from an unspecified area of northwestern South America could have 150+ potential parental species (10,440 species combinations). Clearly, the difficulty of hybrid diagnosis is directly proportional to taxonomic species diversity and geographic scope.

Diagnostic assumptions of character analysis.—In diagnosing putative hybrids, I assumed that mensural characters, such as wing and bill length, were polygenic and additive and that the morphology of hybrids does not exceed that of the parental species (Falconer 1981). Plumage characters in hybrids may resemble a mosaic of the parental species or be inherited intact from one parent, depending on the number of encoding genes and their interaction (Hutt 1949, Buckley 1982). Hypothetically, hybrids may exhibit a wide range of plumage phenotypes. The major pigments in bird plumage, melanins, carotenoids, and porphyrins, appear to be under separate genetic control and mutually independent between feather tracts. The inheritance of structural colors, which dominate the plumage of hummingbirds, is poorly understood (Fox & Vevers 1960, Lucas & Stettenheim 1972), but the complexity of color-producing structures suggests a polygenic mode of inheritance.

What little is known about inheritance in hybrid hummingbirds is summarized by Banks & Johnson (1961) and Short & Phillips (1966). Strongly contrasting patterns of non-structural color (e.g., rufous and black rectrices of *Selasphorus* sp.) are expressed in some fashion in all crosses. There is reason to doubt that the same is always true, however, for plumage characters exhibiting brilliant structural color. For example, the coronal iridescence found in species of *Calypte* is evident in five examples of *C. anna* × *Selasphorus sasin* and one specimen of *C. anna* × *Stellula calliope* (although it is never as extensive on the hybrids as it is on *C. anna*), but is lacking in the single known *C. anna* × *Archilochus alexandri* hybrid (Banks & Johnson 1961). This suggests either that few genes control the color of coronal plumage or that phenotypic expression is controlled by a modifer in these species. The shape of gorget feathers, rectrices, and remiges of hybrids is generally intermediate between those of the parental species, reflecting a polygenic mode of inheritance.

Banks & Johnson (1961) assumed that hybridization in hummingbirds does not produce traits of species or genera other than those involved in the particular cross. This assumption rules out the possibility of atavistic characteristics—those not found in either parental species but which reflect a pattern postulated to be ancestral or the result of mixed alleles encoding polygenic traits. Although atavism is well known in certain anseriform hybrids (e.g., Harrison & Harrison 1963), it has not been documented in hybrid hummingbirds.

This study was geared toward the identification of apomorphic character states in putative hybrids. The mosaic expression of parental autapomorphies in a number of characters is the best indicator of hybridity of a unique specimen and provides the only direct evidence of parentage. However, because many plumage characters are polygenic, the expression of parental apomorphies may be obscured in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the expression of a combination of plesiomorphic characters unique to a single pair of parental species.

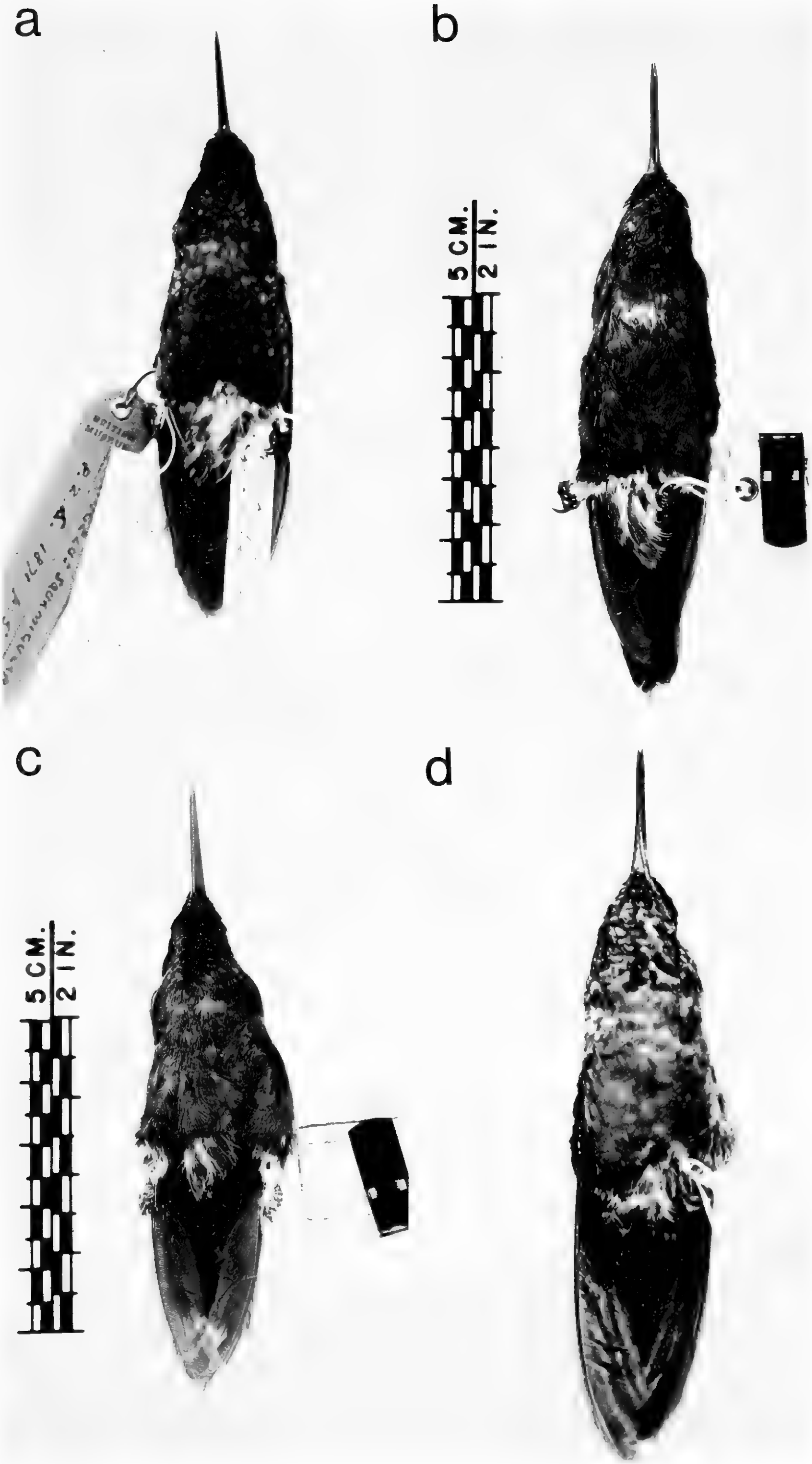
Results

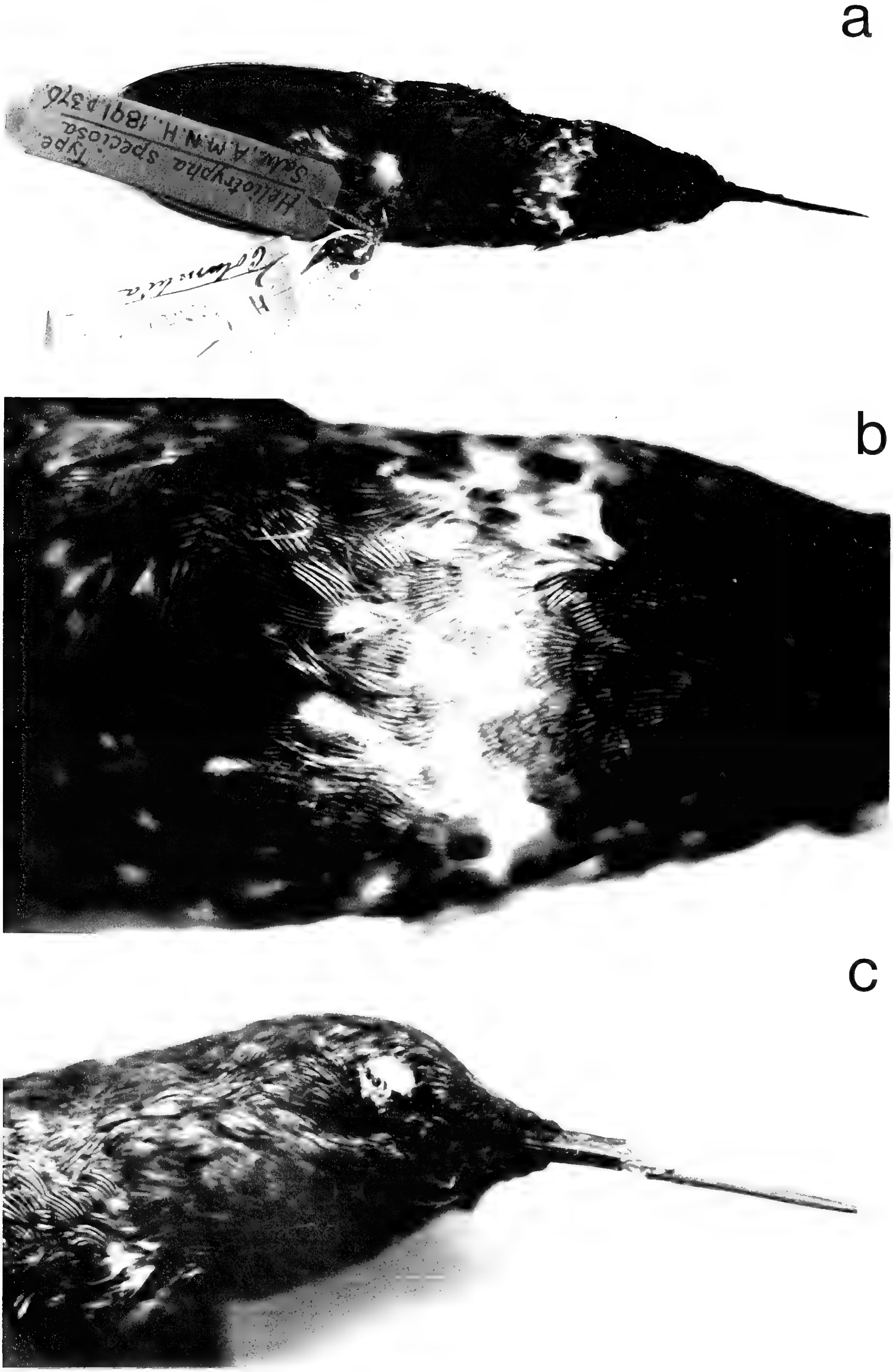
The original labels of GTS specimens are marked "Columbia" (sic), "Colombia," "New Grenada," or "Bogotá Collection." Thus, the geographic pool can only be defined in general terms. Berlioz & Jouanin (1944) showed that the vast majority of skins

Fig. 2 Feet and tarsi of "green-throated sunangels" (a = FMNH 46286; b = FMNH 46294), *Heliangelus amethysticollis* (c, male), and *Eriocnemis cupreoventris* (d, male). Note downy leg puffs on tibias of a, b, and d.

→

Fig. 3. Ventral view of "green-throated sunangels": (a) type of "*Heliangelus squamigularis*"; (b) FMNH 46286; (c) syntype of "*Heliotrypha simoni*" (FMNH 46294); (d) "*Heliotrypha speciosa*" (MNHN).


a
b
5 CM.
2 IN.
c
5 CM.
2 IN.
d


a
Heliotrypha speciosa. Type.
Salv. A.M.N.H. 1891.376.
Colombia
H
b
c

prepared in the "Bogotá" method were collected in the northern Andes and adjacent lowlands, a region roughly encompassed by the present boundaries of Colombia. In the absence of unequivocal locality data for any of the "green-throated sunangels," the geographic pool of potential parental species must initially include all hummingbirds recorded from Colombia, a total of 143 species in 61 genera (Hilty & Brown 1986).

There are two major lineages of hummingbirds, the Phaethornithinae and Trochilinae. As *Heliangelus* and related genera belong to the Trochilinae, I treat the subfamily Phaethornithinae as an outgroup. I identified all species of hummingbirds that occur in Colombia that shared with GTS one or both of the following characters that are apomorphic with respect to species in the outgroup: (1) lengthened downy tibial plumes (leg puffs) (Fig. 2); and (2) a brilliant gorget that contrasts with adjacent plumage and extends from the chin posteriorly to the upper breast (Figs. 3, 4). With the exception of GTS, no taxon exhibits both of these characters. It follows that if GTS are hybrids, then one parental species contributed leg puffs and the other the brilliant gorget.

Species representing four genera of hummingbirds, *Boissonneaua, Eriocnemis, Haplophaedia,* and *Ocreatus,* have downy tibial plumes that exceed those of GTS in length. Narrowing the pool of potential parental contributors of the brilliant gorget is more difficult. Including taxa with brilliantly reflective throats that do not contrast with adjacent plumage, species representing most of genera of the subfamily Trochilinae could be the gorgeted parent. However, only species of *Heliangelus* have gorgets that are similar in structure, shape, and size to those of GTS. Thus, a first review based on two apormophic characters limits the potential parental species to five of the 61 genera of Colombian hummingbirds.

Reduction of the species pool is supported by comparison of general morphology. The remiges, rectrices, body plumage, and bill of GTS are unspecialized and lack many of the elaborations that are common within trochiline hummingbirds. Assuming polygenic inheritance of these structures, if GTS are hybrids, then their parental species must be morphologically unspecialized. Sexual dichromatism within the series of GTS specimens, if any, is minor (Fig. 1). Collections of sexually dichromatic species of hummingbirds from Bogotá collections are often sexually skewed in favor of brightly colored adult males (Graves, in prep.). Plumage of immature males of these species may resemble that of females. Because immature GTS specimens do not differ significantly in appearance from adults (which suggests that the sexes are similar), sexual bias in collecting due to appearance of GTS specimens is unlikely. Assuming a 1:1 sex ratio the probability of finding only males or females in a random sample of 13 (number examined) individuals is $P < 0.0002$ (Binomial test). However, as pointed out by Haldane (1922), the heterogametic sex (♀ in birds) may be rare or absent in F_1 hybrids. Therefore, for diagnostic purposes I entertained the possibility that the sample of GTS specimens was exclusively male.

By structural criteria alone, 106 species (47 genera including *Ocreatus* and *Boissonneaua*) may be eliminated from the pool of potential parental species. These include species with specialized bills (e.g., *Ensifera ensifera, Schistes geoffroyi*), remiges (e.g., *Campylopterus falcatus, Aglaeactis cupripennis*), rectrices (e.g., *Ocreatus underwoodii, Acestrura mulsant*), and body plumage (e.g., *Colibri coruscans, Lophornis stictolo-*

←

Fig. 4. Type of "*Heliotrypha speciosa*": (a) ventral view; (b) enlargement of upper breast showing white pectoral band; (c) side view of head showing sloping profile forehead and thick bill.

pha). External morphology of the remaining 37 species representing 14 genera (*Klais, Chlorestes, Lepidopyga, Chrysuronia, Goldmania, Goethalsia, Amazilia, Adelomyia, Anthocephala, Urosticte, Phlogophilus, Heliangelus, Eriocnemis, Haplophaedia*) is relatively unspecialized. These bear further scrutiny as potential parental species of GTS.

GTS have unpatterned rectrices and uniformly dark bills. This suggests that species with spotted or patterned rectrices (e.g., *Amazilia* sp., *Anthocephala floriceps, Adelomyia melanogenys, Phlogophilus hemileucurus*) or markedly bicolor lower ramphotheca (e.g., *Amazilia* spp.) can be eliminated, leaving species from three genera (*Heliangelus, Eriocnemis, Haplophaedia*) as potential parental species of GTS. Excepting these, all other species may be rejected from the species pool by two or more criteria (available from the author). In sum, rejection of species whose distinctive characters (some of which are apomorphic) are not found in GTS, reduces the species pool to nearly the same subset of species that share apomorphic characters with GTS.

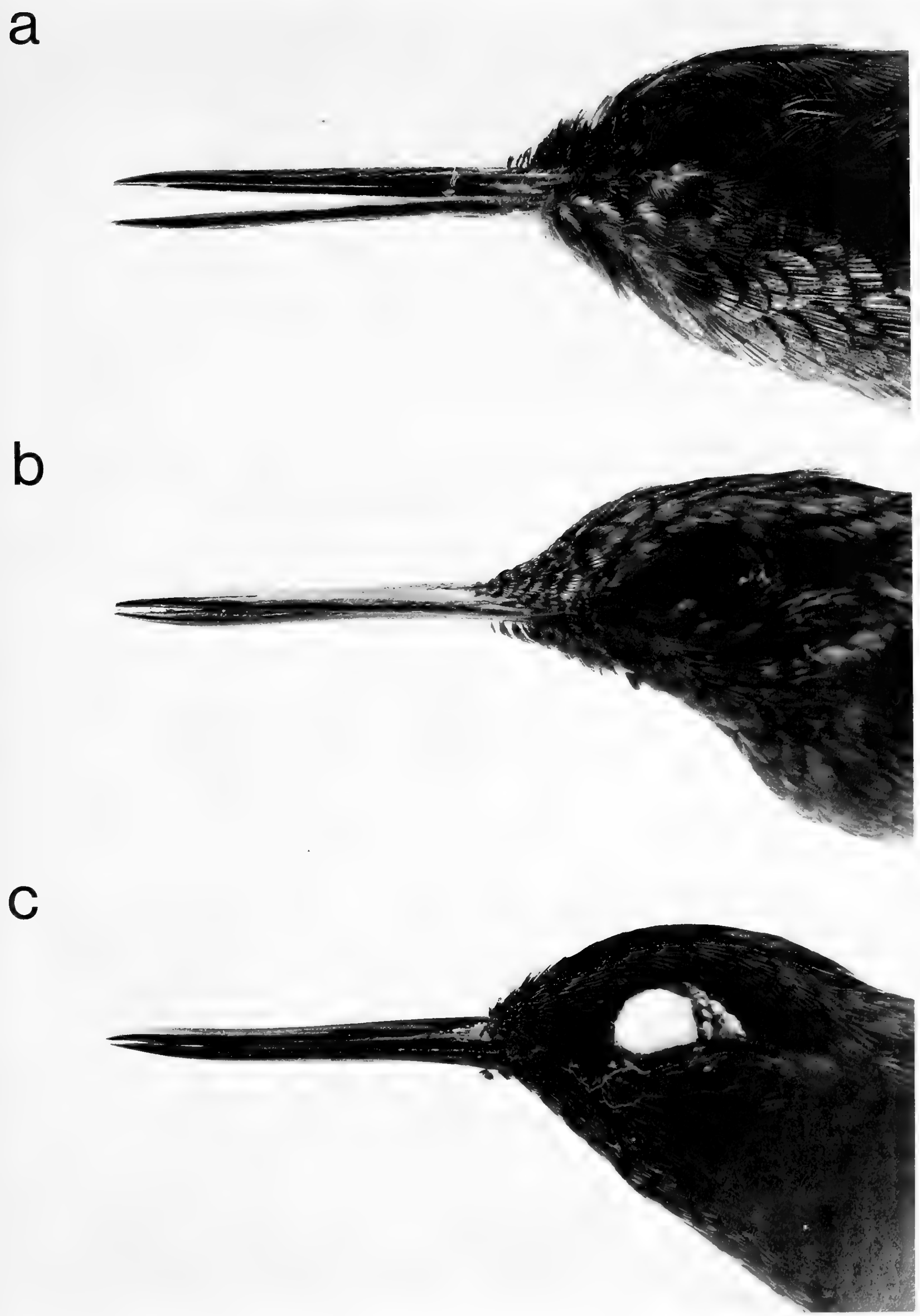
Berlioz (1936) noted the downy tibial plumes of the MNHN specimen, *Heliotrypha speciosa,* and suggested that some species of Colombian puffleg (*Eriocnemis* spp., *Haplophaedia* spp.) was one of its parents. He concluded that the entirely green body plumage and non-brilliant undertail coverts of this specimen seemed to preclude the possibility of a cross with a species of *Eriocnemis* (with brilliant violet or blue undertail coverts) and that only one hybrid combination was possible, *Haplophaedia aureliae* × *Heliangelus exortis.* Berlioz's statement on undertail coverts may be extended to other GTS specimens—none of the specimens I examined exhibit the structural brilliance found in many species of puffleg (e.g., *Eriocnemis vestitus, E. luciani, E. cupreoventris, E. mirabilis, E. alinae, E. derbyi*). Undertail coverts of the potential *Heliangelus* parental species vary from pure white to gray with white margins. Contrary to Berlioz's reasoning, the hybrid progeny of *Eriocnemis* sp. × *Heliangelus* sp. might be expected to have green undertail coverts with white or grayish-white margins, similar to those of GTS.

One character of GTS that has not received mention by previous investigators is the extensive distribution of brilliant green reflections from the body plumage. These reflections extend posteriorly to the vent and upper tail coverts and are particularly apparent when specimens are viewed head-on in direct light. Barbule modifications of this type are well-developed in several species of *Eriocnemis* (e.g., *E. vestitus, E. cupreoventris*) but are weakly developed or lacking in both species of *Haplophaedia.* Several species of *Heliangelus* (e.g., *H. exortis, H. amethysticollis, H. viola*) exhibit brilliant reflections on the upper breast but lack them posteriorly when viewed head-on in direct light. The presence of brilliantly reflective plumage (similar to that of GTS specimens) on the flanks and abdomen of hypothetical *Haplophaedia* spp. × *Heliangelus* spp. hybrids would represent a clear case of "atavism," a phenonemon that has not been demonstrated in trochiline hybrids.

Several other characters contradict Berlioz's hypothesis that *Haplophaedia aureliae* is involved in the parentage of GTS. Both sexes of *H. aureliae* have bronze crowns and uppertail coverts that contrast with the green back and rump. The dorsum of GTS specimens lacks such contrast, and, in fact, some specimens are brightest on the

→

Fig. 5. Head profiles of "green-throated sunangels" (a = FMNH 46286, b = FMNH 46294) and *Haplophaedia aureliae* (c). Nasal operculum of *H. aureliae* is more inflated and exposed than in "green-throated sunangels" and *Heliangelus* spp.


a
b
c

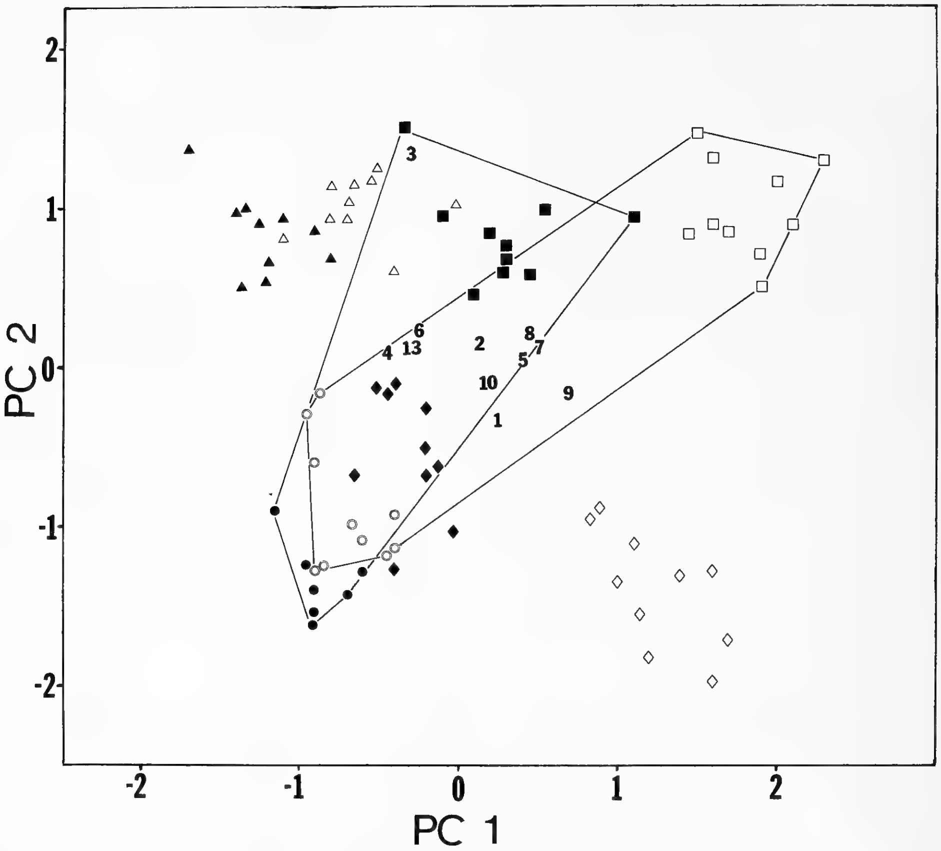


Fig. 6 Bivariate plot of Principal Component factor scores of "green-throated sunangels" and some of their potential parental species. Diamonds = *Heliangelus exortis.* Circles = *Eriocnemis cupreoventris.* Triangles = *Haplophaedia aureliae.* Squares = *Heliangelus amethysticollis.* Hollow and solid symbols represent males and females, respectively. Numbers represent "green-throated sunangel" specimens from Table 1. Lines envelop groups of males and females of *Heliangelus amethysticollis* × *Eriocnemis cupreoventris.*

uppertail coverts. Northern races of *Haplophaedia aureliae* (e.g., *H. a. aureliae, H. a. caucensis*), especially females, have white or grayish white abdomens and lower breasts speckled peripherally with green. Feathers of the ventral midlines of females and immature males of Colombian species of *Heliangelus* have wide buffy margins. Consequently, the venters of hypothetical female hybrids of *H. aureliae* × *Heliangelus* spp. would be extensively buffy, not green as in GTS.

Another important character is the relationship between the nasal operculum and the anterior extension of feathering on the bill of GTS specimens (Fitzpatrick et al. 1979) (Fig. 5). In *Heliangelus exortis* and *H. amethysticollis,* feathering extends anteriorly to the distal edge of the nasal operculum but does not cover it. Feathering in *Haplophaedia* spp. does not reach the distal edge of the operculum, which is inflated and exposed. In *Eriocnemis,* feathers extend to the distal edge of the nasal operculum, or slightly beyond, imparting a sloped appearance to the forehead in profile. Feathering and forehead profile of GTS is somewhat intermediate between that found in *Heliangelus exortis* or *H. amethysticollis* and several species of *Eriocnemis,* but differs from

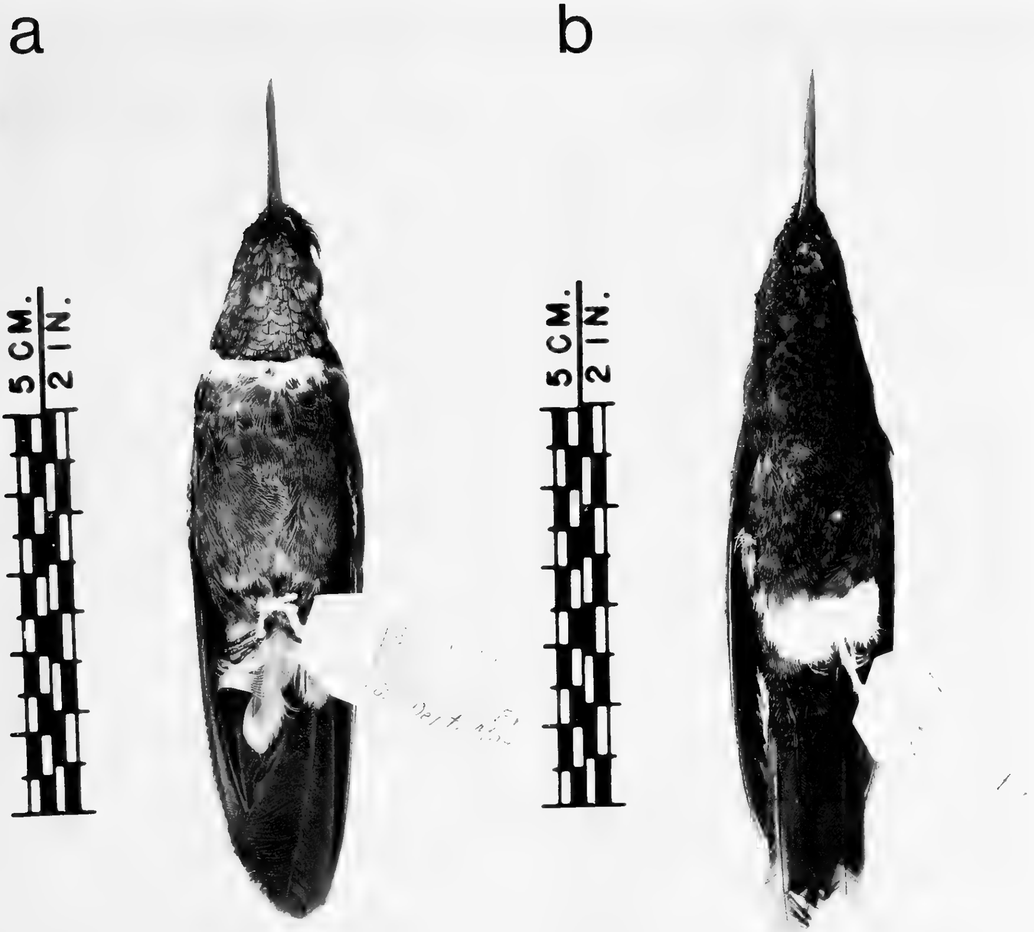


Fig. 7. Males of the two most probable parental species of "green-throated sunangels" examined in this study: (a) *Heliangelus amethysticollis*; (b) *Eriocnemis cupreoventris*.

that of *H. aureliae* or *H. lugens*. This and the other characters mentioned above indicate that both species of *Haplophaedia* may be rejected as potential parental species of GTS and support the hypothesis that the puffleg parent is some species of *Eriocnemis*.

Of the seven species of *Eriocnemis* (excluding *E. godini,* which is of uncertain status) that occur north of Ecuador, all but *E. cupreoventris* can be rejected as a parental species of GTS. Both sexes of *E. mosquera* (see Bleiweiss [1988] for measurements) and *E. luciani* have deeply forked tails and are significantly larger than GTS specimens or any of its possible *Heliangelus* parents. Neither of these puffleg species occur in the Eastern Cordillera in sympatry with *Heliangelus amethysticollis* and hypothetical hybrids between these species and *H. exortis* would have tails more deeply forked than in any GTS specimen. In addition, GTS lack white bases to throat feathers found in those species and the greenish outer rectrices of

Table 2.—Ranges of measurements (mm) of potential parental species of "green-throated sunangels." Specimens from a number of localities were chosen in order to incorporate the range of intraspecific variation found in Colombian populations.

Species	Sex	n	Wing chord	Outermost rectrix	Innermost rectrix	Culmen
Heliangelus exortis	♂	10	64.0–67.6	44.8–50.0	32.1–34.5	13.3–15.0
	♀	10	56.9–60.9	38.9–41.3	29.7–33.9	14.2–16.8
Heliangelus amethysticollis	♂	10	65.1–71.8	43.6–48.8	41.4–46.0	14.8–16.0
	♀	10	60.5–65.6	35.9–42.4	36.9–39.6	15.5–17.1
Eriocnemis cupreoventris	♂	15	58.8–65.2	40.6–45.3	24.3–28.4	17.8–19.6
	♀	7	58.2–60.6	38.7–42.6	23.2–26.3	16.7–17.9
Haplophaedia aureliae	♂	10	59.1–62.8	35.4–41.3	32.6–37.6	17.3–19.6
	♀	10	55.3–58.9	32.8–37.8	32.3–36.1	16.2–20.1

E. mosquera. E. mirabilis and *E. alinae* are small, have restricted ranges in the northern Andes, and possess several apomorphic characters that are not expressed in GTS. *E. derbyi* is sexually dichromatic and divergent in tail structure and plumage (e.g., black leg puffs) and can be conclusively rejected as a possible parent of GTS. *E. vestitus* is moderately sexually dichromatic but both sexes possess a small violet (male) or blue (female) gorget on the upper throat. Hypothetical *Heliangelus* spp. × *E. vestitus* hybrids of both sexes would probably have a small gorget of some shade of purple or pink. Female hybrids would be buffier and less green on the breast and lower belly than are GTS.

E. cupreoventris exhibits weak sexual dichromatism, lacks a contrasting gorget, and is similar in size to both GTS and possible *Heliangelus* parents. The nasal operculum is partially covered with feathers in both sexes. When viewed head-on in direct light, the body plumage of adult males reflect a brilliant golden-green anteriorly changing to bluish-green on the upper tail coverts and to coppery-gold on the breast and belly. Females are slightly duller below. These characters make *E. cupreoventris* the most probable parental puffleg species of GTS.

The probable sunangel parent can be limited to the only two species with extensive distributions in the Colombian Andes, *H. exortis* and *H. amethysticollis.* (*H. mavors, H. strophianus,* and *H. spencei* possess apomorphies not found in GTS.) Both species occur sympatrically with *E. cupreoventris* in the Eastern Cordillera (see Hilty & Brown 1986). *H. amethysticollis* differs from *H. exortis* primarily in having a well-defined white pectoral band below the throat of both sexes, a larger, more extensive gorget in males, and a less deeply forked tail. Intergeneric hybrids involving these species may best be distinguished by mensural characters of the parental species (Table 2). Additional descriptions of potential parental species can be found in Salvin (1892), Zimmer (1951), Bleiweiss (1985a, b), and Hilty & Brown (1986).

Measurements of the most probable parental species of GTS (*H. exortis, H. amethysticollis, E. cupreoventris*; *H. aureliae* included for comparison) overlap extensively (Table 2). I compared the measurements of these species and GTS specimens. Under the diagnostic assumptions used in this study, a GTS specimen could not be the hybrid progeny of a pair of species if the measurements of the specimen occurred outside the cumulative range (±0.5 mm for wing and tail; ±0.2 mm for culmen) of their measurements. Statistics were not performed because the reference samples were chosen to maximize ranges of measurements. This procedure is conservative because it assumes that the inheritance of quantitative characters is mutually inde-

Table 3.—Comparison of "green-throated sunangel" (GTS) measurements with the cumulative range of measurements for combinations of potential parental species (*Heliangelus amethysticollis, H. exortis, Eriocnemis cupreoventris, Haplophaedia aureliae*). A male or female symbol indicates that all measurements of a particular "green-throated sunangel" specimen fall within the range of measurements (by sex) for that combination of species. Numbers in parentheses refer to specimens listed in Table 1 for which all measurements were available. Ratios at the bottom of each column denote the minimum number of males and maximum number of females possible assuming that all "green-throated sunangels" represented hybrids of those species. Binomial *P*-values are given, assuming a 1:1 sex ratio.

GTS	*H. amethy.* × *E. cupreo.*	*H. amethy.* × *H. aureliae*	*H. exortis* × *E. cupreo.*	*H. exortis* × *H. aureliae*
(1)	♂	♂	♂	♂
(2)	♂♀	♂♀	♂	♂
(3)	♂	♂♀	—	♂
(4)	♂	♂	♂	♂
(5)	♂	♂	♂	♂
(6)	♂	♀	♂	♂
(7)	♂	♂	—	♂
(8)	♂	♂	—	♂
(9)	♂	♂	—	♂
(10)	♂♀	♂♀	♂	♂
(13)	♀	♂♀	♂♀	♂♀
♂:♀	8:3 $P \leq 0.08$	6:5 $P \geq 0.20$	6:1 $P \leq 0.05$	10:1 $P \leq 0.005$

pendent. Unfortunately, this procedure rules out few hybrid possibilities (Table 3). None of the possible pairs of parental species can be rejected for 7 of 11 of the GTS specimens.

Multivariate morphological relationships (Table 4) of potential parental species and GTS specimens are illustrated by the first two axes of a Principal Components Analysis in Fig. 6. Inspection of factor scores revealed that most GTS specimens are clustered near the center of the bivariate plot. Only one specimen (type of *H. speciosa*) falls within the envelope outlining the factor scores for *H. aureliae* and *H. amethysticollis* and none occurs in the *H. exortis* × *E. cupreoventris* envelope. Assuming that the inheritance of polygenic size and shape characters is reflected in the spread of factor scores, these pairs of species are not involved in the parentage of GTS, with the possible exception of the type of *H. speciosa*. All GTS specimens fall within the factor score envelope of *H. amethysticollis* × *E. cupreoventris*, and ten of eleven specimens fall within the *H. exortis* × *H. aureliae* envelope. However, as noted previously with univariate comparisons, if GTS are the progeny of *H. exortis* × *H. aureliae*, they would be predominately male. This fact, and a variety of plumage characters previously discussed suggest that GTS are not hybrids of the latter two species. The scatter of GTS factor scores within the *H. amethysticollis* × *E. cupreoventris* envelope shows that an even sex ratio is possible. With the exception of *H. speciosa*, plumage characters and measurements of GTS specimens are con-

Table 4.—Factor loadings for the first two principal components from analysis of "green-throated sunangels" and potential parental species (see Fig. 6).

	I	II
Variable		
Wing chord	0.91	0.10
Outermost rectrix	0.85	−0.39
Central rectrix	0.67	0.72
Culmen	−0.72	0.32
Variance explained		
Percent	62.5	19.6
Cumulative	62.5	82.1

sistent with the hypothesis that they represent hybrids of *H. amethysticollis* and *E. cupreoventris* (Fig. 7). Note, however, that the wing chord of AMNH 483682 (Table 1), which is probably a female, is significantly shorter than any specimen in the sample of these two species.

The position of *H. speciosa* on the bivariate plot is well removed from the other GTS specimens. *H. speciosa* differs from other GTS specimens in having a broad white pectoral band (Fig. 4) instead of a few semi-concealed spots, a shallowly-forked tail, and a slightly longer bill. The presence of a white pectoral band and the conformation of the gorget of *H. speciosa* indicates that a white-banded species of *Heliangelus* (e.g., *H. amethysticollis*) is one of the parental species. The well-developed leg puffs of *H. speciosa* (fide M. P. Walters) indicate that the other parental species is a puffleg. The anterior extension of feathering over the nasal operculum of *H. speciosa,* however, indicates that the other parent could not be *H. aureliae* which is similar to it in size and shape. *H. speciosa* lies within the PCA envelope for *H. cupreoventris* × *H. amethysticollis.* Despite the difference in appearance of *H. speciosa* from other GTS specimens, it seems probable that they represent the same hybrid cross. Additional study of the specimen may be required to verify this fact. If true, then *H. speciosa* represents an extreme hybrid phenotype that resembles its sunangel parent much more than its puffleg parent.

Conclusions

With the possible exception of *H. speciosa,* GTS specimens examined in this study, for which measurements were available, are probably hybrids of *Heliangelus amethysticollis* × *E. cupreoventris.* Berlioz's (1936) hypothesis that the MNHN specimen and perhaps others were hybrids of *Haplophaedia aureliae* and *Heliangelus exortis* is not supported by the data. Because the hypothesis of hybridity cannot be rejected, GTS cannot be considered as valid taxa. Additionally, the data (especially the variability and inconsistency of plumage characters) do not support the hypothesis that GTS, taken as a whole, represent population samples of one or more valid species.

Geographic origin.—*H. amethysticollis* and *E. cupreoventris* are sympatric in Andean forests and shrublands (2000–3000 m elevation) in the northern half of the Eastern Cordillera. Thus, GTS specimens could actually have been collected in the environs of "Bogotá." Mulsant & Verreaux (1872) reported that the type of *Heliotrypha barrali* was collected on the Río Saldana, Department of Tolima, in the Central Cordillera of the Colombian Andes. However, as previously mentioned, the original labels of *H. barrali* and other specimens lack specific locality data and in the absence of corroborating evidence, the possible Central Cordilleran origin of the type of *H. barrali* can be dismissed.

Nomenclature.—Hybrids are individuals and not taxa. Thus, the names *Heliangelus squamigularis* Gould, 1871, *Heliotrypha barrali* Mulsant & Verreaux, 1872, *Heliotrypha speciosa* Salvin, 1891, and *Heliotrypha simoni* Boucard, 1892, are available only for the purposes of homonymy in taxonomy and should not be used in the popular literature. For the purposes of field guides, these hybrids may be referred to collectively as "green-throated sunangels."

Discussion

Hybrid diagnoses can be simple or extremely complex depending on circumstances. Factors that affect the success of hybrid diagnoses include: (1) the number of hybrid individuals and their age, sex, and hybrid composition (e.g., F_1, backcross); (2) the number of distinctive plumage and morphological characters on the hybrid; (3) the number of species in the putative hybrid's taxonomic group; (4) and knowledge of the hybrid's taxonomic group and of the regional avifauna where the hybrid originated. (The most challenging diagnoses are of hybrids represented by a unique, unsexed, possibly immature specimen without specific locality data, which belongs to a speciose, dull-plumaged, and poorly known taxonomic group from a poorly collected region of high species diversity!)

Ideally, parental species are identified with certainty, but failing this, what result justifies the considerable effort expended in the average hybrid diagnosis? In terms of value to future researchers, it is far better to have a short list of species that includes the correct pair of parents, than an exact determination of parental species that may be wrong (errors of this sort are frequently perpetuated in the literature; see Graves 1988). Rejection of any species from the pool of potential parental species must be based on the unequivocal violation of diagnostic assumptions, and there is no logical reason for reducing the species pool beyond the limits suggested by the data. Conclusive knowledge of what species or species combinations are *not* parents, as well as those that might be parents of a hybrid is far more valuable than perhaps recognized by most taxonomists, especially when the majority of species fall into the former category. Species in the latter category constitute the nucleus for future analyses.

Acknowledgments

R. Banks, M. R. Browning, P. Cannell, F. Gill, S. Olson, and R. Zusi commented on an earlier version of the manuscript. Banks, R. Bleiweiss, T. Schulenberg, and Zusi reviewed a later incarnation. I thank them for their suggestions and criticism. I thank J. Becker, H. James, C. Jouanin (MNHN), M. Robbins (ANSP), and M. Walters (BM) for providing measurements or answering detailed questions about specimens, Becker and Jouanin for providing excellent color transparencies of specimens for my use, and V. Krantz for preparing illustration prints. M. Farmer deserves special thanks for translating French. I am also grateful to the curators and staff of the American Museum of Natural History and the Academy of Natural Sciences of Philadelphia (ANSP) for providing access to collections and the Field Museum of Natural History for loaning GTS specimens. Lastly, I would like to thank R. L. Zusi for patiently answering untold thousands of my questions about hummingbird systematics over the past few years.

Museum research was supported by grants from the Smithsonian Research Opportunities Fund and the Frank M. Chapman Memorial Fund of the American Museum.

I dedicate this paper to Jacques Berlioz and Christian Jouanin in recognition of their pioneering work on hummingbird hybrids.

Literature Cited

Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—Condor 63:3–28.

Berlioz, J. 1936. Note sur l'identite probable du type d'*Heliotrypha simoni* Boucard (Trochilides).—Bulletin du Museum National D'Histoire Naturelle, Paris 14:233–236.

———. 1964. La collection de Trochilides A. L. Butler.—Oiseau 34:91–105.

———, and C. Jouanin. 1944. Liste de Trochilides trouves dans les collections commerciales de Bogota.—Oiseau 14:126–155.

Bleiweiss, R. 1985a. Variation and population structure of the Tourmaline Sunangel, *Heliangelus exortis exortis* (Aves, Trochilidae).—American Museum Novitates 2811:1–14.

———. 1985b. Iridescent polychromatism in a female hummingbird: is it related to feeding strategies?—Auk 102:701–713.

———. 1988. Systematics and geographic variation in the Golden-breasted Puffleg *Eriocnemis mosquera* (Aves, Trochilidae).—American Museum Novitates 2913:1–8.

Boucard, A. 1892. A complete list up to date of the hummingbirds found in Columbia, with descriptions of several supposed new species.—The Humming Bird 2:73–87.

———. 1895. Genera of humming birds. Vol. 5, Part 1. Bournemouth, London.

Buckley, P. A. 1982. Avian genetics. Pp. 21–110 *in* M. Petrak, ed., Diseases of cage and aviary birds. 2nd ed. Lea and Febiger, Philadelphia, 680 pp.

Chapman, F. M. 1917. The distribution of bird-life in Colombia.—Bulletin of the American Museum of Natural History 36:1–729.

Cory, C. B. 1918. Catalogue of birds of the Americas. Part 2, No. 1.—Field Museum of Natural History Zoological Series 13:1–313.

Falconer, D. S. 1981. Introduction to quantitative genetics. 2nd ed. Longman, New York, 340 pp.

Fitzpatrick, J. W., D. E. Willard, and J. W. Terborgh. 1979. A new species of hummingbird from Peru.—Wilson Bulletin 91:177–186.

Fox, H. M. and G. Vevers. 1960. The nature of animal colours. Macmillan, New York, 246 pp.

Gould, J. 1871. Descriptions of six new hummingbirds.—Proceedings of the Zoological Society of London 1871:503–505.

Graves, G. R. 1988. Evaluation of *Vermivora* × *Oporonis* hybrid wood-warblers.—Wilson Bulletin 100:285–289.

Gray, A. P. 1958. Bird hybrids. Commonwealth Agricultural Bureaux, Bucks, England, 390 pp.

Greenway, J. C., Jr. 1978. Type specimens of birds in the American Museum of Natural History. Part 2.—Bulletin of the American Museum of Natural History 161:1–305.

Haldane, J. B. S. 1922. Sex-ratio and unisexual sterility in hybrid animals.—Journal of Genetics 12:101–109.

Harrison, J. M., & J. G. Harrison. 1963. Comments on a hybrid Red Shoveler × Northern Shoveler.—Bulletin of the British Ornithological Club 83:21–25.

Hartert, E. 1922. Types of birds in the Tring Museum. B. Types in the general collection. Trochili.—Novitates Zoologicae 29:403–412.

Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, 836 pp.

Hutt, F. B. 1949. Genetics of the fowl. McGraw-Hill, New York, 590 pp.

Jouanin, C. 1950. Catalogue systematique des types de Trochilides du Museum National d'Histoire Naturelle de Paris.—Bulletin du Museum National d'Histoire Naturelle de Paris 22:1–27.

Lucas, A. M., & P. R. Stettenheim. 1972. Avian anatomy—integument. Agricultural handbook 362. United States Department of Agriculture, Washington, D.C.

Meyer de Schauensee, R. M. 1949. Birds of the Republic of Colombia. Part 2.—Caldasia 23:381–644.

———. 1966. The species of birds of South America. Livingstone Press, Narberth, Pennsylvania, 577 pp.

Morony, J. J., Jr., W. J. Bock, & J. Farrand, Jr. 1975. Reference list of the birds of the world. American Museum of Natural History, New York.

Mulsant, E., & J. Verreaux. 1872. Description d'une espece nouvelle d'oiseau moche.—Annales Societe Linneenne de Lyon 18:106–107.

Parkes, K. C. 1984. An apparent hybrid Black-billed × Yellow-billed Cuckoo.—Wilson Bulletin 96: 294–296.

Peters, J. 1945. Check-list of birds of the world. Vol. 5. Museum of Comparative Zoology, Cambridge, Massachusetts, 306 pp.

Salvin, O. 1891. Descriptions of new species of Upupae and Trochili in the collection of the British Museum.—The Annals and Magazine of Natural History (6th series) 7:374–378.

———. 1892. Catalogue of birds in the British Museum, Vol. 16.

Short, L. L., and A. R. Phillips. 1966. More hybrid hummingbirds from the United States.—Auk 83:253–265.

Simon, E. 1921. Histoire naturelle des Trochilidae (synopsis et catalogue). Paris, 416 pp.

Zimmer, J. T. 1951. Studies of Peruvian Birds. No. 61. The genera *Aglaeactis, Lafresnaya, Pterophanes, Boissonneaua, Heliangelus, Eriocnemis, Haplophaedia, Ocreatus,* and *Lesbia.*—American Museum Novitates 1540:1–55.

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Appendix

Comparative Description of "Green-throated Sunangels"

Descriptions of structural colors are unusually subjective and actual color varies with the angle of inspection and direction of light. For this reason I use general color descriptions. Numbers in parentheses refer to specimens in Table 1.

The crown, nape, back, and rump are medium green. Uppertail coverts are medium green to bluish-green. There is no contrast between crown and back. When viewed head-on in direct light, scattered feathers on crown (5), back, wings, and upper tail coverts show brilliant golden-green to green reflections. A brilliant green frontlet, variable in intensity and definition, is found in most adults (absent in 10), but is faint or lacking in immatures. When present, the frontlet is small (1, 2, 4, 6, 8, 11, 12), similar in size to that found in *H. exortis* or *H. amethysticollis.* Prominence of the frontlet is affected by variations in skin preparation. Lores, auriculars, and neck at the sides of the throat are medium green, but appear much darker when viewed head-on. A small white postocular spot is present. A brilliant gorget is found in all specimens but is variable in size, color, and degree of contrast with adjacent plumage. Gorget margins are somewhat irregular and indistinct in all adult specimens. Gorget color is variable and can be characterized (viewed head-on) as bluish-green (4) and silvery-green (2, 9, 13) to silvery bluish-green (7) in immatures, and from bluish-green (5) and pale green (12) to silvery-green (1, 3, 6, 8, 10, 11) in adults. In indirect light, gorgets of some specimens emit faint coppery or pinkish reflections. Color variation appears to be fairly continuous and color characterizations are arbitrary. For example, "silvery-green" includes various shades of pale metallic green (= "leaden" of Salvin 1892). Gorgets of immatures are oval in shape, wider posteriorly and may be surrounded by dull, lax plumage (7). Gorgets of adults are larger, contrast less with adjacent plumage, and may have irregular margins (5). Brilliant gorget feathers are rounded and about the size of those in male *Heliangelus* sp. (e.g., *H. exortis*), but become progressively smaller toward the chin and malar regions in adults. The upper and lower breast, abdomen, and flanks (except 2) are medium green. Feathers along the midline of immatures may have narrow buffy margins. Brilliant golden-green or green reflections (or faint coppery in 5) are scattered over the breast, abdomen, and flanks when viewed head-on. Plumage of immatures is duller than in adults. The type of *H. speciosa* (3) differs from other GTS specimens in having a large white pectoral patch spotted with green discs and darker underparts with few brilliant reflections. White or buffy spots, mostly subterminal, are present on two to ten feathers of the upper pectoral area on most specimens (1, 2, 7, 8, 9, 10, 11, 13). Undertail coverts are variable in length (not exceeding half the length of the tail) and are medium green or bluish-green with narrow to broad white or grayish white margins; basal barbs in some specimens are long and downy. Central rectrices are dark green to bronzy green; outer retrices are bluish-black. Depth of tail fork varies from 3.8 to 10.5 mm. Outer web of outermost rectrix is well-developed (> ½ width of inner web). The outermost rectrix ranges from 8.0 to 9.5 mm in width and is more acuminate in shape than in *H. exortis* or *H. amethysticollis*. Tibial feathers (leg puffs) are white or buffy (2), variable in length (2.5 to 8 mm), and more or less downy in texture. [The presence of leg puffs on (1) cannot be determined from photographs of specimens or published descriptions]. The remiges are unmodified (e.g., not emarginate) and dull dark brown in color. Outer webs of primaries of some specimens have a faint bronzy-green sheen. Bills are unmodified and straight and dark blackish-brown. The upper mandible of (3) is broken (Fig. 4). Feathering extends anteriorly on the bill to the distal edge of the nasal flange (not inflated), somewhat obscuring it. Feet are dark brown or dark blackish brown.

Additional notes on plumage can be found in Berlioz (1936).

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 26–34

A NEW SPECIES OF *CUORA* (REPTILIA: TESTUDINES: EMYDIDAE) FROM THE RYUKYU ISLANDS

Carl H. Ernst and Jeffrey E. Lovich

Abstract.—A new species of Asian box turtle, *Cuora evelynae,* from the Ryukyu Islands is described and compared with *C. flavomarginata* from Taiwan and southern China. Recognition is based on its pattern of very large light colored pleural blotches (length of blotch at its medial height 49–72% of medial length of pleural) that at their dorsal border coalesce to form lateral stripes in 52% of adults examined, its large light brown plastral blotch which is indented at the bridge, and the usual presence of less than 10 rows of large scales on the anterior surface of the forelimbs. A discriminant function is given that separates *C. evelynae* from *C. flavomarginata.* Geological history of the Ryukyu Islands is discussed, in view of speciation of *C. evelynae.*

The yellow-margined box turtle, *Cuora flavomarginata* (Gray, 1863) occurs in southern China, Taiwan, and the Ryukyu Islands (Iverson 1986). Even though these localities have been long isolated (Inger 1947), no consistent differentiation of these turtle populations has been reported previously.

Hsu (1930) described a subspecies, *Cuora f. sinensis,* from Tungting Lake, Hunan, China, as differing from the nominate Taiwanese population on the basis of having the anterior border of the plastron obtusely emarginate, each plastral scute with deeply cut parallel lines, each marginal with its posterior angle slightly overlapping the next with the degree of overlap most pronounced in the posterior third of the marginals so that the posterior carapacial rim is somewhat serrated, a small notch between the anal scutes, and a much shorter tail. Pope (1935) commented that with the exception of the longer tail (which may be sexual dimorphic), all the other characters used by Hsu are either common variants expected in most emydid turtles or differences generally correlated with age, but Pope thought that until direct comparison between Chinese and Taiwanese *C. flavomarginata* could be made, it was best to consider the two populations as distinct subspecies. Tanaka & Sato (1983) have referred to the turtles on the Ryukyu Island of Iriomote as *Cuora f. flavomarginata* indicating an affinity with the population on Taiwan. However, Fang (1934) had critically compared specimens from Taiwan and the Ryukyu Islands with Hsu's diagnostic characters and found that the mainland Chinese turtles could not be differentiated from the insular populations.

Recent examination and comparison of *C. flavomarginata* from these three populations has shown that turtles from the Ryukyu Islands can be distinguished from those of the other two populations and represent an undescribed species.

Methods and materials.—Sixty-six turtles were examined (Ryukyu Islands, 38; Taiwan, 14; China, 14). Sexes were determined by the characters given by Ernst & Barbour (1989). Straight-line measurements of each specimen were taken with dial calipers accurate to 0.1 mm. Variables included: the greatest carapace length, carapace width and depth at the level of the seam separating vertebrals 2 and 3, marginal width (the difference between the carapacial width and the width across the pleurals taken between the points of juncture of the marginals and pleurals at the level of the seam between vertebrals 2 and 3), greatest plastron length, greatest width and length of both plastral lobes, least bridge length, greatest width and length of the cervical scute and all vertebrals and medial seam lengths of all plastral scutes (Gul., Hum., Pect., Abd., Fem., An.). Careful notes and drawings were made of head, neck, limb, carapacial and plastral patterns. Colors were recorded from living turtles and color transparencies. Shell proportions were expressed as ratios of one measurement to another. Several ratios proved useful in our description (abbreviations used in text are given in parentheses): width/length of cervical scute (W/L CS), width/length of designated vertebrals (W/L 1st, V W/L 2nd V, etc.), marginal width/carapacial width (MW/CW), marginal width/carapacial length (MW/CL), carapacial width/carapacial length (CW/CL), carapacial depth/carapacial length (D/CL), carapacial depth/carapacial width (D/CW), length of light-colored blotch at its medial heights on pleural scute 2/total length of pleural scute 2 at the same point (PBL/PSL), plastral length/carapacial length (PL/CL), bridge length/plastral length (B/PL), bridge length/carapacial length (B/CL), length of the anterior plastral lobe/plastral length (APL/PL), width of anterior plastral lobe/plastral length (APW/PL), width of anterior plastral lobe/length of anterior plastral lobe (APW/APL), length of posterior plastral lobe/plastral length (PPL/PL), width of posterior plastral lobe/plastral length (PPW/PL), and width of posterior plastral lobe/length of posterior plastral lobe (PPW/PPL). The number of rows of large scales at the lateral edge of the antebrachium between the claw of digit 5 and the first horizontal skin fold proximal to the elbow (presented in text as FLSR) was recorded.

Statistical techniques were executed using SYSTAT (Wilkinson 1986) and STATGRAPHICS (STSC 1986). Males and females were combined for analysis since statistically significant size differences were not detected ($\bar{x}$ male CL, 137.6 mm; $\bar{x}$ female CL, 143.3 mm: ANOVA, F = 0.98; df = 1,39; $P = 0.33$). Juveniles (23) were included in all analyses due to small total sample size (66). Males, females and juveniles were evenly distributed between population samples. Variables were transformed for parametric analysis as follows: those based on proportions, such as the interanal seam length (An) and PBL/PSL, were arcsine square root transformed, FLSR was square root transformed, and natural logarithms were taken of all others to reduce variance (Lewontin 1966, Moriarty 1977). Principal components analysis (PCA) was used as a data reduction technique to identify orthogonal factors and their important variables. Interanal seam length (An) was excluded from this step because it had previously been identified to vary independently of population. Variables with high factor loadings were used in subsequent analyses as were factor scores (Kachigan 1986). Following PCA, differences among populations were tested using multivariate analysis of variance (MANOVA) as suggested by Willig et al. (1986). Following identification of differences among these putative populations, a three-group discriminant function analysis was conducted using the raw variables selected with PCA. Discriminant scores were calculated by multiplying these variables by their associated unstandardized canonical coefficients and summing the products. Each specimen was then plotted along the axes providing maximal separation of the a priori groups. Levels of significance were set a priori at alpha = 0.05.

Specimens from the following collections were examined: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Field Museum of Natural History (FMNH), George Mason University (GMU), Museum of Comparative Zo-

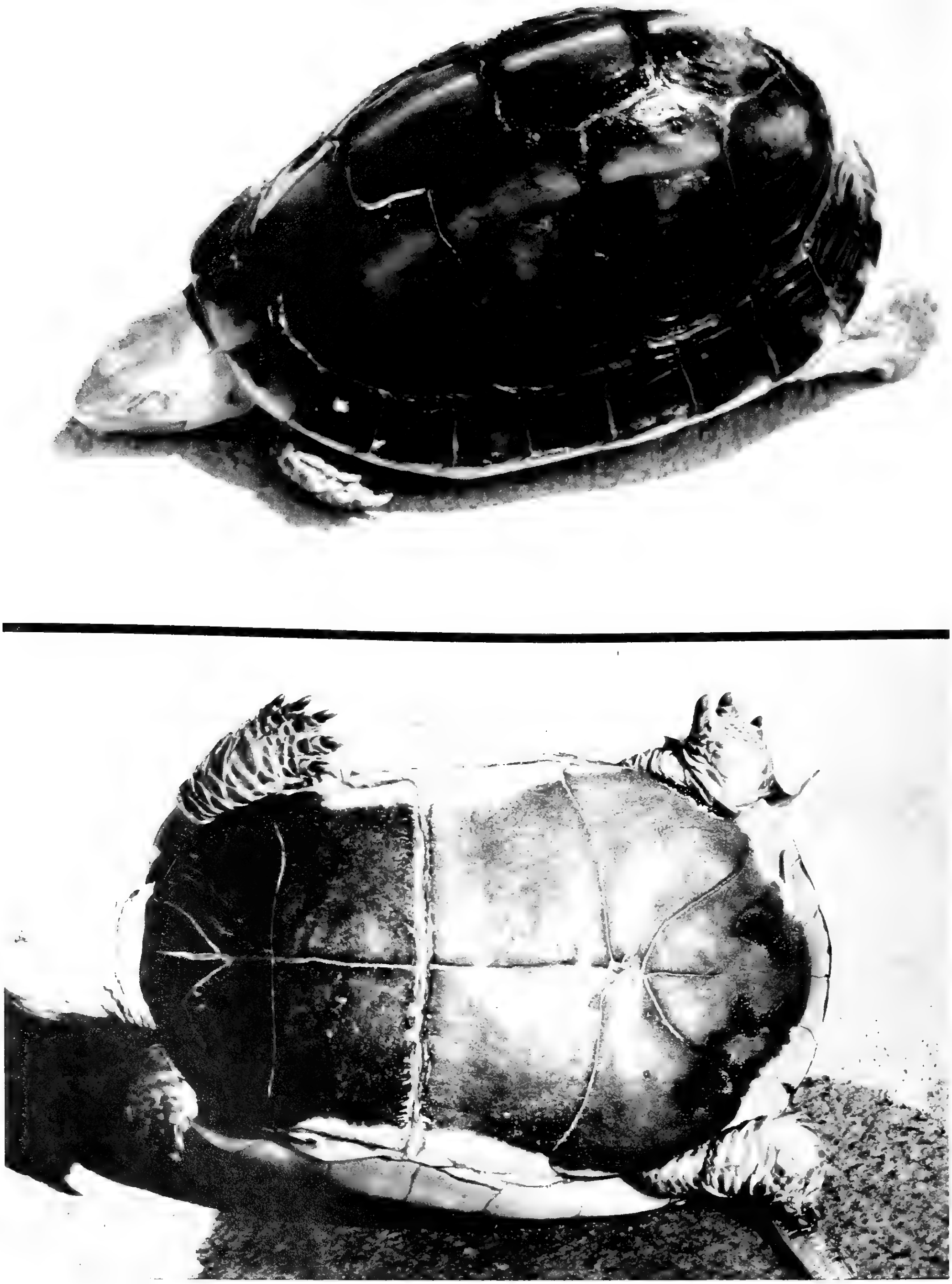


Fig. 1. Carapace and plastron of *Cuora evelynae,* new species (AMNH 50804).

Table 1.—Summary statistics for significant variables by populations. Means (mm) are followed by one standard error in parentheses. Probabilities are given for univariate F-tests between localities. Refer to text for abbreviations.

Variable	Population (n) Ryukyu Islands (35)	Taiwan (13)	China (14)	Probability
CW	90.6 (3.2)	74.9 (6.7)	92.0 (5.7)	0.03
APW	63.7 (2.5)	50.8 (5.3)	67.2 (4.5)	0.01
PPW	71.4 (3.0)	57.0 (6.3)	76.3 (5.3)	0.02
Gul	19.7 (0.7)	16.4 (1.7)	19.6 (1.2)	0.05
Hum	6.0 (0.4)	6.6 (0.6)	8.8 (0.8)	0.01
Abd	32.3 (1.5)	24.4 (2.8)	28.9 (2.4)	0.02
FLSR	8.8 (0.2)*	10.8 (0.6)	8.9 (0.2)	<0.001
PBL/PSL (%)	64.6 (0.5)	34.2 (1.0)	35.3 (0.4)	<0.001

* Includes four additional specimens not included in other statistical analyses.

ology, Harvard University (MCZ), Naturhistorisches Museum Wien, Vienna (NHMW), United States National Museum of Natural History (USNM), William P. McCord, Hopewell Junction, New York, personal collection (WPM), and William H. Randel, Hatboro, Pennsylvania, personal collection (WHR).

Results and discussion.—Turtles from the Ryukyu Islands showed two pattern differences from the other two populations. The pleural blotch in these specimens was larger (PBL/PSL; $\bar{x} = 65\%$) than those of turtles from Taiwan (34%) and mainland China (35%). The pleural blotch accounted for significantly different proportions of the pleural scute length (PBL/PSL) between populations (ANOVA; F = 703.08; df = 2,59; $P < 0.0001$). In 14 of 27 adults (52%) from the Ryukyu's the blotches were so large as to coalesce dorsally, forming two lateral light longitudinal stripes in addition to the normal medial stripe (Fig. 1). No specimens from either Taiwan or China had lateral stripes. The shape and coloration of the dark medial blotch on the plastron also varied (Fig. 1). Turtles from Ryukyu usually had a large, hourglass-shaped blotch, indented at the bridge, which was light brown in color; those from the other two populations had large dark brown to black blotches with straight sides or only a very shallow indentation at the bridge. Summary statistics and univariate test probabilities between populations are given for all significant variables in Table 1. Eight variables, about six more than expected at alpha = 0.05, show significant differences among populations.

The first three factors generated by PCA for 28 variables accounted for 93 percent of the total variance (Factor I—84%, eigenvalue = 23.49, Factor II—6%, eigenvalue = 1.65, Factor III—3%, eigenvalue = 0.96). The highest loadings in Factor I are all size related mensural variables. PPL had the highest loading in Factor I (0.997). The proportion of pleural blotch coloration (PBL) had the highest loading in Factor II (0.790). FLSR had a very high negative loading (−0.729) in Factor II. MW had the highest loading in Factor III (0.920). All other variables were highly correlated with these four and add little to the analysis, so they were not analyzed further. Factor scores for Factor I did not differ significantly between populations (ANOVA; F = 2.45; df = 2,50; $P = 0.10$), nor did scores for Factor III (ANOVA; F = 0.46; df = 2,50; $P = 0.64$). However, Factor II scores did (ANOVA; F = 55.85; df = 2,50; $P < 0.001$). Differences among populations were suggested by MANOVA when all three sets of factor

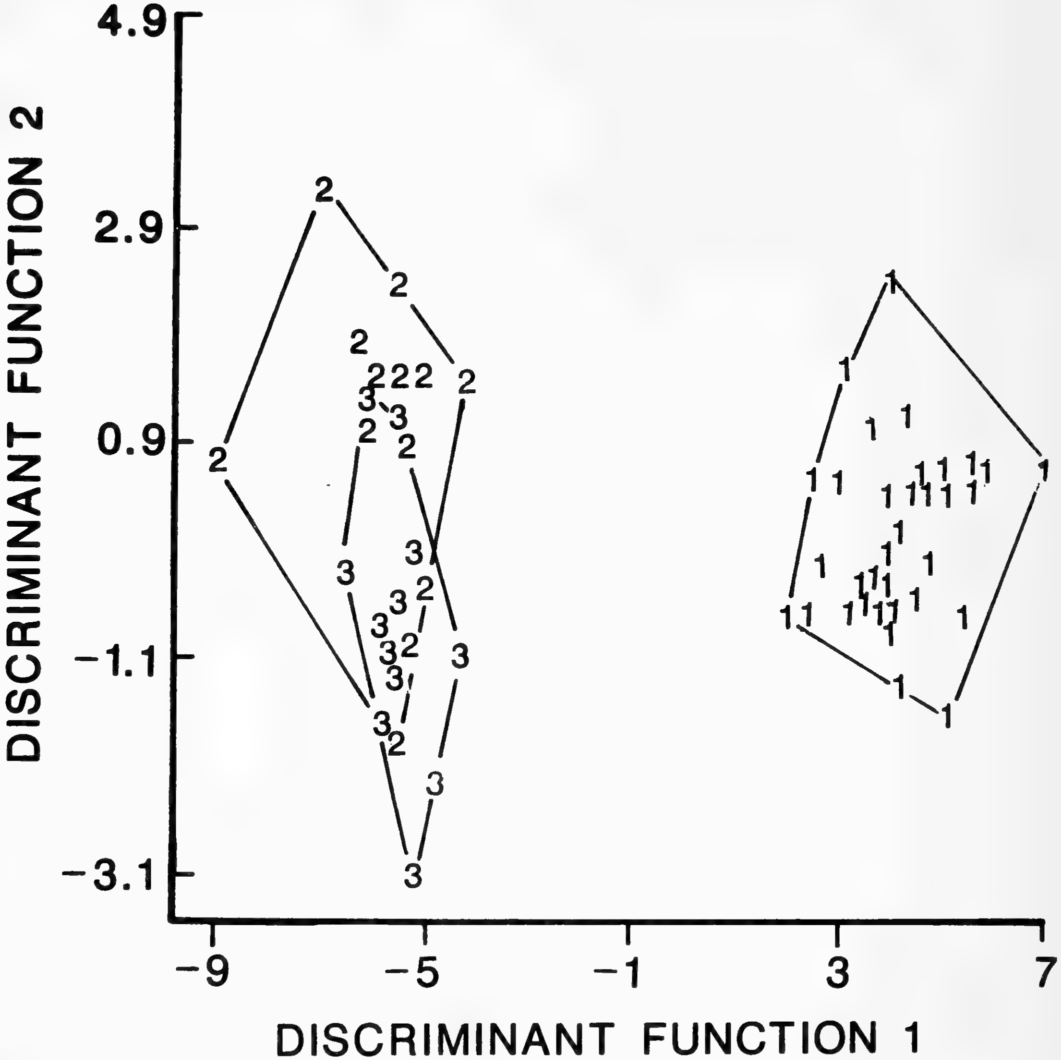


Fig. 2. Discriminant function analysis of turtle populations from the Ryukyu Islands(1), Taiwan(2), and southern China(3) for the characters PPL, PBL/PSL, MW, and FLSR. Polygons define extreme values of each cluster. Numbers represent individual turtles.

scores were included (Wilks' Lambda = 0.23; F = 17.76; df = 6,96; $P < 0.001$). Univariate F-tests for the highest loading variable in each factor were as follows: Factor I—PPL (ANOVA; F = 2.83; df = 2,59; $P = 0.07$), Factor II—PBL (ANOVA; F = 703.08; df = 2,59; $P < 0.001$), Factor III—MW (ANOVA; F = 0.92; df = 2,59; $P = 0.40$). Differences were again demonstrated using MANOVA for these three variables (Wilks' Lambda = 0.04; F = 82.64; df = 6,114; $P < 0.001$).

FLSR differed significantly between populations (ANOVA; F = 9.07; df = 2,56; $P < 0.001$). Specimens from Taiwan had a mean of 10.8 while those from the Ryukyu Islands and China had means of 8.8 and 8.9 respectively.

Variables with high loadings (PPL, PBL, FLSR, MW) were entered into a discriminant function analysis and each specimen was classified into a predicted population. The first and second discriminant functions provide significant ($P < 0.001$) discrimination between populations (Fig. 2). The function correctly classified 100% of the Ryukyu specimens, 92% of those from mainland China, and 77% of the specimens from Taiwan. Discriminant scores (DS) are > -1 for specimens from the Ryukyus and < -1 for specimens of *C. flavomarginata* from China and Taiwan based on the following discriminant function: DS = −18.6013 + 33.7378(PBL/PSL) + 0.02580(FLSR) + 0.01970(MW) + 0.00960(PPL). This function correctly classified all specimens of both species.

Although closely related to *C. flavomarginata,* the turtle population in the Ryukyu's can be distinguished by the combination of characters listed above. Since it is allopatric, and has apparently been isolated for more than a million years (see discussion below), we believe it to be at least an incipient species and have treated it as such, rather than as a subspecies of *C. flavomarginata.*

Cuora evelynae, new species

Fig. 1

Holotype.—CAS 26113, adult male; Ishigaki Shima, Ryukyu Islands, Japan; Victor Kuhne, 5–11 May 1910.

Paratypes.—CAS 21026-21029, 26102-26112, 26801 (five adult males, eleven adult females); AMNH 50804 (adult female); MCZ 56064 (adult male); USNM 34076-34079 (adult male, adult female, two juveniles) from the type-locality.

Diagnosis.—A domed species of *Cuora* with a yellow head; a dark brown to black carapace with a large yellow to light brown blotch which at its medial height extends 49–72% ($\bar{x} = 64.6$) across the middle of each pleural, and at its dorsal border coalesces to form lateral stripes in 52% of adults; a large pale brown plastral blotch, which is indented at the bridge; the plastron lacking a medial posterior notch; most adults with at least a partially obliterated interanal seam, and usually less than 10 ($\bar{x} = 8.8$) rows of large scales on the anterior surface of the foreleg (a character shared with the mainland Chinese population).

Description (from all specimens examined).—Carapace length to 164 mm (males 159, females 164), elliptical, domed (D/CL 0.41–0.52, $\bar{x} = 0.468$; D/CW 0.57–0.71, $\bar{x} = 0.648$; CW/CL 0.67–0.80, $\bar{x} = 0.725$); widest at marginals 8, highest at posterior of vertebral 2 or vertebral 3. Carapace sides straight, anterior marginals flared, posterior marginals at best only slightly serrated with no medial notch. Marginals over bridge downturned (MW 6.4–18.7 mm, $\bar{x} = 10.86$; MW/CW .056–.16, $\bar{x} = 0.108$; MW/CL 0.04–0.12, $\bar{x} = 0.078$). Marginals large, and approximately the same width throughout. Carapacial scutes in young individuals are rugose because of growth annuli; those of older turtles are worn smooth. Cervical scute rectangular to triangular, longer than wide (W/LCS 0.46–0.95, $\bar{x} = 0.782$). Vertebrals 3–5 wider than long, vertebral 2 usually longer than wide (79% of adults) and vertebral 1 may be either wider than long (53% of adults) or longer than wide (47% of adults). Vertebrals 4 and 5 widest, vertebral 5 posteriorly flared, vertebral 1 slightly flared anteriorly and only contacting marginal 1. Three low longitudinal keels present; medial keel most pronounced and extending along all 5 vertebrals, lateral keels extend from posterior of pleural 1 through pleural 4 and may disappear with age. Color black to dark brown; rim of marginals yellow. Medial yellow stripe always present. Areolae of pleurals and vertebrals yellow or light brown. Light areolae of pleurals large (PBL/PSL 0.49–0.72, $\bar{x} = 0.646$), and tend to coalesce at their dorsal borders to form lateral light stripes in 52% of adults (Fig. 1). Undersides of marginals yellow.

Plastron length to 160 mm (males 154, females 160), shorter than carapace in 23(85%) specimens (PL/CL 0.93–1.01, $\bar{x} =$

0.973), movable hinge between the pectoral and abdominal scutes. Posterior lobe longer and wider than anterior lobe (APL/PL 0.40–0.44, $\bar{x}$ = 0.420; PPL/PL 0.57–0.61, $\bar{x}$ = 0.586; APW/PL 0.49–0.57, $\bar{x}$ = 0.524; PPW/PL 0.55–0.62, $\bar{x}$ = 0.592; APW/CW 0.67–0.75, $\bar{x}$ = 0.712; PPW/CW 0.75–0.87, $\bar{x}$ = 0.800). Anterior lobe rounded in front; posterior lobe rounded in rear, usually without a medial notch. Bridge moderate (B/CL 0.27–0.37, $\bar{x}$ = 0.311; B/PL 0.28–0.39, $\bar{x}$ = 0.318); axillary and inguinal scutes generally lacking, or small. Average plastral formula Abd. > An. > Pect. > Gul. > Fem. > Hum.; 14 (40%) had this formula, but 4 other formulae occurred; 23 (66%) had Abd. > An., 11 (31%) had An. > Abd., 21 (60%) had Fem. > Hum., 14 (40%) had Hum. > Fem. Intergular and interanal seams often obliterated in large individuals. Plastron and bridge yellow, with a large pale brown medial blotch occurring on all scutes and indented at the bridge (Fig. 1).

Head narrow, snout slightly projecting; upper jaw with slight medial hook. Dorsally, the head is lemon-yellow to olive. Laterally behind the orbit and jaws, is a large yellow blotch that encloses the tympanum. This blotch is dark bordered dorsally. A second smaller yellow blotch lies dorsally and behind the first, and extends across the top of the head to touch a similar blotch from the other side just in front of the cervical skin fold. Jaws and chin immaculate yellow. Neck yellow to olive with no pattern.

Digits partially webbed. Forelimbs with large scales (6–11 rows, $\bar{x}$ = 8.8), 29 of 34 individuals (85.3%) had less than 10 rows; outer surface olive brown or yellow to reddish-brown, inner surface and sockets yellow. Hindlimbs with smaller scales, colored similar to forelimbs; hindfoot olive to brown with large scales at heel and ankle. Tail yellow dorsally and bordered by two olive or brown stripes, tip yellow.

Males with moderately concave plastra, and longer, thicker tails with the vent beyond the carapacial rim. Females with flat plastra and smaller tails with the vent beneath the posterior marginals.

Cuora evelynae is known only from the islands of Iriomote, Ishigaki, and Okinawa (Iverson 1986); the Okinawa specimen (MCZ 55838) may represent an escaped captive. These turtles probably originated from mainland China or Taiwan at a time when the Ryukyus were connected by a land bridge, or only separated by shallow water. Subsequent submergence of the land bridge isolated the Ryukyu population thus allowing for speciation to occur.

Based on the reports of Yabe & Aoki (1923), Yabe (1929a, b), and Hanzawa (1935), Inger (1947) has presented a summary of the geology of these islands. The Ryukyu cordillera arose in the late Permian or early Mesozoic Era. It seems to have broken into several mountain masses between the Permian and upper Eocene. After the Eocene there have been many fluctuations in sea level great enough to have altered radically the area available for use by terrestrial or semi-terrestrial animals such as *C. evelynae.* From the upper Eocene through the lower Oligocene, Iriomote and Ishigaki were probably submerged (Yabe & Aoki 1923, Hanzawa 1935), but the islands emerged again during the middle and upper Oligocene. Three additional submergences took place, finally ending in the middle Pleistocene, during which at least the highest points of Iriomote and Ishigaki were above sea level. Between these latter submergences, Iriomote and Ishigaki probably had direct land connections with China through Taiwan, and it was then that the parent stock of *C. evelynae* may have reached the islands. However, the possibility of turtles rafting from Taiwan on the Kuroshio Current can not be excluded (Lovich et al. 1985). Final inundation of this land bridge during the early to middle Pleistocene, about 1.5 million years ago, presumably isolated the turtles on the islands and subsequently separated Iriomote and Ishigaki. Inger (1947) proposed a similar scenario to explain present variation in the amphibian fauna of the Ryukyus, which also shows strong Oriental affinities.

Ye (1985) summarized the fossil record of *Cuora* in China, Taiwan and Japan, emphasizing specimens of *C. flavomarginata.* The earliest records for the genus are from the late Miocene (approximately 8 million years ago) of Yunnan, and Pleistocene remains are known from Kyushu and Honshu, Japan. This raises the possibility that the Ryukyu Islands population of *C. evelynae* may have reached there by island hopping along the Japanese archipelago. However, since no fossils of the genus are known from Korea and no living species of *Cuora* reaches there, it is more likely that movement was in the opposite direction and that the Kyushu and Honshu turtles came from mainland China by way of Taiwan and the Ryukyus.

Other material.—Cuora evelynae: CAS 21015-24, 26114-15; GMU 730-31; MCZ 7997, 55838. *Cuora flavomarginata*: AMNH 110181; CAS 10834-40; FMNH 121225-26, 127324, 216515; GMU 975; NHMW 29515, 29518; USNM 140825; WPM 1-5(live); WHR 1-7(live).

Etymology.—The genitive noun used as the specific epithet honors Dr. Ernst's wife Evelyn for her years of encouragement and help, and for her contributions to the study of turtle helminths.

Acknowledgments

Thanks are given to those individuals who allowed examination of turtles in their collections. Dr. George R. Zug and two anonymous reviewers offered valuable suggestions for improvement of the manuscript. Manuscript preparation was supported by DOE grant DE-AC09-76SR00819 to the University of Georgia, Savannah River Ecology Laboratory.

Literature Cited

Ernst, C. H., & R. W. Barbour. 1989. Turtles of the world. Smithsonian Institution Press, Washington, D.C., 313 pp.

Fang, P. W. 1934. Notes on some chelonians of China.—Siensia 4:145–199.

Gray, J. E. 1863. Observations on the box tortoises, with the descriptions of three new Asiatic species.—Proceedings of the Zoological Society of London 1863:173–179.

Hanzawa, S. 1935. Topography and geology of the Riukiu Islands.—Tohoku Imperial University Science Report, (2) Geology 18:1–61.

Hsu, H.-F. 1930. Preliminary note on a new variety of *Cyclemys flavomarginata* from China.—Contributions from the Biological Laboratory of the Science Society of China, Zoological Series 6:1–7.

Inger, R. F. 1947. Preliminary survey of the amphibians of the Ryukyu Islands.—Fieldiana:Zoology 32:296–350.

Iverson, J. B. 1986. A checklist with distribution maps of the turtles of the world. Privately printed, Paust Printing, Richmond, Indiana, 283 pp.

Kachigan, S. K. 1986. Statistical analysis. Radius Press, New York, 589 pp.

Lewontin, R. C. 1966. On the measurement of relative variability.—Systematic Zoology 15:141–142.

Lovich, J. E., C. H. Ernst, & S. W. Gotte. 1985. Geographic variation in the Asiatic turtle *Chinemys reevesii* (Gray) and the status of *Geoclemys grangeri* Schmidt.—Journal of Herpetology 19:238–245.

Moriarty, D. J. 1977. On the use of the variance of logarithms.—Systematic Zoology 26:92–93.

Pope, C. J. 1935. Natural history of Central Asia, Volume X. The reptiles of China. American Museum of Natural History, New York, 604 pp.

STSC. 1986. Statgraphics users guide. STSC Inc., Rockville, Maryland.

Tanaka, S., & F. Sato. 1983. Brief observation of the mating behavior of the box turtle *Cuora flavomarginata* in nature.—Biological Magazine, Okinawa 21:75–76.

Wilkinson, L. 1986. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Illinois.

Willig, M. R., R. D. Owen, & R. L. Colbert. 1986. Assessment of morphometric variation in natural populations: the inadequacy of the univariate approach.—Systematic Zoology 35:195–203.

Yabe, H. 1929a. The latest land connection of the Japanese Islands to the Asiatic continent.—Proceedings of the Imperial Academy of Tokyo 5: 167–169.

———. 1929b. Geologic age of the latest continental stage of the Japanese Islands.—Proceedings of the Imperial Academy of Tokyo 5:430–433.

———, & R. Aoki. 1923. A summary of the stratigraphical and paleontological studies of the Cainozoic of Japan.—Proceedings of the Pan-Pacific Science Congress (Australia) 1:954–969.

Ye, X. 1985. Studies on fossils of *Cuora* of China and Japan.—Acta Herpetologica Sinica 4:81–87.

(CHE) Department of Biology, George Mason University, Fairfax, Virginia 22030; (JEL) Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, South Carolina 29801.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 35–38

A NEW OCELLATED FROG (CENTROLENIDAE) FROM WESTERN COLOMBIA

John D. Lynch

Abstract.—A new species of *Centrolenella* (*C. ignota*) is described from cloud forests of the Cordillera Occidental in Colombia. The new species is most closely allied to the Ecuadorian *C. anomala,* the only other brown centrolenid known.

Knowledge about the Neotropical frog family Centrolenidae has increased from a view of a small family of one or two dozen species seemingly centered in Central America in 1950 to a modest-sized family of at least 65 species centered in Colombia. Our current ideas of relationships within the family are much in need of study and largely reflect the perspectives of the Costa Rican fauna (Savage 1967, Savage & Starrett 1967, Starrett & Savage 1973). Lynch & Duellman's (1973) arrangement closely paralleled that from Costa Rica but emphasized the fact that many species from northwestern South America seem to strain the Costa Rican arrangement.

Lynch & Duellman (1973) named one peculiar species from the Amazonian slopes of the Andes in Ecuador as *Centrolenella anomala* because it was tan, not green, in life. They treated the species as the sole member of a species group (op. cit.:58).

While collecting on the western flank of the Farallones de Cali in western Colombia in July 1979, I obtained a series of a small centrolenid that initially I thought to be *C. anomala* because it was tan at night. During the day the animals changed to olive-brown. The Colombian frogs are intermediate, at least in part, between *C. anomala* and the other ocellated *Centrolenella.*

Centrolenella ignota, new species
Fig. 1

Holotype.—ICNMNH 14748, an adult male, 24.4 mm SVL, from a series collected at Peñas Blancas, Farallones de Cali, ca 6 km by road SW Pichindé, Depto. Valle de Cauca, Colombia, 1900 m, 4 Jul 1979 by Humberto Carvajal and John D. Lynch.

Paratypes.—ICNMNH 14749-77, KU 209763-65, taken with the holotype.

Diagnosis.—1) vomerine teeth and odontophores absent; 2) bones very pale green in life; 3) parietal peritoneum white, visceral peritoneum clear; 4) color in life tan-brown to very pale olive with black ocelli containing orange or yellow centers; in preservative, very pale lavender with black ocelli; 5) outer fingers with basal webbing **III** 3^{+}–3^{-} **IV**; 6) webbing on foot **I** 2^{-}–2^{+} **II** 1½–2½ **III** 1½–2⅔ **IV** 3^{-}–1⅔ **V**; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with elevated warts corresponding to ocelli; 9) arms and legs lacking dermal fringes; 10) humeral spine absent; 11) lower three-fourths of tympanum visible, directed anterolaterally with slight posterior inclination.

Centrolenella ignota is most similar to *C. anomala* but differs in lacking the dark brown flecks that are interspersed among the ocelli and in lacking the spicules on the skin of the dorsum; furthermore, *C. ignota* has subanal tubercles. The two species may differ as well in that *C. ignota* has pale green bones (white in the only specimen of *C. anomala* ever captured) and has traces of green pigmentation (*C. anomala* never exhibited any green cast in its dorsal pattern).

Description.—Adults small, snout-vent length in males 22.3–25.4 mm ($\bar{x} = 23.9$ [S.E. = 0.12], n = 31), in two females 24.2

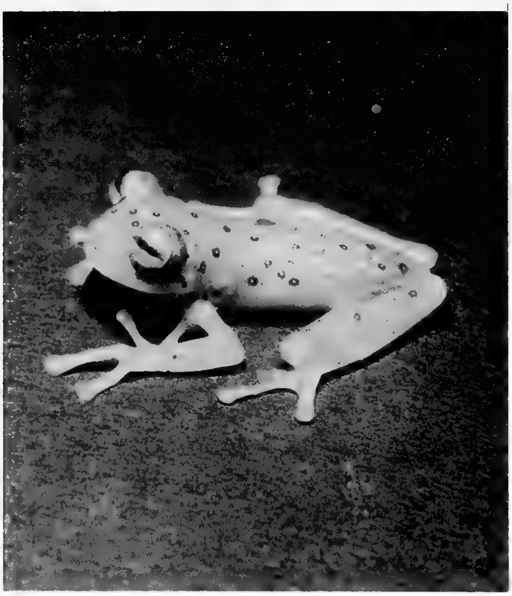


Fig. 1. *Centrolenella ignota,* topotype (ICNMNH 18007, male, 23.8 mm SVL).

and 24.4 mm; head wider than body; width of head 31.5–34.8% ($\bar{x}$ = 33.4 ± 0.1, n = 35) of snout–vent length; snout short, high, truncate in dorsal and lateral profiles; canthus rostralis round; loreal region flat; lips not flared; nostrils at tip of snout; internarial region concave, nostrils proturberant, directed anterolaterally; eye to nostril distance 53.1–75.0% ($\bar{x}$ = 62.5 ± 1.0, n = 35) eye length; eyes large, directed anterolaterally; width of upper eyelid 76.0–114.3% ($\bar{x}$ = 96.7 ± 1.4, n = 35) interorbital distance; supratympanic fold obsolete; tympanic annulus distinct, tympanum round to slightly higher than long, directed dorsolaterally with slight posterior inclination; length of tympanum 18.8–27.6% ($\bar{x}$ = 22.7 ± 0.4, n = 35) eye length; choanae large, round, not concealed by palatal shelf of maxillary arch; no vomerine odontophores or teeth; tongue round to ovoid, bearing a shallow notch posteriorly, posterior edge not adherent to floor of mouth; males with vocal slits posterolateral to tongue; males with median subgular vocal sac.

Forelimb moderately slender; no humeral spine or hook; no ulnar tubercles or folds; palmar tubercle round to ovoid, larger than oval thenar tubercle; no supernumerary tubercles on palm; subarticular tubercles low, basal tubercles broader than long, more distal ones round; fingers with lateral keels; median edge of fourth and lateral edge of third fingers bearing fleshy ridge (confluent with basal webbing); webbing formula **III** 3^{+}–(2¾–3^{-}) **IV**; first finger longer than second; all fingers bearing discs, discs rounded apically but broader than long (subtruncate); discs of fingers II–IV largest, but all discs larger than tympanum; males with swollen base of thumb, non-spinous nuptial pad on dorsal surface of thumb (metacarpal section only); hind limbs slender; length of shank 52.1–58.7% ($\bar{x}$ = 55.0 ± 0.3, n = 35) snout–vent length; tarsal tubercles and folds absent; inner metatarsal tubercle oval, flat; outer metatarsal tubercle apparently absent; no supernumerary plantar tubercles; subarticular tubercles small, round; toes about one-half webbed; webbing formula **I** (2–2^{-})–(2^{+}–2¼) **II** (1½–1⅔)–(2½–2⅔) **III** (1¼–1½)–(2½–3^{-}) **IV** (2¾–3^{+})–(1½–1¾) **V**; discs of toes smaller than those of fingers, round to subtruncate.

Skin of dorsal surfaces smooth to very finely shagreened, lacking spicules; white spots are elevated flat warts; venter and posterior surfaces of thighs bearing flat areolations; anal opening under a short transverse flap at upper level of thighs; pair of enlarged flat warts on posteroventral surface of thighs (subanal warts).

Color in preservative: Cream above with pale violet stippling over head, dorsum, and upper surfaces of limbs (this stippling is very fine and provides a pale lavender wash to the dorsal surfaces); dorsum bearing dense violet stippling around bases of white warts (forming ocelli); ocelli generally on top of head, back, and on shank but, in some individuals, also on side of head, top of thigh, and tarsus near heel; ventral surfaces cream.

Color in life: Pale tan to olive-brown above with black ocelli having orange (or yellow) centers; tips of digits yellow; parietal peritoneum white; bones very pale green; iris whitish gray with a gold cast and black reticulation.

Remarks.—When the majority of specimens were collected (4 Jul 1979), the area was receiving a light rain. During the rain the frogs were calling actively on vegetation 0.5 to 2 m above a sluggish stream (average width 0.5 m). Females were found sitting on vegetation. Some individuals were found as much as two meters away from the stream in dense vegetation. The call of *C. ignota* is a series of chirps.

The discovery of *C. ignota,* with its non-green coloration, provides evidence that the coloration of *C. anomala* is probably natural (some colleagues have doubted that brown centrolenids exist). The nearest relatives of *C. ignota* appear to be *C. anomala* and *C. cochranae.* These three species have small ocelli on the dorsum bearing reddish centers (orange-tan in *C. anomala,* red in *C. cochranae,* orange or yellow in *C. ignota*) and exhibit virtually the same head shape and degree of webbing; differences among the three species are slight. In addition to coloration differences, they differ in the presence of subanal warts (absent in *C. anomala*), vomerine dentition (usually present in *C. cochranae*), skin texture (spicules in *C. anomala* and *C. cochranae*), and adult size (*C. cochranae* is larger than the other two, *cochranae* males are 23.8–26.7 mm snout–vent length and females are 27.2–30.0 mm snout–vent length).

At present, I consider *C. ignota* and *C. anomala* to be sister species and consider *C. cochranae* the sister species of the pair of tan/brown species. The conjectured synapomorphies are (1) brown pigmentation (shared by *anomala* and *ignota*) and (2) small ocelli on elevated warts. The plesiomorphic conditions are (1) green pigmentation (true for all other centrolenid frogs) and (2) no ocelli (true for nearly all other centrolenids, see below).

There are only two other species of centrolenids having ocelli (*C. ocellata* and *C. ocellifera*). Each has more webbing on the hand than the three previously cited and each has larger ocelli that are not on elevated warts (also cream or pale yellow in life). It is tempting to assert that the ocelli constitute a synapomorphy for these five species but a case could be made for arguing that the ocelli of *C. ocellata* and *C. ocellifera* are not homologous to the ocelli of *C. anomala, C. cochranae,* and *C. ignota* but rather are homologous to the open reticulation found in the dorsum of centrolenids of the *fleischmanni* group. The published illustration of *C. grandisonae* in Cochran and Goin (1970) shows ocelli, although in their description it is apparent that they did not find ocelli in that species. *Centrolenella grandisonae* has red (flat and elevated) warts on the dorsum. Upon preservation the red disappears leaving cream spots.

Etymology.—The trivial name is Latin (*ignotus*), for strange, and is used to reflect the annectent coloration of *C. ignota* between that of *C. anomala* and the green coloration seen in most species of the genus.

Acknowledgments

I thank Humberto Carvajal for assistance in the field and Stephen C. Ayala, William E. Duellman, and Pedro M. Ruiz for provision of working space. Museum abbreviations used in the text refer to collections at the Instituto de Ciencias Naturales in Bogotá (ICNMNH) and the Museum of Natural History at the University of Kansas (KU).

Literature Cited

Cochran, D. M., & C. J. Goin. 1970. Frogs of Colombia.—Bulletin of the United States National Museum 288:1–655.

Lynch, J. D., & W. E. Duellman. 1973. A review of the centrolenid frogs of Ecuador, with descriptions of new species.—University of Kansas Museum of Natural History, Occasional Papers 16: 1–66.

Savage, J. M. 1967. A new tree-frog (Centrolenidae) from Costa Rica.—Copeia 1967(2):325–331.

———, & P. H. Starrett. 1967. A new fringe-limbed tree-frog (family Centrolenidae) from lower Central America.—Copeia 1967(3):604–609.

Starrett, P. H., & J. M. Savage. 1973. The systematic status and distribution of Costa Rican glass-frogs, genus Centrolenella (family Centrolenidae), with description of a new species.—Bulletin of the Southern California Academy of Science 72:57–78.

School of Biological Sciences, The University of Nebraska, Lincoln, Nebraska 68588.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 39–62

ON THE VALIDITY OF THE INDO-PACIFIC CARDINALFISHES *APOGON AUREUS* (LACEPÈDE) AND *A. FLEURIEU* (LACEPÈDE), WITH DESCRIPTION OF A RELATED NEW SPECIES FROM THE RED SEA

John E. Randall, Thomas H. Fraser, and Ernest A. Lachner

Abstract.—Two large species of Indo-Pacific cardinalfishes of the genus *Apogon,* subgenus *Ostorhinchus,* previously identified either as *A. aureus* (Lacepède) or *A. fleurieu* (Lacepède), are shown to be distinct. Their most characteristic color marking is a black bar encircling the caudal peduncle. They are separated by gillraker counts (22–27 for *aureus,* 19–23 for *fleurieu*) and the form of the black peduncular marking (a spot on juvenile *fleurieu,* expanding to a bar in adults; always a bar in *aureus,* typically broader dorsally and ventrally to a slight hourglass shape. Both species occur from East Africa (only *fleurieu* in the Red Sea) to the western Pacific; *fleurieu* is known only from continental shelf localities except for the Seychelles. A third species with a black peduncular bar, *A. pselion,* is described as new from specimens from the northern Red Sea. It is more slender (depth 2.8–3.4 in SL), small (largest 41.3 mm SL), and distinctive in life color (four dusky yellow stripes on head separated by blue lines, one stripe continuing as a yellow band midlaterally on body).

The Apogonidae (popularly known as cardinalfishes) is one of the largest families of tropical fishes; the great majority of these fishes are found in the marine environment. Apogonids are small (only a few species exceed 20 cm total length), with two separate dorsal fins (the first of VI to VIII spines), II anal spines, a double-edged preopercle, large eyes, and a large oblique mouth. Most are nocturnal, and those for which the reproductive strategy is known are mouth brooders.

Fraser (1972) recognized three subfamilies and 20 genera in the family. Nelson (1984) wrote that there are about 192 species, but it is clear from the number of undescribed species on museum shelves and probably more that remain to be discovered in the sea that well over 200 species will eventually be recorded.

There has long been confusion over the correct specific name for a large species of *Apogon* with a broad black bar posteriorly on the body which occurs in the Indian Ocean and western Pacific. Most authors have used the name *Apogon aureus* (Lacepède) for this fish, but some (Gon 1987, gave 12 references[1]) have called it *A. fleurieu* (Lacepède). Lacepède (1802:23) described the latter as *Ostorhinchus fleurieu*; his illustration from a drawing by Commerson was published as fig. 2 of pl. 32 in volume 3 of Histoire Naturelle des Poissons (1801) (reproduced by Gon 1987: fig. 2). Lacepède's description, obviously based on Commerson's drawing and not a specimen, appeared in volume 4 (1802:23). Because no teeth are apparent on the drawing, Lacepède assumed that they were fused to form dental plates like those of scarids, diodontids, and tetraodontids. This led Whitley (1959) to

---

[1] Weber & de Beaufort (1929:319) used *Apogon aureus,* not *A. fleurieu.*

regard *fleurieu* as an oplegnathid. Smith (1961) realized that Lacepède's figure is an apogonid. He wrote, "Most workers have refused to accept Lacepede's *fleurieu* on the grounds that it is not an Apogonid fish. To me his 1802, Pl 32, fig. 2 of *fleurieu* represents nothing else, . . ."

Fraser (1972) discussed the controversy in detail. He opted for the use of *Apogon aureus* (which was described by Lacepède, 1802:253, 273, 275, as *Centropomus aureus*) because the description of *Ostorhinchus fleurieu* "does not agree with any apogonid". He was influenced in his decision by Lacepède's description of the dentition, the apparent lack of a lateral line, and the high number of rays of the second dorsal fin (14). He concluded, "Perhaps the best course of action would be the rejection of the name on the basis that it is an unidentifiable taxon."

The second author suspected as early as 1974 that two species had been confused under the presumed synonymous names *Apogon aureus* and *A. fleurieu.* About five years ago both junior authors had determined that there were indeed two species and differentiated them by gillraker count and the form of the dark peduncular bar. In one species both juveniles and adults have a well-defined dark peduncular bar that is usually expanded dorsally and ventrally to form a slight hourglass shape. Juveniles of the other species have a dark spot centroposteriorly on the peduncle which expands with growth to form a solid bar, but without dorsal and ventral expansions. At that time the junior authors were inclined to preserve the name *Apogon fleurieu* for one species and describe the other as new. They were subsequently joined by the senior author, and with the analysis of more specimens and the original Lacepède accounts of the two species, it was concluded that both the names *fleurieu* and *aureus* should be recognized. In the meantime Gon (1987) reviewed the problem of Lacepède's apogonid names *fleurieu* and *aureus.* Like Smith (1961), he regarded Lacepède's illustration of *fleurieu* as identifiable and placed *aureus* in its synonymy. He designated a neotype for *fleurieu* (BPBM 15821, 94 mm SL, from Papua New Guinea) and illustrated it.

Lacepède's figure of *fleurieu* exhibits a peduncular bar that is narrower dorsally and ventrally, thus typical of a specimen that had a peduncular spot as a juvenile but had not yet developed a complete bar. It is clear from Gon's (1987) description of *fleurieu* and his material that he had both species. Unfortunately he chose a specimen with the hourglass peduncular bar as the neotype of *fleurieu.* If we were to follow Gon in his neotype designation, we would need to describe the other species as new. We prefer to link *fleurieu* to the species with the peduncular bar like Lacepède's figure bearing this name, thus leaving the species with the hourglass bar as *aureus.* It may be argued that Lacepède's description of *Centropomus aureus* is not diagnostic for either of these species. However, the type localities of Mauritius and Réunion strongly suggest that the one with the hourglass bar was the species described by Lacepède. We have examined specimens of this species from six collections from Mauritius. Unfortunately, all are in poor condition and none merits neotype designation. The other species, *A. fleurieu,* is known thus far only from continental shelf localities except for three lots from the Seychelles which are stranded continental fragments (for discussion see Springer 1988:128–129).

In retaining the name *Apogon aureus* for the species which is the best represented of the two in museum collections and most often reported in the literature by this name, we are being less disruptive to nomenclatural stability than if we were to adopt the name *fleurieu* for this fish.

Because of the great similarity of *Apogon aureus* and *A. fleurieu* we have included literature records of these two species and plotted the distributions of Fig. 1 only from specimens reported in sufficient detail to permit identification (generally this meant a good illustration) or from the examination of specimens.

As pointed out by both Fraser (1972) and Gon (1987), the recognition of *Apogon fleurieu* as a valid taxon will result in *Ostorhinchus* Lacepède (type series, *O. fleurieu* Lacepède) replacing *Nectamia* Jordan as a subgenus of the genus *Apogon.* See Fraser (1972) for a diagnosis of *Ostorhinchus* (as *Nectamia*).

Bleeker (1874) recorded *Dipterodon hexacanthus* Lacepède (1801:pl. 30, fig. 2; 1802: 166, 168) as a junior synonym of *Amia* (=*Apogon*) *aurea* Lacepède. He was followed by Day (1875) and Weber & de Beaufort (1929) (though questioned). Barnard (1927) stated that this nominal species cannot be included in the synonymy of *aureus* because the description of the dentition is not that of an *Apogon.* Fowler & Bean (1930), however, did not agree with Barnard, pointing out that both *Ostorhinchus fleurieu* and *Dipterodon hexacanthus* have a dark transverse band across the caudal peduncle. They added, "The large teeth shown in the figure of the latter we think an error in engraving." Fraser (1972) admitted that *D. hexacanthus* could be an apogonid, but at best a *Cheilodipterus,* not an *Apogon.* He wrote, "I treat this name as a *nomen dubium,* perhaps involving a member of the Apogonidae." Gon (1987) accepted Fraser's opinion, and we also concur.

Specimens of a third species of *Apogon* with a dark peduncular bar that were collected by the senior author and colleagues in the northern Red Sea represent an undescribed species. Though notably smaller than either *aureus* or *fleurieu,* this species could easily be misidentified as the young of the former. The purpose of the present paper is to provide descriptions of all three species and to differentiate them.

Apogonid material for the present study has been examined at or obtained from the following institutions: Australian Museum, Sydney (AMS); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS, SU); Hebrew University, Jerusalem (HUJ); Museum National d'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); Queensland Museum, Brisbane (QM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); J. L. B. Smith Institute of Ichthyology, Grahamstown (RUSI); Tel Aviv University, Ramat Aviv (TAU); U.S. National Museum of Natural History, Washington, D.C. (USNM); and Western Australian Museum, Perth (WAM).

Lengths given for specimens are standard length (SL), measured from the front of the upper lip to the base of the caudal fin (posterior end of hypural plate); body depth is the depth from the base of the anterior dorsal spines; body width is measured just posterior to the gill opening; head length is measured from the front of the upper lip to the end of the opercular membrane, and snout length from the same anterior point to the fleshy edge of the orbit; orbit diameter is the greatest fleshy diameter and interorbital width the least bony width; caudal peduncle depth is the least depth, and caudal peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and soft rays are measured to their extreme base; caudal concavity is the horizontal distance between verticals at the tips of the shortest and longest caudal rays.

Pectoral-ray counts include the rudimentary upper ray; lateral-line scale counts are made to the base of the caudal fin (hence do not include the pored scales posterior to the hypural plate); gillraker counts are made on the first gill arch and include all rudiments; the count of the upper-limb rakers is given first; the raker at the angle is contained in the lower-limb count.

Counts of the rays of the median fins are the same for all three species. Pectoral-ray

Table 1.—Gillraker counts of species of *Apogon.*

	Upper limb				Lower limb							Total gillrakers								
	5	6	7	8	14	15	16	17	18	19	20	19	20	21	22	23	24	25	26	27
aureus (total)		73	93	8			10	84	39	34	4				6	59	40	29	30	7
Comoros			35	4					5	31	3							5	28	6
Other localities		73	58	4			10	84	34	3	1				6	59	40	24	2	1
fleurieu (total)	30	129	4		1	49	90	23				1	16	46	74	26				
Red Sea	9	43	1			13	38	2					3	16	31	3				
Seychells	2	34	3				24	15						2	19	18				
Other localities	19	52			1	36	28	6				1	13	28	24	5				
pselion	15	25			4	15	20					4	7	19	11					

counts are nearly always 14. Gillraker counts, however, are useful in distinguishing the new species and *Apogon fleurieu* from *A. aureus* (Table 1).

Tables 2–4 present proportional measurements of specimens of the three species as percentages of the standard length. Body and fin proportions are given in the text to the nearest 0.05.

Paratypes of the new species are listed chronologically by date of collection. Data in parentheses in the description of the new species refer to paratypes.

Apogon aureus (Lacepède)

Figs. 1–4; Tables 1, 2

Centropomus aureus Lacepède, 1802:253, 273, 275 (type localities, Mauritius and Réunion).

Apogon roseipinnis Cuvier in Cuvier & Valenciennes 1829:490 (type locality, Sri Lanka).—Valenciennes in Cuvier & Valenciennes 1830:553 (Ambon).

Apogon annularis var. *roseipinnis* (non Cuvier) Günther, 1859:239 (in part) (Hong Kong).

Apogon annularis (non Rüppell) Playfair & Günther, 1867:20 (Zanzibar).—Boulenger, 1887:655 (Muscat, Oman).

Amia aurea Bleeker, 1874:48 (Indonesian localities).—Bleeker, 1873–1876:92, pl. 337, fig. 1.

Apogon aureus Macleay, 1883:236 (Port Moresby, New Guinea).—Sauvage, 1891: 142 (Sulawesi, Sri Lanka, Mauritius, and Madagascar).—Weber & de Beaufort, 1929:319 (Indonesian localities, northern New Guinea).—Munro, 1955:120, pl. 21, fig. 329 (Sri Lanka).—Woodland & Slack-Smith, 1963:31 (Heron Island, Great Barrier Reef).—Ida & Moyer, 1974:114, fig. 5B (Miyake-jima, Japan).—Masuda et al., 1975:204, pl. 37G (southern Japan).—Burgess & Axelrod, 1975:1447, fig. 10 (Vanuatu).—Fourmanoir & Laboute, 1976: 288 (figure with erroneous color) (New Caledonia).—Burgess & Axelrod, 1976:

Table 2.—Proportional measurements of specimens of *Apogon aureus* expressed as a percentage of the standard length.

	BPBM 23388	SU 27353	SU 27353	BPBM 19410	CAS 62567	BPBM 30648	BPBM 30648	BPBM 15921	SU 27367	BPBM 20151
Standard length (mm)	33.1	49.9	56.2	70.5	76.8	87.2	91.0	94.0	99.6	108.5
Body depth	35.2	38.8	40.0	39.4	40.3	41.4	40.2	42.5	44.0	41.4
Body width	15.7	16.0	16.4	15.9	16.3	15.0	15.3	15.9	17.2	14.8
Head length	40.3	39.6	38.6	41.1	39.9	41.7	40.4	40.3	38.7	39.3
Snout length	8.8	8.9	8.9	9.3	9.3	8.9	9.5	9.1	8.7	9.8
Orbit diameter	15.8	14.2	14.0	13.8	14.3	14.4	14.4	14.5	12.6	13.5
Interorbital width	9.6	9.7	8.9	9.6	9.9	9.7	9.9	9.8	9.1	9.3
Upper jaw length	20.9	20.2	19.6	20.1	20.4	20.4	21.0	21.1	19.8	20.3
Caudal peduncle depth	14.2	16.8	17.5	17.7	17.2	16.6	17.4	17.0	17.4	17.6
Caudal peduncle length	24.1	23.6	23.7	22.8	24.5	23.5	22.0	23.0	23.4	21.9
Predorsal length	42.3	40.7	41.0	43.3	42.2	43.2	41.7	43.5	41.7	41.8
Preanal length	63.3	62.8	63.0	63.7	64.5	65.4	65.7	65.9	65.1	64.1
Prepelvic length	39.3	40.2	38.0	40.6	40.2	40.4	41.5	41.7	40.0	39.7
Length of first dorsal spine	3.5	3.2	4.3	3.1	3.9	4.3	4.0	4.1	3.2	3.9
Length of second dorsal spine	9.6	9.8	10.6	10.1	10.8	11.4	10.2	11.2	9.0	10.6
Length of third dorsal spine	17.6	20.6	broken	21.4	20.8	22.4	23.1	21.6	21.1	23.5
Length of fourth dorsal spine	17.5	20.2	broken	21.4	20.6	22.1	22.4	20.7	broken	22.2
Length of spine of second dorsal fin	14.8	16.6	16.0	16.9	16.3	16.1	17.0	17.9	15.5	15.4
Length of longest dorsal ray	25.4	broken	26.0	28.1	24.9	27.5	27.8	27.6	25.2	26.7
Length of first anal spine	4.1	4.2	3.8	4.4	4.6	3.6	4.4	5.1	3.6	4.7
Length of second anal spine	14.7	16.0	15.7	14.5	15.9	16.0	16.2	17.2	14.7	15.5
Length of longest anal ray	23.5	25.3	24.4	24.9	26.0	24.1	23.6	24.2	23.0	broken
Caudal fin length	35.0	broken	broken	35.2	36.2	35.5	35.7	broken	33.5	32.4
Caudal concavity	12.4	—	—	12.9	12.0	13.1	12.9	—	10.2	10.1
Pectoral fin length	26.9	26.5	25.2	27.1	27.2	28.1	28.7	28.9	26.4	27.2
Pelvic spine length	14.9	16.0	16.3	16.7	15.9	15.5	16.6	17.2	15.1	16.6
Pelvic fin length	21.7	23.0	24.0	26.4	24.6	24.4	25.8	26.3	23.9	25.5

Table 3.—Proportional measurements of specimens of *Apogon fleurieu* expressed as a percentage of the standard length.

	BPBM 18258	USNM 191704	HUJ 11922	BPBM 27638	BPBM 27638	USNM 212416	USNM 212416	USNM 212416	BPBM 19811	BPBM 31874
Standard length (mm)	32.9	42.0	52.9	60.3	65.2	70.6	77.7	82.2	96.2	102.1
Body depth	35.2	36.2	36.7	38.4	39.9	38.0	40.6	40.9	41.5	41.7
Body width	16.4	16.2	16.4	16.9	17.4	17.3	17.3	17.8	16.6	16.7
Head length	42.5	40.2	39.7	41.4	40.5	40.9	39.8	41.4	39.6	39.6
Snout length	9.1	9.4	9.5	9.3	9.6	9.5	9.3	9.7	9.4	9.5
Orbit diameter	16.7	14.6	13.6	13.3	13.6	13.5	13.2	13.6	13.1	12.9
Interorbital width	9.9	9.6	9.8	9.5	9.6	8.9	9.3	9.1	8.8	8.9
Upper jaw length	21.6	20.0	19.8	19.9	20.7	20.2	20.3	21.3	20.7	19.9
Caudal peduncle depth	15.8	16.6	16.1	17.1	16.8	16.2	16.7	16.1	16.8	16.7
Caudal peduncle length	23.7	23.3	22.2	21.6	22.1	23.0	21.9	20.8	22.0	21.0
Predorsal length	42.7	41.2	43.0	42.8	42.0	41.5	41.3	43.2	43.2	42.0
Preanal length	65.4	62.0	61.1	63.4	65.1	63.4	65.8	66.1	64.4	65.5
Prepelvic length	39.8	37.0	38.5	39.2	39.9	40.4	40.0	41.4	39.8	39.8
Length of first dorsal spine	3.6	3.9	3.2	3.3	3.8	4.1	4.1	3.1	3.1	3.3
Length of second dorsal spine	10.8	11.6	broken	11.4	10.3	10.4	10.9	10.0	9.4	9.0
Length of third dorsal spine	20.3	19.0	19.3	21.9	20.2	20.0	21.0	20.6	20.7	19.2
Length of fourth dorsal spine	19.2	18.6	19.5	21.6	19.9	broken	21.0	21.5	21.7	20.9
Length of spine of second dorsal fin	16.7	17.2	16.2	16.3	15.7	15.9	16.7	16.4	16.1	15.8
Length of longest dorsal ray	27.3	27.4	26.5	27.2	27.1	25.8	27.3	28.1	25.4	26.5
Length of first anal spine	4.1	4.8	broken	4.8	4.7	4.3	4.9	4.8	4.7	4.0
Length of second anal spine	15.8	16.2	14.6	15.7	15.8	14.8	15.6	15.6	16.2	14.7
Length of longest anal ray	24.2	broken	23.7	24.8	23.3	23.4	24.6	23.7	22.8	broken
Caudal fin length	33.4	broken	33.8	33.5	33.3	32.2	32.2	33.6	32.2	broken
Caudal concavity	11.4	—	9.8	11.9	9.7	10.9	11.6	10.0	10.3	—
Pectoral fin length	26.6	26.1	26.1	27.4	26.3	26.2	27.7	27.8	26.3	25.6
Pelvic spine length	17.2	16.4	15.5	16.7	16.3	15.7	16.0	15.6	15.5	14.8
Pelvic fin length	24.0	23.6	23.6	26.2	25.8	24.8	24.4	25.3	23.7	23.6

Table 4.—Proportional measurements of type specimens of *Apogon pselion* expressed as a percentage of standard length.

	Holotype	Paratypes								
	BPBM 21515	USNM 213387	BPBM 18261	TAU 9670	BPBM 18261	BPBM 31988	BPBM 31988	BPBM 31988	USNM 213383	USNM 213383
Standard length (mm)	36.2	20.6	23.2	26.5	33.5	33.8	36.6	39.2	39.6	41.3
Body depth	34.0	29.6	31.2	30.0	35.3	33.2	33.4	35.5	34.9	33.1
Body width	14.4	15.5	14.2	12.2	14.0	14.7	15.2	15.6	16.6	15.0
Head length	39.2	38.8	39.0	39.4	39.3	39.2	39.1	38.4	40.7	38.8
Snout length	10.2	9.7	9.9	9.5	9.3	9.2	9.1	9.2	9.4	9.7
Orbit diameter	14.0	15.5	15.1	15.2	15.1	14.5	13.9	13.7	13.5	13.1
Interorbital width	8.0	8.5	8.4	7.5	8.3	8.1	8.2	8.0	7.5	7.7
Upper jaw length	19.9	19.9	20.2	19.3	20.9	19.8	20.5	19.2	20.7	19.5
Caudal peduncle depth	15.2	11.7	13.3	12.2	14.7	14.2	15.8	15.5	12.3	14.3
Caudal peduncle length	24.4	24.8	25.8	24.1	25.6	24.7	25.0	24.0	25.3	25.5
Predorsal length	40.2	42.4	41.0	41.4	42.2	41.8	40.5	41.9	41.7	40.7
Preanal length	62.2	60.8	61.0	60.0	62.6	60.3	60.7	62.5	62.7	61.5
Prepelvic length	38.2	37.9	38.4	37.8	39.1	37.8	38.2	38.2	40.1	37.5
Length of first dorsal spine	3.3	3.2	3.9	3.4	3.3	3.6	4.0	3.8	2.8	3.6
Length of second dorsal spine	11.0	12.4	12.7	11.7	11.6	11.5	10.4	11.5	10.5	10.2
Length of third dorsal spine	18.9	18.4	19.8	20.7	18.5	20.0	18.1	18.4	18.9	18.7
Length of spine of second dorsal fin	15.0	broken	16.2	14.7	15.5	14.8	14.2	15.3	14.4	14.7
Length of longest dorsal ray	24.6	broken	26.0	broken	24.7	23.7	23.9	25.5	broken	broken
Length of first anal spine	4.7	4.8	5.3	5.4	4.3	5.3	4.9	5.0	3.8	4.0
Length of second anal spine	13.1	15.0	15.9	14.4	13.8	13.3	14.2	13.1	14.3	broken
Length of longest anal ray	20.4	broken	22.8	broken	20.7	20.7	19.9	21.7	broken	broken
Caudal fin length	31.0	broken	30.5	broken	31.3	32.3	29.0	27.8	broken	broken
Caudal concavity	8.4	—	8.8	—	9.0	8.0	9.1	9.4	—	—
Pectoral fin length	24.9	24.5	24.6	broken	25.2	24.8	22.5	25.3	24.5	23.3
Pelvic spine length	14.1	15.1	15.9	15.1	14.9	14.2	14.2	15.0	13.9	14.4
Pelvic fin length	22.1	20.9	23.3	22.6	22.2	22.5	21.9	23.0	22.8	22.5

1678, fig. 25 (Great Barrier Reef).—Allen & Steene, 1979:28 (Christmas Island, Indian Ocean).—Schroeder, 1980:145, fig. (western Sulu Sea, Philippines).—Russell, 1983:47 (southern Great Barrier Reef).—Hayashi & Kishimoto, 1983:27, pl. 5, fig. 21 (Iriomote Island, Ryukyus and Osezaki, Shizuoka Prefecture).—Shen, 1984: 48, figs. 304–6a, 6c (Taiwan).—Masuda et al., 1984:147, pl. 131 I (southern Japan).—Gloerfelt-Tarp & Kailola, 1984: 145, 327, fig. on 144 (off Bali).—Gon in Smith & Heemstra, 1986:549, pl. 48, fig. 175.3 (East Africa south to Durban).—Shao & Chen, 1986:93, fig. 38 (Taiwan).—Allen & Steene, 1987, pl. 35, fig. 2 (Christmas Island, Indian Ocean).—Al-Baharna, 1986:71, fig. (Bahrain).

Amia fleurieu (non Lacepède) Fowler, 1918: 65 (Philippines).—Fowler, 1927:274 (Philippines).—Fowler & Bean, 1930 (Philippine and Indonesian localities and Borneo).

Apogon fleurieu (non Lacepède) Smith, 1949:207, pl. 22, fig. 481 (Natal and Mozambique).—Fourmanoir, 1957:83, fig. 59 (Comoro Islands).—Shen & Lam, 1977:177, fig. 21 (Taiwan) (misspelled *fleurien*).—Gon, 1987:140, fig. 1 (in part).

Ostorhynchus fleurieu (non Lacepède) Smith, 1961:399, pl. 46D (in part).—Smith & Smith, 1963:20, pl. 60D (Seychelles).

Gronovichthys aureus Munro, 1967:244, 251, pl. 29, fig. 432 (New Guinea).

Diagnosis.—A species of the genus *Apogon,* subgenus *Ostorhinchus,* with dorsal rays VII–I,9; pectoral rays 14 (rarely 13 or 15); lateral-line scales 24; median predorsal scales 5; total gillrakers 22–27; preopercular ridge smooth, the posterior margin and most of ventral margin serrate; body depth 2.25–2.85 in SL; interorbital width 4.05–4.35 in head; posterior nostril usually only slightly larger than anterior; pale (coppery with iridescence in life) with a black bar encircling posterior caudal peduncle in both young and adult, its midlateral width one-half to two-thirds orbital diameter, its upper and lower edges expanded to form a slight hourglass shape, a broad blackish stripe from front of snout to orbit, continuing behind eye, this stripe bordered by a blue line in life; a narrow blackish streak (blue in life) on maxilla and continuing a short distance posterior; a small blackish spot on each lateral-line scale; a row of dark dashes basally in anal fin; maximum standard length about 125 mm.

Description.—Dorsal rays VII–I,9, all rays branched, the last to base; anal rays II,8, all rays branched, the last to base; pectoral rays 13(2), 14(64), 15(4), the upper two and lower one or two unbranched; pelvic rays I,5; principal caudal rays 17, the upper and lower unbranched; upper and lower procurrent caudal rays 8 or 9, the posterior two segmented; lateral-line scales 24 (plus 4 pored scales posterior to caudal-fin base, the last long and pointed); scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 5, the fourth and fifth deeply indented posteriorly in the midline; circumpeduncular scales 12 (minimum zigzag count); gillrakers 6–8+16–20, 1–2 upper and 0–1 lower as rudiments, the total count 22–25; pseudobranchial filaments 16 in a 33 mm specimen, 27 in a 92 mm one, and 32 in a 108.5 mm one; branchiostegal rays 7; predorsal bones 3; vertebrae 10+14.

Body moderately deep, the depth 2.25–2.85 in SL, and compressed, the width 2.1–2.8 in depth; head length 2.4–2.6 in SL; dorsal profile of head slightly convex to straight except for rounded front of snout; snout length 4.0–4.65 in head; eye large; the orbit diameter 2.55–3.05 in head; interorbital space flat to slightly convex with median and lateral longitudinal ridges, the least width 4.05–4.35 in head; caudal peduncle depth 2.2–2.85 in head; caudal peduncle length 1.65–1.85 in head.

Mouth large, the maxilla reaching to or slightly posterior to a vertical at rear edge of pupil, the upper jaw length 1.9–2.1 in head; mouth oblique, forming an angle of about 35° to horizontal axis of head and body; posterior margin of maxilla slightly rounded to slightly concave, the corners rounded; supramaxilla not present; lower jaw projecting, knob-like; upper jaw with a broad band of villiform teeth except for gap at symphysis, the teeth of the outer rows slightly incurved and inwardly depressible, the teeth of the inner rows at side of jaw very small; a narrow band of villiform teeth in lower jaw, with three or four rows at front of jaw and a single row posteriorly, the inner teeth longer than outer; vomer with one to two rows of small teeth forming a V-shape with rounded apex; palatines with a single irregular row of small teeth. Tongue broadly triangular, the tip moderately pointed.

Anterior nostril a short membranous tube located in front of center of orbit nearly half distance to anterior end of snout; posterior nostril ovate to slit-like, without a rim, located obliquely dorsoposterior to anterior nostril, the internarial distance about 1.5 times greater than distance from posterior nostril to orbit; posterior nostril usually only slightly larger than anterior; large openings, one in front of anterior nostril, one below internarial space and one at edge of interorbital space, leading to broad subsurface channels; a pair of prominent pores on tip of lower jaw; numerous small sensory pores over dorsal surface of head, side of snout, suborbital region, naked part of preopercle, and mandible.

A single, poorly developed, flat, obtuse spine on opercle at level of upper edge of pupil; preopercular ridge smooth; posterior margin, rounded corner, and most of ventral margin of preopercle serrate (35 serrae on 33 mm specimen, 73 on 92 mm fish).

Lateral line conspicuous, very slightly arched anteriorly, then paralleling dorsal contour of body and ending midlaterally a short distance onto base of caudal fin; scales ctenoid; head naked except for cheek, opercle, subopercle, and nape; no scales on dorsal and anal fins except for a very low sheath of small scales on extreme base of second dorsal and anal fins; basal part of caudal fin with progressively smaller scales that extend about half distance to posterior margin; paired fins naked except for triangular scaly process basally on lower surface of pelvic fins.

Origin of first dorsal fin above base of third lateral-line scale; first dorsal spine slender and short, about one-third length of second spine; second dorsal spine 3.6–4.3 in head; third dorsal spine longest (though only slightly longer than fourth), 1.65–2.3 in head; first dorsal soft ray longest, 1.45–1.6 in head; origin of anal fin below base of third dorsal soft ray; anal spine small, 3.4–4.45 in length of second spine; second anal spine 2.35–2.85 in head; first anal soft ray longest, 1.55–1.75 in head; caudal fin forked, the caudal concavity 3.15–3.9 in head, the fin length 2.75–3.1 in SL; third or fourth pectoral rays longest, 1.4–1.5 in head; origin of pelvic fins slightly anterior to upper base of pectorals; pelvic fin tips extending well beyond anus, often to origin of anal fin, the first soft ray longest, 1.5–1.85 in head.

Color in alcohol pale to light brown with a dark brown bar encircling posterior caudal peduncle, its midlateral width about one-half to two-thirds orbit diameter, its upper and lower edges usually expanded to produce a slight hourglass shape; a dark brown stripe from front of snout, broadening as it passes to orbit, and continuing diffusely a short distance posterior to eye, its edges often darker brown; tip of snout dark brown; a narrow brown streak on maxilla and continuing a short distance beyond it; lower opercle, subopercle, thorax, and lower abdomen of some specimens partly silvery; tubular anterior nostril pale; a small dark brown spot on underside of each lateral-line scale, usually visible externally (more evident on anterior than posterior scales); fins pale except anterior part of first dorsal fin, proximal upper and lower edges of caudal fin and lateral edge of pelvic fins which are dusky, and a dark brown line basally in anal fin, interrupted by each ray, which diverges

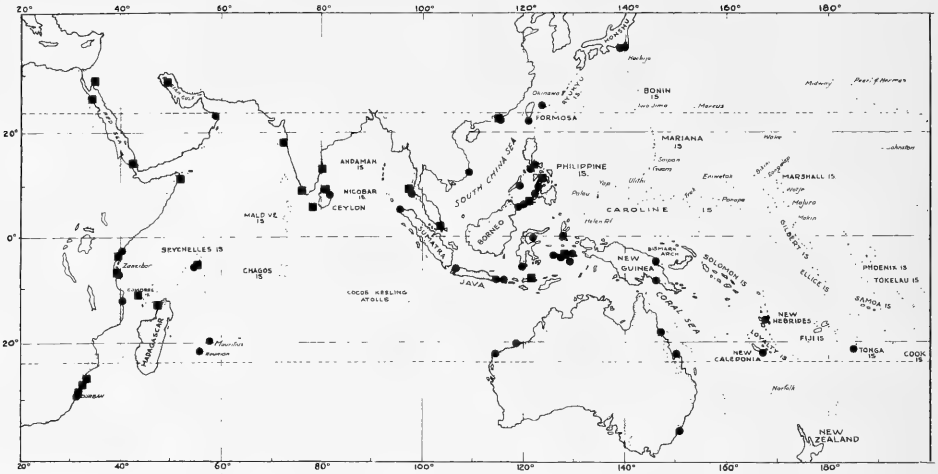


Fig. 1. Distributions of *Apogon aureus* (●) and *A. fleurieu* (■).

outward from midbase of fin to end in a streak on last ray; peritoneum pale; digestive tract black; gillrakers dusky.

Color in life coppery with iridescence, paler posteriorly, becoming golden on postorbital head and side of body; a black bar across posterior caudal peduncle, broader dorsally and ventrally; a blackish stripe, edged in bright blue, from front of snout through eye, continuing diffusely a short distance behind eye where the blue margins tend to break up into dashes and spots; some individuals with a few indistinct bluish spots anteriorly on side of body; tip of lower jaw blackish; a bright blue line on upper lip, extending across maxilla, and continuing a short distance posterior to maxilla; lateral line pale with a series of small blackish spots, one per scale (spots progressively fainter, and often absent, posteriorly); median fins with pale orange-yellow membranes and salmon pink rays, the anterior part of the first dorsal fin dusky orange; distal part of lobes of second dorsal, anal, and caudal fins sometimes red; base of anal fin with a narrow orange band separated from an adjacent outer narrow blue band by a black line on membranes of fin; pectoral fins pale yellowish with light orange rays; pelvic fins with yellow membranes and orange rays, the lateral edge dusky bluish.

Remarks.—As mentioned above, *Apogon aureus* is very similar to *A. fleurieu*; previously these two taxa were considered synonymous. See the Remarks of the following account (of *fleurieu*) for discussion of their similarities and differences.

Apogon aureus occurs from the coast of East Africa to the western Pacific where it ranges from southern Japan to Sydney, New South Wales; it is known from the following islands: Madagascar, Rèunion, Mauritius, Seychelles, Sri Lanka, Christmas, Indonesia, Philippines, Taiwan, New Guinea, Vanuatu, and New Caledonia. With the exception of the Tonga Islands where the senior author has observed and photographed the species underwater, it is not known from the islands of Micronesia and Polynesia. In spite of much collecting, it has not been taken at the atolls of the Maldives or Chagos Archipelago. It has not been observed or collected in the Red Sea or Persian Gulf and is as yet unknown from the coasts of India, Burma, and Thailand. It has, however, been recorded from the Gulf of Oman (as *Apogon annularis*) by Boulenger (1887); Boulenger's specimen from Muscat was examined at the British Museum (Natural History).

Collections of this species have been made in the depth range of 1–30 m from coral reefs or rocky substrata where there are caves

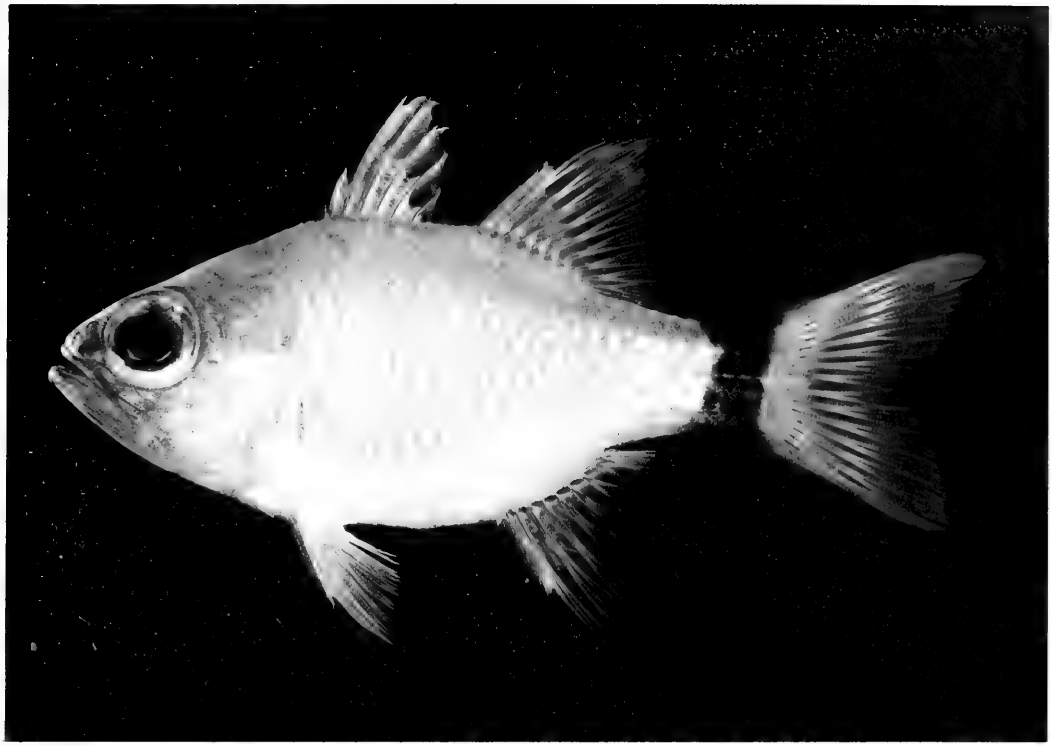


Fig. 2. Adult of *Apogon aureus*, BPBM 30648, 92 mm SL, Port Moresby, Papua New Guinea.

or crevices to provide shelter by day. The senior author photographed the species off northeastern Bali in 40 m. It does not normally occur in areas subject to much wave action. The localities where collections have been made in only a few meters of water are all in well-protected bays or lagoons.

Apogon aureus is generally encountered in small aggregations, sometimes mixed with *A. apogonides* (Bleeker). As noted by Ida & Moyer (1974), it is unusually bold for an apogonid and will venture a short distance from shelter to approach a diver if he remains still. It leaves the shelter of the reef shortly before sunset for nocturnal feeding, mainly on the larger zooplankton.

In 1975 John E. McCosker and associates collected 39 specimens (CAS 35490) of a cardinalfish identified as *Apogon aureus* at Grande Comore, Comoro Islands, in caves in 20–30 m. These fish are immature and range in SL from 37–55 mm. We took routine meristic data on all 39 specimens. The lower-limb gillraker count is high, 18–20 (see Table 1, under *aureus*). Since no other differences could be found between the Comoro fish and typical *aureus,* we provisionally identify them as *A. aureus.* It is hoped that future collecting at these islands will result in specimens of the adult of this form and a record of its life color.

Material examined.—East Africa: RUSI 3205, 54 mm. Kenya: Mombasa, BMNH 1913.4.7.51, 92 mm. Zanzibar: BMNH 1867.3.7.555, 84 mm; RUSI 3167, 86 mm. Mozambique: Bazaruto Island, RUSI 3168, 80 mm. Pinda, RUSI 3164, 86.5 mm. Mozambique Island, RUSI 3165, 3: 64.5–87 mm. Natal: Durban, BMNH 1916.9.23.14, 81 mm; RUSI 11655, 8: 86–92 mm; SU 31278, 68 mm. Madagascar: MNHN 8762, 73 mm; USNM 17104, 3: 78–83 mm. Nossi Bé, USNM 212408, 2: 62–79 mm. Mauritius: BMNH 1934.2.22.11, 98 mm; BMNH

Fig. 3. Juvenile of *Apogon aureus,* BPBM 23388, 32 mm SL, Taiwan.

1937.5.26.9, 98 mm; BMNH 1941.4.18.17, 97 mm; BPBM 20151, 5: 105–118 mm; MNHN 8759, 3: 66–81 mm; RUSI 1158, 3: 99–108 mm. Seychelles: Mahé, RUSI 3166, 71 mm. Gulf of Oman: Muscat, BMNH 1887.11.11.65, 99 mm; BMNH 1901.1.30.48, 64 mm. Sri Lanka: Trincomalee, USNM 212422-24, 10: 61–88 mm; USNM 212587, 86.5 mm; MNHN 8700, 74.5 mm, holotype of *Apogon roseipinnis.* Sumatera (Sumatra): Weh, RMNH 12730, 4: 43–84 mm. Viet Nam: Nha Trang Bay, CAS 62567, 52: 74–95 mm; CAS 62568, 7: 90.5–98 mm. Jawa (Java): Jakarta, RMNH 12731, 86.5 mm. Java Sea, RMNH 12733, 77 mm. Sulawesi (Celebes): MNHN 60, 56.5 mm. Gulf of Tomini, Dodepo and Pasejogo Islands, USNM 171278, 2: 64–71 mm. Simba Strait, USNM 171290, 48.5 mm. Makassar Island, USNM 171294, 8: 24–51 mm. Buton Strait, Labuan Blanda Island, USNM 171292, 3: 35–46 mm. Selayar, RMNH 10020, 84 mm. Bali, BPBM 32247, 3: 45–48 mm. Lombok, BPBM 30047, 87 mm. Molucca Islands: Ambon, BPBM 19410, 5: 70.5–86 mm; MNHN 8699, 2: 79–80 mm; MNHN 8706, 73 mm; RMNH 8158, 5: 70–89 mm; USNM 210441, 26 mm. Buru (Bouro), USNM 171281, 4: 55–78 mm; Tomahu Island (near Buru), USNM 171283, 62–77 mm; USNM 212425, 72 mm. Seram (Ceram), BMNH 1858.4.21.175,180, 2: 70–81 mm. Bacan (Batjan), RMNH 13056, 76 mm. Gillolo Island, USNM 171280, 78 mm. Makyan Island, USNM 171291, 73 mm; USNM 171276, 7: 75–87 mm. Saparua Island, USNM 210076, 4: 75–81 mm; USNM 210357, 44: 22–81 mm. Tidore Island (south of Ternate), USNM 171282, 3: 80–83 mm; Dowarra Island, USNM 171290, 47 mm. Banda Islands: Banda Neira, USNM

Fig. 4. Underwater photograph of *Apogon aureus,* about 95 mm TL, Bali.

213077, 49 mm. Western Australia: Ashmore Reef, AMS I.26742-024, 2: 32–33 mm. Northwest Cape, AMS I.19641-004, 2: 97–97.5 mm. Dampier Archipelago, Rosemary Island, AMS I.19688-006, 2: 41–44.5 mm. Warroora, QM I.10263, 103 mm. Borneo: Sabah, Darvel Bay, Danawan and St. Amil Islands, USNM 171268, 2: 72.5–73 mm. Philippines: Sulu Archipelago, Singaan Island, USNM 171279, 3: 57–73 mm. Simaluc Island and Simaluc Sibi Sibi Island, USNM 171275, 7: 41–80 mm. Jolo, SU 27367, 6: 92.5–107 mm. Tumindao Island, USNM 171277, 85 mm. Mindanao: Basilan Island, USNM 171288, 86 mm. Tonquil Island, USNM 171269, 2: 77–80 mm. Malanipa Island, USNM 171273, 2: 64–81 mm. Tulnalutan Island, USNM 171270, 64 mm. Inamucan Bay, USNM 171274, 90 mm. Murcielagos Bay, USNM 171284, 3: 71–75 mm. Negros: SU 27353, 7: 50.5–98 mm. Dumaguete, BPBM 26513, 82 mm; BPBM 28579, 81 mm; SU 53318, 3: 53.5–93 mm. Mindoro: Galera Bay, USNM 171267, 2: 43–73 mm; USNM 171293, 3: 42–80 mm. Marinduque: Santa Cruz Island, USNM 171285, 2: 45–51 mm. Luzon: Batangas, USNM 171272, 6: 42–93 mm. Hong Kong: BMNH 1856.11.17.73, 67 mm. Taiwan: BPBM 23388, 32 mm. Papua New Guinea: southeast New Guinea, AMS I.266, 95.5 mm. Port Moresby, AMS I.17537-003, 3: 88.5–92 mm; BPBM 15921, 94 mm (invalid neotype of *Apogon fleurieu,* see Remarks, under *A. fleurieu*); BPBM 30648, 7: 85–92 mm. Madang, AMS I.17086-008, 2: 55–65 mm; BMNH 1974.5.25.1608–1609, 2: 52–63 mm; USNM 212426-27, 8: 30.5–62 mm. Queensland: Great Barrier Reef, Palm Island, ANSP 122321, 80 mm. One Tree Island, AMS I.20206-006, 3: 53–60.5 mm. New South Wales: Sydney Harbor, AMS I.16777.001, 57 mm; AMS I.17734-001, AMS I.18850-004, 47.5 mm; ANSP 135507, 5: 52–61 mm.

Apogon fleurieu (Lacepède)
Figs. 1, 5–7; Tables 1, 3

Ostorhinchus fleurieu Lacepède, 1801:pl. 32, fig. 2; 1802:23 (type locality, Pacific Ocean).

Apogon annularis var. *roseipinnis* (non Cuvier) Günther, 1859:239 (in part) (Ambon).

Apogon annularis (non Rüppell) Klunzinger, 1870:713 (Red Sea).

Apogon aureus (non Lacepède) Day, 1875: 61, pl. 16, fig. 8 (Madras, India).—Randall, 1983:63, fig. 82 (Red Sea).—Allen & Steene, 1987:pl. 55, figs. 1, 2 (Similan Islands, Andaman Sea).

Apogon (*Amia*) *aureus* (non Lacepède) Klunzinger, 1884:22 (Quseir, Egypt).—Botros, 1971:296 (Red Sea).

Ostorhynchus fleurieu Smith, 1961:399 (in part).—Kotthaus, 1970:62, figs. 245, 246, 250 (southern Red Sea).

Apogon (*Nectamia*) *fleurieu* Dor, 1984:112 (Red Sea).—Kuronuma & Abe, 1986:99, pl. 10 (Persian Gulf).

Apogon (*Ostorhinchus*) *fleurieu* Gon, 1987: 140 (in part).

Apogon sp. Allen & Steene, 1987:pl. 35, fig. 5 (Phuket, Thailand).

Diagnosis.—A species of the genus *Apogon,* subgenus *Ostorhinchus,* with dorsal rays VII–I,9, pectoral rays 14 (rarely 13 or 15); lateral-line scales 24; median predorsal scales 5; gillrakers 19–23; preopercular ridge smooth, the posterior margin and most of ventral margin serrate; body depth 2.4–2.85 in SL; interorbital space 4.05–4.6 in head; posterior nostril usually only slightly larger than anterior; pale (coppery with iridescence in life), the young with a blackish spot midlaterally on posterior caudal peduncle which expands to a broad blackish bar in adults (dark bar not distinctly broader dorsally and ventrally); a broad blackish stripe from front of snout to orbit and continuing diffusely behind eye (stripe bordered above and below by a blue line in life); a narrow brown streak (blue in life) on maxilla and a short distance posterior to it; a small blackish spot on each lateral-line scale (may be faint or absent posteriorly); a line of dark brown dashes basally in anal fin. Maximum size about 105 mm SL.

Description.—Dorsal rays VII–I,9, all rays branched, the last to base; anal rays II,8, all rays branched, the last to base; pectoral rays 14 (rarely 13 or 15); the upper two and lower two or three unbranched; pelvic rays I,5; principal caudal rays 17, the upper and lower unbranched; upper and lower procurrent caudal rays 7–8, the posterior two segmented; lateral-line scales 24; scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 5, the fourth and fifth deeply indented posteriorly in median line; circumpeduncular scales 12; gillrakers 5–6 (rarely 7)+15–16 (rarely 14 or 17), 1–2 upper and 0–1 lower as rudiments, the total count 19–23; pseudobranchial filaments increasing in number with size from 17 in 29 mm specimen to 29 in 102 mm specimen; branchiostegal rays 7; predorsal bones 3; vertebrae 10+14.

Body moderately deep, the depth 2.4–2.85 in SL, and compressed, the width 2.15–2.5 in depth; head length 2.35–2.5 in SL; dorsal profile of head straight except for rounded front of snout; snout length 4.15–4.65 in head; eye large, the orbit diameter 2.55–3.1 in head; interorbital space flat to slightly convex with median and lateral longitudinal ridges, the width 4.05–4.6 in head; caudal peduncle depth 2.35–2.7 in head; caudal peduncle length 1.7–2.0 in head.

Mouth large, the maxilla reaching to or posterior to a vertical at rear edge of pupil, the upper jaw length 1.9–2.1 in head; mouth oblique, forming an angle of about 35° to horizontal axis of head and body; posterior edge of maxilla slightly rounded to slightly concave, the corners rounded; supramaxilla not present.

Dentition, nostrils, pores, and scales essentially as described for *Apogon aureus.*

A single, poorly developed, flat, opercular spine at level of upper edge of pupil, the dorsal and ventral margins of the spine forming an angle of 90° or more at the tip; preopercular ridge smooth; posterior margin and most of ventral margin of preopercle serrate (28 serrae on 29 mm specimen and 94 on a 96 mm fish).

Origin of first dorsal fin above base of third lateral-line scale; first dorsal spine slender and short, about one-third length of second spine; second dorsal spine 3.45–4.4 in head; third or fourth dorsal spine longest, 1.8–2.1 in head; first dorsal soft ray longest, 1.45–1.6 in head; origin of anal fin below base of third dorsal soft ray; first anal spine very small, 3.25–3.85 in length of second anal spine; second anal spine 2.45–2.75 in head; first anal soft ray longest, 1.6–1.75 in head; caudal fin forked, the caudal concavity 3.5–4.15 in head, the fin length 2.95–3.1 in SL; third or fourth pectoral rays longest, 1.45–1.6 in head; pelvic fin tips reaching posterior to anus but not beyond origin of anal fin, the first soft ray longest, 1.55–1.75 in head.

Color of adults in alcohol light brown with a dark brown bar about three-fourths orbit diameter in width posteriorly on caudal peduncle, the upper and lower edges of bar not broader than central part; a dark brown stripe from front of snout, broadening as it passes to orbit, and continuing diffusely a short distance behind eye; a dark brown streak usually present on side of maxilla of adults which extends diagonally downward behind end of maxilla; tubular anterior nostril pale; a small dark brown spot on underside of each lateral-line scale, the spots progressively smaller and less pigmented posteriorly; edge of eye dark brown except ventrally; dorsal fins pale or slightly dusky anteriorly, particularly the first dorsal fin; anal fin pale, the leading edge sometimes dusky, with a narrow dark brown line of dashes at base which diverges outward from midbase to end in a streak on last ray; caudal fin usually with some dusky pigment proximally on upper and lower edges; paired fins pale except for a dusky lateral edge on pelvics; peritoneum pale; digestive tract black; gillrakers dusky. Some specimens largely silvery over lower opercle, subopercle, thorax and ventral part of abdomen.

Juveniles of about 30 mm SL are pale with a round diffuse dark brown spot midlaterally on posterior part of caudal peduncle about the size of pupil or slightly larger; the dark stripe on the side of the snout is only faintly developed. With growth the peduncle spot gradually expands dorsally and ventrally to form the bar typical of adults (this attained at a SL of about 75 to 80 mm); the stripe on the head becomes more darkly pigmented, and the dark spots along the lateral line develop and become progressively darker.

Color in life coppery with iridescence, becoming golden on side of body and postorbital part of head; peduncular spot of juveniles and bar of adults black; edges of blackish stripe on head bright blue, these margins often breaking into dashes or spots posterior to eye; occasional individuals with a few blue spots anteriorly on side of body; a bright blue line on side of maxilla and a short distance beyond; lower edge of eye orange; median fins pale salmon, more of this color on rays than membranes, the leading edges of dorsal and anal fins and proximal upper and lower edges of caudal fin slightly dusky; an orange line at base of anal fin (broader posteriorly), separated from an outer adjacent blue line by a row of blackish dashes, one per membrane; pectoral fins pale salmon; pelvic fins with pale yellowish membranes and light orange rays, a narrow dusky leading edge and orange submarginal band.

Remarks.—Apogon fleurieu shares many characters with *A. aureus*: essentially the same body and fin proportions (compare

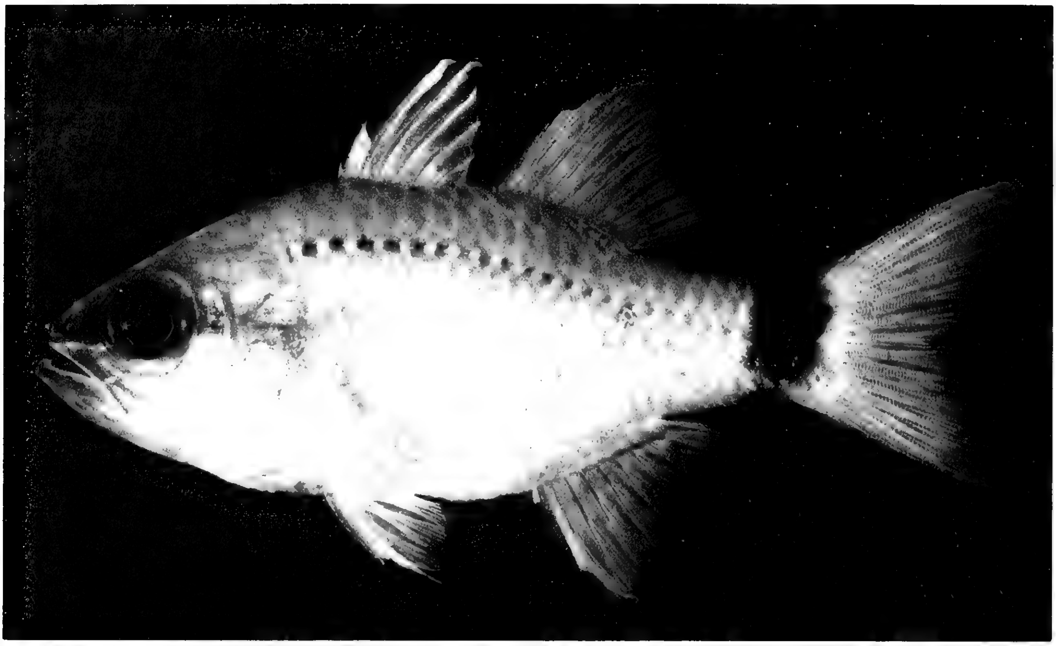


Fig. 5. Adult of *Apogon fleurieu,* BPBM 19811, 96 mm SL, Gulf of Aqaba, Red Sea.

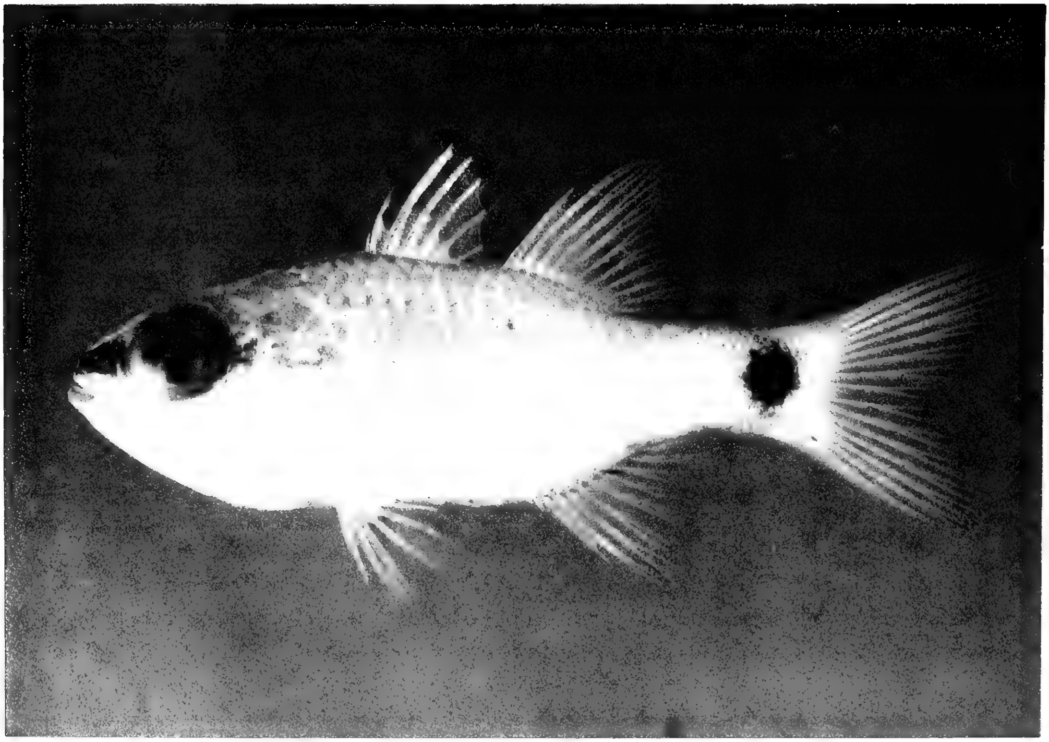


Fig. 6. Juvenile of *Apogon fleurieu,* BPBM 18258, 33 mm SL, Gulf of Aqaba, Red Sea.

Fig. 7. Underwater photograph of *Apogon fleurieu,* about 100 mm TL, Gulf of Aqaba, Red Sea.

Tables 2 and 3), meristic data except gillraker counts, relatively large size, and such color features as the coppery-golden ground color, black peduncular bar in adults, blue-edged blackish stripe on head; blue line on maxilla, row of blackish spots along lateral line, row of dark dashes basally in the anal fin, dusky leading edges of dorsal, anal, and pelvic fins, and dusky proximal upper and lower edges of the caudal fin.

The two species differ in gillraker counts (19–23 for *fleurieu,* compared to 22–27 for *aureus*) and the nature of the dark peduncular marking. Juveniles of *aureus* have a solid bar across the posterior part of the caudal peduncle (Fig. 3) in contrast to a diffuse dark spot for *fleurieu* (Fig. 6). The dark peduncular bar of *aureus* is sharply defined and usually expanded dorsally and ventrally to form a slight hourglass shape. The bar of adult *fleurieu* is not as well defined, is slightly broader laterally than that of *aureus,* and lacks the expanded upper and lower parts usually seen on *aureus.*

There appears to be a difference in the maximum size attained by these two cardinalfishes. *A. aureus* often exceeds 90 mm SL, the largest reported, 121 mm SL (RUSI 12345, from off Durban). Only 28 specimens of *fleurieu* of 423 examined exceed 90 mm SL, the largest, BPBM 31874, 102 mm SL, from the northern end of the Gulf of Aqaba. A specimen of 98 mm SL taken in the Persian Gulf was lost in shipment to the Bishop Museum, but a color photograph of it is on file at the Museum.

Two specimens of *A. fleurieu* from Hong Kong (SU 60820, 61–62 mm SL) and two from off Somalia (USNM 212415, both 63 mm SL) are fully mature females.

Apogon fleurieu is known from the Red Sea, coast of East Africa south to Durban, Seychelles, Persian Gulf, India, Sri Lanka, Andaman Sea (Similan Islands and off Burma), Ambon, southern Malaysia, Hong Kong, and Philippines. Gerald R. Allen sent us an underwater photograph of this species from Flores, Indonesia. As mentioned, all of the collection sites except the Seychelles are on continental shelves (if the islands of Indonesia and the Philippines may be regarded as on the Asian continental shelf), and the Seychelles are continental in origin.

Six lots of *A. fleurieu* were collected by trawling from the R/V *Anton Bruun,* three off western India (17°41′N–20°N, 70°–71°33′E) in 71–97 m, two off Somalia in 25–31 m, and one in the Andaman Sea at 9°54′N, 97°42′E in 73 m. The shallowest collection of the species was made in 0–7 m off Kovalam, Kerala, southwestern India by the senior author and William F. Smith-Vaniz.

The specimens of *A. fleurieu* from the Seychelles have a higher average number of gillrakers than other localities, and those from the Red Sea have slightly higher counts than other localities (Table 1). Seychelles specimens also attain larger size, in general, than those from other localities. All but five of the twenty-eight specimens which are longer than 90 mm SL were collected from these islands.

Although there are many localities where *Apogon fleurieu* and *A. aureus* seem not to coexist, they do overlap in such localities as East Africa, Seychelles, Sri Lanka, Indonesia, Philippines, and Hong Kong. Both species were collected together at one station in Sri Lanka (USNM 212411 and 212424).

The International Code of Zoological Nomenclature, 3rd Edition, 1985, Article 75, Neotypes, p. 157, (b), Circumstances admitted, states, "A neotype is to be designated only in connection with revisory work, but only in exceptional circumstances. . . ." Article 75, (b)(i), p. 157 states, "The expression 'revisory work' refers to a critical study of the nominal species-group taxon in question, regardless of the scope of the work in which it is published." Other statements of the "Code" not satisfied by the account of Gon (1987) are listed on p. 159, (d), Qualifying conditions, "A neotype is validly designated only when it is published with the following particulars:" (2) "data and description sufficient to ensure recognition of the specimen designated."

Material examined.—Red Sea: Gulf of Aqaba, BPBM 19811, 96 mm; BPBM 18258, 2: 28.5–33 mm; BPBM 31874, 102 mm; HUJ 11321, 62 mm; HUJ 11909, 2: 32.5–55.5 mm; HUJ 11912, 2: 32.5–34.5 mm; HUJ 11920, 2: 33–34 mm; HUJ 11922, 41: 29.5–69 mm; MNHN 1988-689, 2: 38.5–44 mm; NSMT-P.29514, 2: 38.5–43.5 mm; RUSI 3170, 9: 34.5–64.5 mm; RUSI 27672, 2: 37.5–44 mm; USNM 191657, 22: 49–87 mm; USNM 191704, 51: 30–50 mm; WAM P.29707-001, 2: 37–41 mm. Somalia: 11°14–18′N, 51°8′E, USNM 212415, 28: 61.5–82 mm; USNM 212416, 13: 59–82 mm. Kenya: Mombasa, BPBM 27315, 63 mm. Zanzibar: USNM 212405, 86 mm; USNM 212406, 81 mm; USNM 212407, 34: 23–29 mm. Mozambique: Inhaca, RUSI 1733, 9: 29–77 mm; RUSI 1835, 2: 79–83 mm; RUSI 3169, 2: 67–95.5 mm. Delagoa Bay, ANSP 97470, 2: 37–43 mm. Natal: Sodwana Bay, RUSI 9207, 15: 29–46 mm. Madagascar: Nossi Bé, USNM 212408, 2: 59–76 mm. Seychelles: Mahé, ANSP 153774, 91.5 mm; ANSP 153775, 23: 41–101 mm; RUSI 3175, 51 mm; USNM 212409, 75: 34–100 mm. Cosmoledo Group, Assumption Island, RUSI 3176, 44.5 mm. India: off Bombay, USNM 212418, 74 mm; USNM 212419, 3: 77–80.5 mm; USNM 212420, 9: 65.5–75 mm. Kerala, Kovalam, BPBM 27638, 5: 60.5–65.5 mm. Wadge Banks, USNM 212410, 79 mm. Sri Lanka: Trincomalee, USNM 212411-14, 15: 21–77 mm. Andaman Sea: off southern end of Burma, USNM 212421, 10: 52.5–67 mm. Indonesia: Ambon, BMNH 1855.3.24.41, 92 mm. Malaysia: Johore, SU 30409, 90.5 mm. Hong Kong: 22°18′N, 114°23′E, SU 60820, 3: 61–63.5 mm. Philippines: Jolo Island, USNM 171287, 10: 76–89 mm;

USNM 171289, 73 mm. Masbate, Cataingan Bay, USNM 212417, 9: 19–26 mm.

Apogon pselion, new species
Figs. 8, 9; Tables 1, 4

Holotype.—BPBM 21515, male, 36.2 mm, Red Sea, Gulf of Aqaba, Sinai Peninsula, El Himeira, coral knoll, 12 m, rotenone, J. E. Randall and O. Gon, 25 Apr 1977.

Paratypes.—TAU 9670, 26.5 mm, Red Sea, Gulf of Suez, Abu Zneiman, rotenone, L. Fishelson, 22 Sep 1967; TAU 9669, 2: 29.0–30.5 mm, Gulf of Aqaba, Eilat, rotenone, D. Popper, 22 Jan 1969; USNM 213381, 36.0 mm, Gulf of Aqaba, Sinai Peninsula, El Himeira, 0–18 m, rotenone, V. G. Springer et al., 16 Jul 1969; USNM 213382, 2: 33.5–35.5 mm, El Himeira, 8–16 m, V. G. Springer et al., 19 Jul 1969; USNM 213383, 7: 39.3–41.3 mm, Sinai Peninsula, east coast, Ras Burqa, 9–15.5 m, rotenone, V. G. Springer et al., 21 Jul 1969; USNM 213385, 38.0 mm, just north of Ras Burqa, to 11 m, rotenone, V. G. Springer et al., 23 Jul 1969; USNM 213387, 11: 20.6–36.8 mm, El Himeira, 21.5–27.5 m, V. G. Springer et al., 9 Sep 1969; CAS 60679, 2: 24.6–35.7 mm, NSMT-P.44623-24, 2: 24.5–35.1 mm, RUSI 27056, 2: 22.0–34.4 mm, WAM P.29386-001, 2: 25.2–35.0 mm—all with same data as USNM 213387; BPBM 13381, 32.7 mm, Gulf of Aqaba, Eilat, off marine biological laboratory, reef in 43 m, rotenone, J. E. Randall and D. Popper, 6 Jun 1972; BPBM 18261, 6: 23.2–36.9 mm, Sinai Peninsula, east coast, Coral Island, east side, 30 m, quinaldine, J. E. Randall and O. Gon, 24 Sep 1974; BPBM 31988, 6: 33.8–39.6 mm, MNHN 1977-827, 5: 32.5–37.5 mm—both lots with same data as holotype.

Diagnosis.—A species of the genus *Apogon,* subgenus *Ostorhinchus,* with dorsal rays VII–I,9; pectoral rays 13–14 (usually 14); lateral-line scales 24; median predorsal scales 4; gillrakers 19–22; preopercular ridge smooth, the posterior margin and rear half of ventral margin of preopercle serrate; body depth 2.8–3.4 in SL; interorbital space 4.55–5.4 in head; posterior nostril more than twice as large as anterior; four dusky golden yellow stripes on head separated by blue lines, the midlateral stripe passing from snout, through eye, and continuing along side of body as a brassy yellow stripe; a black bar encircling posterior caudal peduncle.

Description.—Dorsal rays VII–I,9, all rays branched, the last to base; anal rays II,8, all rays branched, the last to base; pectoral rays 14(13–14), the upper two and lower three unbranched; pelvic rays I,5; principal caudal rays 17, the upper and lower unbranched; upper and lower procurrent caudal rays 7, the posterior two segmented; lateral-line scales 24 (plus 3 scales posterior to end of hypural plate); scales above lateral line to origin of first dorsal fin 2; scales below lateral line to origin of anal fin 5½; median predorsal scales 4, the fourth scale deeply indented medially on the posterior edge and the third scale slightly indented posteriorly; circumpeduncular scales 12; gillrakers 6+15 (5–6+14–16), 2–3 upper and 0–1 lower as rudiments; pseudobranchial filaments 15 (10–16); branchiostegal rays 7; predorsal bones 3; vertebrae 10+14.

Body moderately elongate, the depth 2.95 (2.8–3.4) in SL, and compressed, the width 2.35 (1.9–2.5) in depth; head length 2.55 (2.45–2.6) in SL; dorsal profile of head straight except for rounded front of snout; snout length 3.85 (3.95–4.3) in head; eye large, the orbit diameter 2.8 (2.5–3.0) in head; interorbital space flat to slightly convex, the width 4.9 (4.55–5.4) in head; caudal peduncle about twice as long as deep, the least depth 2.6 (2.5–3.3) in head.

Mouth large, the maxilla reaching to or slightly posterior to a vertical through rear edge of pupil, the upper jaw length 1.95 (1.9–2.05) in head; mouth oblique, forming an angle of about 35° to horizontal axis of head and body; posterior edge of maxilla slightly concave; no supramaxilla present; lower jaw projecting, the tip dorsoventrally thickened;

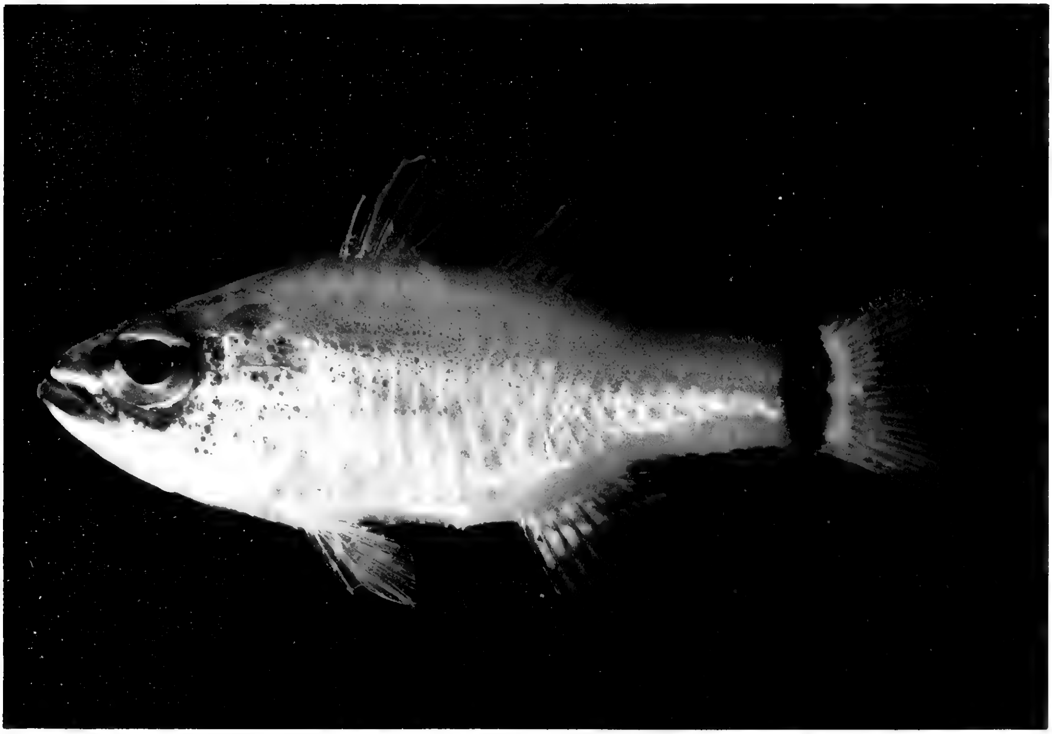


Fig. 8. Holotype of *Apogon pselion,* BPBM 21515, 36.2 mm SL, Gulf of Aqaba, Red Sea.

villiform teeth in a narrow band in jaws, with two rows at front of upper jaw (except for a gap at symphysis) and about five rows at side of jaw (teeth of inner rows on side of jaw very small); front of lower jaw with about three rows of teeth narrowing to one at side of jaw; a single irregular row of very small teeth forming a V on vomer; a single row of very small teeth on palatines; tongue broad at base tapering to lanceolate form with expanded rounded tip.

Anterior nostril a short membranous tube directly anterior to center of eye half the distance to front of snout; posterior nostril ovate without a raised rim, its largest diameter two or more times greater than diameter of anterior nostril, located dorsoposterior to anterior nostril closer to edge of orbit than anterior nostril; numerous small pores readily visible dorsally on head, scattered over surface of preopercle and along its anterior margin, on suborbital rim, and mandible.

A single, poorly developed, flat opercular spine, its tip forming an angle slightly greater than 90°; posterior margin of preopercle serrate (33 serrae on holotype), the serrae smaller on upper margin than the broadly rounded corner; lower margin of preopercle serrate about half distance from middle of rounded corner to end of free edge; preopercular ridge not serrate.

Lateral line conspicuous, very slightly arched anteriorly, then paralleling dorsal contour of body and ending midlaterally a short distance posterior to caudal-fin base (three pored scales posterior to end of hypural); scales weakly ctenoid; head naked except operculum and nape; no scales on fins except for a low sheath at extreme base of dorsal and anal fins and small scales on base of caudal fin which extend at most half distance to posterior margin.

Origin of first dorsal fin above base of third lateral-line scale; first dorsal spine slender and short, about one-fourth length of second spine, 11.9 (9.8–14.5) in head; third dorsal spine longest, 2.1 (1.9–2.15) in

Fig. 9. Underwater photograph of *Apogon pselion,* about 40 mm TL, Eilat, Gulf of Aqaba, Red Sea.

head; first dorsal soft ray longest, 1.6 (1.5–1.65) in head; origin of anal fin below base of second dorsal soft ray; first anal spine small, about one-third length of second anal spine, 8.35 (7.3–10.7) in head; second anal spine 3.0 (2.45–2.95) in head; first anal soft ray longest, 1.9 (1.7–1.9) in head; caudal fin forked, its length 3.2 (3.1–3.6) in SL, the caudal concavity 4.7 (4.1–4.9) in head; third and fourth pectoral rays longest, 1.55 (1.5–1.75) in head; first and second pelvic rays longest, 1.75 (1.65–1.85) in head.

Color of holotype in alcohol: pale with a black bar encircling posterior caudal peduncle and extending slightly onto caudal-fin base, this bar widest on side of peduncle (bar width about half orbit diameter); a very diffuse and faint dusky midlateral stripe on body; a narrow dusky stripe from front of upper lip to middle of front edge of orbit; a narrow dusky stripe from front of lower jaw to lower edge of eye and merging with broad dusky area on side of postorbital head; fins pale except for a dusky stripe near base of second dorsal and anal fins; peritoneum pale to slightly dusky; digestive tract black.

Color of holotype when fresh: body pale pinkish gray, overlaid with iridescent bluish silver ventrally, with a midlateral brassy yellow stripe faintly edged in pale iridescent blue, and a black bar encircling posterior caudal peduncle and adjacent caudal-fin base; head with four dusky golden yellow stripes separated by pale blue lines; median fins transparent bluish, the rays edged in pale salmon, the second dorsal and anal fins with a pale blue-edged dusky light orange band near base; paired fins transparent with pale salmon rays.

Remarks.—This species is given the specific name *pselion* from the Greek noun for bracelet or anklet, in reference to its most distinctive color marking, the ring of black around the posterior caudal peduncle.

Apogon pselion coexists in the northern Red Sea with the related *A. fleurieu.* The former is a much smaller species (the largest specimen 41.3 mm SL). At this size *A. fleurieu* has a diffuse dark spot posteriorly on the side of the peduncle whereas *A. pselion* at all sizes represented by our material has a solid black bar. *A. pselion* could be confused by its color pattern in preservative with the young of *A. aureus* (though the latter is not known from the Red Sea), which already has a completely formed black peduncular bar at sizes as small as 33 mm SL. Most specimens of these two species can be distinguished by gillraker counts (see Table 1).

Apogon pselion may be differentiated from both *aureus* and *fleurieu* by its more elongate body (the depth 2.8–3.4 in SL, compared to 2.25–2.85 for the other two species), narrower interorbital space (4.55–5.4 in head, compared to 4.05–4.6 for the other two species), shorter fins, in general (compare Tables 2–4), three instead of four lateral-line scales posterior to end of hypural plate, and life color. *A. aureus* and *A. fleurieu* lack the four yellow stripes on the head and lateral yellow stripe on the body, and *A. pselion* lacks the series of small dark spots along the lateral line.

Apogon pselion is at present known only from the Gulfs of Aqaba and Suez; it may be confined to the northern Red Sea where the water temperature is distinctly cooler than the central and southern part of the Sea. No specimens have been collected in rotenone stations from the Red Sea coasts of Sudan, Ethiopia, or Saudi Arabia. The type material has been obtained from reefs in the depth range of about 10 to 43 m.

Acknowledgments

We thank the following persons for the loan of specimens and/or pertinent information for the present study: Gerald R. Allen, M. Eric Anderson, Marie Louise Bauchot, David Catania, Martine Desoutter, Lev Fishelson, Anthony C. Gill, Daniel Golani, Ofer Gon, Menachem Goren, Douglass F. Hoese, Susan L. Jewett, Alwyne C. Wheeler, and Jeffrey T. Williams. Richard L. Pyle took radiographs for us. The manuscript was reviewed by Gerald R. Allen, William D. Anderson, Jr., Ofer Gon, and Victor G. Springer.

Literature Cited

Al-Baharna, W. S. 1986. Fishes of Bahrain. Directorate of Fisheries, Bahrain, 294 pp.

Allen, G. R., & R. C. Steene. 1979. The fishes of Christmas Island, Indian Ocean.—Australian National Parks and Wildlife Service, Special Publication no. 2:1–81.

———, & ———. 1987. Reef fishes of the Indian Ocean. T. F. H. Publications, Inc., Neptune City, New Jersey, 240 pp.

Barnard, K. H. 1927. A monograph of the marine fishes of South Africa.—Annals of the South African Museum XXI part 2:vii + 419–1065.

Bleeker, P. 1873–1876. Atlas Ichthyologique des Indes Orientales Néêrlandaises. Frêderic Muller, Amsterdam, volume 7, 126 pp.

———. 1874. Révision de espèces indo-archipélagiques du groupe des Apogonini.—Natuurkundige Verhandelingen der Hollandsche Maatschappij der Wetenschappen, Series 2, 3(1):1–82.

Botros, G. A. 1971. Fishes of the Red Sea.—Oceanography and Marine Biology, An Annual Review 9:221–348.

Boulenger, G. A. 1887. An account of the fishes obtained by Surgeon-Major A.S.G. Jayakar at Muscat, East Coast of Arabia.—Proceedings of the Zoological Society of London 43:653–667.

Burgess, W., & H. R. Axelrod. 1975. Pacific marine fishes. Book 6, Fishes of Melanesia. T. F. H. Publications, Inc., Neptune City, New Jersey, pp. 1383–1654.

———, & ———. 1976. Pacific marine fishes. Book 7, Fishes of the Great Barrier Reef. T. F. H. Publications, Inc., Neptune City, New Jersey, pp. 1655–1925.

Cuvier, G., & A. Valenciennes. 1829. Histoire Naturelle des Poissons. F. G. Levrault, Paris, volume 3, xxviii + 500 pp.

———, & ———. 1830. Histoire Naturelle des Poissons. F. G. Levrault, Paris, volume 6, xxiv + 559 pp.

Day, F. 1875–1878. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. William Dawson & Sons Ltd., London, volume 1, xx + 778 pp.

Dor, M. 1984. CLOFRES—Checklist of the fishes of the Red Sea. The Israel Academy of Sciences and Humanities, Jerusalem, xxii + 427 pp.

Fourmanoir, P. 1957. Poissons téléostéens de eaux malgaches du Canal de Mozambique.—Memoirés de l'Institut Scientifique de Madagascar, Serie F. Oceanographic 1:1–316.

———, & P. Laboute. 1976. Poissons de Nouvelle Caledonie et des Nouvelles Hébrides. Les Éditions du Pacifique, Papeete, 376 pp.

Fowler, H. W. 1918. A list of Philippine fishes.—Copeia 58:62–65.

———. 1927. Notes on the Philippine fishes in the collection of the Academy.—Proceedings of the Academy of Natural Sciences of Philadelphia 79:255–297.

———, & B. A. Bean. 1930. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the Families Amiidae, . . . and Serranidae, obtained by the United States Bureau of Fisheries Steamer "Albatross" . . . Philippine Islands and adjacent seas.—Bulletin of the United States National Museum 100 (10):ix + 1–334.

Fraser, T. H. 1972. Comparative osteology of the shallow water cardinalfishes [Perciformes: Apogonidae] with the reference to the systematics and evolution of the family.—Ichthyological Bulletin, J. L. B. Smith Institute of Ichthyology 24:v + 105.

Gloerfelt-Tarp, T., & P. J. Kailola. 1984. Trawled fishes of Southern Indonesia and Northwestern Australia.—Australian Development Assistance Bureau, Australia; Directorate General of Fisheries, Indonesia; German Agency for Technical Cooperation, Federal Republic of Germany, 406 pp.

Gon, O. 1987. Redescription of *Apogon* (*Ostorhinchus*) *fleurieu* (Lacepède, 1802) with notes on its synonymy.—Japanese Journal of Ichthyology 34(2):138–145.

Günther, A. 1859. Catalogue of the Acanthopterygian fishes in the collection of the British Museum. Taylor and Francis, London, volume 1, xxxi + 524 pp.

Hayashi, M., & H. Kishimoto. 1983. Fish faunas of Iriomote-Island, Ryukyu Islands III. Apogonidae (Apogoninae).—Scientific Reports of the Yokosuka City Museum 31:15–46.

Ida, H., & J. T. Moyer. 1974. Apogonid fishes of Miyake-jima and Ishigaki-jim, Japan, with description of a new species.—Japanese Journal of Ichthyology 21(3):113–128.

Klunzinger, C. B. 1870. Synopsis der Fische des Rothen Meeres. Part 1. Percoiden-Mugiloiden.—Verhandlungen der Kaiserlich-Königlichen zoologisch-botanischen Gesellschaft in Wien 20:669–834.

———. 1884. Die Fische des Rothen Meeres. I. Theil. Acanthopter. ver. Owen. E. Schweizerbart'sche, Stuttgart, ix + 133 pp.

Kotthaus, A. 1970. Fische de Indischen Ozeans. A. Systematischer Teil, VIII Percomorphi (2).—"Meteor" Forschungsergebnisse, Series D (Biology) 6:56–75.

Kuronuma, K., & Y. Abe. 1986. Fishes of the Arabian Gulf. Kuwait Institute for Scientific Research, Kuwait, xiii + 356 pp.

Lacepède, B. G. E. 1801. Histoire Naturelle de Poissons. Chez Plassen, Paris, volume 3, xxvii + 558 pp.

———. 1802. Histoire Naturelle de Poissons. Chez Plassan, Paris, volume 4, xliv + 728 pp.

Macleay, W. 1883. Contribution to a knowledge of the fishes of New Guinea.—Proceedings of the Linnean Society of New South Wales 7:224–250.

Masuda, H., C. Araga, & T. Yoshino. 1975. Coastal fishes of Southern Japan. Tokai University Press, Tokyo, 382 pp.

———, K. Amaoka, C. Araga, T. Uyeno, & T. Yoshino, eds. 1984. The fishes of the Japanese Archipelago. Tokai University Press, Tokyo, 2 volumes, English version, xxii + 437 pp., plate section, 370 pls.

Munro, I. S. R. 1955. The marine and fresh water fishes of Ceylon. Department of External Affairs, Canberra, xvi + 351 pp.

———. 1960. Handbook of Australian fishes, no. 35.—Fisheries Newsletter 19(10):141–144.

———. 1967. The fishes of New Guinea. Department of Agriculture, Stock and Fisheries, Port Moresby, New Guinea, xxxvii + 651 pp.

Nelson, J. S. 1984. Fishes of the world. John Wiley & Sons, New York, 2nd edition, xv + 523 pp.

Playfair, R. L., & A. C. L. G. Günther. 1867. The fishes of Zanzibar. John van Voorst, London, xiv + 153 pp.

Randall, J. E. 1983. Red Sea reef fishes. IMMEL Publishing Co., London, 192 pp.

Russell, B. C. 1983. Annotated checklist of the coral reef fishes in the Capricorn-Bunker Group, Great Barrier Reef, Australia.—Great Barrier Reef Marine Park Authority, Special Publication Series 1:1–184.

Sauvage, H. E. 1891. Histoire Naturelle des Poissons in Histoire Physique, Naturelle et Politique de Madagascar. l'Imprimerie Nationale, Paris, volume 16, 543 pp.

Schroeder, R. E. 1980. Philippine shore fishes of the Western Sulu Sea. Bureau of Fisheries and Aquatic Resources and National Media Production Center, Manila, xvi + 266 pp.

Shao, K. T., & J. P. Chen. 1986. Ten new records of cardinalfishes from Taiwan, with a synopsis of the Family Apogonidae.—Journal of the Taiwan Museum 39(2):61–104.

Shen, S. C. 1984. Coastal fishes of Taiwan. Shih-chieh Shen, private publisher, Taipei, 190 pp.

———, & C. Lam. 1977. A review of the cardinalfishes (Family Apogonidae) from Taiwan.—Acta Oceanographica Taiwanica Science Reports of the National Taiwan University 7:154–192.

Smith, J. L. B. 1949. The sea fishes of Southern Africa. Central News Agency Ltd., Cape Town, xvi + 550 pp.

———. 1961. Fishes of the family Apogonidae of the Western Indian Ocean and the Red Sea.—Ichthyological Bulletin, Department of Ichthyology, Rhodes University 22:374–418.

———, & M. M. Smith. 1963. The fishes of Seychelles. The Department of Ichthyology, Rhodes University, Grahamstown, 215 pp.

Smith, M. M., & P. C. Heemstra, eds. 1986. Smiths' sea fishes. Macmillan South Africa (Publishers) (Pty) Ltd., Johannesburg, xx + 1047 pp.

Springer, V. G. 1988. The Indo-Pacific blenniid fish genus *Ecsenius*.—Smithsonian Contributions in Zoology 465:iv + 134 pp.

Weber, M., & L. F. de Beaufort. 1929. The fishes of the Indo-Australian Archipelago. 5. Anacanthini, Allothriognathi . . . Percomorphi: Families: Kuhliidae . . . Centropomidae. E. J. Brill Ltd., Leiden, xiv + 458 pp.

Whitley, G. P. 1959. Ichthyological snippets.—The Australian Zoologist 12, part 4:310–323.

Woodland, D. J., & R. J. Slack-Smith. 1963. Fishes of Heron Island, Capricorn Group, Great Barrier Reef.—Department of Zoology, University of Queensland Papers 2(2):15–69.

(JER) Bishop Museum, Box 19000-A, Honolulu, Hawaii 96817-0916; (THF) Environmental Quality Laboratory, 1009 Tamiami Trail, Port Charlotte, Florida 33952; (EAL) Dept. Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 63–85

LIVING CASSIDULOIDS (ECHINODERMATA: ECHINOIDEA): A KEY AND ANNOTATED LIST

Rich Mooi

Abstract.—A key to the 30 known living species of cassiduloids is provided which includes abbreviated geographic and bathymetric data. All species are illustrated for the first time in a single work. An annotated list of genera and species includes basic taxonomic information, remarks upon systematic affinities, more detailed discussions of geographic and bathymetric ranges, and summaries of general biology and habitat preferences.

The order Cassiduloida (sensu Kier 1962) consists of some 800 species of irregular echinoids, most of which are known only as fossils. Kier (1962:1) characterized this order as comprising "all those 'irregular' echinoids having petals, phyllodes, and bourrelets (the floscelle)." However, this general description also applies to such forms as clypeasteroids, which have not only well-developed petaloids, but also what can be interpreted as floscelles consisting of interambulacral bourrelets and reduced phyllodes with buccal and large food groove podia (sensu Mooi 1986). This, along with great variation in the major features used to characterize the families within the order Cassiduloida (for example, the periproct varies in position from aboral and in a deep groove to submarginal), renders it difficult to unambiguously define the order Cassiduloida without using features common to other major irregular echinoid groups. Lack of unique unifying characters leads to suspicions that the group is not monophyletic. I am at present preparing a phylogenetic revision of the living cassiduloid species that should shed light on this problem. In spite of the possibility that the Cassiduloida as defined by Kier (1962) may not be a natural group, it remains convenient to refer to this assemblage as the "cassiduloids." For the purposes of this paper, this group includes all those shallow burrowing irregular echinoids with a relatively high test, short spines, a posteriorly placed periproct, and well-developed floscelle.

Although abundant as Mesozoic and Cenozoic fossils, the cassiduloids have dramatically decreased in number since the Eocene (Kier 1974, Suter 1988). Studies of the pattern of decline of the cassiduloids (Suter 1988) and the evolution of other major irregular echinoid groups (Mooi 1987) have made desirable a review of the distinguishing features of, and basic biological information on, the Recent taxa of the Cassiduloida. In his monograph of the echinoids, Mortensen (1948) listed 27 Recent species of cassiduloids, including the 5 species in the Neolampadidae which he thought constituted a separate family within the order. Since Mortensen's work, three new species of cassiduloids have been described (Krau 1954, Baker 1983, Mooi 1990), and additional morphological and biogeographic information has become available, particularly for the poorly known neolampadids (McKnight 1968). Kier (1962) never mentioned the Neolampadidae in his revision of the Cassiduloida and did not offer a reason for their exclusion. Although Philip (1963) raised the family Neolampadidae to subordinal rank (Neolampadina) within the Cassiduloida, only its familial standing is recognized here, pending phylogenetic revision of the living taxa in the order.

The most recent key to the cassiduloids is that of Mortensen (1948). In light of information accumulated over the past 40 years, a new, illustrated key to the living species of the group is needed. The key and annotated list include the neolampadids and the cassiduloid genus *Oligopodia,* which Kier (1962) also omitted from his revision. For the first time in a single work, all the known Recent species are figured. I have included brief comments on taxonomy, affinities, and geographic and bathymetric ranges as well as a summary of what has become known of the biology of some of the species since Mortensen (1948).

List of Recognized Taxa

- Phylum Echinodermata Bruguière, 1789
  - Subphylum Echinozoa Haeckel in Zittel, 1895
    - Class Echinoidea Leske, 1778
      - Subclass Euechinoïdea Bronn, 1860
        - Infraclass Acroechinoidea A. B. Smith, 1981
          - Cohort Irregularia Latreille, 1825
            - Superorder Microstomata A. B. Smith, 1984
              - Series Neognathostomata A. B. Smith, 1981
                - Order Cassiduloida Claus, 1880
                  - Family Echinolampadidae Gray, 1851
                    - Genus *Echinolampas* Gray, 1825
                      - *Echinolampas ovata* (Leske, 1778)
                      - *Echinolampas alexandri* de Loriol, 1876
                      - *Echinolampas chuni* (Döderlein, 1905)
                      - *Echinolampas crassa* (Bell, 1880)
                      - *Echinolampas depressa* Gray, 1851
                      - *Echinolampas keiensis* (Mortensen, 1948)
                      - *Echinolampas koreana* H. L. Clark, 1925
                      - *Echinolampas rangii* Desmoulins, 1837
                      - *Echinolampas sternopetala* A. Agassiz & H. L. Clark, 1907
                      - *Echinolampas sumatrana* (Döderlein, 1905)
                    - Genus *Conolampas* (A. Agassiz, 1883)
                      - *Conolampas sigsbei* (Agassiz, 1878)
                      - *Conolampas diomedea* Mortensen, 1948
                      - *Conolampas malayana* Mortensen, 1948
                      - *Conolampas murrayana* Mortensen, 1948
                  - Family Cassidulidae L. Agassiz & Desor, 1847
                    - Genus *Cassidulus* Lamarck, 1801
                      - *Cassidulus caribaearum* Lamarck, 1801
                      - *Cassidulus infidus* Mortensen, 1948
                      - *Cassidulus mitis* Krau, 1954
                      - *Cassidulus malayanus* (Mortensen, 1948)
                    - Genus *Eurhodia* Haime in d'Archiac & Haime, 1853
                      - *Eurhodia relicta* Mooi, 1990
                    - Genus *Oligopodia* Duncan, 1889
                      - *Oligopodia epigonus* (van Martens, 1865)

- Genus *Rhyncholampas* A. Agassiz, 1869
  - *Rhyncholampas pacificus* (A. Agassiz, 1863)
- Genus *Studeria* Duncan, 1891
  - *Studeria recens* (A. Agassiz, 1879)

Family Apatopygidae Kier, 1962

- Genus *Apatopygus* Hawkins, 1920
  - *Apatopygus recens* (Milne Edwards, 1863)
  - *Apatopygus occidentalis* H. L. Clark, 1938
- Genus *Porterpygus* Baker, 1983
  - *Porterpygus kieri* Baker, 1983

Family Neolampadidae Lambert, 1918

- Genus *Neolampas* A. Agassiz, 1869
  - *Neolampas rostellata* A. Agassiz, 1869
- Genus *Anochanus* Grube, 1868
  - *Anochanus sinensis* Grube, 1868
- Genus *Aphanopora* de Meijere, 1902
  - *Aphanopora echinobrissoides* de Meijere, 1902
- Genus *Nannolampas* Mortensen, 1948
  - *Nannolampas tenera* (de Meijere, 1902)
- Genus *Tropholampas* H. L. Clark, 1923
  - *Tropholampas loveni* (Studer, 1880)

Key to the Living Cassiduloids

The following key relies on morphology of the test and external appendages, particular aspects of which are illustrated in Figs. 1–5. The species themselves are illustrated at the end of the key, in Figs. 6–12 (see Annotated List). When a species is encountered within the key, an abbreviated description of its range is given in square brackets, followed by a statement of its known bathymetric range. Nomenclatural authorities and other taxonomic information can be found in the annotated list of species that follows the key. Anatomical terminology is that of Mooi (1989).

1\. Petaloids strongly developed (Figs. 6–11); respiratory podia with well-developed inner and outer pores; phyllodes conspicuous; bourrelets moderately to strongly developed 2

– Petaloids completely absent (Fig. 12); when present, aboral podia are single-pored, and not developed into respiratory podia; phyllodes inconspicuous, usually lacking inner series of phyllopores; bourrelets poorly developed or lacking 26

2\. Apical system monobasal, without separate genital plates (Fig. 1a); naked zone present medially on oral surface (except in *Studeria recens* [Fig. 10d]), although not always strongly developed (Figs. 6–10); anal sulcus absent, or typically (except in *Cassidulus malayanus* [Fig. 9c]) short and shallow (Figs. 6–10); buccal podia present; globiferous pedicellariae absent 3

– Apical system tetrabasal, with separate genital plates (Fig. 1b); naked zone absent (Fig. 11); anal sulcus long and very deep (Fig. 11); buccal podia absent; globiferous pedicellariae present 24

3\. Periproct just submarginal (Figs. 6–8); anal sulcus absent; three large, triangular plates along adoral edge of periproctal membrane (Fig. 2a);

ophicephalous pedicellariae with distal, closed oval ring of gripping teeth (Fig. 3a); many calcite spicules in stem of non-respiratory podia 4

– Periproct aboral or marginal (Figs. 9, 10); anal sulcus present, often weakly developed; more than four or five large plates in adoral part of periproctal membrane (Fig. 2b); ophicephalous pedicellariae with distal, U-shaped row of distal teeth (Fig. 3b); no spicules in stem of non-respiratory podia, but some spicules may occur in sucker tip of podium 17

4\. Test margin oval in outline with periproct on slight posterior projection, or rostrum (Figs. 6, 7); oral surface concave (Figs. 6, 7); peristome slightly displaced anteriorly; primary aboral spination relatively dense, average distance between spine tubercles less than 1.5 times primary spine tubercle diameter (*Echinolampas*) 5

– Test margin almost circular in outline, rostrum very short, or absent (Fig. 8); oral surface flat (Fig. 8); peristome central, or slightly displaced posteriorly; primary aboral spination relatively sparse, average distance between spine tubercles more than twice primary spine tubercle diameter (*Conolampas*) . 14

5\. Columns of respiratory podia in each petaloid very unequal in length, shorter column less than 60% length of longer in petaloid of ambulacra I and V (Figs. 6e, 7a, b, d) 6

– Columns of respiratory podia in each petaloid not very unequal in length, shorter column more than 65% length of longer in petaloid of ambulacra I and V (Figs. 6a–d, 7c, e) 9

6\. Peristome oval, bourrelets not projecting into peristome; peristome width more than 17% test width 7

– Peristome pentagonal, bourrelets slightly projecting into peristome; peristome width less than 15% test width 8

7\. Test width greater than 85% test length; ambitus broadly rounded in cross section; oral surface tumid [northeastern Central America, Yucatan, southeastern U.S., Greater and Lesser Antilles to northeastern South America; 30–310 m] ....
..... *Echinolampas depressa* (Fig. 6e)

– Test width less than 85% test length; ambitus relatively sharp in cross section; oral surface somewhat flattened [Japan; 150–500 m]
. *Echinolampas sternopetala* (Fig. 7d)

8\. Apical system more than 40% test length away from anterior edge of test; test almost conical; ambitus relatively sharp in cross section; oral surface flattened [Kepulauan Kai, southern Philippines; 245–400 m] ....
..... *Echinolampas keiensis* (Fig. 7a)

– Apical system less than 35% test length away from anterior edge of test; test smoothly arched in side view; ambitus broadly rounded in cross section; oral surface tumid [Korean Strait; 73 m] ....
..... *Echinolampas koreana* (Fig. 7b)

9\. Petaloids wide, eight or more primary spine tubercles in row across interporiferous zone half-way down petaloid of ambulacrum V; peristome pentagonal, bourrelets slightly projecting into peristome 10

– Petaloids narrow, fewer than eight primary spine tubercles in row across interporiferous zone half-way down petaloid of ambulacrum V; peristome oval, bourrelets not projecting into peristome 12

10. Test smoothly arched antero-posteriorly; ambitus broadly rounded in cross section; oral surface tumid; tuberculation of aboral surface fine, more than 100 primary spine tubercles in 25 mm²; outer pore of each respiratory podial pore pair circular or subcircular [Red Sea, northern Indian Ocean to western Australia; 9–75 m] .... *Echinolampas ovata* (Fig. 6a)
- Test with relatively sharp ambitus; oral surface somewhat flattened; tuberculation of aboral surface coarse, fewer than 100 primary spine tubercules in 25 mm²; outer pore of each respiratory podial pore pair strongly elongate 11

11. Test high, height greater than 50% test length; tuberculation of aboral surface very coarse, fewer than 50 primary spine tubercules in 25 mm² [South Africa; 25–500 m] . ... *Echinolampas crassa* (Fig. 6d)
- Test low, height less than 50% test length; tuberculation of aboral surface not very coarse, more than 70 primary spine tubercles in 25 mm² [west coast of Africa, Cape Verde Islands; shallow to 1670 m] .... *Echinolampas rangii* (Fig. 7c)

12. Apical system almost central, more than 45% test length from anterior edge of test; width of periproct less than 15% test width; more than five primary spine tubercles in row across interporiferous zone halfway down petaloid of ambulacrum V [Sumatra; 371 m] .... *Echinolampas sumatrana* (Fig. 7e)
- Apical system slightly anterior, less than 45% test length from anterior edge of test; width of periproct more than 16% test width; five or fewer primary spine tubercles in row across interporiferous zone half-way down petaloid of ambulacrum V 13

13. Test relatively wide, width greater than 85% test length; phyllodes widened, interrupting taper of ambulacra as they approach peristome [Red Sea, Indian Ocean, Malaysia; 8–365 m] .... *Echinolampas alexandri* (Fig. 6b)
- Test relatively narrow, width less than 85% test length; phyllodes narrow, ambulacra tapering smoothly as they approach peristome [Sumatra; 371 m] .... *Echinolampas chuni* (Fig. 6c)

14. Spine tubercles on oral surface sparsely distributed, fewer than seven in 25 mm² in interambulacrum 5 next to peristome; outer pore of each respiratory pore pair round [West Indies; 120–800 m] .... *Conolampas sigsbei* (Fig. 8a)
- Spine tubercles on oral surface relatively densely distributed, 10 or more in 25 mm² in interambulacrum 5 next to peristome; outer pore of each respiratory pore pair elongate 15

15. Peristome approximately central; periproct approximately half its own length away from ambitus; interporiferous zone of petaloids relatively wide, more than twice as wide as single column of respiratory podia as measured at a point half-way down anterior petaloid [Maldives; 230 m] .... *Conolampas murrayana* (Fig. 8d)
- Peristome slightly posterior; periproct almost as far from ambitus as it is long; interporiferous zone of petaloids relatively narrow, less than twice as wide as a single column of respiratory podia as measured at a point half-way down anterior petaloid 16

16. Longest column of respiratory podia in each petaloid reaches ambitus when viewed from above

[Philippines; 265 m] .... *Conolampas diomedeae* (Fig. 8b)

– Longest column of respiratory podia in each petaloid ends well short of ambitus when viewed from above [eastern Indonesia, southern Philippines; 245–400 m] .... *Conolampas malayana* (Fig. 8c)

17\. Peristome longer than wide 18

– Peristome circular, or wider than long 19

18\. Periproct slightly longer than wide [Indian Ocean, Malaysia; 35–140 m] ... *Oligopodia epigonus* (Fig. 10b)

– Periproct wider than long [northern South America; 57–112 m] . ... *Eurhodia relicta* (Fig. 10a)

19\. Naked zone absent from medial area of oral surface; three gonopores; columns of respiratory podia in each petaloid equal in length [Arafura Sea; 236 m] ....*Studeria recens* (Fig. 10d)

– Large naked zone in medial area of oral surface; four gonopores; columns of respiratory podia in each petaloid unequal in length, with columns Ia, IIb, IIIb, IVa, and Vb the shortest of each pair 20

20\. Large forms, test of adults over 40 mm in length; more than 70 respiratory podia in anterior petaloid of adults; more than 20 podial pores in anterior phyllode [Gulf of California to west coast of Panama, Galapagos; 2–130 m] .... *Rhyncholampas pacificus* (Fig. 10c)

– Relatively small forms, test of adults less than 30 mm in length; fewer than 60 pore pairs in anterior petaloid of adults; fewer than 15 podial pores in anterior phyllode (*Cassidulus*) 21

21\. Periproct longer than wide, located aborally, about half the distance from the apical system to the posterior edge; anal sulcus long, narrow, without conspicuous hood over periproct [Indonesia; 250–290 m] ...*Cassidulus malayanus* (Fig. 9c)

– Periproct round, or wider than long, located aborally, considerably more than half the distance from the apical system to the posterior edge; anal sulcus short, wide, with small but distinct hood over periproct 22

22\. Test height greater than 50% test length; periproct subcircular; fewer than 45 respiratory podia in anterior petaloid of adults [East coast of South America?; shallow water, precise locality and depth data unavailable] *Cassidulus infidus* (Fig. 9b)

– Test height less than 50% test length; periproct distinctly wider than long; more than 45 respiratory podia in anterior petaloid of adults 23

23\. Apical system less than 40% test length from anterior edge; test relatively wide, more than 80% test length [Belize, Bahamas to Barbados; very shallow, 2–10 m] ... . *Cassidulus caribaearum* (Fig. 9a)

– Apical system approximately 40% test length from anterior edge; test relatively narrow, less than 80% test length [Sepetiba Bay, Brazil; shallow water, precise depth data unavailable] .... *Cassidulus mitis* (Fig. 9d)

24\. Three gonopores; petaloids slightly reduced, fewer than 16 pore pairs in ambulacrum III of large adults; peristome roughly pentagonal [Three Kings Islands, New Zealand; 90–300 m] .... *Porterpygus kieri* (Fig. 11c)

– Four gonopores; at least 17 pore pairs in ambulacrum III of large adults; peristome transversely oval, or roughly triangular (*Apatopygus*) 25

25\. Test large, adults commonly reaching 40 mm in length; more than 20 hydropores in madreporic plate; valves of globiferous pedicellariae with short blade and a single pair of long, distal, fang-like teeth (Fig. 4a) [New Zealand; 5–145 m] . *Apatopygus recens* (Fig. 11a)

– Test small, adults usually less than 20 mm in length; fewer than 15 hydropores in madreporic plate; valves of globiferous pedicellariae with long, narrow blade and two pairs of long, distal, fang-like teeth (Fig. 4b) [southern and southwestern Australia; 17–40 m] .... *Apatopygus occidentalis* (Fig. 11b)

26. Periproct on ambitus, or slightly submarginal, not in deep anal sulcus 27

– Periproct aboral, in deep anal sulcus 29

27. Apical system sunken to form aboral "marsupium" in females; podial pores entirely absent from aboral ambulacra; four gonopores [South Africa; 135–350 m] .... *Tropholampas loveni* (Fig. 12e)

– Apical system not sunken in females; podial pores present in aboral ambulacra; two or three gonopores (four in rare individuals) .. 28

28. Apical system monobasal, without separate genital plates; typically three gonopores (rarely four, never two); valves of ophicephalous pedicellariae lacking thorns on proximal "handle" (Fig. 5a) [West Indies, Mediterranean; 145–1260 m] ..... *Neolampas rostellata* (Fig. 12a)

– Apical system tetrabasal, with separate genital plates; two gonopores; valves of ophicephalous pedicellariae with prominent thorns on proximal part of "handle" on largest valve (Fig. 5b) [East Indies, Timor Sea; 390 m] .... *Nannolampas tenera* (Fig. 12d)

29. Apical system sunken to form aboral "marsupium" [China Sea; depth unknown] .... *Anochanus sinensis* (Fig. 12b)

– Apical system not sunken [East Indies, northern and northeastern Australia; 350–710 m] .... *Aphanopora echinobrissoides* (Fig. 12c)

Annotated List of Cassiduloid Genera and Species

This list of genera is arranged by family according to Kier & Lawson (1978), which is in turn largely based on Kier (1962). I depart from their arrangement only in not recognizing the family Pliolampadidae Kier, 1962, pending phylogenetic revision of that group to resolve systematic problems that Kier (1962) himself acknowledged. As a result, *Eurhodia* (which Kier placed in the Pliolampadidae) is here placed in the Cassidulidae, following Mooi (1990). *Studeria* is also provisionally recognized as a cassidulid. *Oligopodia,* which Kier & Lawson (1978:125) listed among the "doubtful nominal genera," is here considered to be a cassidulid as well, as its similarity to some members of the genus *Eurhodia* suggests. Species described after 1948 are placed in the genera and families to which they were assigned by the original authors. Generic synonymies can be found in Kier (1962), and complete species descriptions and synonymies in Mortensen (1948), Krau (1954), Baker (1983), and Mooi (1990). The type species for each genus is indicated by an asterisk (*). Within families, genera are listed alphabetically after the type genus, and species are listed alphabetically within genera. Illustrations of these taxa (Figs. 6–12) follow this same arrangement.

Order Cassiduloida Claus, 1880

Family Echinolampadidae Gray, 1851

Echinolampas Gray, 1825

Echinolampas ovata (Leske, 1778)*

Fig. 6a

Geographic range.—A widespread species occurring in the Red Sea and the tropical

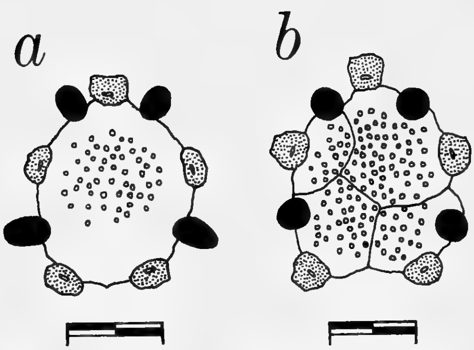


Fig. 1. Apical systems of cassiduloids: a, Monobasal system of *Cassidulus caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands]; b, Tetrabasal system of *Apatopygus recens* (Milne Edwards, 1863) [USNM E16325]. Hydropores represented by open circles, gonopores in solid black, ocular plates shaded, genital plates unshaded, anterior towards top of page. Scale bar is 1 mm long.

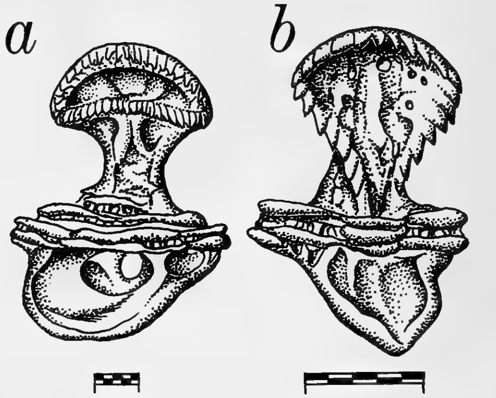


Fig. 3. Valves from ophicephalous pedicellariae of echinolampadids and cassidulids: a, *Conolampas sigsbei* (A. Agassiz, 1878) [USNM E12941] showing closed oval of distal teeth; b, *Cassidulus caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands] showing U-shaped, open row of distal teeth. Scale bars are 50 μm long.

Indian Ocean eastward to the northwestern coast of Australia.

Bathymetric range.—9 to 75 m (Mortensen 1948).

Remarks.—Several attempts have been made to subdivide the genus *Echinolampas* into separate genera and subgenera (Mortensen 1948). None of these schemes have become universally accepted, and Kier (1962:107) finally decided "that all these sections and subgenera are based on characters too variable to be of generic distinction." In spite of Kier's (1962) attempt to revive the name *Echinolampas oviformis* (Gmelin, 1789) for *Echinolampas ovata,* recent authors (Clark & Rowe 1971, Dollfus & Roman 1981) have argued convincingly for the retention of Leske's (1778) old name. This species apparently can be found in the littoral zone of the Red Sea (Dollfus & Roman 1981). This is supported by observations of this species in the intertidal, on fine carbonate sand without mud at Ashmore Reef, N. W. Australia (Lyle Vail, pers. comm.). At this locality, *E. ovata* also appears to have a diurnal activity cycle, "burrowing through the sand with about half of their test exposed" at night, but remaining more deeply burrowed during the day (Lyle Vail, pers. comm.). McNamara & Philip (1980) speculated that this species lives slightly inclined, with the posterior deeper in the substrate, buried in the sand up to the level of the petaloids.

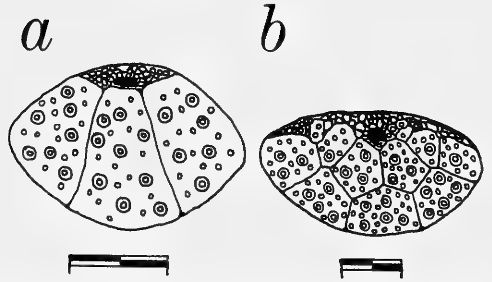


Fig. 2. Periproctal plate patterns of echinolampadids and cassidulids: a, *Echinolampas depressa* Gray, 1851 [USNM E12929]; b, *Cassidulus caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands]. Periproct in solid black, primary spine tubercles represented by two concentric circles, miliary spine tubercles by single open circle, aboral is towards top of page. Scale bars are 1 mm long.

Echinolampas alexandri de Loriol, 1876
Fig. 6b

Geographic range.—The Red Sea and throughout the Indian Ocean and Malaysia.

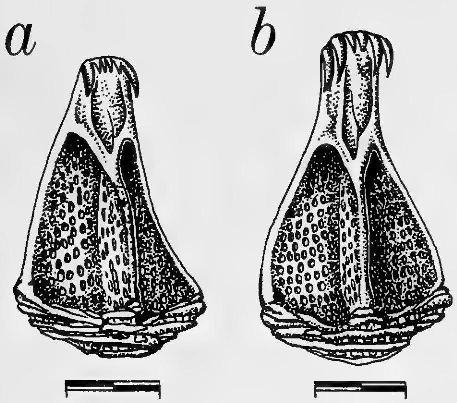


Fig. 4. Valves from globiferous pedicellariae of apatopygids: a, *Apatopygus recens* (Milne Edwards, 1863) [USNM E11089] showing single pair of fang-like teeth; b, *Apatopygus occidentalis* H. L. Clark, 1938 [after Baker 1983] showing two pairs of fang-like teeth. Scale bars are 100 μm long.

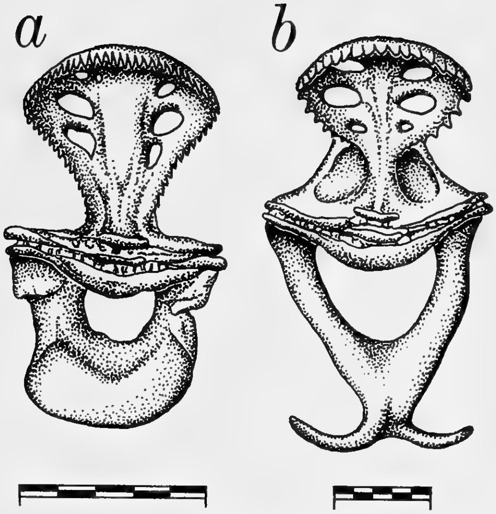


Fig. 5. Valves from ophicephalous pedicellariae of neolampadids: a, *Neolampas rostellata* A. Agassiz, 1869 [USNM E20529], illustrating absence of thorns on "handle"; b, *Nannolampas tenera* (de Meijere, 1902) [after Mortensen 1948] showing presence of thorns on "handle." Scale bars are 50 μm long.

Bathymetric range.—8 to 365 m.

Remarks.—Mortensen (1948) reported two subspecies (*E. alexandri sibogae* and *E. alexandri forcipulata*) to which Dollfus & Roman (1981) added a third (*E. alexandri arctambulacrum*). Mortensen (1948) felt that *E. ovata* and *E. alexandri* were very distinct, but because of variation in both species, Dollfus & Roman (1981) suggested that there is considerable overlap in morphology. Although more material from all parts of their ranges will be necessary before a complete comparison can be made, based on differences in petaloid width and peristome shape (see key, above), it would appear that *E. ovata* and *E. alexandri* are good species.

Echinolampas chuni (Döderlein, 1905)
Fig. 6c

Geographic range.—Known only from two denuded specimens from Sumatra (Döderlein 1906).

Bathymetric range.—From a single "Valdivia" station at 371 m.

Remarks.—No new information has come to light since Döderlein's (1906) and Mortensen's (1948) descriptions. Since the only known specimens were dead when collected, nothing is known of the biology of this species.

Echinolampas crassa (Bell, 1880)
Fig. 6d

Geographic range.—Known only from the South African coast.

Bathymetric range.—Mortensen (1948) says 25 to 500 m, but Thum & Allen (1975) record it from as shallow as 12 m.

Remarks.—The ecology of this species is amongst the best known of all cassiduloids. Thum and Allen (1975:362) reported that this echinoid prefers the ripple slopes of ripple beds composed of biogenic substrates (75–95% calcium carbonate), and that it is "an indirect deposit feeder and habitually burrows during feeding," being frequently overlain by 30 to 50 mm of substrate. They also estimated a growth rate of approximately 5 mm of test length per year. Their largest specimen was about 125 mm in length, suggesting (p. 373) "that this lamp urchin must be rather long-lived." Thum &

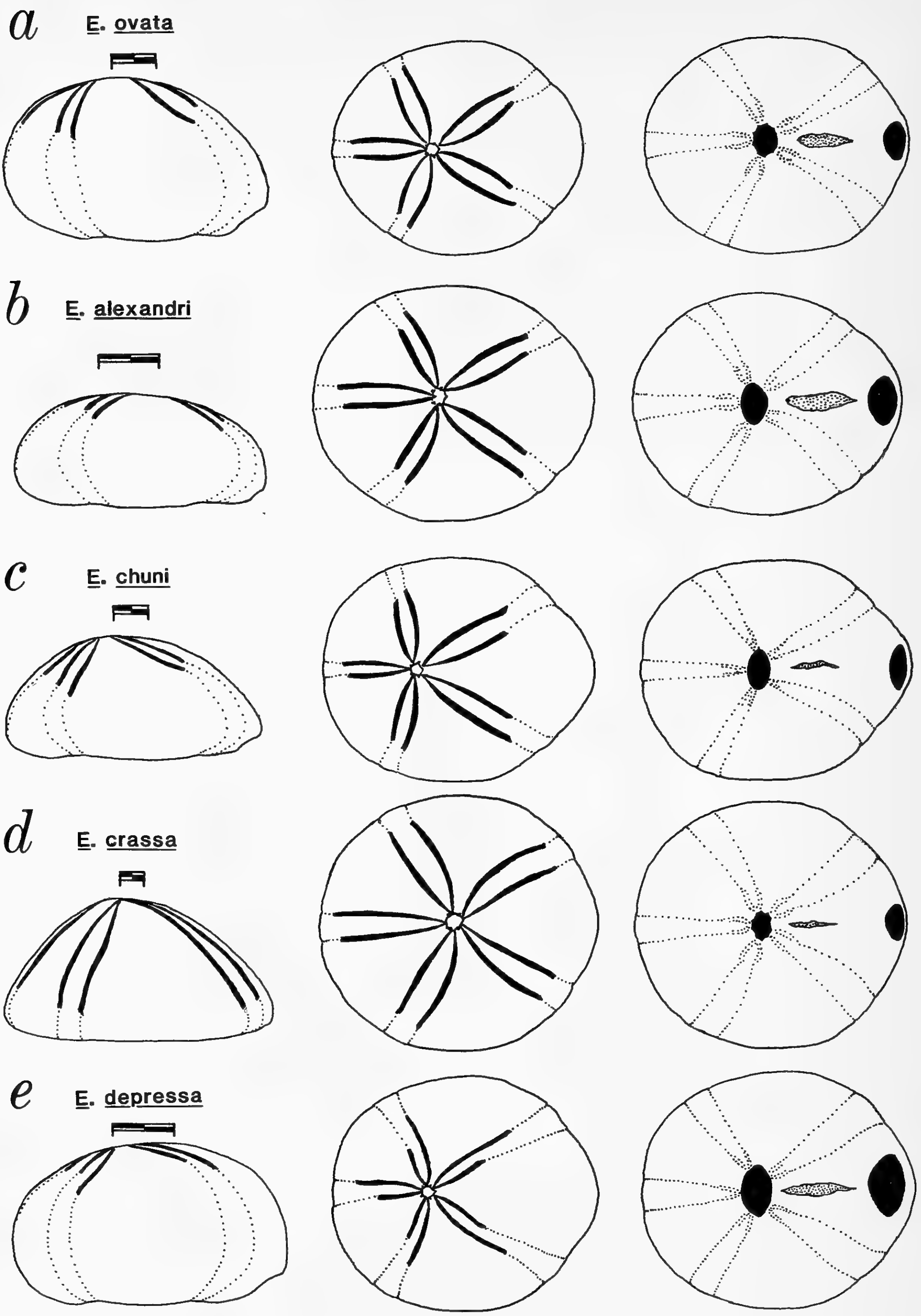


Fig. 6. Family Echinolampadidae, genus *Echinolampas*: a, *E. ovata* (Leske, 1778) [after Mortensen 1948]; b, *E. alexandri* de Loriol, 1876 [after Mortensen 1948]; c, *E. chuni* (Döderlein, 1905) [after Döderlein 1906]; d, *E. crassa* (Bell, 1880) [after Mortensen 1948]; e, *E. depressa* Gray, 1851 [Florida Department of Natural Resources I3562]. From left to right for each species: lateral view, aboral view, oral view. Anterior end is to the left. Petaloids, peristomes, and periprocts in solid black, naked zone stippled. All scale bars are 10 mm long.

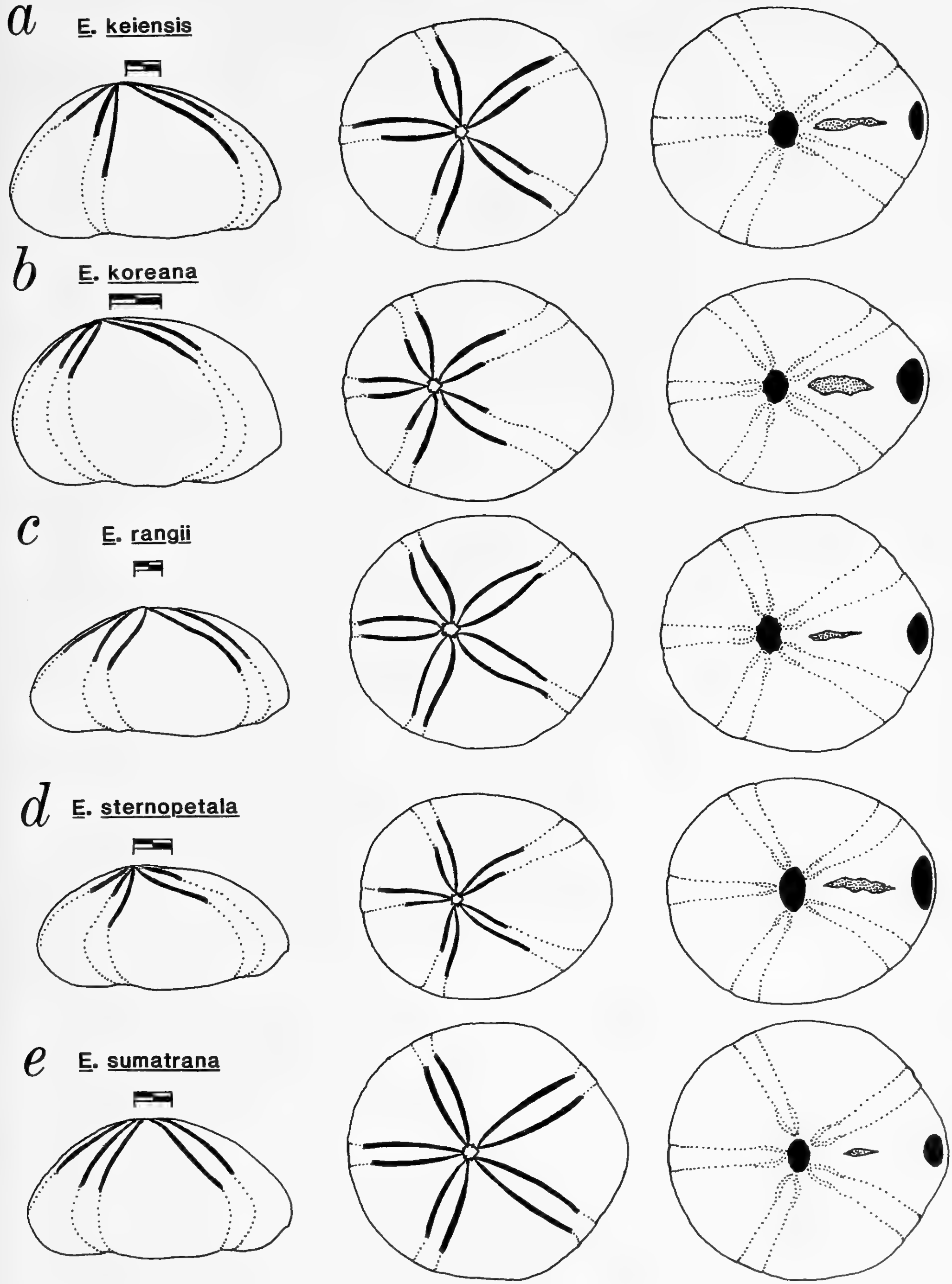


Fig. 7. Family Echinolampadidae, genus *Echinolampas* (cont'd): a, *E. keiensis* (Mortensen, 1948) [after Mortensen 1948]; b, *E. koreana* H. L. Clark, 1925 [after Clark 1925 and Mortensen 1948]; c, *E. rangii* Desmoulins, 1837 [after Agassiz 1872]; d, *E. sternopetala* A. Agassiz & H. L. Clark, 1907 [after Mortensen 1948]; e, *E. sumatrana* (Döderlein, 1905) [after Döderlein 1906]. Conventions as in Fig. 6. All scale bars are 10 mm long.

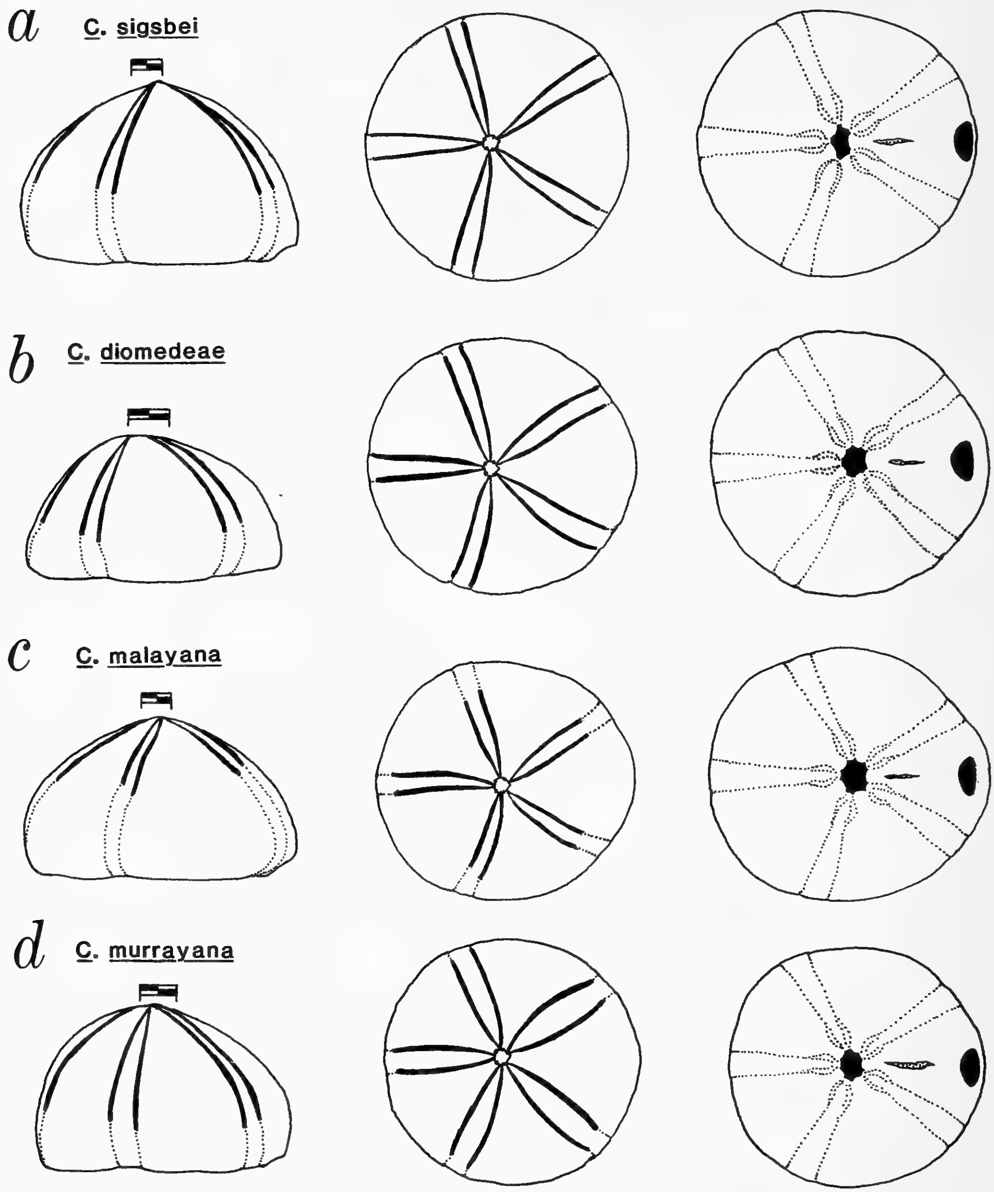


Fig. 8. Family Echinolampadidae (cont'd), genus *Conolampas*: a, *C. sigsbei* (A. Agassiz, 1878) [after Kier 1962]; b, *C. diomedeae* Mortensen, 1948 [after Mortensen 1948]; c, *C. malayana* Mortensen, 1948 [after Mortensen 1948]; d, *C. murrayana* Mortensen, 1948 [after Mortensen 1948]. Conventions as in Fig. 6. All scale bars are 10 mm long.

Allen (1976:27) later analyzed the breeding behavior of *E. crassa,* discovering a "remarkable synchrony of gonad tissue mass both within and between sexes." They also compared ambient substrate and gut content particle dimensions, and suggested that larger particles are excluded from the diet because of the fixed mouth size, and smaller ones because the animal has difficulty manipulating them (Thum & Allen 1976). These echinoids feed using the oral podia to lift particles to the peristome and can also

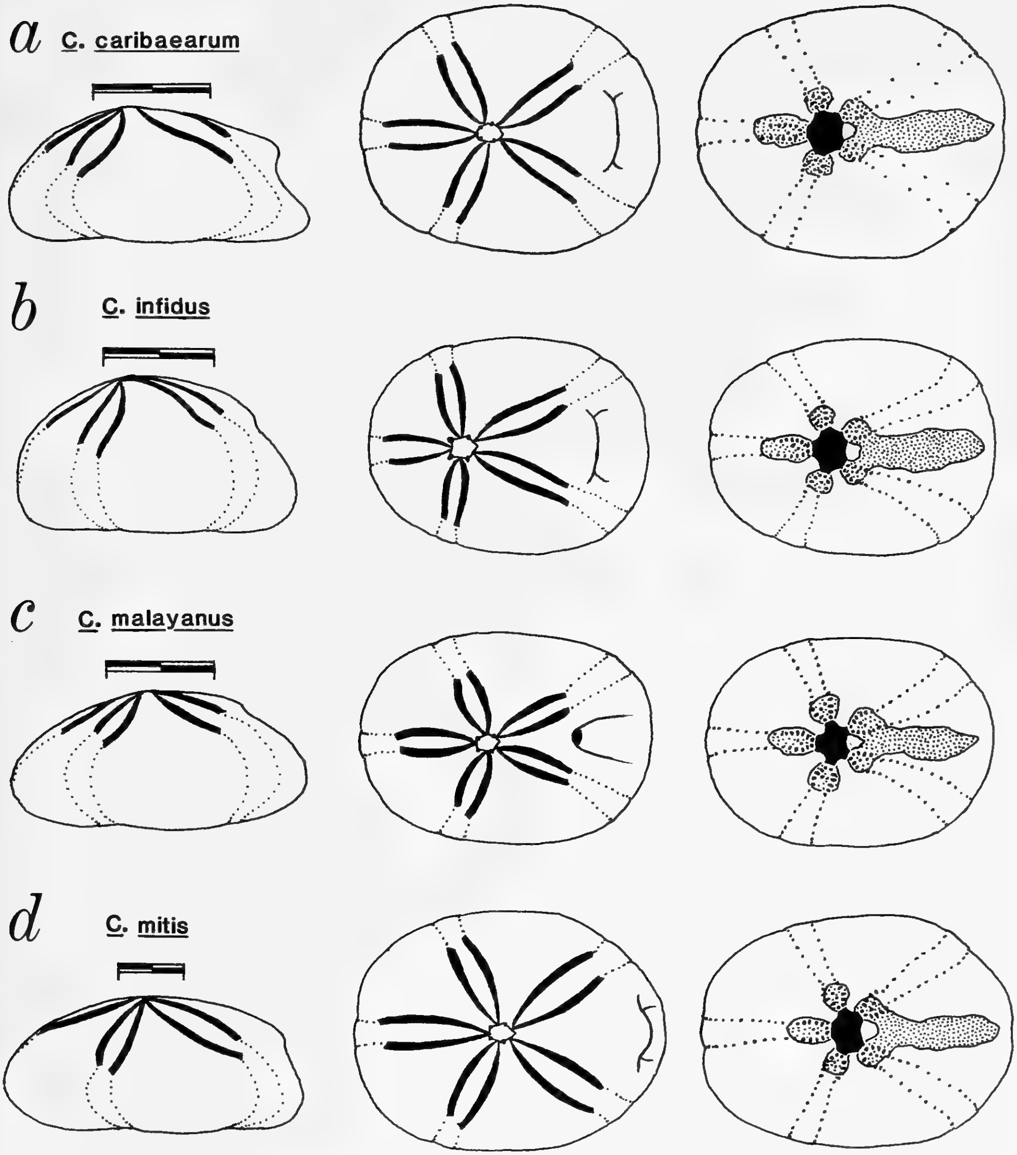


Fig. 9. Cassidulidae, genus *Cassidulus*: a, *C. caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands]; b, *C. infidus* Mortensen, 1948 [after Mortensen 1948]; c, *C. mitis* Krau, 1954 [after Krau 1954]; d, *C. malayanus* (Mortensen, 1948) [after Mortensen 1948]. Conventions as in Fig. 6. All scale bars are 10 mm long.

use the circum-oral bourrelet spines to elevate particles into the mouth (Thum & Allen 1976). Cram (1971) described the early life history and larval morphology of *E. crassa,* reporting that metamorphosis occurred at about 40 days after fertilization.

Echinolampas depressa Gray, 1851
Figs. 2a, 6e

Geographic range.—From eastern Central America as far north as the north coast of the Yucatan, the southeastern U.S., both coasts of Florida, the Greater and Lesser

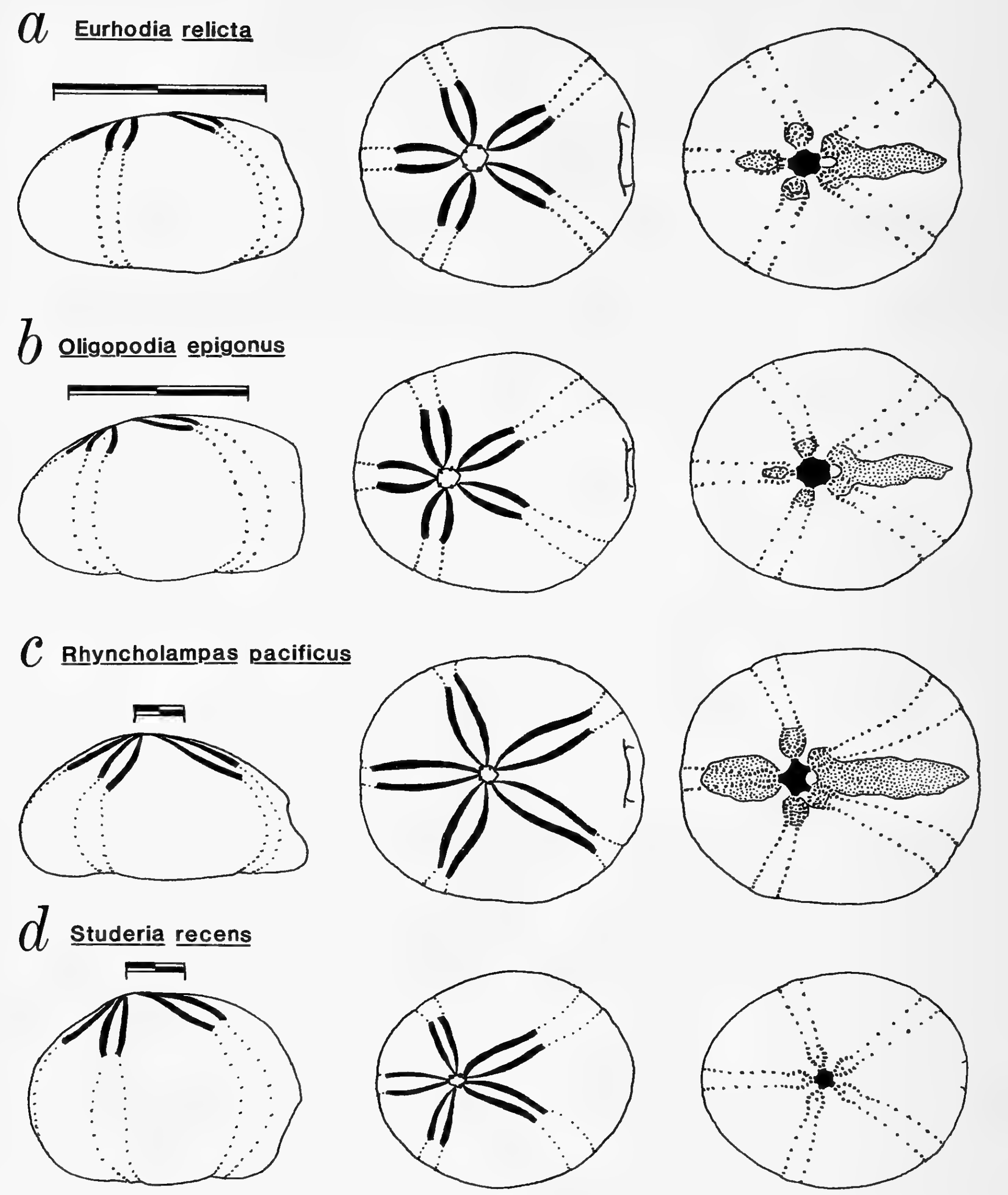


Fig. 10. Cassidulidae (cont'd): a, *Eurhodia relicta* Mooi, 1990 [Holotype, USNM E20480]; b, male *Oligopodia epigonus* (van Martens, 1865) [USNM E35684]; c, *Rhyncholampas pacificus* (A. Agassiz, 1863) [after Kier 1962]; d, *Studeria recens* (A. Agassiz, 1879) [after Agassiz 1881]. Conventions as in Fig. 6. All scale bars are 10 mm long.

Antilles south to northeastern South America as far east as French Guyana.

Bathymetric range.—30 to 310 m (Serafy 1979).

Remarks.—Märkel (1978) described the Aristotle's lantern from juveniles of this species. The lantern disappears as the animal approaches 5 mm in length and does

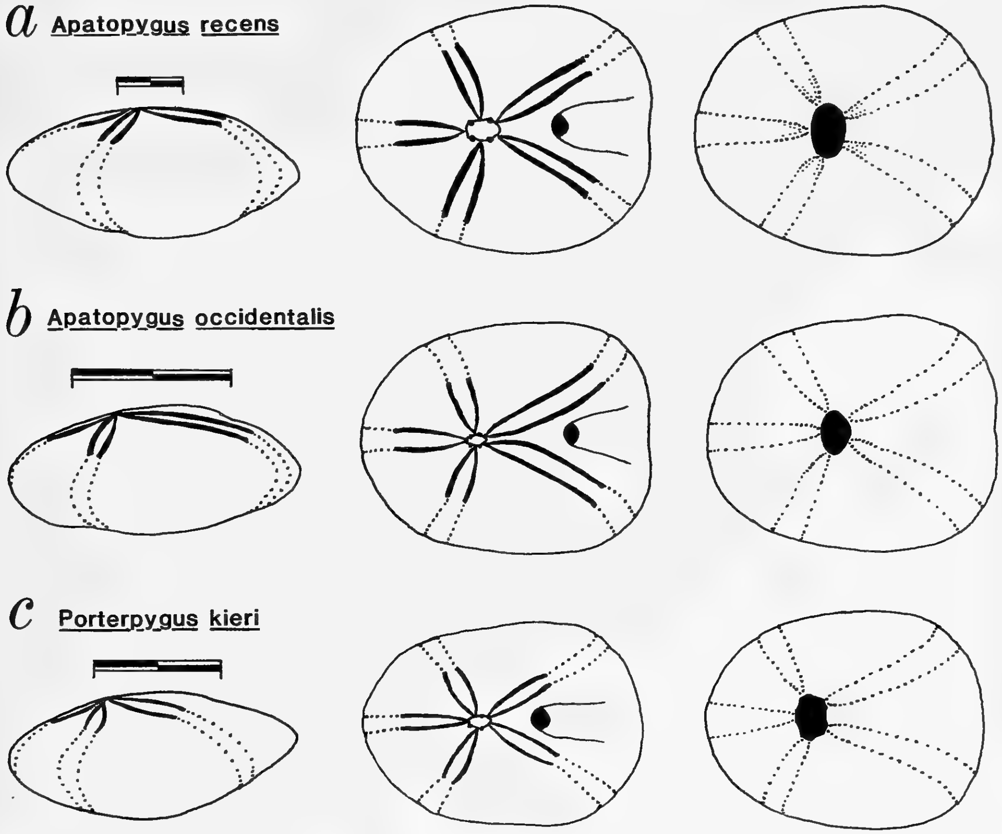


Fig. 11. Apatopygidae: a, *Apatopygus recens* (Milne Edwards, 1863) [USNM E16325]; b, *Apatopygus occidentalis* H. L. Clark, 1938 [after Baker 1983]; c, *Porterpygus kieri* Baker, 1983 [after Baker 1983]. Conventions as in Fig. 6. All scale bars are 10 mm long.

not appear to function at all in the feeding of the echinoid. Serafy (1979) documented the occurrence of this species in the Gulf of Mexico on carbonate sands consisting largely of calcareous algal fragments. In spite of the apparent frequency with which this species is collected, little else is known of its ecology.

Echinolampas keiensis (Mortensen, 1948)
Fig. 7a

Geographic range.—Known only from Kepulauan Kai (Kei Islands) and from off Zamboanga in the southern Philippines (Mortensen 1948).

Bathymetric range.—245 to 400 m (Mortensen 1948).

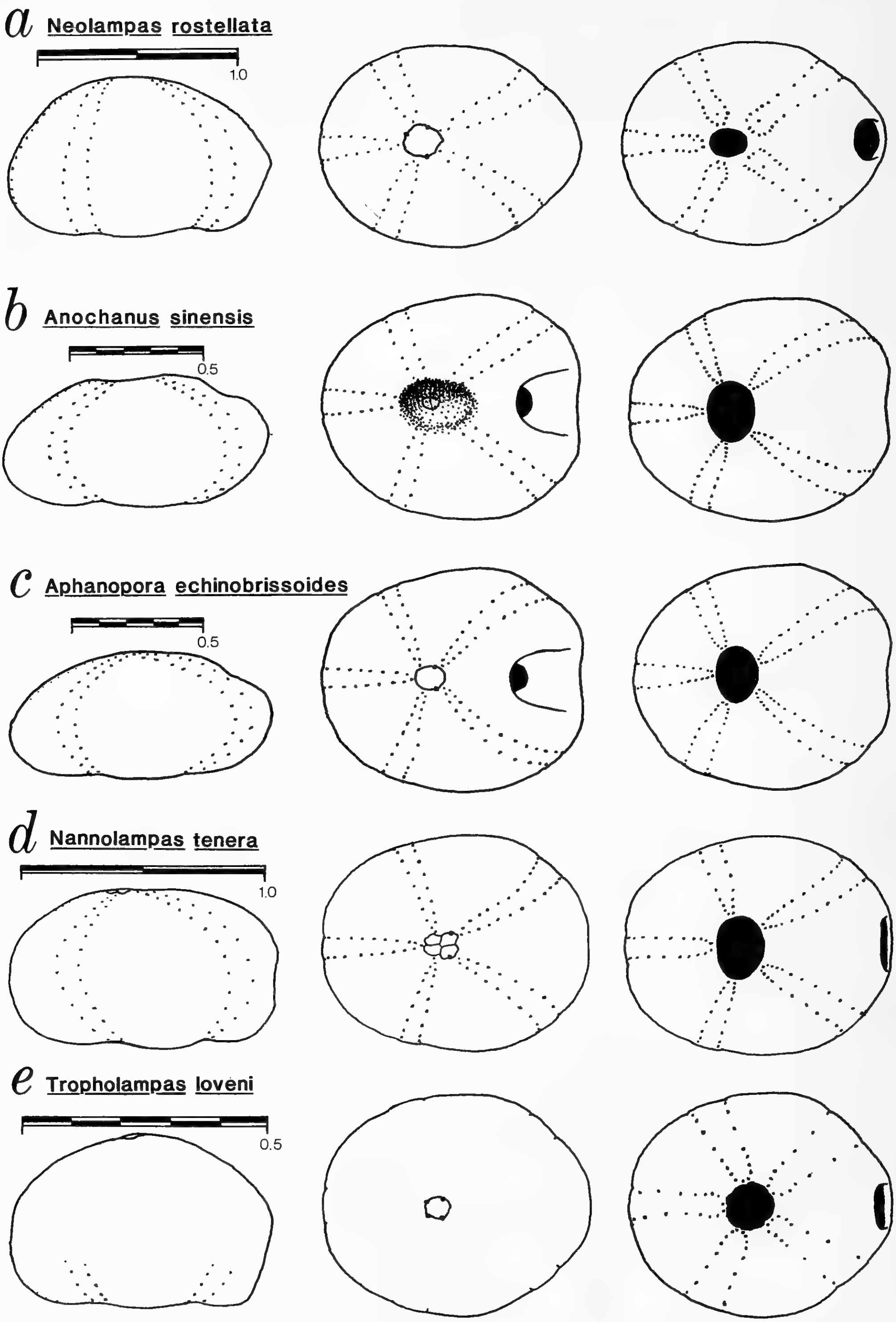
Remarks.—This species has apparently not been encountered since Mortensen's (1948) original description. *E. keiensis* was originally placed in a separate genus, *Planilampas* Mortensen, 1948 along with *Echinolampas sternopetala* (see below).

Echinolampas koreana H. L. Clark, 1925
Fig. 7b

Geographic range.—From the Korean Strait (Clark 1925) and western Japan (Nisiyama 1968).

Bathymetric range.—73 to 100 m.

Remarks.—Clark (1925) compared his new species with *E. sternopetala,* and Nisiyama (1968) compared *E. koreana* with *E. alexandri. E. koreana* differs from both


a Neolampas rostellata
1.0
b Anochanus sinensis
0.5
c Aphanopora echinobrissoides
0.5
d Nannolampas tenera
1.0
e Tropholampas loveni
0.5

of the other species in having a much higher test and a pentagonal peristome. It also lacks the distinctive inequality in the length of the respiratory podial columns so strongly developed in the petaloids of *E. sternopetala.* For these reasons, I would agree with Mortensen (1948) in suggesting that these species are not particularly closely related. Nisiyama (1968) appears to be the only author to have published on *E. koreana* since Clark (1925) described it from a single specimen. Nothing has been published on the biology of this species.

Echinolampas rangii Desmoulins, 1837
Fig. 7c

Geographic range.—Apparently from the west coast of Africa (Senegal) and the Cape Verde Islands (Mortensen 1948).

Bathymetric range.—Mortensen (1948) recorded it from 1570 to 1670 m, but stated that it is undoubtedly also known from "shallow" water without suggesting an upper limit.

Remarks.—No work has been published on this species since Mortensen (1948).

Echinolampas sternopetala A. Agassiz & H. L. Clark, 1907
Fig. 7d

Geographic range.—Known only from Japanese waters from Sagami Bay to Kagoshima Bay (Shigei 1986).

Bathymetric range.—100 to 500 m (Shigei 1986).

Remarks.—Mortensen (1948) made this the type species of a new genus, *Planilampas,* which he erected largely on the basis of the flatness of the oral surface. Kier (1962) synonymized this genus with *Echinolampas.* Shigei (1986) described *Echinolampas sternopetala* from Sagami Bay, Japan, but provided no comments on substrate type or ecology.

Echinolampas sumatrana (Döderlein, 1905)
Fig. 7e

Geographic range.—Known from a single denuded test collected off Sumatra.

Bathymetric range.—From a single "Valdivia" station at 371 m.

Remarks.—Mortensen (1948) agreed with Döderlein (1906) in suggesting that more specimens of *E. sumatrana* were necessary before it could be firmly established that it was distinct from *E. crassa.* However, differences in peristome shape and petaloid width (see key, above) seem to indicate that *E. sumatrana* is distinct from *E. crassa.*

Conolampas (A. Agassiz, 1883)
Conolampas sigsbei (A. Agassiz, 1878)*
Figs. 3a, 8a

Geographic range.—Throughout the Greater and Lesser Antilles, west coast of Florida, and the north and northeastern coasts of the Yucatan.

Bathymetric range.—120 to 800 m.

Remarks.—Mooi (1990) recently summarized what little is known of the biology of this species, suggesting that it lives on the surface of the sediment, not burrowed, and feeds on relatively fine carbonate substrates. Judging from the flatness of the oral surface and overall similarity in spination and test shape, other species of *Conolampas* probably have similar habits.

←

Fig. 12. Neolampadidae: a, *Neolampas rostellata* A. Agassiz, 1869 [MCZ 2739]; b, presumed female *Anochanus sinensis* Grube, 1868 [reconstructed from Mortensen 1948 and McKnight 1968]; c, presumed male *Aphanopora echinobrissoides* de Meijere, 1902 [after McKnight 1968]; d, *Nannolampas tenera* (de Meijere, 1902) [after Mortensen 1948]; e, male *Tropholampas loveni* (Studer, 1880) [after Mortensen 1948 and MCZ 4507]. Conventions as in Fig. 6. All scale bars in mm.

Conolampas diomedeae Mortensen, 1948
Fig. 8b

Geographic range.—Mortensen (1948) recorded a single specimen (the holotype) from off Mindoro Island in the Philippines. David & de Ridder (1989) describe an additional seven specimens from the Philippines.

Bathymetric range.—Mortensen's (1948) specimen was dredged from 265 m, David and de Ridder's (1989) from stations between 181 and 195 m.

Remarks.—David & de Ridder's (1989) specimens are the only ones collected since Mortensen's (1948) description. They provide some biometrics and figures, but no information on the biology of this species.

Conolampas malayana Mortensen, 1948
Fig. 8c

Geographic range.—Known only from Kepulauan Kai (Kei Islands) and off Zamboanga in the southern Philippines (Mortensen 1948).

Bathymetric range.—245 to 400 m.

Remarks.—No new information since Mortensen (1948) discovered the species.

Conolampas murrayana Mortensen, 1948
Fig. 8d

Geographic range.—Only two specimens known from off the Maldive Islands in the Indian Ocean.

Bathymetric range.—Dredged from 229 m.

Remarks.—No new information since Mortensen (1948).

Family Cassidulidae L. Agassiz & Desor, 1847

Cassidulus Lamarck, 1801

Cassidulus caribaearum Lamarck, 1801*
Figs. 1a, 2b, 3b, 9a

Geographic range.—Belize, Central America, and from the Bahama Islands south through the Virgin, Leeward, and Windward Islands to Barbados.

Bathymetric range.—Very shallow water, from less than 1 m to probably no deeper than 10 m. Agassiz (1872) reported fragments from 197 m, but it is not at all certain whether these actually represent *C. caribaearum.*

Remarks.—Some confusion has arisen on the spelling of the species name, recent papers reporting it as *C. cariboearum* (Kier 1975) and *C. caribbearum* (Gladfelter 1978). As Mortensen (1948) recorded, Lamarck's original and correct spelling is *C. caribaearum.* Kier (1975) described this species as living buried in coarse sand at Carrie Bow Cay, Belize. Gladfelter (1978) reported that *C. caribaearum* broods its young among the aboral spines and was locally abundant in coarse, oolitic carbonate sand in very shallow water. He also described locomotion in this species, which uses "ditaxic waves, passing from the front to the rear of large movable spines on the lateral portions of the ventral surface; this mechanism is unique among echinoids" (p. 149). *C. caribaearum* feeds in much the same way as described for *Echinolampas crassa* (see above), but apparently does not rely as much on activities of the circum-oral spination (Gladfelter 1978). Gladfelter (1978) also studied reproductive biology and seasonal variation in population density in this widely distributed, but surprisingly seldom encountered, shallow water cassiduloid.

Cassidulus infidus Mortensen, 1948
Fig. 9b

Geographic range.—Known only from a single specimen labeled "Bahia" (Mortensen 1948). Probably from the east coast of South America.

Bathymetric range.—No depth record exists for the holotype, but Mortensen (1948) felt that it probably occurs in shallow water.

Remarks.—Although Krau (1954) compared her new species, *C. mitis,* with *C. infidus,* she relied on Mortensen's (1948) description, as no new information has been published on the latter, poorly known species.

Cassidulus mitis Krau, 1954
Fig. 9c

Geographic range.—Known only from Sepetiba Bay, near Rio de Janeiro, Brazil.

Bathymetric range.—Krau (1954) did not provide precise depth data, but said that the new species was collected from "shallow waters."

Remarks.—Tommasi & Lima-Verde (1970) synonymized *Cassidulus delectus* Krau, 1960 with *C. mitis* and noted that *C. mitis* broods its young in a manner similar to that of *C. caribaearum* (Gladfelter 1978).

Cassidulus malayanus (Mortensen, 1948)
Fig. 9d

Geographic range.—Only two known specimens, both from Kepulauan Kai (Kei Islands), according to Mortensen (1948).

Bathymetric range.—Approximately 250–290 m (Mortensen 1948).

Remarks.—Mortensen (1948) described this species as a member of the genus *Procassidulus* Lambert, 1918. The latter genus was erected by Lambert (1918) to replace *Cassidulus,* which he thought was preoccupied (Mortensen 1948). Kier (1962) synonymized *Procassidulus* with *Rhynchopygus* d'Orbigny, 1856. *Rhynchopygus* is stated by Kier (1962) to have a tetrabasal apical system. According to Mortensen (1948), *Procassidulus malayanus* has a "compact" (=monobasal) apical system and so cannot be a *Rhynchopygus.* Since this species is so much like other species in *Cassidulus,* it appears best to place *C. malayanus* in this genus, at least until more material becomes available. Mortensen (1948:225) reported that the two specimens he studied were taken from a "sandy bottom."

Eurhodia Haime in d'Archiac & Haime, 1853
Eurhodia relicta Mooi, 1990
Fig. 10a

Geographic range.—Only two specimens known, the holotype from off western Surinam, paratype from off Venezuela (Mooi 1990).

Bathymetric range.—Dredged from 57 and 112 m, respectively.

Remarks.—The type species of the genus is *Eurhodia morrisi* Haime in d'Archiac & Haime, 1853. *E. relicta* apparently occurs in terrigenous, siliceous substrates (Mooi 1990), but little else is known of its biology.

Oligopodia Duncan, 1889
Oligopodia epigonus (van Martens, 1865)*
Fig. 10b

Geographic range.—Mortensen (1948) recorded this species from off the east coast of Africa, the Malaysian region, off Jolo in the Philippines, and the Bonin Islands. Because specimens from off the northeast coast of Somalia, South Africa, Tonga, and New Zealand can be found in the U.S. National Museum (USNM), it would appear that this species ranges from the western Indian Ocean eastward through Indonesia and the Philippines all the way to the South Pacific Ocean. This means that *O. epigonus* has the largest range of any known living species of cassiduloid.

Bathymetric range.—Live specimens are recorded from 35 to 141 m. Mortensen reported dead specimens from 5 to 390 m, suggesting that the bathymetric range could be much greater than the live specimens indicate.

Remarks.—Females of this species have gonopores many times larger than those of the male (Mortensen 1948). Although once thought to be closely related to *Apatopygus, Oligopodia* differs in having a monobasal apical system and in ambulacral plate pattern and overall test shape. This genus appears to be much more closely related to *Eurhodia,* as noted by Mooi (1990). Mortensen (1948:232) said that "it is not rare in places with a suitable bottom, viz. a coarse sandy or even gravelly bottom" and reported that it occasionally is found in substrates with a high percentage of calcareous algal fragments.

Rhyncholampas A. Agassiz, 1869
Rhyncholampas pacificus
(A. Agassiz, 1863)*
Fig. 10c

Geographic range.—The tropical eastern Pacific Ocean, from the Gulf of California to the Gulf of Panama. Also known from the Galapagos Islands (Mortensen 1948).

Bathymetric range.—Clark (1925) said that it occurs from 7 to 130 m, but in his description of *Rhyncholampas,* Agassiz (1872) recorded it from water less than 2 m deep.

Remarks.—The biology of this large species of cassidulid is surprisingly poorly known. Agassiz (1872) mentioned that the living echinoid lives partially buried in the substrate up to the level of the petaloids, but no other direct observations of living specimens have since been reported.

Studeria Duncan, 1891
Studeria recens (A. Agassiz, 1879)
Fig. 10d

Geographic range.—Agassiz (1881) recorded the species from the Arafura Sea, south of Papua-New Guinea.

Bathymetric range.—Dredged from 236 m.

Remarks.—According to Kier (1962), the type species of the genus is *Studeria elegans* (Laube, 1869) because this was the only species included in the original description of the genus. Many previous authors had considered *S. recens* to be the type of *Studeria.* There is some uncertainty that *S. recens* is a *Studeria,* but there are strong similarities (except in overall test shape) between this species and Kier's (1962) figure of *S. subcarinatus* (Goldfuss, 1928). *S. recens* also fits the description of the genus (Kier 1962: 216), particularly with respect to the 3 gonopores, strongly developed bourrelets, and absence of an oral, medial naked zone. Kier (1962) synonymized *Hypselolampas* H. L. Clark, 1917 (which included *H. recens*) with *Studeria* because of a lack of significant characters separating *S. recens* from other members of *Studeria* Duncan, 1891. No other occurrences of this poorly known species have been published since Agassiz's (1881) description and nothing is known of its biology apart from the fact that it was collected from mud.

Family Apatopygidae Kier, 1962
Apatopygus Hawkins, 1920
Apatopygus recens (Milne Edwards, 1863)*
Figs. 4a, 11a

Geographic range.—Known only from New Zealand.

Bathymetric range.—6 to 146 m.

Remarks.—The behavior and general biology of this well-known species have been described by Higgins (1974). The echinoid burrows to a depth of approximately 30 mm into coarse sands or fine gravels composed of terrigenic material and high proportions of broken shell. Higgins (1974:513) suggested that *A. recens* is "an almost continuous deposit feeder," but did not describe the manner by which food is collected.

Apatopygus occidentalis
H. L. Clark, 1938
Figs. 4b, 11b

Geographic range.—Five specimens are known from along the western and southern coasts of Australia (Baker 1983).

Bathymetric range.—17 to 40 m (Baker 1983).

Remarks.—Although Baker (1983) provided a detailed redescription of this very rare species, almost nothing is known of its general biology.

Porterpygus Baker, 1983
Porterpygus kieri Baker, 1983*
Fig. 11c

Geographic range.—Known only from five specimens collected near Three Kings Islands, New Zealand (Baker 1983).

Bathymetric range.—Dredged from approximately 90 to 300 m.

Remarks.—Baker (1983:172) suggested that the discovery of this second genus attributable to the family Apatopygidae "supports the isolation of Kier's Apatopygidae as a separate family." Nothing is known of the biology of this species.

Family Neolampadidae Lambert, 1918
Neolampas A. Agassiz, 1869
Neolampas rostellata A. Agassiz, 1869*
Figs. 5a, 12a

Geographic range.—West Indian waters and the Eastern Atlantic, particularly Florida, across the Atlantic to the Moroccan coast, and the Mediterranean.

Bathymetric range.—Mortensen (1948) reported the species from 145 to 1260 m.

Remarks.—Examination of specimens in the National Museum of Natural History (USNM) and the Museum of Comparative Zoology, Harvard (MCZ) reveals that, as in *Oligopodia,* females of this species have much larger gonopores than the males. Although this species is fairly well known from North American waters, its preference for deep waters has prevented direct observation of habits.

Anochanus Grube, 1868
Anochanus sinensis Grube, 1868*
Fig. 12b

Geographic range.—Reported only from the China Sea.

Bathymetric range.—No depth record available for the only known specimen.

Remarks.—Both Mortensen (1948) and McKnight (1968) have suggested that *Anochanus sinensis* may be the female of *Aphanopora echinobrissoides* (see below). Because the only known specimen has never been completely figured, the drawings presented here have been based on the similar *Aphanopora* and the description given in Mortensen (1948).

Aphanopora de Meijere, 1902
Aphanopora echinobrissoides de Meijere, 1902*
Fig. 12c

Geographic range.—Mortensen (1948) recorded the species from the Timor and Sulu Seas, and McKnight (1968) described two specimens from an area approximately 150 miles north of Norfolk Island.

Bathymetric range.—The Timor and Sulu specimens were found at 350 to 390 m, and McKnight's (1968) specimens were dredged from 710 m.

Remarks.—This species might actually be sexually dimorphic, with the females (possibly represented by *Anochanus sinensis,* see above) possessing an aboral brood cavity at the apical system. Therefore, the males would probably not have a sunken apical system, as figured by McKnight (1968). McKnight (1968) redescribed the species from material representing a range extension. However, his specimens were denuded tests, which prevented any speculation on the biology of the species.

Nannolampas Mortensen, 1948
Nannolampas tenera (de Meijere, 1902)*
Figs. 5b, 12d

Geographic range.—Known only from the Timor Sea.

Bathymetric range.—From a single "Siboga" station, at 390 m.

Remarks.—Mortensen (1948) assigned *Neolampas tenera* de Meijere, 1902 to a new genus, *Nannolampas,* because the latter species has a tetrabasal apical system. Nothing is known of the biology of *N. tenera.*

Tropholampas H. L. Clark, 1923
Tropholampas loveni (Studer, 1880)*
Fig. 12e

Geographic range.—South African coast, Cape Peninsula to Cape St. Francis (Mortensen 1948).

Bathymetric range.—Dredged from 135–350 m (Mortensen 1948).

Remarks.—The females of this species have a strongly developed aboral "marsupium" at the apical system, and the males have only a very slightly sunken apical system. In spite of the markedly different positions of the periproct, Mortensen (1948) thought that *Tropholampas* was closely related to *Anochanus* on the basis of common possession of an adapical brood cavity.

Acknowledgments

I would like to thank David Pawson, Malcolm Telford, and an anonymous reviewer for reading early versions of the paper, and Cindy Ahearn for her tireless efforts in locating collection data. Personal support was provided by a Natural Sciences and Engineering Research Council of Canada Postdoctoral Fellowship and additional funding by the Smithsonian Institution.

Literature Cited

Agassiz, A. 1872–1874. Revision of the Echini.—Memoirs of the Museum of Comparative Zoology 3:383–762.

———. 1881. Report on the scientific results of the voyage of the H.M.S. "Challenger" during the years 1873–1876, Zoology, Vol. III, Part IX, Report on the Echinoidea. London, England, Longmans & Company, 321 pp.

Baker, A. N. 1983. A new apatopygid echinoid genus from New Zealand (Echinodermata: Cassiduloida).—Records of the National Museum of New Zealand 2(15):163–173.

Clark, A. M., & F. W. E. Rowe. 1971. Monograph of the shallow-water Indo-west Pacific echinoderms. London, British Museum (Natural History), 238 pp.

Clark, H. L. 1925. A catalogue of the Recent sea-urchins (Echinoidea) in the collection of the British Museum (Natural History). London, England, Oxford University Press, 250 pp.

Cram, D. L. 1971. Life history studies on South African echinoids (Echinodermata) 2. *Echinolampas* (*Palaeolampas*) *crassa* (Bell) (Echinolampadidae).—Transactions of the Royal Society of South Africa 39(3):339–352.

David, B., & C. de Ridder. 1989. Echinodermes: Échinides irréguliers. Résultats des campagnes MUSORSTOM, volume 4.—Mémoires du Muséum Nationale d'Histoire Naturelle Paris (Serie A) 143:203–227.

Döderlein, L. 1906. Die Echinoiden der deutschen Tiefsee-Expedition.—Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899 5(2):61–290.

Dollfus, R. P., & J. Roman. 1981. Les échinides de la Mer Rouge. Paris, Bibliothèque Nationale, 145 pp.

Gladfelter, W. B. 1978. General ecology of the cassiduloid urchin *Cassidulus caribbearum* [*sic*].—Marine Biology 47(2):149–160.

Higgins, R. C. 1974. Observations on the biology of *Apatopygus recens* (Echinoidea: Cassiduloida) around New Zealand.—Journal of Zoology London 173:505–516.

Kier, P. M. 1962. Revision of the cassiduloid echinoids.—Smithsonian Miscellaneous Collections 114(3):1–262.

———. 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids.—Journal of Paleontology 48 (supplement) Paleontological Society Memoirs 5:1–95.

———. 1975. The echinoids of Carrie Bow Cay, Belize.—Smithsonian Contributions to Zoology 206:1–45.

———, & M. H. Lawson. 1978. Index of living and fossil echinoids 1924–1970.—Smithsonian Contributions to Paleobiology 34:1–182.

Krau, L. 1954. On a new species of Recent sea urchin, *Cassidulus mitis,* order Cassiduloida, Echinoidea, found on the coast of Sepetiba Bay.—Memorias do Instituto Oswaldo Cruz 52(2):455–475.

Lambert, J. 1918. Considerations sur la classification des échinides atelostomes.—Mémoires de la Société Academique de l'Aube ser., 3 55:9–54.

Leske, N. G. 1778. Additamenta ad Jacobi Theodori Klein naturalem dispositionem Echinodermatum et lucubratiunculam de aculeis echinorum marinorum. Lipsiae, 214 pp.

Märkel, K. 1978. On the teeth of the Recent cassiduloid *Echinolampas depressa* Gray, and on some Liassic fossil teeth nearly identical in structure (Echinodermata, Echinoidea).—Zoomorphologie 89:125–144.

McKnight, D. G. 1968. Some echinoids and ophiuroids from off Norfolk Island and from Wanganella Bank.—New Zealand Journal of Marine and Freshwater Research 2:204–213.

McNamara, K. J., & G. M. Philip. 1980. Tertiary species of *Echinolampas* (Echinoidea) from southern Australia.—Memoirs of the National Museum, Victoria 41:1–14.

Mooi, R. 1986. Non-respiratory podia of clypeasteroids (Echinodermata, Echinoides): II. Diversity.—Zoomorphology 106:75–90.

———. 1987. A cladistic analysis of the sand dollars (Clypeasteroida: Scutellina) and the interpretation of heterochronic phenomena. Unpublished Ph.D. dissertation, University of Toronto, Canada, 208 pp.

———. 1989. Living and fossil genera of the Clypeasteroida (Echinoidea: Echinodermata): An illustrated key and annotated checklist.—Smithsonian Contributions to Zoology 488:1–51.

———. 1990. A new "living fossil" echinoid (Echinodermata) and the ecology and paleobiology of Caribbean cassiduloids.—Bulletin of Marine Science 46:(in press).

Mortensen, T. 1948. A monograph of the Echinoidea, 4(1). Holectypoida, Cassiduloida. Copenhagen, Denmark, C. A. Reitzel, 471 pp.

Nisiyama, S. 1968. The echinoid fauna from Japan and adjacent regions, Part 2.—Palaeontological Society of Japan Special Papers 13:1–491.

Philip, G. M. 1963. Two Australian Tertiary neolampadids and the classification of cassiduloid echinoids.—Palaeontology 6(4):718–726.

Serafy, D. K. 1979. Memoirs of the Hourglass cruises. St. Petersburg, Florida, Florida Department of Natural Resources, 120 pp.

Shigei, M. 1986. The sea urchins of Sagami Bay collected by His Majesty the Emperor of Japan. Tokyo, Japan, Maruzen, 204 pp.

Suter, S. J. 1988. The decline of the cassiduloids: Merely bad luck?—Proceedings of the International Echinoderms Conference, Victoria, 1987, pp. 91–95.

Thum, A. B., & J. C. Allen. 1975. Distribution and abundance of the lamp urchin *Echinolampas crassa* (Bell) 1880 [*sic*] in False Bay, Cape.—Transactions of the Royal Society of South Africa 41(4):359–373.

———, & ———. 1976. Reproductive ecology of the lamp urchin *Echinolampas crassa* (Bell), 1880 [*sic*] from a subtidal biogenous ripple train.—Transactions of the Royal Society of South Africa 42(1):23–33.

Tommasi, L. R., & J. S. Lima-Verde. 1970. Observações sôbre *Cassidulus mitis* Krau, 1960 [*sic*, should be 1954] (Cassiduloida, Echinoidea).—Boletim Instituto Oceanografico Sao Paulo 18(1): 1–9.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 86–94

A NEW SPECIES OF HALOPHILOUS WATER-STRIDER, *MESOVELIA POLHEMUSI,* FROM BELIZE AND A KEY AND CHECKLIST OF NEW WORLD SPECIES OF THE GENUS (HETEROPTERA: MESOVELIIDAE)

Paul J. Spangler

Abstract.—A new species of water strider, *Mesovelia polhemusi,* from mangrove cays in the Stann Creek District of Belize is described, illustrated by line drawings and scanning electron micrographs, and compared with *M. hambletoni* Drake & Harris, a similar species, and *M. halirrhyta* Polhemus from Costa Rica, the only other described halophilous species included in *Mesovelia.* A key to males and a checklist of the 10 species presently described from the Western Hemipshere are included.

According to the classification of the Mesoveliidae by Andersen & Polhemus (1980), there are 23 species and subspecies of *Mesovelia* described for the world fauna; 14 from the Old World and 9 from the New World. Because it is necessary to examine many specimens of the widely distributed *M. mulsanti* to confirm or refute the infraspecific categories cited by Jaczewski (1930), only the nominate subspecies (with *bisignata* as a synonym) is included in the checklist below. The tenth New World species, *Mesovelia polhemusi,* new species, is described below.

The new species of *Mesovelia* was collected during a survey of aquatic and semiaquatic Hemiptera and Coleoptera of mangrove, coral reef, and estuarine habitats in the Stann Creek District of Belize. Collections of a variety of water bugs were made in the Sittee River estuary at Sittee Point, in Placencia Lagoon, and on numerous cays—on Bread and Butter Cay, the reef crest at Carrie Bow Cay, Man of War Cay, Round Cay, Twin Cays, Wee Wee Cay, and cays on the Blue Ground Range.

Specimens of *Mesovelia polhemusi,* new species, were found only on the mangrove cays where they occurred on mud flats among the prop-roots of red mangrove and the pneumatophores of black mangrove during ebb tide and on the surface of the salt water or resting on emergent vegetation when the tide was incoming or full.

The first specimen of this undescribed species was found in April 1986 while I was examining mud flats between the dense tangle of roots of the red mangrove *Rhizophora mangle* L. That find led to a concerted search for more specimens and some were ultimately found. They did not seem to be widely dispersed but some were found among pneumatophores of black mangrove, *Avicennia nitida* Jacquin. In order to obtain some information on the abundance of this species, counts of specimens were made for 8 plots of 1 m among the pneumatophores. The number of specimens from the plots varied from 0 to 18 with 6 being the mean of the sample. During the fieldwork in 1986, the bugs were difficult to find but abundant specimens were found on numerous cays during subsequent trips as listed under the type data below. During limited collecting on the mainland in freshwater estuarine habitats *Mesovelia mulsanti* White was found to be abundant but no specimens of *M. polhemusi* were obtained. This new species probably occurs widely on the many cays along the coast of Belize and perhaps it will be found on the mainland if more intensive collecting efforts are made there.

The specimens of the type series were found on mud flats and the water surface among the prop roots of red mangrove and pneumatophores of black mangrove. Some were hiding in small cracks, fiddler crab burrows, and similar niches until flushed out of hiding. During subsequent field trips other specimens were found running about openly, usually on shaded, damp to muddy soil.

Mesovelia polhemusi, new species
Figs. 1–20

Holotype ♂ (Figs. 1, 2).—Body form and size: Elongate; slightly widening to mid-length of abdomen then converging to end of genital capsule. Length, 2.21 mm; width (across abdomen), 0.64 mm.

Color: Ground color yellowish brown; with indication of a yellowish longitudinal vitta on midline of dorsum. Connexivia light yellowish brown. Legs light yellowish brown except each femur with darker brown subapical band. Antennal segments dark reddish brown except basal segment lighter yellowish brown. Venter yellowish except brown laterally. Body, legs, and antennae with very short yellowish brown, decumbent pubescence.

Head (Figs. 3–5): Length, 0.46 mm; broadened anteriorly to tubercles; width between tubercles, 0.35 mm. Median sulcus posteriorly reaching caudal margin, becoming evanescent anteriorly between eyes. Eyes large (width of eye/interocular space: 0.15/0.21 mm); length, 0.21 mm; with many ommatidia, converging anteriorly. Rostrum extending almost to anterior margin of metacoxae. Antenna (Fig. 19) long, slender; segment 1 stoutest; lengths of segments 1–4: 0.50 mm, 0.34 mm, 0.62 mm, 0.62 mm. Antennal segment 1 with numerous short setae and one long, anteriorly directed, thin seta at distal third. Antennal segments 2, 3, and 4 set with many long, thin setae. Cuticle with dense plastron setae and peg plates (Figs. 3–6).

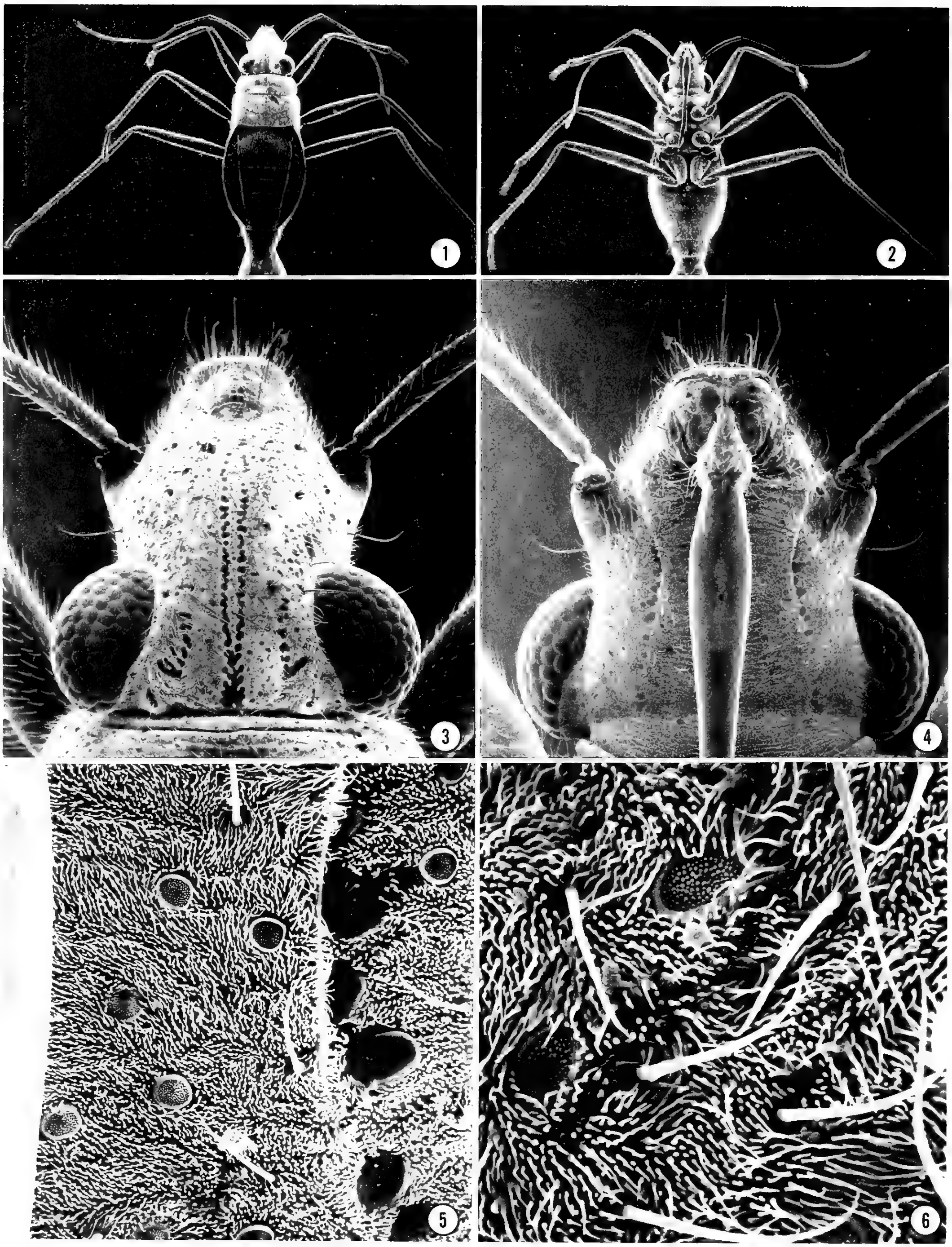
Thorax (Fig. 16): Pronotum and mesonotum granulate along hind margins; metanotum granulate on each side of midline. Pronotum short; posterior margin straight. Midline lengths of pronotum, mesonotum, metanotum = 0.21, 0.20, 0.12 mm. Prosternum with dense plastron setae (Fig. 6). Legs with numerous longer, thin, hairlike setae; metatibia with scattered stiff brown setae. Protibia with grooming comb on apex (Figs. 7, 8). Protarsus (Fig. 9) with long, slender claws (Fig. 10). Right profemur armed beneath with 11 black spines; left profemur with 9 black spines; length of spines equal ¼ to ½ the width of the femur where they arise. Right mesotibia with grooming comb apically (Fig. 11). Right mesofemur armed beneath with 20 black spines (Fig. 12); left mesofemur with 15 black spines of similar length as spines of profemora. All femora moderately stout; tibia and tarsi slender.

Abdomen (Fig. 13): Long, slender. Segment 3 widest. Lengths of abdominal terga 1–7 = 0.12 mm, 0.15 mm, 0.12 mm, 0.15 mm, 0.14 mm, 0.17 mm, 0.23 mm. Median scent pore at anterior third of tergum 4 (Figs. 14, 15). First genital segment (8th abdominal) without spine or cluster of black spinules. Cuticle with peg plates (Fig. 17) and spiracles (Fig. 18).

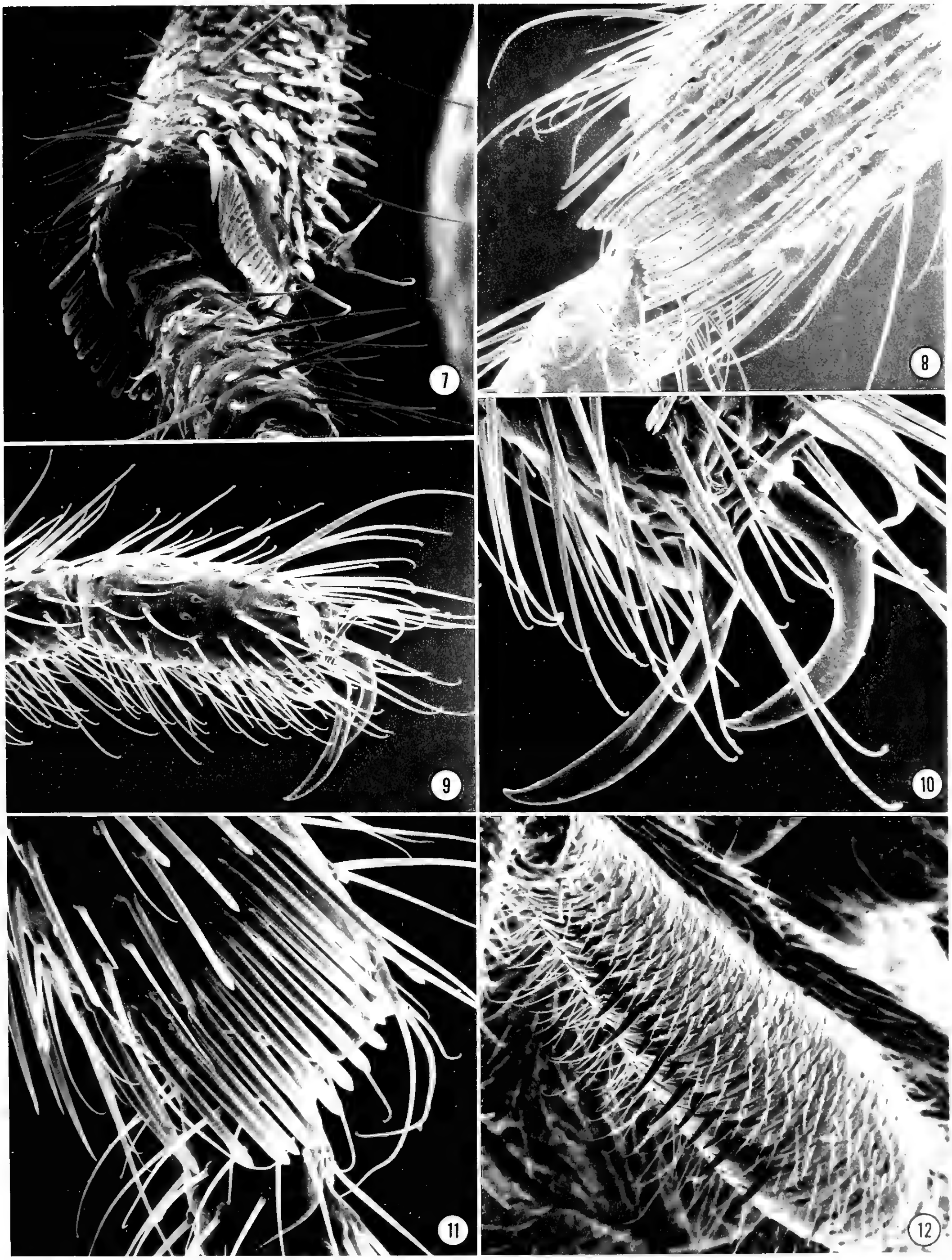
Genitalia: As illustrated (Fig. 20).

Female.—Length, 2.75 mm; width (across abdomen), 1 mm. Fore and middle femora armed beneath with 9 and 16 spines, respectively.

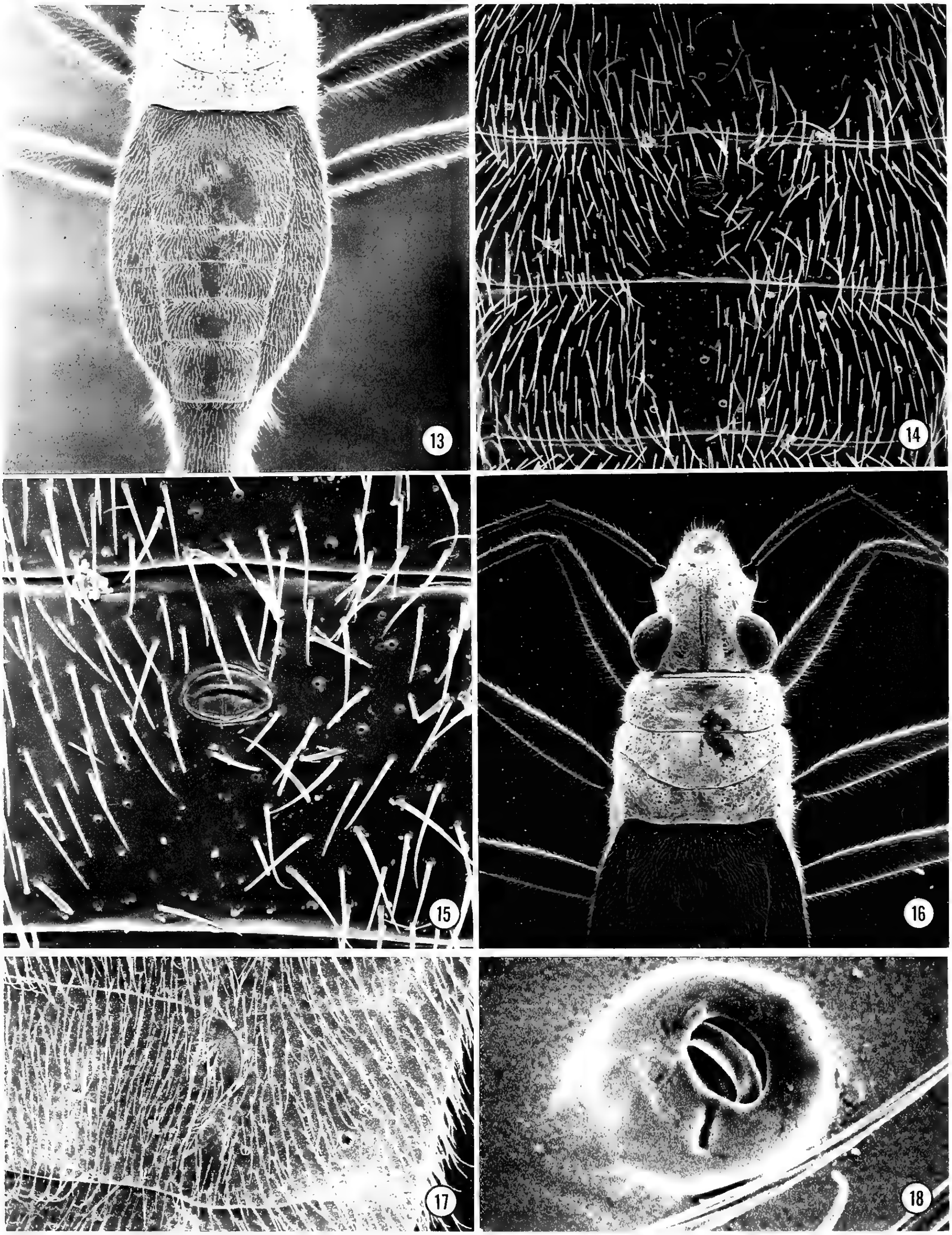
Variations.—The number of spines on the femora was found to be variable. The femoral spines varied as follows (n = 20 for each sex). Profemoral: males, 5–12 ($\bar{x}$ = 10); females, 1–12 ($\bar{x}$ = 7). Mesofemoral: males, 14–21 ($\bar{x}$ = 17); females, 6–17 ($\bar{x}$ = 11). Males (n = 20) ranged in length from 2.11–2.40 mm ($\bar{x}$ = 2.14) and in greatest width from 0.64–0.78 mm ($\bar{x}$ = 0.71). Females (n = 20) ranged in length from 2.33–2.75 mm



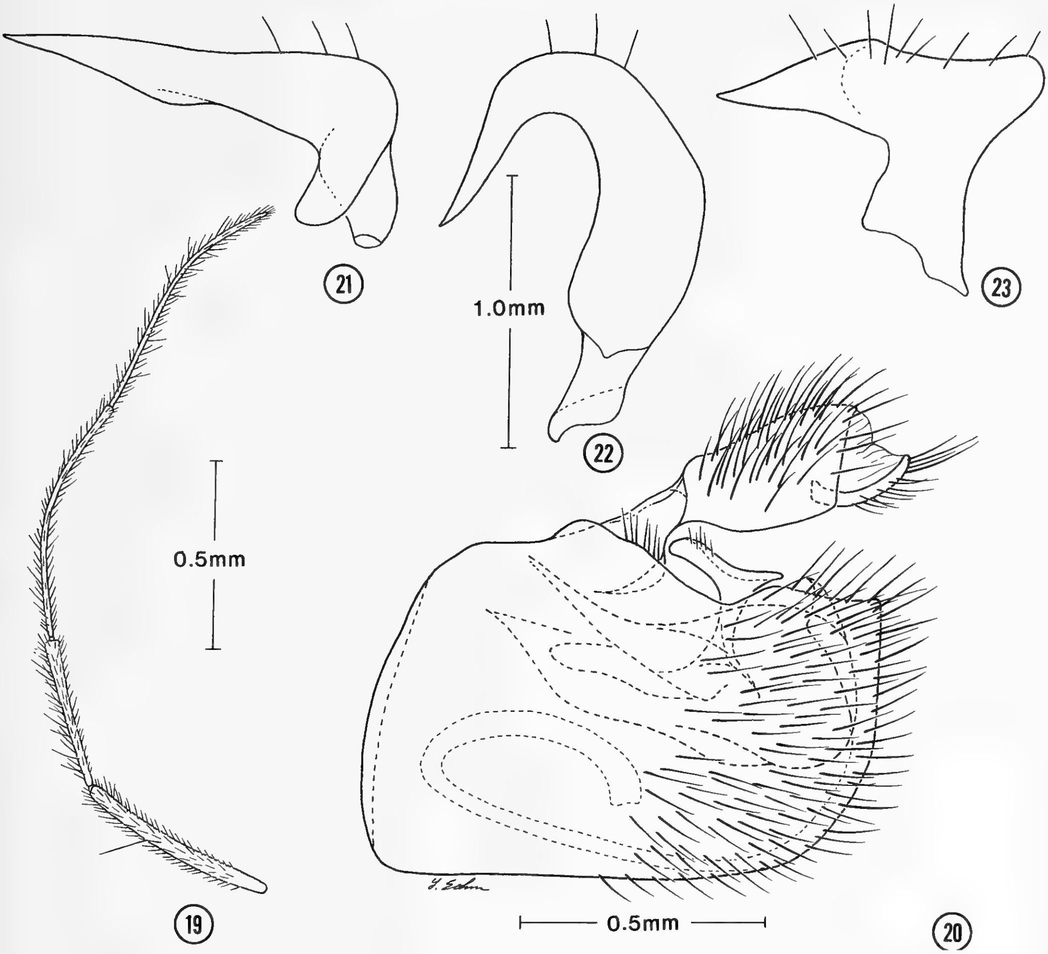
Figs. 1–6. *Mesovelia polhemusi,* n. sp. 1, habitus, dorsal, ×23; 2, habitus, ventral, ×22; 3, head, dorsal, ×150; 4, head, ventral, ×170; 5, plastron setae, ventral surface of head, ×1100; 6, plastron on prosternum, ×2800.



Figs. 7–12. *Mesovelia polhemusi,* n. sp. 7, protibial grooming comb, ×700; 8, protibial grooming comb, ×800; 9, protarsus, ×500; 10, protarsal claws, ×1300; 11, mesotibial grooming comb, ×1000; 12, mesofemur, ×350.



Figs. 13–18. *Mesovelia polhemusi,* n. sp. 13, abdominal terga, ×60; 14, abdominal tergum 4 and scent gland orifice, ×250; 15, abdominal scent gland orifice, ×600; 16, head and thorax, ×60; 17, peg plates and spiracle, side of abdomen, ×300; 18, spiracle, ×5000.



Figs. 19–23. *Mesovelia polhemusi,* n. sp. 19, antenna; 20, genital capsule with clasper. 21, *Mesovelia amoena* Uhler, male clasper. 22, *Mesovelia hambletoni* Drake & Harris, male clasper. 23, *Mesovelia cryptophila* Hungerford, male clasper.

($\bar{x} = 2.32$) and in greatest width from 0.80–1.01 mm ($\bar{x} = 0.93$).

Type data.—Holotype, apterous male: Belize: Stann Creek District: Twin Cays, 18 May 1986, P. J. Spangler and R. A. Faitoute; deposited in the U.S. National Museum of Natural History, Smithsonian Institution. Allotype: Same data as holotype.

Paratypes: Belize: Stann Creek District: Same data as holotype, 37 specimens. Blue Ground Range, 9 Nov 1987, P. J. Spangler and R. A. Faitoute, colln 20, 35 specimens. Bread and Butter Cay, 25 Mar 1988, R. A. Faitoute, colln 25, 15 specimens. Man of War Cay, 16 May 1986, P. J. Spangler and R. A. Faitoute, colln 6, 1 specimen; 8 Nov 1987, P. J. Spangler and R. A. Faitoute, colln 16, 31 specimens. Round Cay (S of Coco Plum), 23 Mar 1988, R. A. Faitoute, colln 19, 7 specimens. Twin Cays: Aanderaa Flats, 19 May 1986, P. J. Spangler and R. A. Faitoute, colln 11, 38 specimens; Aanderaa Flats, 7 Nov 1987, P. J. Spangler and R. A. Faitoute, colln 12, 12 specimens; Aanderaa Flats, 8 Nov 1987, 20 specimens; Aanderaa Flats, 17 Mar 1988, R. A. Fai-

Table 1.—*Mesovelia polhemusi,* lengths of segments of legs (in millimeters).

	Femur	Tibia	Tarsal 1	Tarsal 2	Tarsal 3
Anterior	0.73	0.58	0.04	0.04	0.06
Middle	0.85	0.85	0.08	0.14	0.21
Posterior	1.16	1.35	0.10	0.19	0.15

toute, colln 2, 25 specimens; Aanderaa Flats, 21 Mar 1988, R. A. Faitoute, colln 11, 20 specimens; Hidden Lake, 17 Mar 1988, R. A. Faitoute, colln 4, 36 specimens; northeast side of island, 21 Mar 1988, R. A. Faitoute, colln 12, 1 specimen; West Pond, 18 Mar 1988, R. A. Faitoute; colln 5, 26 specimens. Wee Wee Cay, 24 Mar 1988, R. A. Faitoute, colln 20, 19 specimens.

Paratypes will be deposited in the Museo de Zoologia, Sao Paulo; the American Museum of Natural History, New York, New York; the British Museum (Natural History), London; the California Academy of Sciences, San Francisco, California; the Canadian National Collection, Ottawa; Institute Royal de Histoire naturelle de Belgique, Bruxelles; Instituto de Zoologia Agricola, Facultad de Agronomia, Maracay, Venezuela; Laboratorium voor Zoologische, Oecologie en Taxonomie, Utrecht; the Museum National de Histoire Natural, Paris; Museo Argentina de Ciencias naturales, Buenos Aires; Universidad Nacional de La Plata, La Plata; the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the Snow Entomological Museum, University of Kansas, Lawrence, Kansas; Zoologische Sammlung Bayerischen Staates, München; and the collection of John T. Polhemus, Englewood, Colorado.

Etymology.—This new species, *Mesovelia polhemusi,* is dedicated to my colleague and indefatigable aquatic heteropterist, John T. Polhemus, who has greatly increased our knowledge of these fascinating insects.

Comparative notes.—The male of *Mesovelia polhemusi,* new species, may be separated easily from its congeners by the following combination of characters. Middle femur with a row of black spines; first genital segment (8th abdominal) without spine or cluster of black spinules; length of antennal segment 2 distinctly less than the width of the vertex and one eye. *Mesovelia polhemusi* is most similar to the somewhat variable Ecuadorian species *Mesovelia hambletoni* Drake & Harris (1946) but differs from it by its smaller size (length less than 3 mm vs. more than 3.5 mm), and the male clasper (Fig. 20) not hooklike as on *M. hambletoni* (Fig. 22).

Males of *Mesovelia polhemusi* may be distinguished from the only other described strictly halophilous species of the genus, *Mesovelia halirrhyta* Polhemus (1975), by the absence of the two clusters of spinules on the first genital segment (8th abdominal) and the presence of only 15–20 black spines on the mesofemur vs. 25 spines reported for the 9 specimens in the type series of *M. halirrhyta.*

The only key to the species of *Mesovelia* of the Western Hemisphere is that by Jaczewski (1930) for four of the five species known at that time. In the intervening 59 years, the number of species of *Mesovelia* from the New World has doubled and the following key is provided to the males of the 10 species presently recognized from this hemisphere. Because of similarities between *M. polhemusi* and *M. hambletoni* as well as between *M. cryptophila* and the wide-ranging *M. amoena,* the diagnostic male claspers of these taxa are illustrated and referred to in the key. A complete clasper (Fig. 23) of *M. cryptophila* is also illustrated because Hungerford's (1924b) "freehand sketches of the left genital claspers of male Mesovelias" did not include the base and is misleading.

Key to Males of *Mesovelia* of the Western Hemisphere

1. Mesofemur with a row of prominent black spines ventrally 2
   Mesofemur without row of black spines 7

Table 2.—Checklist of New World *Mesovelia* Mulsant & Rey.

Species	Locality
amoena Uhler, 1894:218 (=*douglasensis* Hungerford, 1924a:142)	USA: Michigan to Florida, Nevada, California, Texas, Hawaiian Islands; Belize; Bonaire; Brazil; Costa Rica; Curacao; Dominican Republic; Mexico; Panama
bila Jaczewski, 1928:77	Argentina; Brazil
blissi Drake, 1949:146	Mexico; Panama
cryptophila Hungerford, 1924b:454	USA: Florida, Iowa, Kansas, Michigan, Mississippi, New Jersey
halirrhyta Polhemus, 1975:245	Colombia; Costa Rica
hambletoni Drake & Harris, 1946:8	Ecuador
mulsanti White, 1879:268 (=*bisignata* Uhler, 1884:274)	Southern Canada; eastern half of USA, Hawaiian Islands; neotropical region to Argentina
polhemusi Spangler, 1990:87	Belize
thomasi Hungerford, 1951:33	Guatemala; Mexico
zeteki Harris & Drake, 1941:276	Brazil; Panama

2(1). First male genital segment (eighth abdominal) with subbasal black-tipped median spine ventrally or two clusters of black spinules ... 3

First male genital segment (eighth abdominal) without spine or cluster of black spinules 6

3(2). First male genital segment (eighth abdominal) with a subbasal black-tipped median spine ventrally . ... *blissi* Drake, 1949

First male genital segment (eighth abdominal) with two clusters of black spinules 4

4(3). First male genital segment (eighth abdominal) with two patches of widely separated black spinules ventrally; each patch with about 40 to 50 spinules .... *thomasi* Hungerford, 1951

First male genital segment (eighth abdominal) with two tightly packed clusters of coarse or thin spinules 5

5(4). Mesofemur with 25 black spines ventrally. Males with two widely separated rows of thin spinules on first genital sternum; each row with three to five spinules. Length, 2.5–2.75 mm .... *halirrhyta* Polhemus, 1975

Mesofemur with 8 to 15 black spines. Males with two tightly packed clusters of stout black spinules on first genital sternum. Length, 3–4 mm .... *mulsanti* White, 1879

6(2). Small species; length less than 3.0 mm. Male clasper, in lateral view, not hooklike; apex blunt anteriorly (Fig. 20) .... *polhemusi,* new species

Large species; length more than 3.5 mm. Male clasper, in lateral view, strongly hooklike; apex acute and directed anteroventrally (Fig. 22) .... *hambletoni* Drake & Harris, 1946

7(1). Sixth male abdominal sternum with posteromedial fringe of black spinules 8

Sixth male abdominal sternum without posteromedial fringe of black spinules 9

8(7). Seventh male abdominal sternum with two clusters of black spinules ...... *bila* Jaczewski, 1928

Seventh male abdominal sternum without black spinules ... . *zeteki* Harris & Drake, 1941

9(7). Prothoracic and mesothoracic pleura and nota (at least laterally) broadly pruinose, with numerous minute shiny black spots. Anterior lobe of pronotum without distinct depressions on each side of midline. Propleuron without longitudinal light streak behind eye. Male clasper, in lateral view, short and robust (Fig. 23) .... *cryptophila* Hungerford, 1924b

Prothoracic and mesothoracic pleura and nota not broadly pruinose, without numerous, minute, shiny, black spots. Anterior lobe of pronotum with a distinct depression (apodeme) on each side of midline. Propleuron usually with longitudinal light streak behind eye. Male clasper, in lateral view, long and slender (Fig. 21) .... *amoena* Uhler, 1894

Acknowledgments

I thank Klaus Ruetzler and the other administrators of the Smithsonian Institution's Caribbean Coral Reef Ecosystem Project for financing the survey of the halophilic Hemiptera and Coleoptera in Belize during which time this undescribed species was discovered. I also thank Young T. Sohn for the line drawings; Robin A. Faitoute for SEM photomicrographs and assistance with the fieldwork in 1986 and 1987 and all of the specimens collected in March 1988; Susann Braden for SEM photomicrographs; John T. Polhemus for constructively reviewing the manuscript; and Phyllis M. Spangler for typing the manuscript into a word processor. This is contribution 284, Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution.

References Cited

Andersen, N. M., & J. T. Polhemus. 1980. Four new genera of Mesoveliidae (Hemiptera; Gerromorpha) and the phylogeny and classification of the family.—Entomologica Scandinavica 11:369–392.

Drake, C. J. 1949. Two new Mesoveliidae with check list of American species (Hemiptera).—Boletin Entomologia Venezolana 7(3–4):145–147.

———, & H. M. Harris. 1946. A new mesoveliid from Ecuador (Hemiptera; Mesoveliidae).—Bulletin of the Brooklyn Entomological Society 41(1):8–9.

Harris, H. M., & C. J. Drake. 1941. Notes on the family Mesoveliidae (Hemiptera) with descriptions of two new species.—Iowa State College Journal of Science 15(2):275–277.

Hungerford, H. B. 1924a. A new *Mesovelia* with some biological notes regarding it (Hemiptera-Mesoveliidae).—The Canadian Entomologist 56:142–144.

———. 1924b. A second new species of *Mesovelia* from the Douglas Lake, Michigan region (Hemiptera-Mesoveliidae).—Annals of the Entomological Society of America 17(4):453–456.

———. 1951. A new *Mesovelia* from Mexico and Guatemala.—Journal of the Kansas Entomological Society 24(1):32–34.

Jaczewski, T. 1928. Mesoveliidae from the state of Paraná.—Annales of the Musei Zoologici Polonici 7(2–3):75–81.

———. 1930. Notes on the American species of the genus *Mesovelia* Muls. (Heteroptera, Mesoveliidae).—Annales Musei Zoologici Polonici 9(1): 3–15.

Polhemus, J. T. 1975. New estuarine and intertidal water-striders from Mexico and Costa Rica (Hemiptera: Gerridae: Mesoveliidae).—Pan-Pacific Entomologist 51:243–247.

Uhler, P. R. 1884. Order IV. Hemiptera. Pp. 204–206 *in* J. S. Kingsley, ed., Standard natural history. S. E. Cassin & Co., Boston, vii + 555 pp.

———. 1894. On the Hemiptera-Heteroptera of the island of Grenada, West Indies.—Proceedings of the Zoological Society of London 1894:167–224.

White, F. B. 1879. List of the Hemiptera collected in the Amazons by Prof. J. W. H. Trail, MA., M.D., in the years 1873–1875, with descriptions of the new species.—Transactions of the Entomological Society of London 267–276.

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 95–99

LUTEOCARCINUS SORDIDUS, NEW GENUS AND SPECIES, FROM MANGROVE SWAMPS IN PENINSULAR MALAYSIA (CRUSTACEA: DECAPODA: BRACHYURA: PILUMNIDAE: RHIZOPINAE)

Peter K. L. Ng

Abstract.—A new genus and species of mangrove-dwelling pilumnid crab of the subfamily Rhizopinae, *Luteocarcinus sordidus,* is described from mangrove swamps in western peninsular Malaysia. It can be separated from other littoral mud-dwelling genera in having a distinctively structured third maxilliped. It is the first rhizopine reported from littoral mangrove substrates.

Crabs of the Indo-West Pacific pilumnid subfamily Rhizopinae Stimpson, 1858 sensu Ng (1987) are small, usually mud-dwelling crabs that are complex taxonomically. Ng (1987) recognized 20 genera with 74 species in the subfamily. However, several of the species, and some of the genera, were only provisionally classified in the Rhizopinae. Almost all occur in sublittoral waters.

In the present paper, a new genus and species, *Luteocarcinus sordidus,* is reported from littoral mangrove areas in western peninsular Malaysia. A diagnosis is provided for the genus and species, and affinities with other taxa discussed. The abbreviations G1 and G2 are used for the male first and second pleopods respectively. Measurements are included for the carapace width and length. Type specimens, consisting of two males and two females, are deposited in the Zoological Reference Collection of the Department of Zoology, National University of Singapore.

Family Pilumnidae Samouelle, 1819
Subfamily Rhizopinae Stimpson, 1858
Luteocarcinus, new genus

Diagnosis.—Anterolateral margin arcuate, without distinct teeth, lobes or indentations, slightly crested, confluent with slightly divergent posterolateral margins. Posterior margin of epistome distinctly separated into four rectangular lobes by three deep clefts; median lobes small, squarish, outer lobes very broadly rectangular. Third maxilliped broad, almost completely covering buccal cavity when closed, not forming any rhomboidal gap; merus large, distinctly wider than ischium, outer anterolateral angle lobiform, rounded, not strongly produced outwards, inner angle produced, tip rounded; ischium quadrate, inner margin gently and evenly rounded; exopod stout, inner margin smooth, without sharp subterminal tooth, distal area expanded to form broad cristiform lobe, distal flagellum well developed, extending beyond width of merus. Male gonopore sternal, opening from coxa of last ambulatory leg via very narrow channel formed by fused adjacent sternites. Male abdomen with seven freely articulating segments; first very narrow, not reaching base of last ambulatory coxa; second narrow; third trapezoidal, lower margin sinuous, upper margin slightly concave, lateral margins slightly concave; fourth to sixth progressively less trapezoidal, more squarish, lateral margins slightly concave to almost straight; seventh distinctly triangular, tip rounded, lateral margins slightly convex.

Type species.—*Luteocarcinus sordidus,* new species, designated herein.

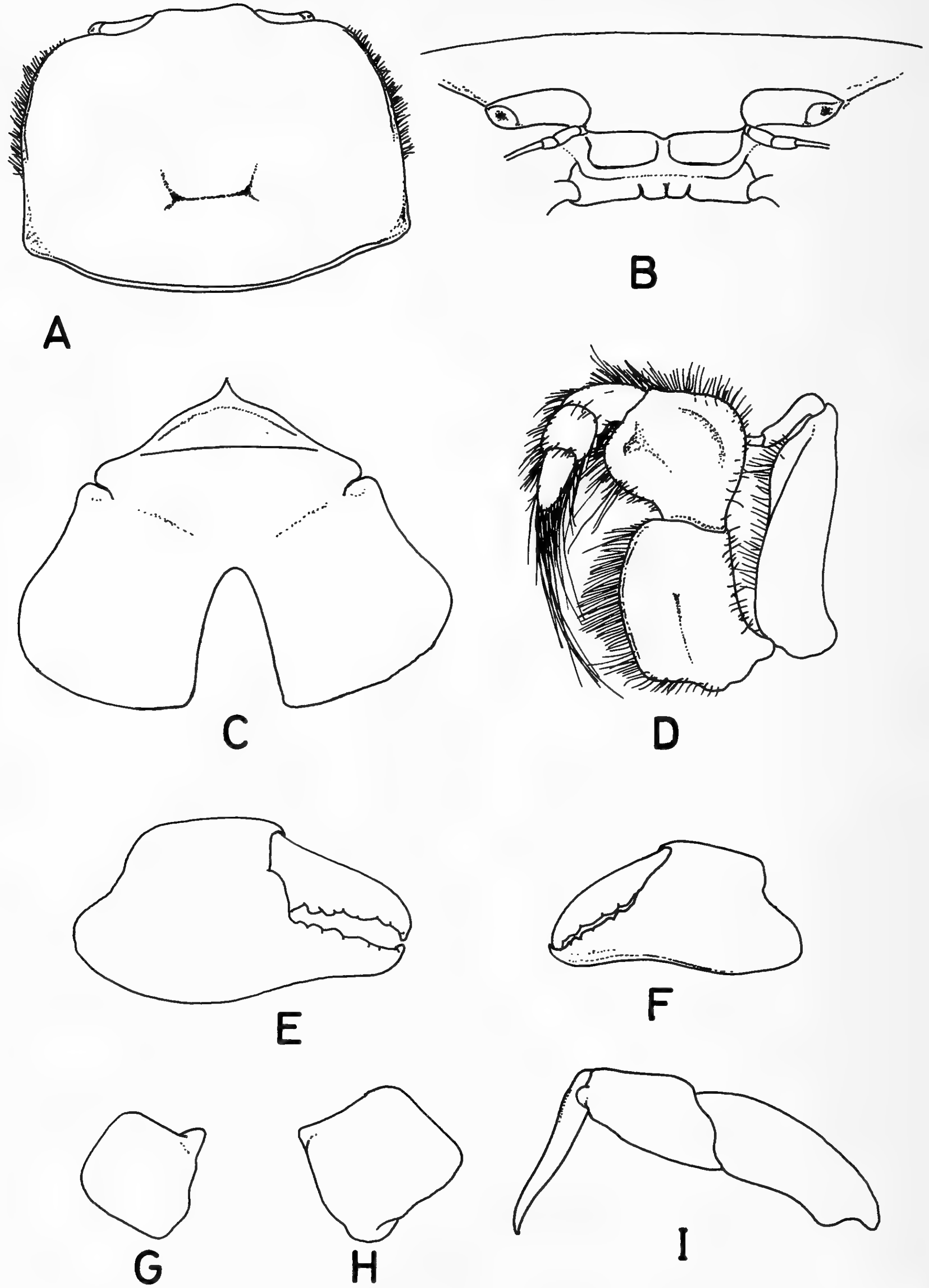


Fig. 1. *Luteocarcinus sordidus* holotype male: A, Carapace; B, Face and dorsal border of epistome; C, Sternum; D, Left third maxilliped; E, Right chela; F, Left chela; G, Left cheliped carpus; H, Right cheliped carpus; I, Dactylus, propodus and carpus of left last ambulatory leg.

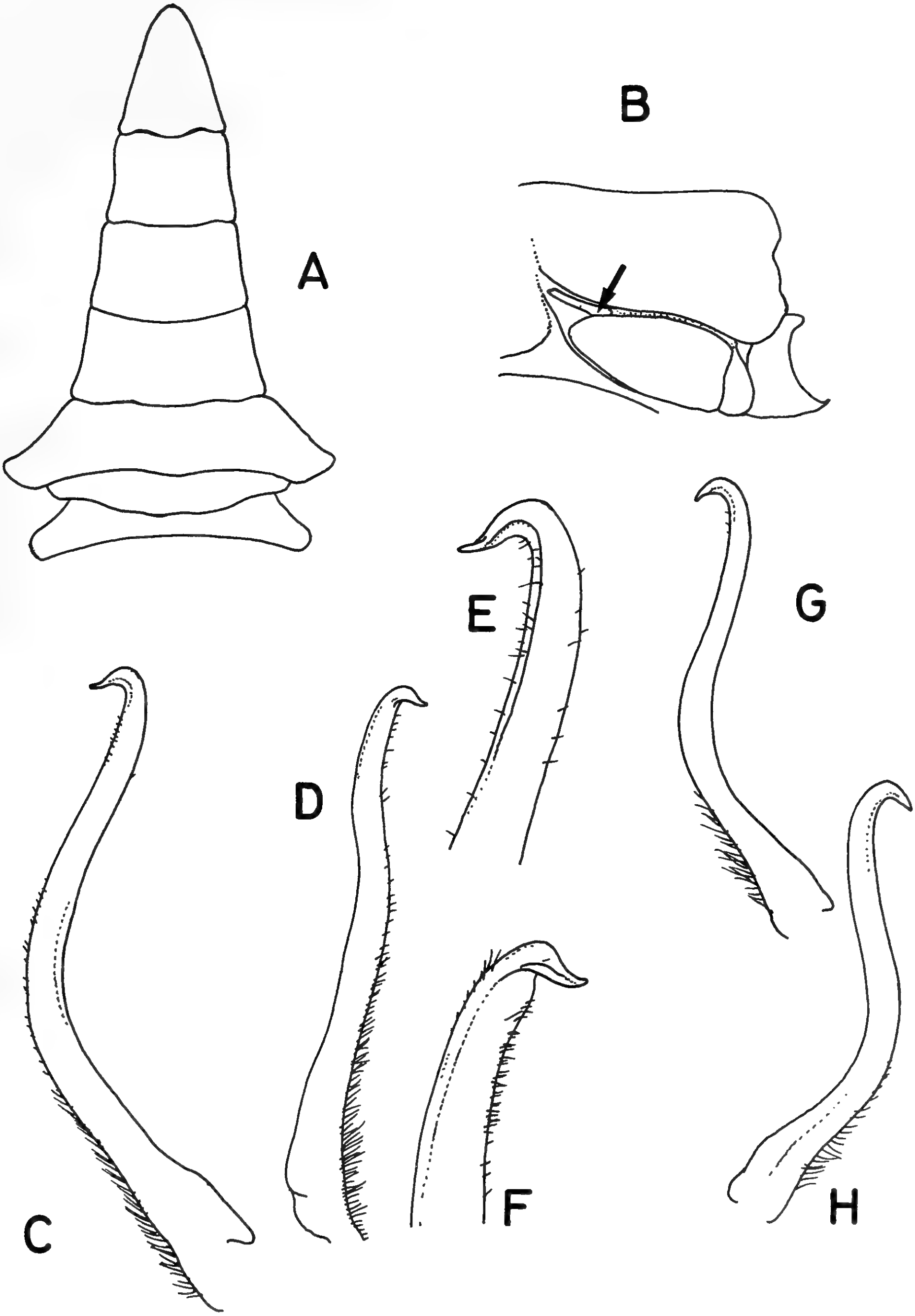


Fig. 2. *Luteocarcinus sordidus* A–F, holotype male; G, H, paratype male. A, Abdomen; B, Left gonopore (arrow); C, E, G, Left G1 (dorsal view); D, F, H, Left G1 (ventral view).

Etymology.—The generic name is derived from the Latin "luteum" for mud; alluding to the muddy mangrove habitat of the type species. The gender is masculine.

Luteocarcinus sordidus, new species
Figs. 1, 2

Typhlocarcinus sp. Sasekumar, 1974:63, 65.
Thyphlocarcinus sp. Sasekumar 1980:22 (spelling erroneous).

Diagnosis.—Carapace transverse, distinctly broader than long; appears slightly trapezoidal, posterolateral margins slightly diverging; surfaces smooth, without granules, almost glabrous except on anterolateral margins, which have numerous short, simple hairs; regions poorly defined, central H-shaped depression distinct but neither deep nor prominent. Eye fitting tightly into orbit, cornea distinct, pigmentation restricted to median part. Frontal margin entire, slightly sinuous, deflexed. Chelipeds asymmetrical in larger males, outer surfaces smooth, almost glabrous; inner angle of carpus with distinct blunt tooth; propodus without distinct projection partly overlapping base of dactylus; fingers shorter than palm. Ambulatory legs not distinctly elongate, segments smooth, unarmed, covered with scattered hairs, second pair longest, upper margin of median part of dactylus of last pair concave, distal part curves gradually downwards, dactylus appearing sinuous. G1 very sinuous, slender, distal part strongly tapered, tip slightly curved upwards; G2 very short, sinuous, without trace of flagellum, distal part strongly dilated forming cup-like structure. Littoral mangrove-dwelling species.

Material.—Holotype male (6.7 by 5.0 mm), Sementa mangroves, Selangor, peninsular Malaysia, leg. K. Sagathevan, 1988; paratype male (4.7 by 3.4 mm), 2 paratype females (5.9 by 4.2 mm, 5.7 by 4.1 mm), mangrove mud, near Batu Pahat, Johore, peninsular Malaysia, leg. P. K. L. Ng, May 1983.

Etymology.—The species name is derived from the Latin "sordida" for dirty, alluding to the appearance of the uncleaned animals.

Remarks.—The characters of *Luteocarcinus* are unusual in their combination, although no one character is unique to it. The most apparent difference is the form of the third maxilliped. The outer anterolateral angle of the merus is not distinctly expanded and appears rounded. This character affiliates it with *Typhlocarcinus* Stimpson, 1858, and *Typhlocarcinops* Rathbun, 1909, genera that are separated from the closely allied *Rhizopa* Stimpson, 1858, *Ceratoplax* Stimpson, 1858, and *Rhizopoides* Ng, 1987, by having the anterolateral angle of their third maxilliped merus rounded and not produced. In the structure of the exopod of the third maxilliped, however, *Luteocarcinus* is closer to the condition of *Rhizopa, Ceratoplax* and *Rhizopoides,* being stout, with the inner margin smooth. In *Typhlocarcinus* and *Typhlocarcinops,* the exopod is more slender and the inner margin has a distinct subterminal tooth. In *Typhlocarcinus* and *Typhlocarcinops,* the ischium is distinctly larger and wider than the merus, the proportions of which are reversed for *Luteocarcinus, Rhizopa, Ceratoplax* and *Rhizopoides.* A new genus has thus been established to accommodate the unusual suite of characters possessed by *Luteocarcinus.*

Sasekumar (1974, 1980) reported an unidentified "*Typhlocarcinus*" species from the mangrove swamps of the Kapar Forest Reserve and the Port Klang river bed, west of Port Swettenham and east of the Strait of Klang in Selangor, peninsular Malaysia. These specimens had been identified and examined by the late Raoul Serène (Sasekumar 1974), but are no longer extant, having been used for experiments (Sasekumar, pers. comm.). K. Sagathevan (pers. comm.), who is studying the ecosystem of the Selangor mangrove swamps, has informed the author that the "*Typhlocarcinus*" fide Serène is not common and is only occasionally seen. Two of the sites where "*Typhlocarcinus* sp." were collected (Sasekumar 1974) are stream beds in the Kapar Forest Reserve. In one (Station 4), a density of 4.3 individuals per square meter was recorded. In another station on the river bed of Port Klang, a density of five individuals per square meter was reported. Both sites in the Kapar Forest Reserve were located in the higher parts of the mangrove.

Sagathevan recently sent the author a collection of small mangrove crabs he had obtained at a Selangor mangrove swamp. Most were *Xenophthalmus pinnotheroides* White, 1846. One male, however, proved to be the unknown Selangor "*Typhlocarcinus.*"

The Selangor specimen proved to be almost identical with three unidentified rhizopine specimens collected by the present author from a mangrove swamp adjacent to Batu Pahat in Johore, southwestern peninsular Malaysia, in 1983. The three Johore specimens are smaller than the Selangor male. Their external carapace and appendage features, however, agree very well. The Selangor male is here made the holotype of *Luteocarcinus sordidus,* the three Johore specimens, paratypes. The G1 of the Johore male, however, does not have the tip distinctly upcurved. This difference is not regarded as significant since the Johore male is smaller than the holotype. The female specimens appear mature, the pleopods being fully setose, but the abdomen only partially covers the sternum. Uncleaned crabs are covered with a thin layer of "pile," resembling pubescence which is easily scraped off.

The rounded outer anterolateral angle of the third maxilliped merus and structure of the first male abdominal segment (not reaching the base of the last pair of ambulatory legs) of *Luteocarcinus sordidus* almost certainly led Serène to identify the earlier Selangor specimens as "*Typhlocarcinus.*" Although *L. sordidus* is close to *Typhlocarcinus,* the form of its third maxilliped argues against its inclusion in that genus.

The genus *Typhlocarcinus* was established for *T. villosus* Stimpson, 1858, from Hong Kong. Since then, additions and transfers have resulted in six species being currently recognized in the genus (Ng 1987). All the known *Typhlocarcinus* species have been described from deeper sublittoral waters, usually in muddy or silty substrates. *Luteocarcinus sordidus* was obtained during low tide on littoral mangrove mud.

The concave dorsal margin of the median part of the last ambulatory dactylus in *L. sordidus,* which makes it appear sinuous, is useful as a species character if used with other external characters. Ng (1987) has commented that since this character (an upcurved or sinuous last dactylus) is also present in other genera (and non-rhizopine taxa as well), and is probably associated with burrowing, it is not useful generically.

Acknowledgments

Thanks are due to Mr. Tan Hong Kim for leading the author through the mangrove swamps of Johore, and for his hospitality and kindness while he was in Batu Pahat. The author is also grateful to Dr. A. Sasekumar and Mr. K. Sagathevan (both Zoology Department, University of Malaya) for their help.

Literature Cited

Ng, P. K. L. 1987. The Indo-Pacific Pilumnidae II. A revision of the genus *Rhizopa* Stimpson, 1858 and the status of the Rhizopinae Stimpson, 1858 (Crustacea: Decapoda: Brachyura).—Indo-Malayan Zoology 4(1):69–111, pl. 1.

Sasekumar, A. 1974. Distribution of macrofauna on a Malayan mangrove shore.—Journal of Animal Ecology 43:51–69.

———. 1980. The present state of mangrove ecosystems in Southeast Asia and the impact of pollution. Malaysia.—South China Sea Fisheries Development and Coordinating Programme, Manila, Philippines, FAO/UNEP 15, SCS/80/ WP/94b:i–vi, 1–80.

Department of Zoology, National University of Singapore, Kent Ridge Campus, Singapore 0511, Republic of Singapore.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 100–102

ON THE STATUS OF *ALPHEUS BARBARA* LOCKINGTON (CRUSTACEA: CARIDEA: ALPHEIDAE)

Mary K. Wicksten

Abstract.—*Alpheus barbara,* described by Lockington (1878) based on a single specimen from California, has not been reported since its description. The type material has been lost. One of the major distinguishing features between *A. barbara* and *A. clamator,* the presence of a spine on the basicerite of the second antenna in the latter species, is inconsistent. Spines on alpheids may be lost, blunt or reduced in old or large individuals. Based on the evidence, *A. barbara* Lockington, 1878 is considered to be a junior subjective synonym of *A. clamator* Lockington, 1877.

In 1878, W. Lockington described a new species of snapping shrimp, *Alpheus barbara,* from Santa Barbara, California. The description was based on the unique type material, a specimen originally reported by J. Kingsley in 1878. Kingsley, however, reported the specimen as *Alpheus clamator* Lockington, 1876. According to Lockington (1878), Kingsley's specimen differed from *A. clamator* by the dissimilar proportions of the articles of the carpus of the second pereopods and the absence of spines on the basicerites of the second antennae and meri of the posterior three pereopods. Neither writer figured the specimen. Both mentioned that it was damaged, missing the rostrum and frontal region of the carapace.

The type specimen, "in the collections of the Peabody Academy of Science at Salem, Massachusetts" or "the Peabody Museum of Yale College" (Kingsley 1878:189), apparently was lost. Neither Holmes (1900) nor Schmitt (1921) reported seeing specimens of the species. No additional material of the supposed species has been reported since the species was described.

In an attempt to compile an accurate list of decapod crustaceans of southern California, I checked records of all species reported in the area. Extensive collections have been made in southern California from the shoreline to the lower continental slopes—the Allan Hancock Foundation, University of Southern California, has over 19,000 specimens of decapod crustaceans, and large collections also exist at Scripps Institution of Oceanography, the California Academy of Sciences and the National Museum of Natural History, Smithsonian Institution. Decapod crustaceans have been collected and studied by environmental agencies, the California Department of Fish and Game, students and researchers from many institutions, park personnel and divers. Despite all of this activity, no further material of *A. barbara* has been reported in the literature or deposited in collections, nor has it been found off western Mexico.

It seems odd that a species in such a well-studied area as southern California would not be found unless it lived in a very inaccessible habitat or occurred in a freshwater site that had been destroyed by human activity. Although exact collecting data was not provided, *Alpheus barbara* probably came from an intertidal or shallow subtidal rocky area. The collector, W. G. W. Harford, collected other alpheids known to live in such habitats (Kingsley 1878). Although there is the remote possibility that the species became extinct, it seems unlikely. Most coastal environmental degradation in southern California has occurred in bays, estuaries and marshlands (Wicksten 1984a).

Kingsley originally referred his specimen to *A. clamator*. This common species is well represented in collections. To determine if *A. barbara* might be misidentified among such material, I examined all of the specimens of *A. clamator* in the collections of the Allan Hancock Foundation. These 1030 specimens have been taken throughout the entire geographic and bathymetric range of the species, and include individuals of both sexes and a wide range of sizes.

When examining the specimens of *A. clamator,* I looked for the differences which Lockington (1878) indicated as different between *A. barbara* and *A. clamator*: the proportions of the articles of the carpus of the second pereopod and absence of spines from the basicerite and meri of the third–fifth pereopods. The proportions of the carpal articles vary slightly and can be difficult to measure exactly without a micrometer. Supposedly, in *A. barbara,* the first two segments of the carpus of the second pereopod are equal in size, while in *A. clamator,* the first segment is 1.3× as long as the second (Kim & Abele 1988). Such a slight difference probably could be easily confused, and is not a useful character for distinguishing between two species.

Of the 1030 specimens of *A. clamator* that I examined, a spine was absent from at least one basicerite in 14 specimens. In 10, the spine was absent on the right but present on the left, and in four, it was absent on the left but present on the right. In addition, in three specimens the spine was blunt or reduced on the right, and in another two it was blunt or reduced on the left. In all, about 2% of individuals of *A. clamator* lack a spine on the basicerite on at least one side. All individuals had spines on the meri of the posterior three pereopods, but these spines could be blunt in large individuals. Animals that were regenerating appendages often had abnormally slender, spineless legs.

At present, three valid species of *Alpheus* are known from southern California: *A. clamator, A. bellimanus* Lockington and *A. californiensis* Holmes (Wicksten 1984b). The major chelae of the latter two species differ greatly in the pattern of spines and sulci from those described by Kingsley for his specimen, so it is unlikely that *A. barbara* could have been confused with either species.

The distinction between *A. barbara* and *A. clamator* was based on three differences. The proportions of the segments of the carpus of the second pereopod could have been misinterpreted without accurate measuring devices: there is little difference between segments "equal" and one being 1.3× as long as the other. The spine on the basicerite is missing in a low proportion of the population of *A. clamator.* In a "damaged" specimen, meral spines might be missing from the posterior pereopods.

In the account by Lockington (1878) describing *A. barbara,* there is no evidence that Lockington ever actually examined Kingsley's specimen. The short description differentiates between *A. clamator, A. bellimanus* and *A. barbara,* but provides no description of the specimen except what was reported by Kingsley. Lockington (p. 472) ended the description by stating, "As Kingsley had only an imperfect specimen, and does not describe the rostrum and front, I cannot be sure that this species belongs to this section" (of alpheids). Based on the description and the evidence of variability within *A. clamator,* I suggest that *Alpheus barbara* Lockington is a junior subjective synonym of *A. clamator* Lockington.

Snapping shrimp of the genus *Alpheus* are known to show considerable within-species variation. The major chelae of males and females often differ in size and shape, as do those of juveniles from adults. Widespread species also can have regional variants. (See, for example, the discussion of *A. floridanus* by Chace 1972:66; and the remarks on variation in the genus *Alpheus* by Banner & Banner 1982:21.) Such within-species variability has confused systematists working on the family and has resulted in many species having extensive lists of synonyms.

Kim & Abele (1988:21) treated *A. barbara* as a valid species "because the absence of a lateral spine on the basicerite is a quite distinct and important character." From my study, it appears that the presence of the spine of the basicerite usually, but not always, is consistent within a single species. I have observed similar variation in spines on the carpal segments of the major chelae of *A. armillatus* Milne Edwards and *A. canalis* Kim & Abele—most individuals of the population have distinct spines, but a few very large (and probably old) individuals have small knobs or no spines at all. Anyone attempting to identify or describe alpheids should be cautious about using presence or absence of spines alone as a distinguishing feature between species, especially when examining a large or old individual.

Literature Cited

Banner, D. M., & A. H. Banner. 1982. The alpheid shrimp of Australia. Part III: The remaining alpheids, principally the genus *Alpheus,* and the family Ogyrididae.—Records of the Australian Museum 34:1–357.

Chace, F. A., Jr. 1972. The shrimps of the Smithsonian-Bredin Caribbean expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia).—Smithsonian Contributions to Zoology 98:1–179.

Holmes, S. J. 1900. Synopsis of California stalked-eyed Crustacea.—Occasional Papers of the California Academy of Sciences 7:1–262.

Kim, W., & L. G. Abele. 1988. The snapping shrimp genus *Alpheus* from the eastern Pacific (Decapoda: Caridea: Alpheidae).—Smithsonian Contributions to Zoology 454:1–119.

Kingsley, J. S. 1878. A synopsis of the North American species of the genus *Alpheus.*—Bulletin of the U.S. Geological and Geographical Survey of the Territories, U.S. Department of the Interior 4:189–199.

Lockington, W. N. 1877. Description of seventeen new species of Crustacea.—Proceedings of the California Academy of Sciences 7:41–48.

———. 1878. Remarks on some new Alphei, with a synopsis of the North American species.—Annals and Magazine of Natural History ser. 5, 1: 465–480.

Schmitt, W. L. 1921. The marine decapod Crustacea of California.—University of California Publications in Zoology 23:1–470.

Wicksten, M. K. 1984a. Early twentieth century records of marine decapod crustaceans from Los Angeles and Orange counties, California.—Bulletin of the Southern California Academy of Sciences 83(1):12–42.

———. 1984b. New records of snapping shrimps (family Alpheidae) from California.—Proceedings of the Biological Society of Washington 97: 186–190.

Department of Biology, Texas A&M University, College Station, Texas 77843.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 103–105

PSEUDOTHELPHUSA GALLOI, A NEW SPECIES OF FRESHWATER CRAB (CRUSTACEA: BRACHYURA: PSEUDOTHELPHUSIDAE) FROM SOUTHWESTERN MEXICO

Fernando Alvarez and Jose Luis Villalobos

Abstract.—A new pseudothelphusid crab from the State of Guerrero, Mexico, is described. Its affinities with four other species present in the Mexican Pacific slope are discussed.

Since the publication of Rodríguez' (1982) monograph on the Pseudothelphusidae, two new species belonging to the genus *Pseudothelphusa* have been described (Alvarez 1987, 1989). The third species, described in this paper, comes from the State of Guerrero in southern Mexico. *Pseudothelphusa galloi,* new species, lacks a defined marginal process on the gonopod like some of its congeners from the Pacific slope of Mexico. This new species was collected by J. P. Gallo while studying the feeding habits of the river otter *Lutra longicaudis annedectens,* which feeds on this and other freshwater crustaceans. Types are deposited in the Carcinological Collection, Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM).

Pseudothelphusa galloi, new species
Fig. 1

Description.—Superior frontal border of carapace formed by small tubercles, divided medially by deep notch posteriorly forming the median groove. In frontal view, front inclined towards central portion. Inferior frontal border well defined, formed by small blunt tubercles, sinuous in frontal view. Dorsal surface of carapace with deep median groove, narrow anteriorly, broader posteriorly. Cervical grooves slightly arched, not reaching anterolateral margin. Carapace regions ill defined, gastric and branchial regions elevated; epigastric lobes well marked. Area between epigastric lobes and superior frontal border inclined anteriorly. Anterolateral margin with 9 denticles between orbit and cervical groove, with 22 to 27 between cervical groove and epibranchial region. Pterygostomian region bearing setae around third maxillipeds. Ratio ischium/exopod of third maxilliped 0.4 to 0.57. Chelipeds unequal, fingers of major chelae gaping, granulated and curved. Palm of cheliped with fine granulation, becoming more dense dorsally and ventrally.

Gonopod with well developed lateral lobe, covering frontal portion of apical cavity; in cephalic view is roughly triangular, ending in two tips. Superior margin of mesial process (mesial crest) curving proximally, forming a rounded, axe-shaped lobe. Marginal process reduced to two small bumps, located anteriorly on mesial crest. Apex cavity elongated along a caudo-cephalic axis, bearing 27 setae with terminal pore restricted to lateral part of cavity. Caudal border thick, decreasing in thickness laterally.

Material examined.—Mexico. Rio La Parota, small tributary of Pinela River (16°46′N, 99°13′W) Municipio Ayutla de los Libres, Estado de Guerrero; 15 Apr 1985; J. P. Gallo; 1 male holotype, c.b. 65.9 mm, c.l. 39.8 mm; 1 male paratype, c.b. 67.8 mm, c.l. 40.4 mm (IBUNAM-EM-3479). Rio Pinela, Municipio Ayutla de los Libres, Estado de Guerrero, 28 Dec 1983; J. P. Gal-

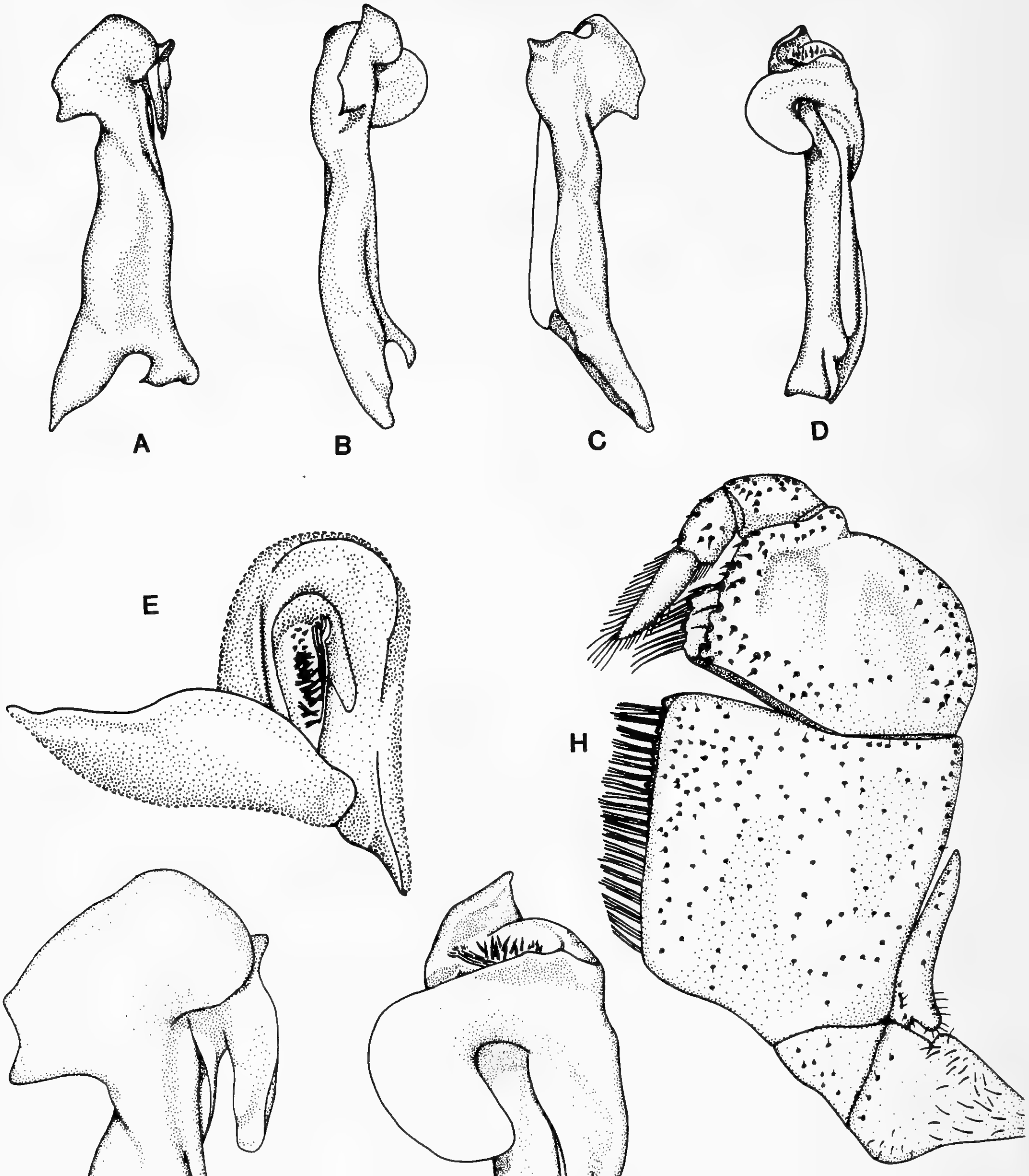


Fig. 1. *Pseudothelphusa galloi,* holotypic male, A–G, left gonopod: A, cephalic view; B, lateral view; C, caudal view; D, mesial view; E, apical view; F, detail of cephalic view; G, detail of mesial view; H, left third maxilliped.

lo; 1 male, c.b. 57.0 mm, c.l. 35.8 mm, 2 females, c.b. 28.0 and 37.3 mm, c.l. 18.2 and 23.6 mm (IBUNAM-EM-3478).

Etymology.—This species is named in honor of Juan Pablo Gallo.

Remarks.—The species shares with *Pseudothelphusa jouyi, P. lophophallus* and *P. sonorae* the vestigial character of the marginal process of the gonopod. However, in *P. jouyi* and *P. lophophallus* these vestiges appear on the mesial crest as a series of acute denticles (Rodríguez 1982, figs. 94a and 96a) and in *P. sonorae* there is only a small protuberance with no denticles (Rodríguez 1982, fig. 97c). In general, the gonopod morphology of *P. galloi* is closer to that of *P. jouyi.*

Acknowledgments

We thank Juan Pablo Gallo for collecting and donating the type specimens and Antonio Cantu for the illustrations. The second author was supported by CONACyT Grant PCCNCNA-031542.

Literature Cited

Alvarez, F. 1987. *Pseudothelphusa mexicana,* a new freshwater crab from the State of Guerrero, Mexico (Brachyura: Pseudothelphusidae).—Proceedings of the Biological Society of Washington 100:1–3.

———. 1989. *Smalleyus tricristatum,* new genus, new species, and *Pseudothelphusa parabelliana,* new species (Brachyura: Pseudothelphusidae) from Los Tuxtlas, Veracruz, Mexico.—Proceedings of the Biological Society of Washington 102:45–49.

Rodríguez, G. 1982. Les Crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Faune Tropicale 22:1–223.

(FA) Department of Zoology, University of Maryland, College Park, Maryland 20742; (JLV) Colección de Carcinología, Instituto de Biología, Universidad Nacional Autónoma de México, Apdo. Postal 70-153, México, D. F. 04510, México.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 106–107

RANGE EXTENSION AND HOST RECORD FOR *DISSODACTYLUS USUSFRUCTUS* GRIFFITH, 1987 (CRUSTACEA: BRACHYURA: PINNOTHERIDAE)

Michel E. Hendrickx

Abstract.—*Dissodactylus ususfructus* Griffith (Pinnotheridae) was found for the first time in the Gulf of California, Mexico, about 19° of latitude north of its previous northernmost record. Among the five specimens collected, two males and one female were found associated with *Clypeaster speciosus* Verrill.

During sampling activities in 1982 and 1985 in the Gulf of California, Mexico, aboard the R/V *El Puma* of the Universidad Nacional Autónoma de México (UNAM; CORTES Cruises), a small series of specimens of *Dissodactylus* Smith (Crustacea: Pinnotheridae) was found among invertebrates and on freshly captured specimens of *Clypeaster* (Echinoidea: Clypeasteridae). Later examination of these specimens demonstrated that they belonged to an undescribed species of *Dissodactylus* and represented the first positive record of the genus on *Clypeaster* for the Pacific. A preliminary description of this species of pinnotherid was prepared at that time (Hendrickx 1987), but was never published.

The genus *Dissodactylus* was recently reviewed by Griffith (1987a) who described two new species for the Pacific coast of America (*D. schmitti* and *D. ususfructus*).

On reading Griffith's paper, it became evident that the material collected in the Gulf of California belonged to *D. ususfructus,* a species already recognized as new by the late S. A. Glassell in the 1930s in a manuscript that he never published (see Griffith 1987a: 402). This species is known only from three localities between Costa Rica and Ecuador, and has not yet had a host species positively identified.

The discovery of *D. ususfructus* in the Gulf of California provides new information on its distribution and ecology. All the specimens reported herein are held in the reference collection of the Estación Mazatlán, UNAM (EMU).

Dissodactylus ususfructus Griffith, 1987

Dissodactylus ususfructus Griffith, 1987a: 401, figs. 3, 8K, 10B, 12D, 14I; 1987b: figs. 7C, 9C, 13B, 17D.

Material examined.—CORTES 1 Cruise, station 19, 6-V-1982, 28°09′30″N, 112°46′30″W, off Cabo San Miguel, Baja California, Mexico, trawling at 30–35 m, sand, 2 ♂♂ c.w. 6.7 and 7.6 mm, 1 ♀ c.w. 6.2 mm (EMU-2635).—CORTES 2 Cruise, station 49B, 19-III-1985, 26°59′N, 111°53′30″W, off Bahía Santa Inés, Baja California, Mexico, trawling at 68 m, 1 ♂ c.w. 5.5 mm (EMU-2636A).—CORTES 2 Cruise, station 50, 20-III-1985, 25°46′N, 109°35′W, off Rio Fuerte, Sinaloa, Mexico, trawling at 96–98 m, muddy sand, 1 ♀ c.w. 7.6 mm (EMU-2636B).

Previous records.—SSE of Judas Point, Costa Rica (Zaca station 214; type locality), off Santa Elena Bay, Ecuador, and SW of Secas Islands, Panama (Griffith 1987a).

Remarks.—The present records extend the known distribution of *D. ususfructus* northward about 19° of latitude, to Cabo San Miguel and to off Rio Fuerte, respectively, on the west and on the east coasts of the Gulf of California.

The positive identification of *Clypeaster* *speciosus* Verrill, 1870 as a host of *D. ususfructus* (CORTES 1 Cruise, station 19) partly confirms the hypothesis of Griffith (1987a: 403), in that this pinnotherid is associated with *Clypeaster.* The possible association of *D. ususfructus* with another species of *Clypeaster, C. europacificus* H. L. Clark, 1944, was suggested by Griffith (1987a) because of the presence of this species of irregular echinoid in successive samples taken by Zaca at station 214, the type locality of *D. ususfructus,* but this had not been confirmed. According to Caso (1980, 1986), both *Clypeaster speciosus* and *C. europacificus* are commonly found throughout the Gulf of California in similar habitats (shallow water to 90 m for *C. speciosus,* 18 to 165 m for *C. europacificus*; mostly on sand). They have also been collected at least once in the same trawl (*Velero III,* station 699-37, Canal Angeles, Gulf of California) (Caso 1980:9, 24), which suggests that they are, at least occasionally, sympatric. The hypothetical association of *D. ususfructus* with two species of *Clypeaster* does not seem unlikely. Indeed, many species of *Dissodactylus* are known to occur on several species or even genera of irregular echinoids (Griffith 1987a, Jangoux 1987).

The bathymetry provided by Griffith (1987a) for *D. ususfructus* is rather imprecise (80–120 m). The present material was found between 30–35 m, at 68 m, and between 96–98 m, on sandy bottom (62 to 100% sand). Other environmental conditions at bottom level were as follows: water temperature, 13.2 to 14.2°C; dissolved oxygen, 1.33 to 3.5 ml O_2/l.

Acknowledgments

I am grateful to Dr. Maria Elena Caso, dean of the Instituto de Ciencias del Mar y Limnología, UNAM, who called my attention to the capture of specimens of *Dissodactylus ususfructus* during the CORTES Cruises. I also thank Drs. J. Bouillon and M. Jangoux for the facilities provided during my stay at the Laboratoire de Biologie Marine, Université Libre de Bruxelles, and Mercedes Cordero H. for aid in preparing and typing the manuscript. This study was partly supported by CONACyT (ICECXNA-021926) and the DGPA, UNAM. This is Contribution 602 of the Instituto de Ciencias del Mar y Limnología.

Literature Cited

Caso, M. E. 1980. Los equinoideos del Pacífico de México. Parte Tercera. Orden Clypeasteroida.—Publicación Especial, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 4:1–252.

———. 1986. Los equinodermos del Golfo de California colectados en las Campañas SIPCO I-II-III a bordo del B/O "El Puma."—Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 13 (1):91–184.

Griffith, H. 1987a. Taxonomy of the genus *Dissodactylus* (Crustacea: Brachyura: Pinnotheridae) with descriptions of three new species.—Bulletin of Marine Science 40(3):397–422.

———. 1987b. Phylogenetic relationships and evolution in the genus *Dissodactylus* Smith, 1870 (Crustacea: Brachyura: Pinnotheridae).—Canadian Journal of Zoology 65:2292–2310.

Hendrickx, M. E. 1987. La faune de crustacés (Stomatopoda et Decapoda) du Golfe de Californie: Taxonomie, aspect écologique et distribution. Thèse de Doctorat, Université Libre de Bruxelles. Vol. I, i–xvii, 1–741; Vol. II, tables 1–210, figs. 1–428.

Jangoux, M. 1987. Diseases of Echinodermata. III. Agents metazoans (Annelida to Pisces).—Diseases of Aquatic Organisms 3(1):59–83.

Instituto de Ciencias del Mar y Limnología, Estación Mazatlán, UNAM, Apdo. Postal 811, Mazatlán, Sinaloa 82000, Mexico.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 108–109

AN EASTERN UNITED STATES RECORD FOR THE WESTERN INDO-PACIFIC CRAB, *HEMIGRAPSUS SANGUINEUS* (CRUSTACEA: DECAPODA: GRAPSIDAE)

Austin B. Williams and John J. McDermott

Abstract.—An ovigerous female of a western Indo-Pacific grapsid crab, *Hemigrapsus sanguineus,* is reported from New Jersey, U.S.A.

During a field trip on 24 Sep 1988, a student member (R. A. Nusbickel) of an invertebrate biology course at Franklin and Marshall College, Lancaster, Pennsylvania, discovered a live ovigerous grapsid crab at Townsends Inlet, Cape May County, New Jersey (39°07′06″N, 74°43′00″W). The crab was taken during an ebbing tide from a *Fucus* covered boulder in the mid-intertidal zone, under the south end of the highway bridge over the inlet. There was slight, but not recent, damage to the crab's left frontal margin. The crab was transported to Lancaster on the same day, where it was maintained at room temperature (ca. 23°) in a one gallon aquarium provided with rocks, *Fucus,* and shallow (ca. 2.5 cm) sea water (ca. 30 ppt). Water was changed daily, but the crab was not fed (however, it may have eaten some of the algae).

On 27 Sep some of the embryos were removed for microscopical examination. They were in the eyed stage (eye pigment 0.057 mm long × 0.029 mm wide), had considerable body pigment, a beating heart, and the yolk was ca. ¼–⅓ of the embryo volume. The eggs were nearly round—mean diameter 0.363 mm, SD 0.015, n = 20.

On 3 Oct the crab was discovered out of the water and oscillating its abdomen. It subsequently entered the water (as it usually did when JJMcD was about to change the water), where it released some embryos, aborted some "prezoeae" (no dorsal spines), and released one zoea having a dorsal spine. At this time the eyes were larger than on 27 Sep (0.114 mm long × 0.057 mm wide), and the yolk was reduced to ca. ⅛ of the embryo volume. Released embryos and zoeae were preserved in glycerine alcohol as were some from 4 Oct.

On the morning of 6 Oct the crab was found dead and was preserved. The crab and larvae are now deposited in the crustacean collection of the National Museum of Natural History, Smithsonian Institution (USNM 239154).

The crab was identified as *Hemigrapsus sanguineus* (de Haan, 1853) by reference to Sakai (1976) and by comparison with specimens in the USNM. The first zoea fits the description of the first zoea of that species (Kurata 1968) and resembles figures of that developmental stage redrafted by Rice (1980).

The carapace of the adult was distinctly patterned or mottled, there were small reddish rounded spots on the upper parts of the chelipeds, and the walking legs were banded. The following morphometric data were obtained with a dial caliper to the nearest 0.05 mm: carapace width 35.8, length 30.7; width between outer orbital teeth 24.95; abdomen width 4th segment 26.2, 5th 25.85, 6th 23.6, telson 14.1; right chela length 17.6, height 9.45; left chela length 17.65, height 9.35.

Hemigrapsus sanguineus is listed by Sakai (1976) as one of the commonest crabs of Japan, having a western Pacific distri-

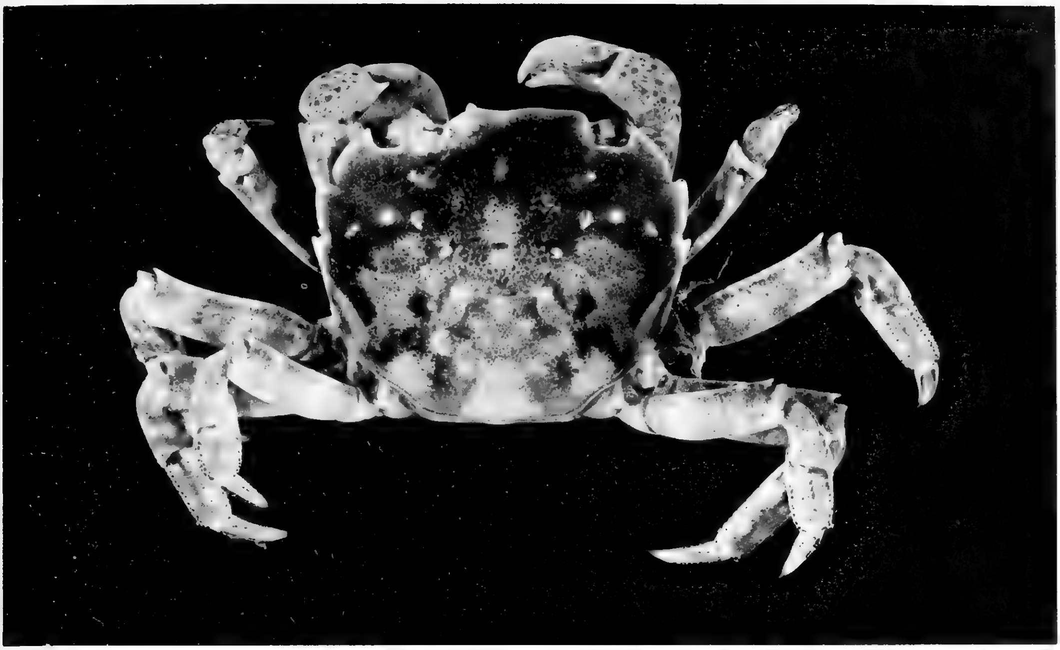


Fig. 1. *Hemigrapsus sanguineus*: mature female collected in New Jersey, U.S.A., dorsal view.

bution extending from Sakhalin, Korea, and north China to Hong Kong, and on all the coasts of Japan from Hokkaido to Okinawa. Occurrence of an ovigerous female in New Jersey may be one of the interesting but potentially distressing introductions that result from world shipping (Carlton 1979). If insemination had taken place before the crab was transported, it may have been a lone immigrant, but if not, at least one male of the species would have been introduced into New Jersey waters with it. The Cape May area should be monitored to see if a population has become established. No other records of this species in the United States are known to us.

Acknowledgment

We thank J. L. Richardson for reviewing the manuscript.

Literature Cited

Carlton, J. T. 1979. Introduced invertebrates of San Francisco Bay. Pp. 427–444 *in* T. J. Conomos, ed., San Francisco Bay the urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California, 493 pp.

Kurata, H. 1968. Larvae of decapod Brachyura of Arasaki, Sagami Bay. II. *Hemigrapsus sanguineus* (de Haan) (Grapsidae).—Bulletin of the Tokai Regional Fisheries Research Laboratory, No. 56:161–165.

Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura.—Transactions of the Zoological Society of London 35:271–424.

Sakai, T. 1976. Crabs of Japan and the adjacent seas.—Kodansha Ltd., Tokyo, 773 pp. (English text), 251 plates (many colored), 461 pp. (Japanese text), as 3 separate volumes.

(ABW) National Marine Fisheries Service-NOAA Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (JJMcD) Department of Biology, Franklin and Marshall College, Lancaster, Pennsylvania 17604-3003.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 110–119

A REDESCRIPTION OF *TIRON ANTARCTICUS* K. H. BARNARD, 1932 (CRUSTACEA: AMPHIPODA: SYNOPIIDAE) WITH AN UPDATED KEY TO THE SPECIES OF *TIRON* LILJEBORG, 1865

Krzysztof Jażdżewski

Abstract.—*Tiron antarcticus* K. H. Barnard (Amphipoda, Synopiidae) is redescribed; drawings of the appendages of the type specimen are presented. A new key for *Tiron* Liljeborg is proposed.

The description of *Tiron antarcticus* by K. H. Barnard (1932) is rather superficial and, with its single figure presenting pereopod 7, cannot satisfy the needs of amphipod taxonomists. This description was sufficient to regard the species as an undoubted member of the genus *Tiron* Liljeborg, but J. L. Barnard (1972) in his survey of the family was unable to put *T. antarcticus* in the key to the species of *Tiron* owing to this inadequate description. The present redescription based on the type material aims at filling this gap.

Material and Methods

The type material, the only available for the species, consists of two female specimens in the collection of the British Museum. They were kindly loaned to the author by this institution. Appendages of the right side of the holotype have been dissected and mounted on slides in polyvinyl lactophenol stained with lignin pink. Specimens and slides are deposited in the British Museum (Natural History) of London. Drawings of the appendages were done from temporary glycerol mounts prior to mounting in permanent slides that were used in final study of some details.

Holotype.—♀ 7.5 mm with bristled oostegites, coll. R.R.S. *William Scoresby,* St. WS 33, South Georgia, 21 Dec 1926, 54°59′S, 35°24′W; tow-net (horizontal haul 130 m, bottom 135 m). Fourteen amphipod species in the sample.

Paratype.—♀? immature 6.5 mm (neither oostegites nor penes traceable), coll. R.R.S. *Discovery,* Sta. 175, Bransfield Strait (South Shetlands), 2 Mar 1927, 63°17′S, 59°48′W; large dredge, 200 m, night. Thirty-three amphipod species in the sample. The only other species in both these two samples was *Epimeria excisipes* K. H. Barnard.

Tiron antarcticus K. H. Barnard
Figs. 1–5

Tiron antarcticus K. H. Barnard, 1932:148–149, fig. 86.

Body slender; head galeate and keeled, rostrum and lateral cephalic lobes sharp. Eyes present, rounded, dorsally appressed. Accessory eye not visible, possibly due to the long preservation of the material but note that accessory eyes were not mentioned by K. H. Barnard (1932: "lower eyes not traceable").

Last four (type) or three (paratype) thoracic segments as well as pleon segments excepting the last one, keeled; last thoracic segment and the said five pleon segments produced dorsally as incised teeth, the last two being the largest.

Antennae rather slender, comparatively

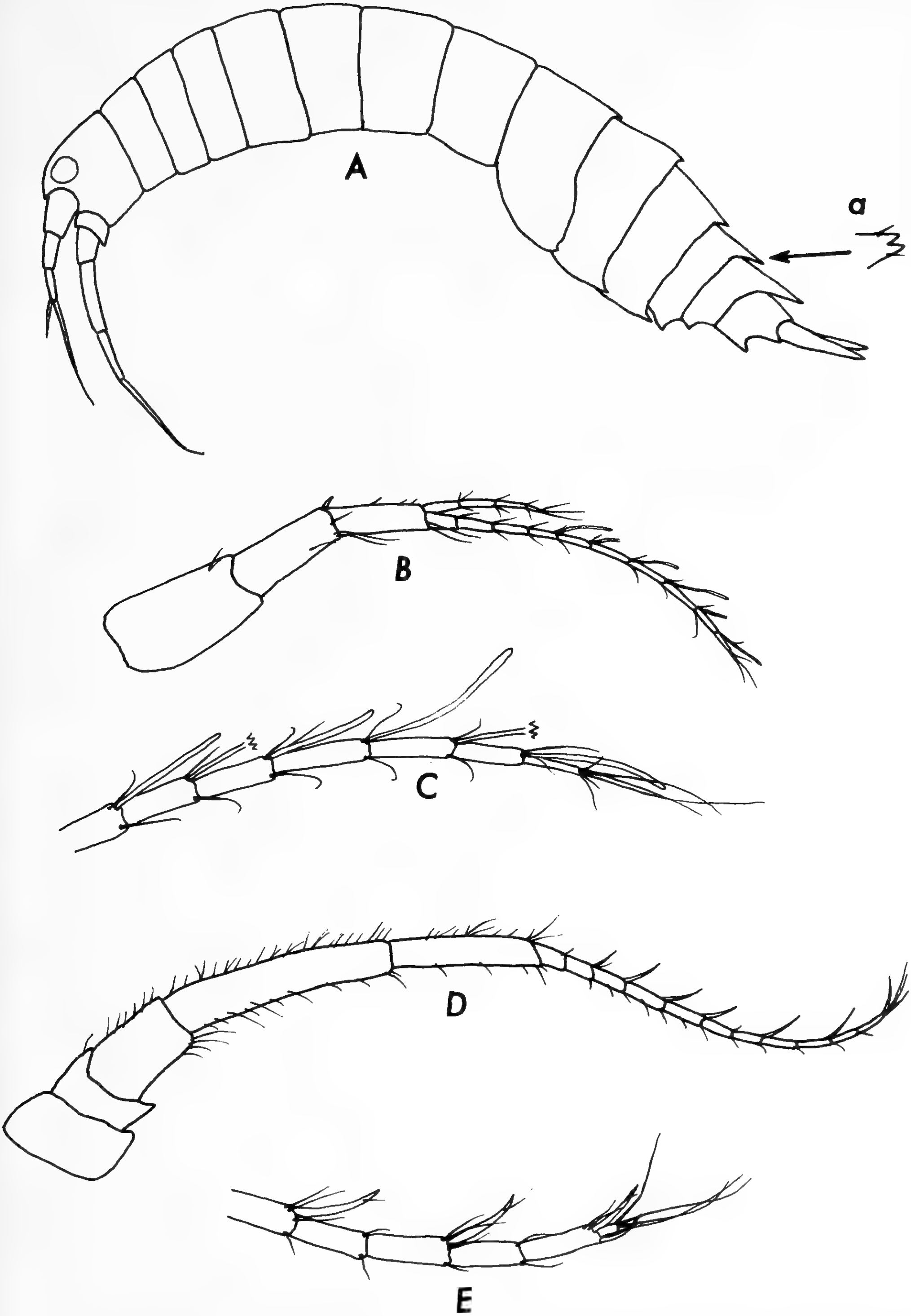


Fig. 1. *Tiron antarcticus,* female, holotype: A, Outline of body, thoracic and abdominal appendages omitted; a, Tooth of urosomite 2, dorsal view; B, Antenna 1; C, Distal part of antenna 1 primary flagellum; D, Antenna 2; E, Distal part of antenna 2 flagellum.

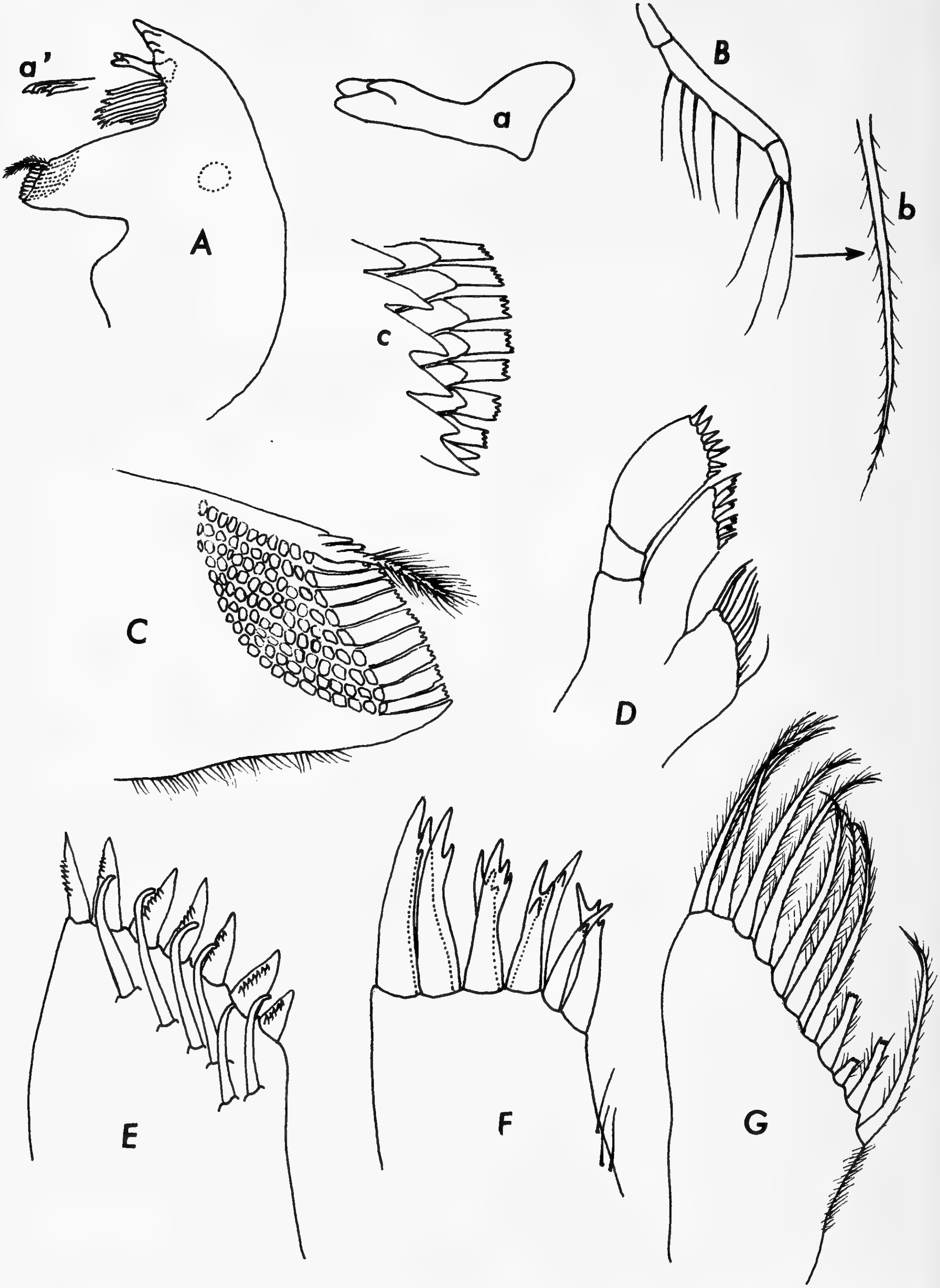


Fig. 2. *Tiron antarcticus,* female, holotype: A, Mandible (place of insertion of mandibular palp indicated by dotted circle); a, Lacinia mobilis; a′, Tip of spine of mandibular spine row; B, Mandibular palp; b, Seta of mandibular palp; C, Pars molaris of mandible; c, Edge of pars molaris; D, Outline of maxilla 1; E, Tip of maxillary palp; F, Tip of outer lobe of maxilla 1; G, Tip of inner lobe on maxilla 1.

short. Antenna 1 as long as about one-fourth of body length, antenna 2 as long as about one-third of body. Antenna 1 very weakly setose. Lengths of peduncular articles of antenna 1 in proportions of 14:11:9. Accessory flagellum long, 4-articulate; primary flagellum with 10 articles, several bearing long, slender aesthetascs (6 in type specimen).

Antenna 2 with elongate articles 4 and 5, their proportion as 3:2. Flagellum with 12 articles (in K. H. Barnard's description 10–11 articles) some of which distally armed with long, slender spines.

Mandible with columnar, triturative molar. Edge of molar provided with three rows of variously shaped teeth. Incisor with four teeth, lacinia mobilis with three teeth followed by row of about eight distally dentate parallel sided spines. Mandibular palp inserted at level of molar, 3-articulated; article 2 three times as long as article 1 and nearly four times as long as article 3; articles 2 and 3 armed with five and three long, delicately feathered setae, respectively.

Lower lip (not dissected) with well developed fleshy inner lobes, outer lobes widely separated.

Maxilla 1 with 2-articulate palp ending with marginal row of seven heavy, dentate spines and submarginal row of six curved setae. Inner plate with marginal row of 11 feathered setae, outer plate with row of nine apically dentate spines.

Maxilla 2: inner plate with medial, submarginal row of feathered setae and one more or less parallel marginal row of such setae; apically these rows ending with some curved, smooth setae and other apically forked and delicately serrated on one side. Outer plate apically with double row of mostly smooth and occasionally curved setae; some feathered setae bordering these rows from inner and outer sides.

Maxilliped with 5-articulate palp. Inner and outer plates apically with several characteristic robust, falcate spines.

Coxae 1–4 suboval to trapezoidal; coxa 4 dominated by coxa 3; coxae 5 and 6 divided by excavation into anterior and posterior lobes, coxa 7 small, pear-shaped. Coxae 1–3 with ventral margins rather richly setose, remaining coxae only with several short setules.

Pereopods 1 and 2 (gnathopods) simple. Article 6 (propus) narrow and elongate with posterior margin armed by several stout, feathered setae. Article 5 (carpus) especially long, nearly twice as long as article 6, densely setose on posterior margin but nearly naked anteriorly. Posterior margin of propus with row of spiny spines. Article 2 (basis) long and narrow, rather densely setose on both margins.

Pereopods 3 and 4 slender, weakly setose, with articles 4, 5 and 6 (merus, carpus and propus) armed posteriorly with some spines.

Pereopods 5–7 subequal in length, but pereopod 6 is longest, these appendages shiny, especially their articles 4, 5 and 6. Articles 2 and 3 of pereopod 6 rather densely setose anteriorly. A distinct increase in the size (width) of articles 2 (basis) and 4 (merus) observed in the sequence from pereopod 5 to pereopod 7; these articles in pereopod 7 with large, overhanging postero-distal lobes. Article 2 (basis) in pereopod 7 posteriorly crenulate with short setules; article 4 (merus) richly armed posteriorly with several groups of spines.

Dactyls of all pereopods ordinary, elongate, with subapical spine and short wire seta.

Six pairs of subovate coxal gills (II–VII pereon segments) and four pairs of oostegites (II–V).

Epimera 1–3 on their posterior margin with increasing number of notches with short setules. Surface of epimera near lower and posterior margins with delicate pilosity. Such pilosity also observed in some other places like outer margin of telson, distal parts of pereopods, mouthparts, etc. Postero-inferior angles of epimera distinctly pointed, this being not exactly consistent with original description of K. H. Barnard (1932: "with a very slightly produced point").

Pleopods normally developed with multiarticulated rami fringed with long feathered setae. Retinaculum composed of two hooked spines and robust feathered seta.

Uropod 1 distinctly longer than uropod 2; in both uropods peduncle and rami armed with spines; exopodites shorter than endopodites by ¼ to ⅓.

Uropod 3 with subequal lanceolate rami twice as long as peduncle. Exopodite 1-articulate, armed mainly with spines; inner margin with some short, feathered setae. Outer margin of endopodite naked, inner margin proximally with long feathered setae (majority of these setae broken in the type specimen but regular row of long feathered setae present in paratype), distally with spines.

Telson fully cleft, long, as long as two last pleon segments and nearly reaching apex of third uropods. Each lobe of telson with row of eight small spines, last one inserted apically in notch. Some few small setules present on upper surface.

Discussion

The nomenclature of *Tiron* species is disordered. The gender of this genus is masculine, the generic name coming from Greek "*τειρων*" (Liljeborg 1865). Therefore, the proper endings of adjectives are "-us" and not "-um" or "-a." According to the International Code of Zoological Nomenclature (1961: art. 30 on the agreement in gender) one should amend the following names of species of *Tiron*:

biocellata to *biocellatus*
intermedia to *intermedius*
spiniferum to *spiniferus.*

One feature that is considered to be of taxonomic importance was wrongly described for *T. antarcticus* by K. H. Barnard (1932) and then repeated in the diagnosis of this species by J. L. Barnard (1972), namely, the dorsal telson armament. It was said to consist of 4–5 "setules" whereas in fact on the upper surface of telson in *T. antarcticus* holotype there are seven small spines (excepting the apical eighth one) arranged in a somewhat irregular row.

According to J. L. Barnard (1972) *T. antarcticus* resembles *T. biocellatus,* which, on the other hand, has mouthparts very similar to *T. tropakis.* The features of *T. antarcticus* distinguishing it most clearly from *T. biocellatus* are the setose second article of the mandibular palp, the lack of dorsal crenulation of pleonites, and the armament of telson (only weak dorsal setules in *T. biocellatus*). In my opinion, the species most similar to *T. antarcticus* is *T. spiniferus*; it follows both from the description and from the figures by G. O. Sars (1895). Good discriminating characters are here the pleonite serration in *T. spiniferus* lacking in *T. antarcticus,* and smooth hind margin of pereopod 7 basis in *T. spiniferus* versus crenulated and setulose hind margin of this article in *T. antarcticus.*

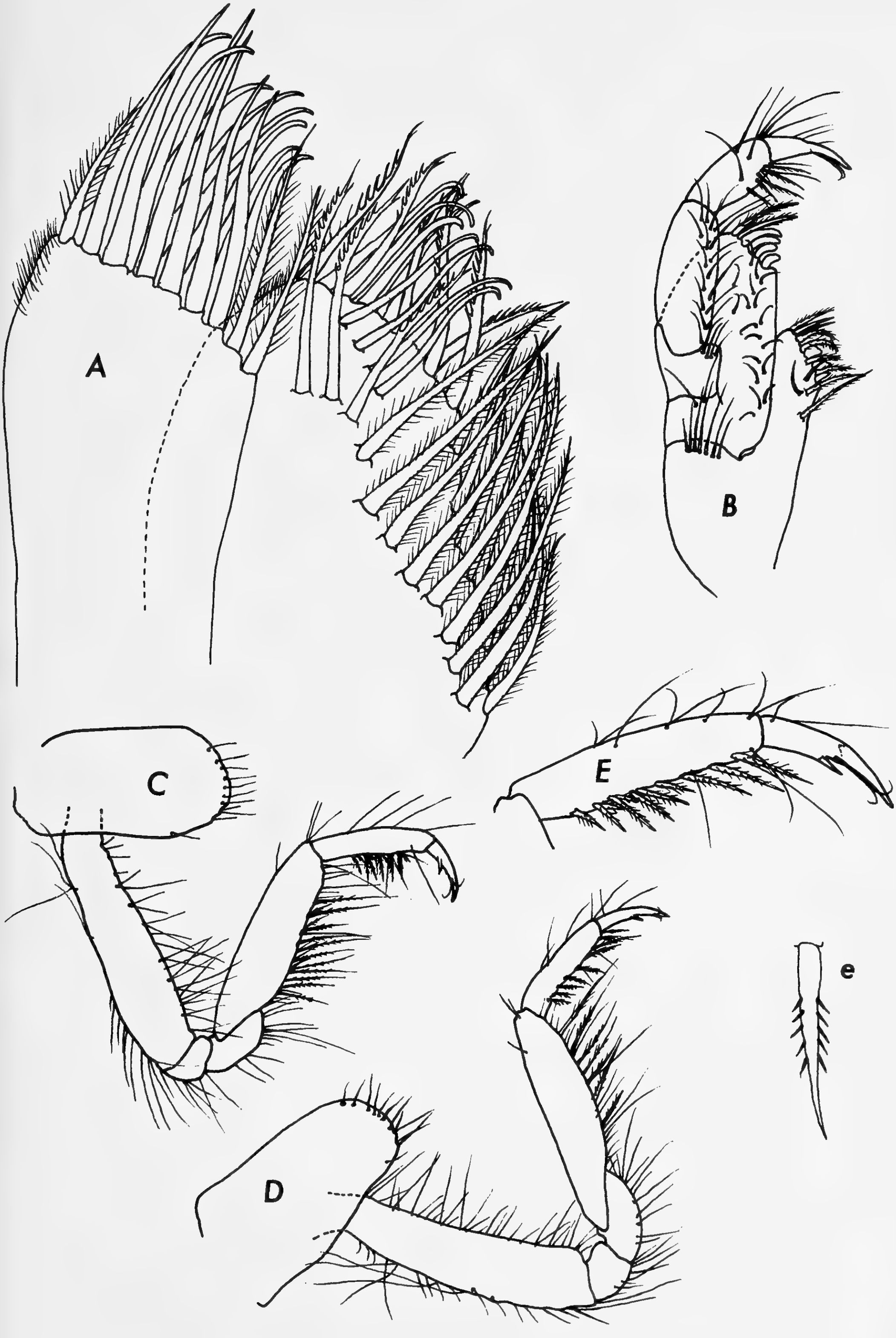
I follow the opinion of Just (1981) that the lack of mandibular palp is not a sufficient reason to create a new genus *Metatiron* Rabindranath (Rabindranath 1972, Ledoyer 1979). Just's survey table of features of eight stubby-legged *Tiron* species clearly shows that one cannot find any other important character to be shared by *Tiron* species lacking mandibular palp.

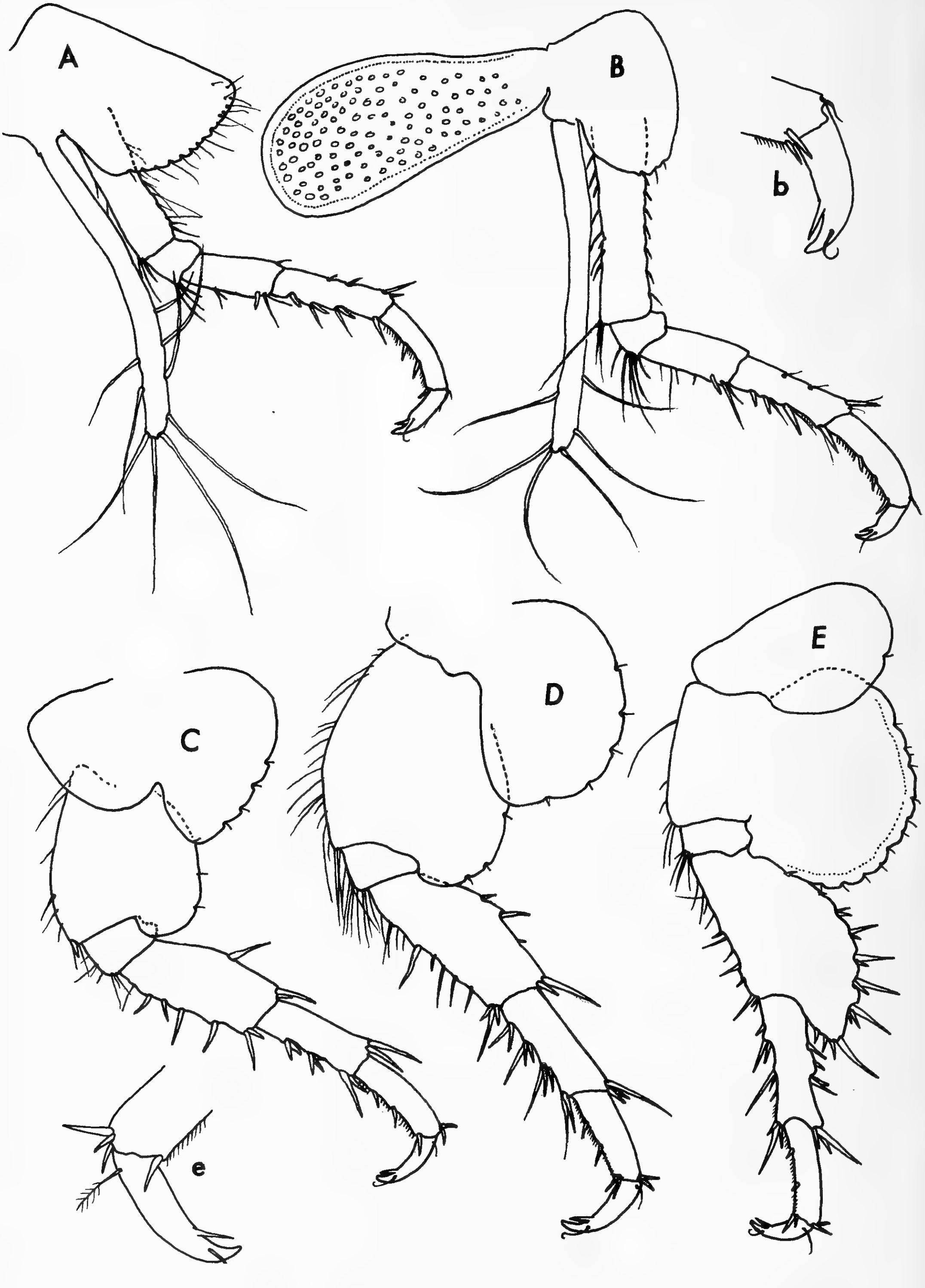
⟶

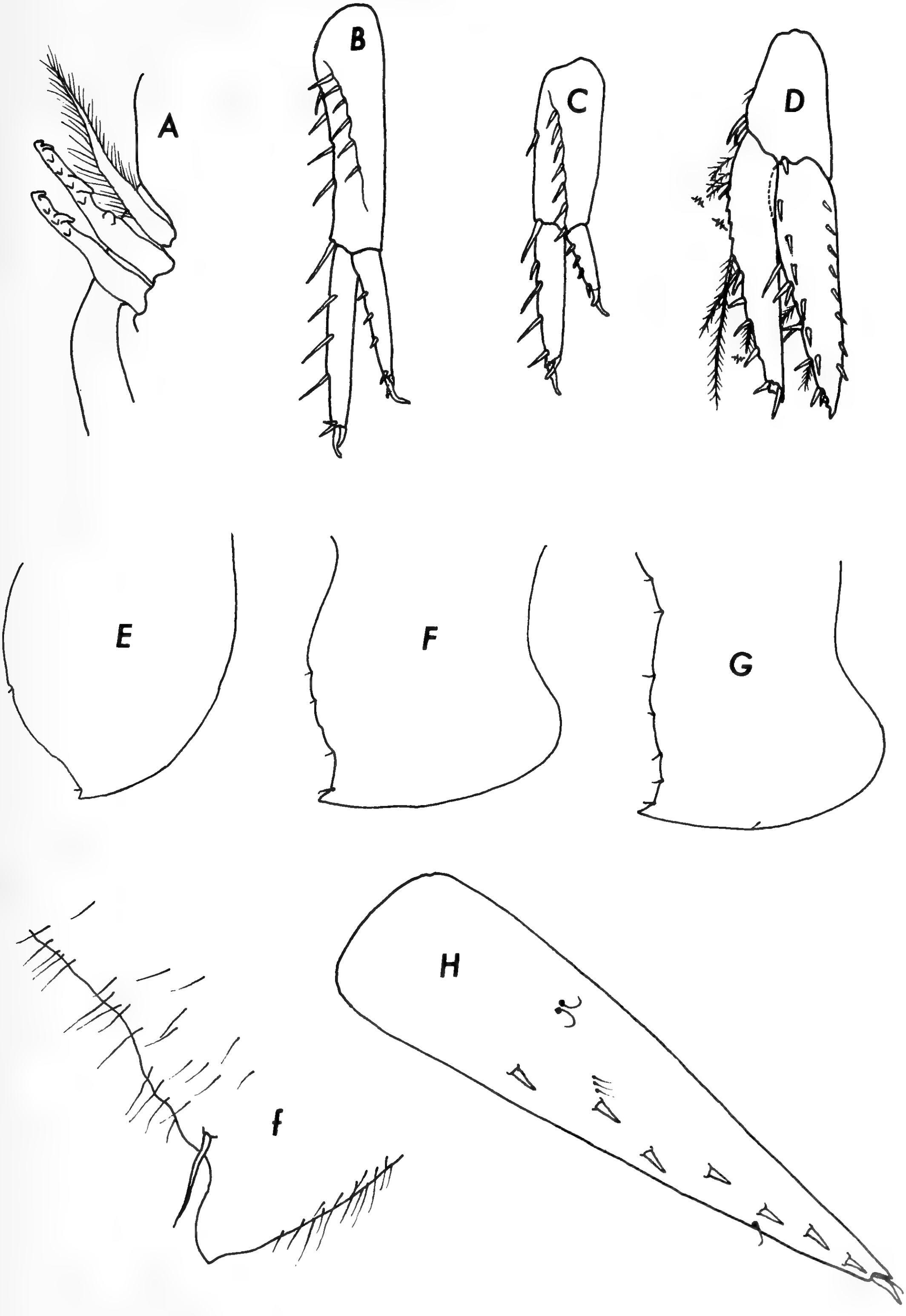
Fig. 3. *Tiron antarcticus,* female, holotype: A, Maxilla 2; B, Maxilliped; C, Pereopod 1 (=gnathopod 1); D, Pereopod 2 (=gnathopod 2); E, Propus and dactylus of pereopod 2; e, Spine on propus of pereopod 2.

Fig. 4. *Tiron antarcticus,* female, holotype: A, pereopod 3 with oostegite; B, Pereopod 4 with coxal gill and oostegite; b, Dactylus of pereopod 4; C, Pereopod 5; D, Pereopod 6; E, Pereopod 7; e, Dactylus of pereopod 7. P. 116.

Fig. 5. *Tiron antarcticus,* female, holotype: A, Retinaculum of pleopod 2; B, Uropod 1; C, Uropod 2; D, Uropod 3; E–G, Epimera 1–3; F, Posterodistal part of epimeron 2; H, Telson (half). P. 117.


A
B
C
D
E
e


A
B
b
C
D
E
e


A
B
C
D
E
F
G
f
H

On the other hand the diagnosis of *Tiron* by J. L. Barnard (1972, p. 83) should be amended by changing the information: "mandible with palp" to "mandible with or without palp," since 5 of 12 known species (*T. bellairsi, T. brevidactylus, T. caecus, T. triocellatus* and *T. tropakis*) lack mandibular palp.

I propose also two other small amendations to J. L. Barnard's diagnosis of *Tiron* (p. 83):

1) to add "usually" in the note that "hands (propus—K. J.) elongate, linear, lacking distinct spines"—since distinct spines are present in *T. brevidactylus* (see Rabindranath 1972);

2) to add "or overreaching" in the note: "uropod 1 reaching apex of uropod 2"—since this is the case at least in *T. antarcticus, T. bellairsi, T. brevidactylus* and *T. spiniferus.*

Key to the Genus *Tiron*

The key presented below is based on the literature data and mainly on the key by J. L. Barnard (1972) and the above mentioned table of Just (1981). The key is updated in the sense that four species are added—namely *T. caecus* Ledoyer, 1979, *T. bellairsi* Just, 1981, *T. triocellatus* Goeke, 1982 and the herein redescribed *T. antarcticus* K. H. Barnard. I have avoided using the feature of accessory eye since I believe that it can be overlooked in long preserved material due to fading. The key presented here will surely need further improvements since for many species we lack data on their morphological variability and sexual dimorphism. One should mention, for instance, that even such a seemingly conservative feature as the condition of the inner lobe of maxilla 1 can be unexpectedly sexually dimorphic as in *T. brevidactylus* where females have four setae and males none (Rabindranath 1972).

1. Pereopods 3–7 with stubby dactyls 2
– Pereopods 3–7 with ordinary, claw-shaped dactyls 10
2. Mandibular palp present 3
– Mandibular palp absent 4
3. Rami of uropod 3 pointed; outer plate of maxilliped normal, ovate 8
– Rami of uropod 3 truncate; outer plate of maxilliped with apical excavation guarded by falcate wings .... *T. thompsoni*
4. Telson with at least several subapical spines 5
– Telson lacking subapical spines 6
5. Posterior margin of basis of pereopod 7 with setules; accessory flagellum with five articles .... *T. tropakis*
– Posterior margin of basis of pereopod 7 smooth, without setules; accessory flagellum with two articles .... *T. caecus*
6. Palp of maxilla 1 slender, much shorter than outer plate; apical spines of uropod 3 exopodite long, nearly one-half of this article length .... *T. bellairsi*
– Palp of maxilla 1 stout, longer than outer plate; apical spines of uropod 3 exopodite short, many times shorter than this article length .. 7
7. Maxillary palp armed with spines and setae at tip only; basis of pereopod 7 lacking special double row of facial setules ..... *T. brevidactylus*
– Maxillary palp armed with setules along major part of its outer margin; basis of pereopod 7 with special double row of facial setules . ... *T. triocellatus*
8. Telsonic medial spine rows absent .... *T. altifrons*
– Telsonic medial spine rows present 9
9. Basis of pereopods 6 and 7 with posterior submarginal row of long, plumose setae .... *T. intermedius*
– Basis of pereopods 6 and 7 lacking special row of setae ..... *T. australis*

10. Posterior margin of basis of pereopod 7 crenulate and setulose 11
- Posterior margin of basis of pereopod 7 smooth ...... *T. spiniferus*

11. Telsonic lobes with row of small spines; article 2 of mandibular palp with several long setae .. *T. antarcticus*
- Telsonic lobes with at most one subapical spine; article 2 of mandibular palp lacking setae .... *T. biocellatus*

Acknowledgments

I am greatly indebted to the staff of the Department of Zoology, British Museum (Natural History), London, and namely to Dr. R. Lincoln, Mr. S. H. Halsey, Mrs. J. Ellis and Mrs. A. Gurney, first for entrusting me with the study of the type specimens of *Tiron antarcticus* and second for their patience in vast but courteous correspondence caused by my too long keeping of the material.

Thanks are due to Dr. J. L. Barnard, Smithsonian Institution, Washington, D.C., for his precious critical comments to this text and for his friendly help.

Literature Cited

Barnard, J. L. 1972. A review of the family Synopiidae (= Tironidae), mainly distributed in the deep sea (Crustacea: Amphipoda).—Smithsonian Contributions to Zoology 124:1–94.

Barnard, K. H. 1932. Amphipoda.—Discovery Reports 5:1–326.

Goeke, G. D. 1982. *Tiron triocellatus,* a new species of amphipod (Gammaridea: Synopiidae) from the western Atlantic and Gulf of Mexico.—Journal of Crustacean Biology 2:148–153.

International Code of Zoological Nomenclature. 1961. International Trust for Zoological Nomenclature, London, 176 pp.

Just, J. 1981. *Tiron bellairsi* sp. n. (Amphipoda, Synopiidae) from coral sand in Barbados with notes on behaviour.—Zoologica Scripta 10:259–263.

Ledoyer, M. 1979. Les gammariens de la pente externe du Grand Récif de Tuléar (Madagascar) (Crustacea Amphipoda).—Memorie del Museo Civico di Storia Naturale di Verona (2)2:1–150.

Liljeborg, W. 1865. Bidrag till kännedomen om underfamiljen Dysianassina inom underordningen Amphipoda bland kräftdjuren.—Upsala Universitets Arsskrift 1865, Upsala, Edquist and Berglund, 25 pp.

Rabindranath, P. 1972. Three species of Gammaridean Amphipoda (Crustacea) from the Trivandrum Coast, India.—Zoologischer Anzeiger 188: 84–97.

Sars, G. O. 1895. An account of the Crustacea of Norway. Volume 1. Amphipoda. Cammermeyers, Christiania, 711 pp.

Department of Invertebrate Zoology and Hydrobiology, University of Łódź, 12/16 Banacha s-t, 90-237 Łódź, Poland.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 120–126

ENSAYARA JUMANE, A NEW SPECIES FROM BELIZE, CARIBBEAN SEA (AMPHIPODA, LYSIANASSIDAE)

J. L. Barnard and James Darwin Thomas

Abstract.—*Ensayara jumane* is described from Belize. It differs from the west Mexican *Ensayara ramonella* J. L. Barnard (1964) in the excavate posteroventral margins of article 2 on pereopods 5–7, and the sparse (9 versus 25) setae on articles 5–6 of gnathopod 1. A new diagnosis for *Ensayara,* a key to species, list of species, references to original descriptions and geographic codes for each species are provided. This is the first record of the genus from the Caribbean Sea.

We present the genus *Ensayara* in the form to appear in Barnard & Karaman (1990), with a key to species, list of species, references to original descriptions and geographic distribution codes from Barnard & Barnard (1983) for each species.

Ensayara J. L. Barnard

Ensayara J. L. Barnard, 1964:79 (*Ensayara ramonella* J. L. Barnard, 1964, original designation).

Diagnosis.—Flagella of antennae short. Mouthparts forming quadrate bundle. Labrum and epistome each produced separately from the prebuccal complex, epistome blunt and weakly dominant in projection. Incisor weakly toothed at opposite corners; molar simple, large, palp attached opposite molar. Inner plate of maxilla 1 poorly setose (0–1); palp biarticulate, large. Inner and outer plates of maxilliped well-developed, palp strongly exceeding outer plate, dactyl well-developed.

Coxa 1 slightly shortened and partly covered by coxa 2, scarcely tapering.

Gnathopod 1 short, simple, article 6 longer than 5, dactyl small, gnathopod 2 minutely chelate, article 6 slightly shorter than article 5.

Pereopod 3 strongly prehensile, parachelate, hand very broad, palm crenulate or spinose.

Inner ramus of uropod 2 without notch. Uropod 3 short, peduncle elongate, inner ramus slightly shortened, outer ramus 2-articulate. Telson short, entire.

Variables.—Peduncle of antenna 1 with three distinct articles (*iara*); coxa 1 large and ordinary (*dentaria*; dactyl of pereopod 7 slender and even (*ramonella*); stunted (*carpinei*).

Remarks.—Better microscopy has resolved article 3 of antenna 1 which is small and mostly obsolescent medially, but has 1.5 rows of facial aesthetascs present.

Relationship.—Like *Endevoura* in the enlarged prehensile pereopod 3 but dactyl of maxilliped unguiform, not bulbous.

Species.—*angustipes* Ledoyer, 1978, 1986 [693]; *carpinei* Bellan-Santini, 1974 [340B]; *dentaria* Hirayama, 1985 [391]; *iara* Lowry & Stoddart, 1983 [776s]; *jumane* Barnard & Thomas, new species, herein [471]; *microphthalma* Ledoyer, 1986 [698]; *ramonella* J. L. Barnard, 1964 [376].

Marine, cosmopolitan in low latitudes, 1–1900 m, 7 species.

Key to the Species of *Ensayara*

1. Article 2 of gnathopod 1 toothed, mandibular palp article 3 with 7 D-setae .... *dentara*
– Article 2 of gnathopod 1 smooth,

mandibular palp article 3 with 1–2 D-setae 2
2. Inner rami of uropods 1–2 with 1 spine each 3
– Inner rami of uropods 1–2 without spines 4
3. Mandibular palp article 3 with 2 D-setae, inner ramus of uropod 3 reaching apex of article 1 on outer ramus, dactyl of pereopod 7 thick .... *carpinei*
– Mandibular palp article 3 with 1 D-seta, inner ramus of uropod 3 not reaching apex of article 1 on outer ramus, dactyl of pereopod 7 ordinary .... *iara*
4. Lateral cephalic lobe very sharp, coxae 2–3 with dense, short setae .... *microphthalma*
– Lateral cephalic lobe blunt, coxae 2–3 with sparse, tiny setae 5
5. Article 2 of pereopod 7 excavate .... *jumane* n. sp.
– Article 2 of pereopod 7 not excavate 6
6. Carpus of pereopod 3 slender (L × W = 18:6), article 3 of antenna 1 free .... *angustipes*
– Carpus of pereopod 3 stout (L × W = 18:11), article 3 of antenna 1 telescoped into article 2 .... *ramonella*

Ensayara jumane, new species

Figs. 1–3

Etymology.—Named for a tribe of Uto-Aztecan Indians from Central America, name a noun in apposition.

Diagnosis.—Lateral cephalic lobe stubby, not subacute; eyes large, deeply pigmented; flagellum of antenna 2 not stubby; article 3 of mandibular palp with only 2 inner (C) setae; palp of maxilla 1 uniarticulate; dactyl of maxilliped with strong nail; coxae 1–4 with 0–1 ventral seta or sparse tiny setules, no dense setal clusters; articles 4–5 of pereopod 3 elongate, article 4 expanded (not linear); article 2 of pereopods 5–7 with posterior setule notches, of pereopods 6–7 posteroventrally excavate; inner ramus of uropods 1–2 naked.

Description.—Lateral cephalic lobes lacking cavity below for insertion of antenna 2; eyes black, one row of clear ommatidia exposed peripherally. Antennae 1–2 very short, reaching equally, article 3 of antenna 1 obsolescent medially, armed with 1.5 rows of aesthetascs in callynophore, primary flagellum with 5 articles, accessory flagellum with 3 articles. Gland cone weak, flagellum of antenna 2 with 5 articles.

Prebuccal mass weakly humped anteriorly. Incisors smooth in middle, convex, laciniae mobiles absent, 2 rakers present, molars massive, subconical with weak spinoserrate distomedial margin, otherwise non-triturative; palp article 1 scarcely elongate, article 2 with 2 apicolateral setae, article 3 with 1–2 inner setae (probably C-type), apex obliquely truncate, with 4 E-setae. Lower lip with fused inner lobes forming broad truncate line, outer plates widely spread, lacking cones, mandibular lobes large. Inner plate of maxilla 1 large, subconical, naked; outer plate with 7 weakly serrate spines, medial margin with thick setules, palp 1-articulate, apex with 3–4 thick and one thin spines. Inner plate of maxilla 2 very short, with 2 apical setae, outer plate more extended but small, with 5 apical setae and 2 basomedial setae on dorsal face. Inner plates of maxillipeds long, slender, with one apicofacial setule and weak, almost fully fused tooth spines on apices, outer plates subfalcate, with several nearly fused tooth-spines on medial margins; palp slender, poorly armed, article 3 with apical comb, dactyl unguiform, with thick apical nail and longitudinal comb.

Coxae 1–4 increasingly elongate, anterior margin of coxa 1 strongly convex, with distal notch and seta, one short midventral but submarginal setule; coxa 2 with 7 tiny and 1 long posteroventral setules; coxa 3 with same; coxa 4 with 15 tiny setules, no corner seta. Article 3 of gnathopod 1 swollen, article 4 tiny, article 5 scarcely lobate, article 6 strongly tapering, simple, dactyl stubby and setulate. Article 3 of gnathopod 2 elongate, articles 5–6 covered with straw-setules, palm weakly produced. Pereopod 3 grossly subchelate, articles 5–6 attached in eusirid fashion (tenuously), humped base of article 6 flexing into hollow of article 5, palm lined with partially chisel-shaped tooth spines, dactyl fitting palm. Pereopod 4 of normal gammaridean structure, with one unlocking setule. Article 2 of pereopod 5 broadly pyriform, posteriorly lobate, margin weakly crenulosetulate; pereopods 6–7 slightly longer than 5, article 2 more narrowly pyriform, posteroventral margin weakly concave, weakly lobate.

Posteroventral corner of epimera 2–3 minutely extended as tooth. Uropods 1–2 poorly spinose, one spine each on dorsolateral and dorsomedial apex of peduncles, uropod 1 with basodorsal spine laterally, each outer ramus with one dorsal spine at midlength, apical nails on rami almost fully immersed. Uropod 3 with one apical spine on peduncle, inner ramus not reaching apex of article 1 on outer ramus, latter with apicomedial tooth, rami serrate apicomedially, article 2 of outer ramus prominent. Telson ovate, with 2 pairs of dorsodistal penicillate setules.

Female "w."—One large egg (room for 2 more). Oostegites vestigial or absent, coxa 5 with tiny broad flap-lobe tightly appressed to proximal base of coxa, lobe bearing 4 vestigial setules; coxa 4 with similar lobe lacking setules, no oostegites found on coxae 2-3. Coxae 1-4 with ventral submarginal setules much longer than in male, whip-like, formula for coxae 1–4 = 1-6-6-14. Gills sac-like, sharply tapering apically, not plaited, lacking basal lobes.

Color.—Ten minutes after preservation, body white, each pereonite with concentrated orange blotch laterally.

Holotype.—USNM 242012, male "t" 2.38 mm.

Type-locality.—Carrie Bow Cay, Belize, Central America, 18 Jun 1982; south side of channel between Carrie Bow Cay and South Water Cay, formalin wash of coral rubble from overhangs 6 m, J. D. Thomas, collector, station JDT-Bel 75C.

Paratypes.—Type locality, male "v" 2.20 mm, female "w" 2.21 mm and 15 other specimens.

Relationship.—Differing from the west Mexican *Ensayara ramonella* J. L. Barnard (1964) in the excavate posteroventral margins of article 2 on pereopods 5–7, and the sparse (9 versus 25) setae on articles 5–6 of gnathopod 1.

Closely similar to *E. angustipes* Ledoyer, 1978, from Mauritius, but differing in the excavate article 2 of pereopod 7, the lack of spines on the inner rami of uropods 1–2, the uniarticulate palp of maxilla 1, and the presence of a strong nail on the dactyl of the maxilliped.

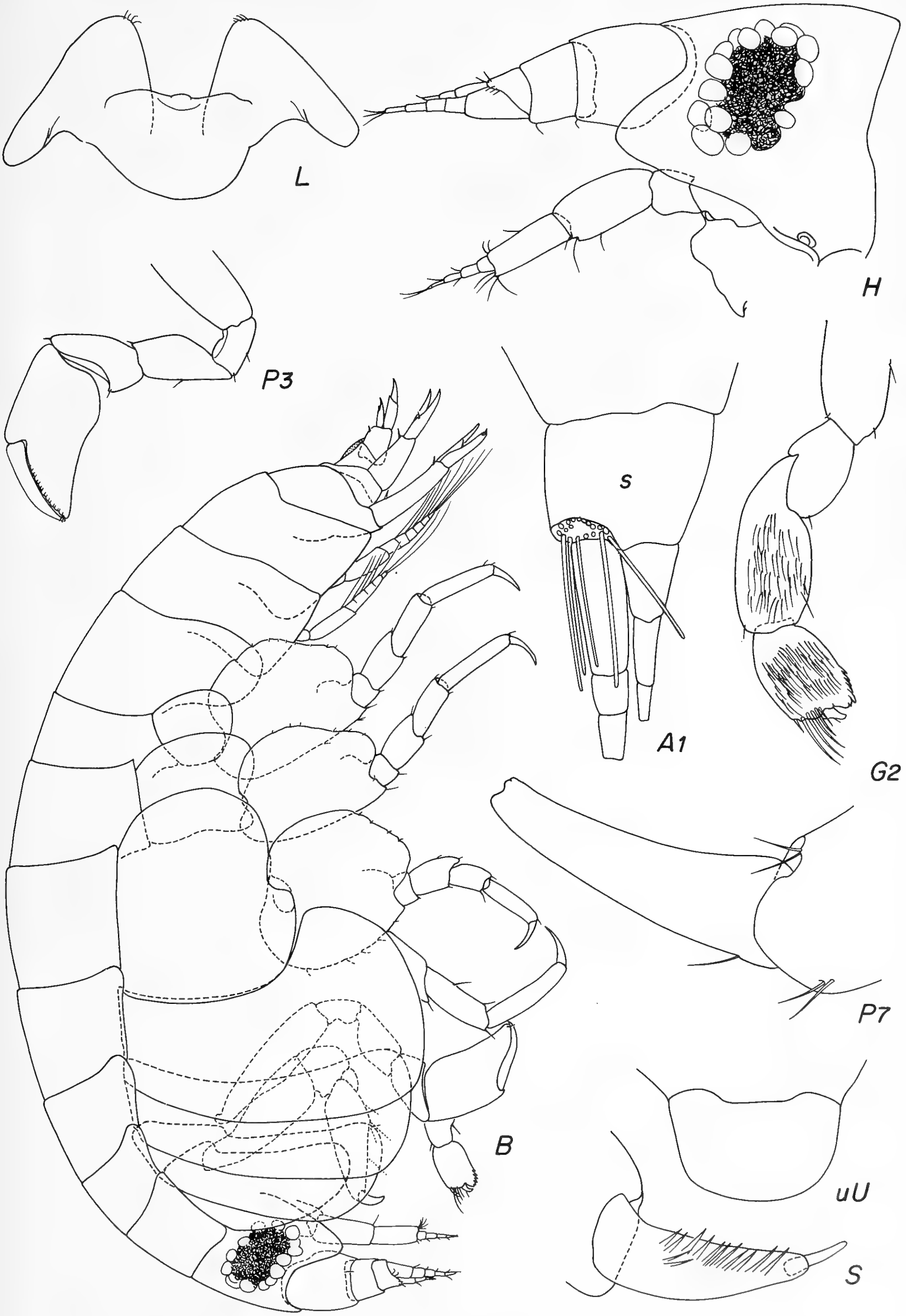
We are not certain about the exactitude of observations in the literature on the con-

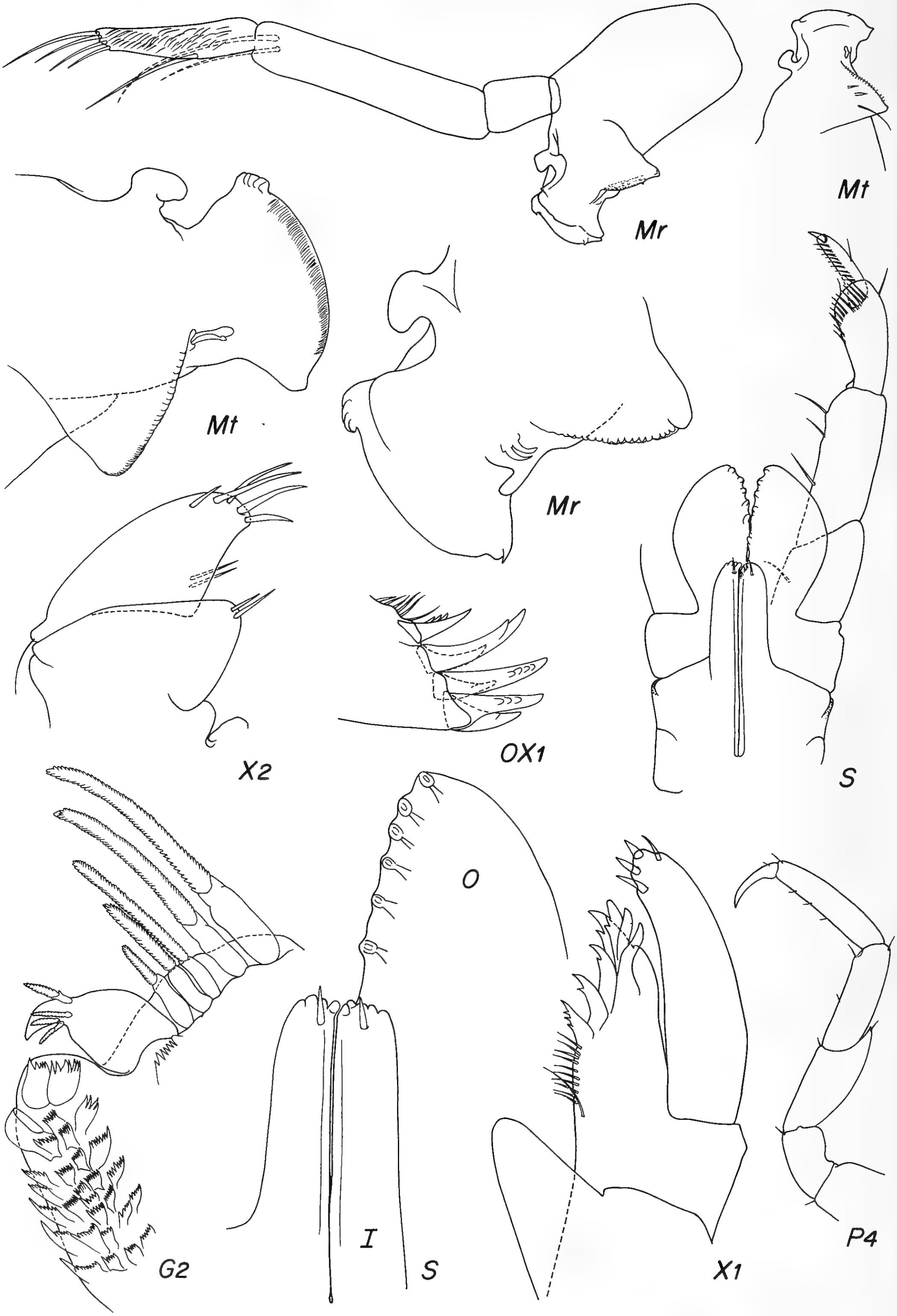
→

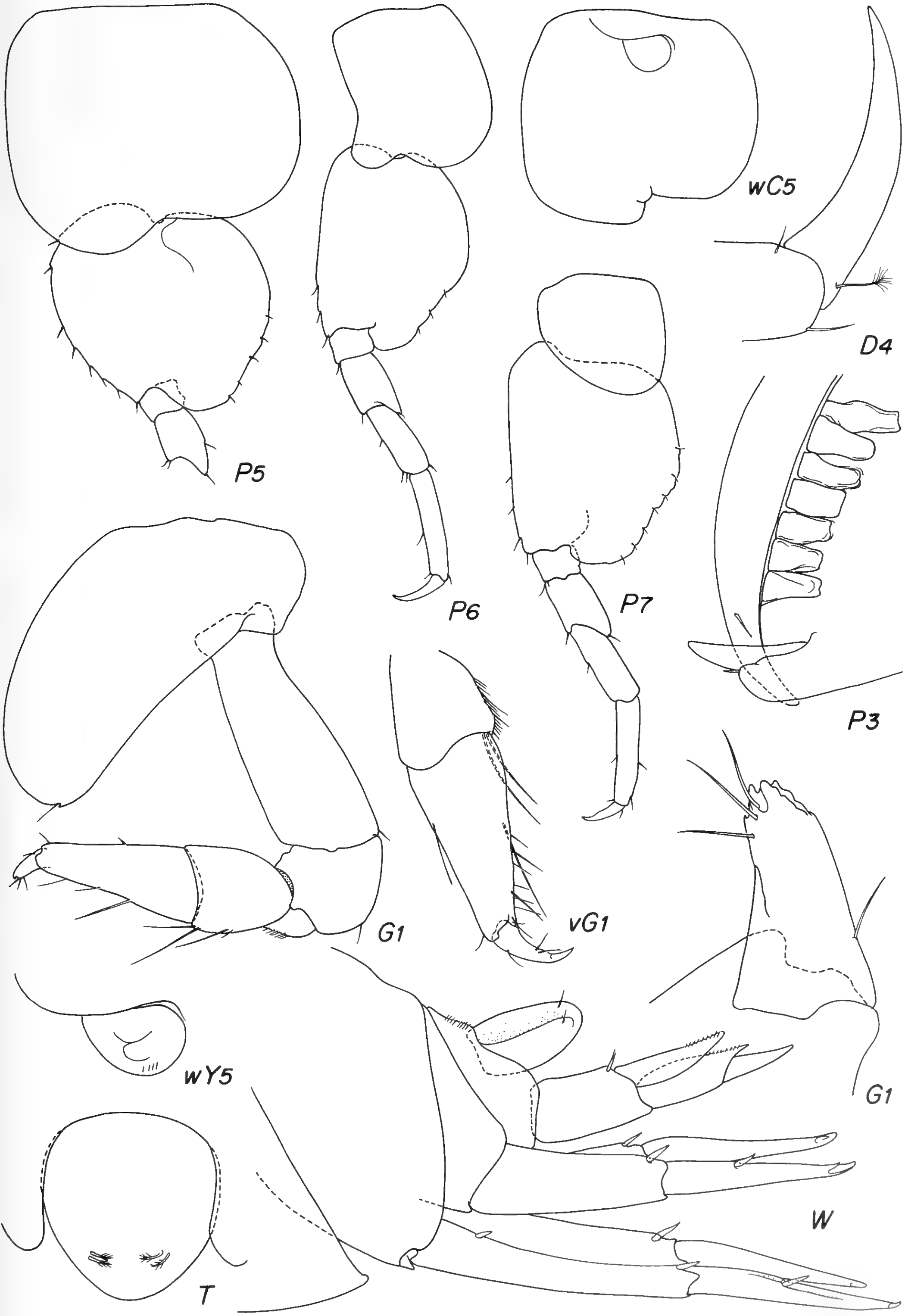
Fig. 1. *Ensayara jumane,* unattributed figures = holotype, male "t" 2.38 mm; u = male "v" 2.20 mm. Legend: Capital letters in figures refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as described below: A, antenna; B, body; C, coxa; D, dactyl; G, gnathopod; H, head; I, inner plate or ramus; L, labium; M, mandible; O, outer plate or ramus; P, pereopod; S, maxilliped; T, telson; U, upper lip; Y, oostegite; r, right; s, setae removed; t, left.

Fig. 2. *Ensayara jumane,* holotype, male "t" 2.38 mm, p. 124.

Fig. 3. *Ensayara jumane,* unattributed figures = holotype, male "t" 2.38 mm; v = male "v" 2.20 mm; w = female "w" 2.21 mm, p. 125.


L
H
P3
s
A1
G2
B
P7
uU
S


Mt
Mr
Mt
Mr
S
X2
OX1
G2
O
I
S
X1
P4


P5
P6
wC5
D4
P7
P3
G1
vG1
G1
wY5
W
T

dition of the nail on the maxillipedal dactyl and the presence or absence of a second (basal) article on the palp of maxilla 1 and these must be confirmed in several of the species by better flattening and higher power microscopy.

Distribution.—Belize, 6 m.

Acknowledgments

Fieldwork for this report was supported by Smithsonian's CCRE committee; this is CCRE Contribution No. 261; we thank Dr. Klaus Ruetzler, head of this program, and Mike Carpenter for their assistance. The second author was supported by NSF Grant 8515186. Linda Lutz of Vicksburg, Mississippi, inked our drawings.

Literature Cited

Barnard, J. L. 1964. Marine Amphipoda of Bahía San Quintin, Baja California.—Pacific Naturalist 4:55–139.

———, & C. M. Barnard. 1983. The freshwater Amphipoda of the world. Mt. Vernon, Virginia: Hayfield Associates, 2 volumes, 849 pp.

———, & G. S. Karaman. 1990. The families and genera of marine gammaridean Amphipoda, except Gammaroidea.—Records of the Australian Museum, Supplement (in press).

Bellan-Santini, D. 1974. Amphipodes bathyaux de Méditerranée.—Bulletin de l'Institut Océanographique, Monaco 721(1427):20 pp., 8 figs.

Hirayama, A. 1985. Taxonomic studies on the shallow water gammaridean Amphipoda of west Kyushu, Japan V. Leucothoidae, Lysianassidae (*Prachynella, Aristias, Waldeckia, Ensayara, Lepidepecreum, Hippomedon* and *Anonyx.*—Publications of the Seto Marine Biological Laboratory 30:167–212.

Ledoyer, M. 1978. Amphipodes gammariens (Crustacea) des biotopes cavitaires organogenes recifaux de l'Île Maurice (Océan Indien).—The Mauritius Institute Bulletin 8:197–332.

———. 1986. Crustacés amphipodes gammariens familles des Haustoriidae à Vitjazianidae.—Faune de Madagascar 59:599–1112.

Lowry, J. K., & H. E. Stoddart. 1983. The shallow-water gammaridean Amphipoda of the subantarctic islands of New Zealand and Australia: Lysianassoidea.—Journal of the Royal Society of New Zealand 13:279–294.

(JLB) NHB-163, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560; (JDT) Reef Foundation, P.O. Box 569, Big Pine Key, Florida 33043.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 127–130

A RANGE EXTENSION TO THE NORTH FOR *MACROCHIRIDOTEA GIAMBIAGIAE* TORTI AND BASTIDA (CRUSTACEA: ISOPODA: VALVIFERA)

Elizabeth Harrison-Nelson and Thomas E. Bowman

Abstract.—*Macrochiridotea giambiagiae* is reported from Rio de Janeiro, Brazil, and slight differences from the original description by Torti and Bastida (1972) are noted. This new record extends the known range of the species more than 1000 km to the north.

The genus *Macrochiridotea* Ohlin, 1901 comprises 11 species confined to the Southern Hemisphere (New Zealand, Falkland Islands, east and west coasts of South America from 23°12′S to 49°29′S): *M. michaelseni* Ohlin, 1901, *M. stebbingi* Ohlin, 1901, *M. kruimeli* Nierstrasz, 1918, *M. setifer* Menzies, 1962, *M. uncinata* Hurley & Murray, 1968, *M. robusta* Bastida & Torti, 1969, *M. giambiagiae* Torti & Bastida, 1972, *M. marcusi* Moreira, 1973, *M. lilianae* Moreira, 1973, *M. mehuinensis* Jaramillo, 1977, *M. australis* (Richardson, 1911) (transferred from *Chiriscus* by Poore 1984). It has been been found at depths ranging from the intertidal to 309 meters, and on substrates varying from mud with fine sand to coarse quartz and calcareous sands. Specimens of this genus may reach 15 mm in length. Moreira (1973) reviewed the genus and provided a revised diagnosis which includes the statement that the inner lobe of maxilla 1 bears 2 apical setae. In fact this lobe bears a single seta in *M. giambiagiae* and the number of setae is unknown in *M. kruimeli, M. michaelseni, M. setifer,* and *M. stebbingi.* The remaining 6 species all have 2 setae.

We report herein a new record for *M. giambiagiae,* which extends this species' known range north by about 5° (1000 km), and slightly increases the known depth range, from 2 to 7 m. Its distribution thus extends from the northern to the southern limits of the Eastern South American Warm Temperate Region as defined by Briggs (1974). It is the most northerly occurring member of the genus.

It is somewhat surprising that *M. giambiagae,* published in 1972 and recorded in the Zoological Record for that year (published in 1978), is not listed in subsequent papers on *Macrochiridotea* by other authors (Moreira 1973, Epelde-Aguirre & Lopez 1975, Jaramillo 1977, Poore 1984), and is not included in Moreira's 1972 review of the genus.

Macrochiridotea giambiagiae
Torti & Bastida
Fig. 1

Macrochiridotea giambiagiae Torti & Bastida, 1972: passim. (Mar del Plata, Argentina; Chuy, Uruguay; Cassino, Brazil).

Material.—Copacabana Beach, Rio de Janeiro, Brazil, 150–300 m from shore in coarse quartz sand, 5–7 m, leg. James D. Thomas, 3–4 May 1985, 1 ♂ (3.5 mm), 2 ♀♀ (1 ovigerous—4.5 mm, 1 non-ovigerous—5.5 mm), 4 juveniles, USNM 241981.—Villa Gesell, Buenos Aires, Argentina, ♀ paratype of *M. giambiagiae* (5.5 mm), USNM 139314.

Description.—Length 1.75 to 5.5 mm. Our specimens have the features diagnostic of *M. giambiagiae,* i.e., dorsal surface of body smooth; head without tubercles, setose on lateral margins, slightly convex dorsally, lateral incisions shallow, eyes small, faintly pigmented (Fig. 1a); 1 seta on endopod of maxilla 1 (Fig. 1c); pereopods 2 and 3 without dactyl (Fig. 1g); male pleopod 2 like that shown by Torti & Bastida (Fig. 1i).

Our material differs from Torti & Bastida's description as follows: article 4 of antenna 1 about ¾ rather than ½ as long as article 2 and with 4 rather than 2 setae on distal margin (Fig. 1b); terminal article of flagellum with 3 rather than 2 apical setae. Exopod of maxilla 1 with 12 spines (Fig. 1c), type material with 9. Palp of maxilla 2 with 5 setae (Fig. 1d), type material with 4; endopod with 8 setae, type material with 6. Tip of pleotelson with 2 small setae medial to posterior pair of long setae (Fig. 1h). The small setae are not shown by Torti & Bastida and could not be seen in our paratype.

Torti & Bastida (1972:21–22) mention that pleonite 1 of *M. giambiagiae* tends to telescope into pereonite 7 and may not be visible in dorsal view. This was true for the 2 largest (4.5 and 5.5 mm) specimens from Rio de Janeiro, but the first segment was visible on the smaller specimens (1.75–3.5 mm).

Torti & Bastida did not note any sexual dimorphism in their 19 females and 3 males, except the appendix masculina on the male pleopod 2, nor did they note any differences between the adult male holotype and another adult male and juvenile male included with their material.

The female paratype of *M. giambiagiae* (USNM 139317, 5.5 mm) from Villa Gesell, Province of Buenos Aires, Argentina (37°28′S, 57°07′W) appears to conform to the description and figures of Torti & Bastida except that the distal process of the carpus of pereopod 1 bears several articulated setae as do our Rio de Janeiro specimens (Fig. 1f). Torti & Bastida's illustrations, which depict the holotype male (4.3 mm) collected at Mar del Plata, Argentina (38°03′18″S, 57°32′30″W), show nonarticulated setae. Our male (3.5 mm) bears articulated setae, thus this characteristic does not appear to be size/age/sex related.

The differences between our specimens and those of Torti & Bastida are slight compared to those separating species of *Macrochiridotea*. If, however, additional collections should show them to be constant, the possibility of assigning distinct specific or subspecific status to the Rio de Janeiro form would have to be considered.

Acknowledgments

We thank James D. Thomas of the Reef Foundation, Big Pine Key, Florida, for providing us with the specimens.

Literature Cited

Bastida, R., & Torti, M. R. 1969. Un nuevo isópodo del genero *Macrochiridothea* de las costas Argentinas (Valvifera, Idoteidae).—Neotropica 15(47):65–72. [In Spanish.]

Briggs, J. C. 1974. Marine zoogeography. New York, McGraw Hill, 475 pp.

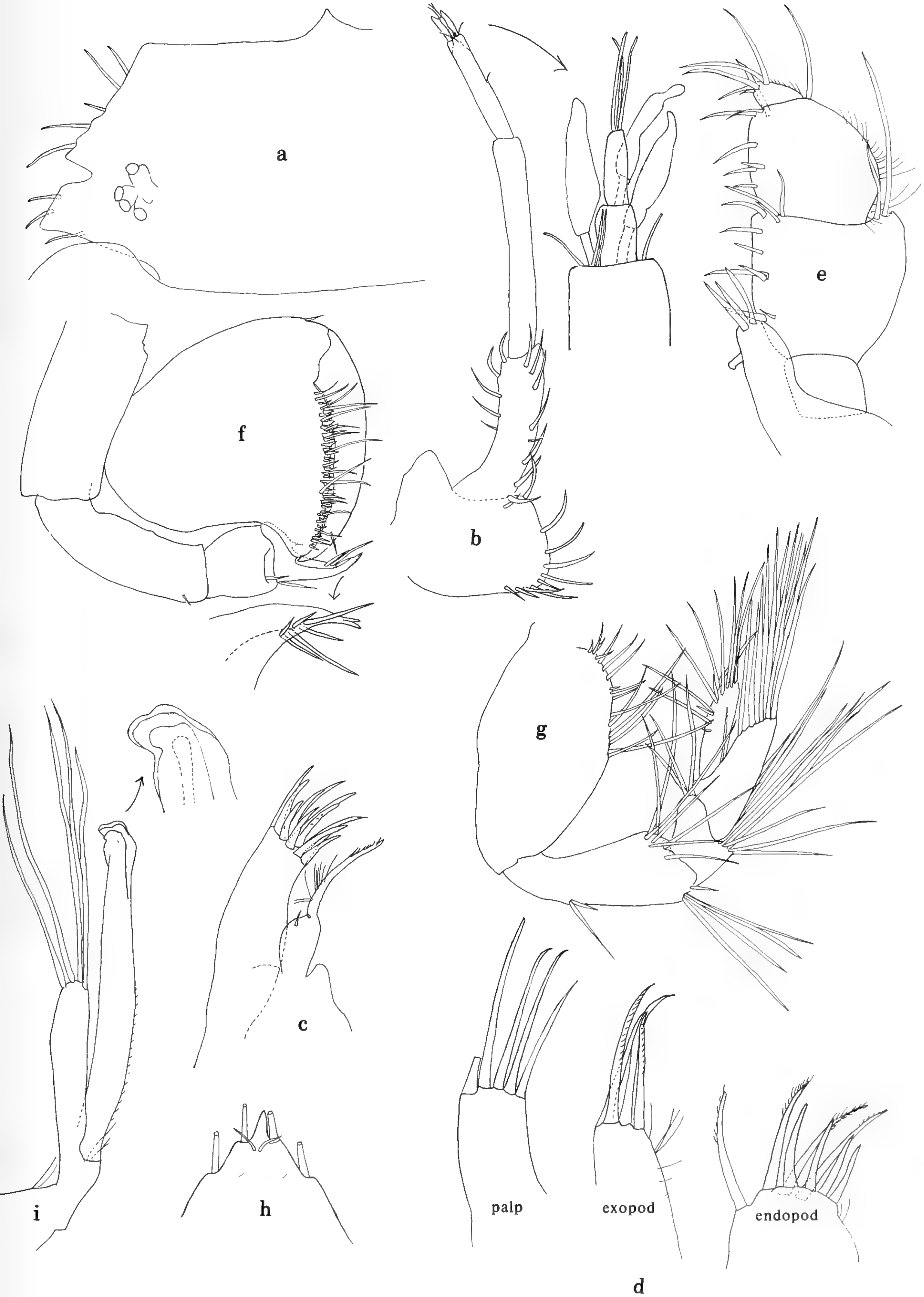
Epelde-Aguirre, A., & Lopez, M. T. 1975. Zonación en el sustrato arenoso de playa Blanca, Bahía de Coronel y observaciones sobre crustáceos poco frecuentes.—Boletín de la Sociedad Biológica de Concepción 49:161–170. [English summary.]

Hurley, D. E., & Murray, R. H. 1968. A new species of *Macrochiridothea* from New Zealand, with notes on the idotheid subfamily Chaetilinae (Crustacea Isopoda: Valvifera.—Transactions of the Royal Society of New Zealand (Zoology) 10(26):241–249.

Jaramillo, E. 1977. *Macrochiridotea mehuinensis* (Valvifera, Idoteidae), nuevo isópodo marino de las costas del sur de Chile.—Studies on the Neotropical Fauna and Environment 12(1):71–80. [English summary.]

→

Fig. 1. *Macrochiridotea giambiagiae,* female, USNM 241981: a, Head, dorsal view; b, Antenna 1; c, Maxilla 1; d, Maxilla 2; e, Maxilliped; f, Pereopod 1, tip of carpus enlarged (medial view); g, Pereopod 2; female, USNM 241982: h, Tip of pleotelson; male, USNM 241983: i, Pleopod 2, endopod with appendix masculina.


a
b
e
f
g
i
c
h
palp
exopod
endopod
d

Menzies, R. J. 1962. The Zoogeography, ecology, and systematics of the Chilean marine isopods. Reports of the Lund University Chile Expedition 1948–49:42.—Lunds Universitets Årsskrift, N.F. Avd. 2, 57(11):1–62.

Moreira, P. S. 1972. On the distribution of species of *Macrochiridothea* Ohlin, 1901 in southern Brazil (Crustacea: Isopoda: Valvifera).—Revista Brasileira de Biología (Rio de Janeiro) 32(3): 395–399.

———. 1973. Species of *Macrochiridothea* Ohlin, 1901 (Isopoda, Valvifera) from southern Brazil, with notes on remaining species of the genus.—Boletim Instituto Oceanográfico, Sao Paulo 22: 11–47.

Nierstrasz, H. F. 1918. Alte und neue Isopoden.—Zoologische Mededeelingen 4(2):103–142, pls. 9, 10.

Ohlin, Axel. 1901. Isopoda from Tierra del Fuego and Patagonia. 1. Valvifera.—Svenska Expeditionen till Magellansländerna 2(11):261–306.

Poore, G. C. B. 1984. Clarification of the monotypic genera *Chiriscus* and *Symmius* (Crustacea: Isopoda: Idoteidae).—Proceedings of the Biological Society of Washington 97:71–77.

Torti, M. R., & Bastida, R. 1972. Presencia del género *Macrochiridothea* Ohlin, 1901 en Uruguay y Brasil: *M. giambiagiae* sp. nov. (Crustacea, Isopoda).—Neotropica 18(55):16–22. [In Spanish with English summary.]

Department of Invertebrate Zoology (Crustacea), NHB Stop 163, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 131–139

HETEROMYSIS MEXICANA, A NEW SPECIES FROM CAMPECHE BANK, GULF OF MEXICO (CRUSTACEA: MYSIDACEA)

Elva Escobar-Briones and Luis A. Soto

Abstract.—*Heteromysis mexicana* is described from waters of Campeche Bank, southern Gulf of Mexico. Its general morphology closely resembles the eurytopic species *H. formosa* Smith, 1873, which is distributed along the western northern Atlantic in subtropical and temperate coastal waters. Available morphologic and ecologic data for 24 species of *Heteromysis* occurring in the Tropical Western Atlantic show no specific latitudinal distribution or host selectivity.

The *Heteromysis* occurring in the Tropical Western Atlantic comprise 26 species, most of which have cryptic habits (Modlin 1987c) and are associated with coralheads, anemones and sponges. The group exhibits considerable adaptive radiation. In the Gulf of Mexico 11 species have been described and 13 more occur in the Caribbean-Antillean region and the Tropical Western Atlantic (Tables 1, 2). Most records in the Gulf are limited to the eastern and northern parts.

This paper presents the description of a new species of *Heteromysis,* the first recorded for the southwestern Gulf of Mexico and summarizes the zoogeography of the *Heteromysis* species recorded in the Tropical Western Atlantic.

Materials and Methods

The specimens reported herein were collected during the research program "Oceanography of the Gulf of Mexico" (OGMEX) conducted aboard the R/V *Justo Sierra* in March 1987. Material collected has been coded as follows: OGMEX.I is the project name and cruise number, in order the following digits represent the year of collection and the station number, and in parentheses is the depth in meters. The number and sex of the individuals captured is designated as 1f (= female), 1m (= male), and 1j (= juvenile).

Hydrographic parameters and sediment texture were determined at the station. Bottom salinity and temperature were recorded with a Niels-Brown CTD sensor. The sediments obtained with a Smith-McIntyre grab were analyzed according to Folk (1969) for the sand and mud size fractions using sediment sieves and the pipette method respectively. Organic content of sediment was determined by the loss on ignition technique, and burnt to 550°C.

Samples were fixed and stored in 70% ethanol. Total length (T.L.), measured with a calibrated ocular micrometer in a dissecting microscope, is the distance along the dorsal midline from the tip of the rostrum to the posterior margin of the telson, excluding apical spines. Illustrations were made with the aid of a camera lucida.

Results

Heteromysis mexicana, new species
Figs. 1A–E, 2A–E, 3A–H, 4A, B

Type material.—Holotype: Male (T.L. 10.2 mm) collected at Campeche Bank, southern Gulf of Mexico, March 1987, obtained from a night trawl sample [OG-

Table 1.—*Heteromysis* species occurring in the Gulf of Mexico. (Additional distributional information in brackets.)

Species	Source	Quadrant
H. beetoni Modlin, 1984	Modlin (1984)	NE
H. bermudensis cesari Băcescu, 1968	Băcescu (1968)	SE (Carib.)
H. dispar Brattegard, 1970	Brattegard (1970)	SE
H. filitelsona Modlin, 1984	Modlin (1984)	NE
H. formosa, Smith, 1873	Stuck et al. (1979b)	NE (eurytop.)
	Tattersall (1951)	NE
H. gomezi Băcescu, 1970	Băcescu (1970)	SE
H. quitarti Băcescu, 1968	Băcescu (1968)	E (Keys)
H. hopkinsi Modlin, 1984	Modlin (1984)	NE
H. mariani Băcescu, 1970	Băcescu (1970)	SE
H. nouveli Brattegard, 1969	Brattegard (1969)	SE (Keys)
H. rubrocineta Băcescu, 1968	Băcescu (1968)	SE

MEX.I-87-52 (168) 1m]. Dissected and mounted on two slides and deposited in USNM, USNM 241592.

Allotype: Female (T.L. 10.3 mm) from same sample. Deposited in USNM, USNM 241593.

Paratypes: Juvenile (T.L. 5.4 mm) from same sample. Deposited in USNM, USNM 241594.

Type locality.—Campeche Bank, southern Gulf of Mexico, Mexico, between 19°31′N, 92°37′W and 19°33′N, 92°37′W.

Description.—Body robust. Carapace (Fig. 1A) with anterior margin produced into small triangular rostrum, posterior margin deeply emarginate, exposing part of thoracic segment 7 and all of 8, anterolateral lobes rounded. Eyes large, oval; cornea large, brown.

Antennular peduncle (Fig. 1B) segment 1 as long as segment 3, with four long setae on conical distolateral process and two setae near middle of distal margin. Segment 2 short with two plumose setae distodorsally. Segment 3 with male lobe located midventrally near distal margin and crowned by a

Table 2.—*Heteromysis* species occurring in the Caribbean Sea and the Western Tropical Atlantic.

Species	Source	Distribution
H. actinae Clarke, 1955	Clarke (1955)	Carib.-Antil.
H. agelas Modlin, 1987	Modlin (1987c)	Bahamas
H. bermudensis Sars, 1885	Tattersall (1951)	Bermuda-Carib.
H. bredini Brattegard, 1970	Brattegard (1970)	Antilles
H. coralina Modlin, 1987	Modlin (1987b)	Fla. Keys
H. disrupta Brattegard, 1970	Brattegard (1970)	Caribbean
H. elegans Brattegard, 1974	Brattegard (1974a)	Caribbean
H. floridensis Brattegard, 1969	Brattegard (1969)	Baham.-Fla. Keys
H. kensleyi Modlin, 1987	Modlin (1987b)	Caribbean
H. mayana Brattegard, 1970	Brattegard (1970)	Caribbean
H. mureseanui Băcescu, 1986	Băcescu (1986)	Brazilian
H. siciliseta Brattegard, 1970	Brattegard (1970)	Caribbean
H. tuberculospina Modlin, 1987	Modlin (1987a)	Caribbean
H. venezuelensis Băcescu, in press	Băcescu, in press	Caribbean
Heteromysis sp. A Brattegard, 1974	Brattegard (1974a)	Caribbean

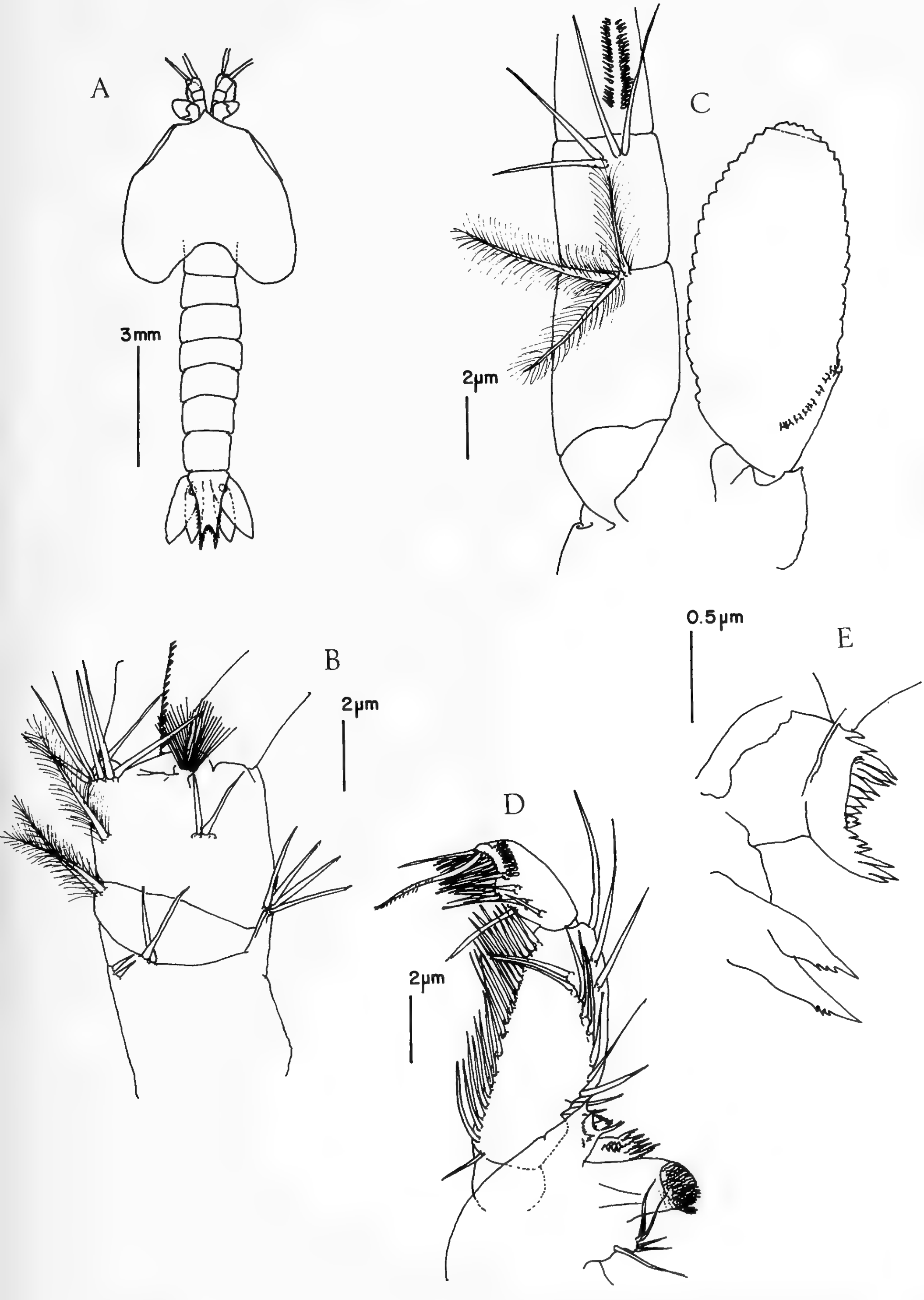


Fig. 1. *Heteromysis mexicana* (male 10.2 mm). A. Dorsal view; B. antennular peduncle; C. antennal scale; D. left mandlible and mandibular palp; E. detail of left mandible lacinia mobilis and accessory blades.

dense tuft of hairs, two simple setae ventrally at midlength, one plumose seta medially at midlength and seven setae distomedially. Antennular flagellum with stout spinules along proximal half.

Antennae (Fig. 1C) peduncle segment 1 short, compressed; segment 2 twice length of segment 1 and 1.6 times length of segment 3, with three plumose setae at middle of distal margin; segment 3 with four setae near middle of distal margin; flagellum with two rows of setules along entire length. Antennal scale as long as or slightly longer than peduncle, 2.3 times as long as maximum width with distal tip articulated; lateral margin nearly straight, medial margin convex, entire margin setose, dorsal surface with nine proximal setae.

Mouthparts (Figs. 1D, E, 2A–D), mandibular palp 3-segmented, segment 1 narrow, segment 2 broad, lateral margin with 19 simple setae, one setae in proximal dorsal position, medial margin with curved row of 10 simple setae and three simple setae distally, segment 3 lateral margin sinuous, with four long submarginal plumose setae proximally, nine surface pectinate spinules, 23–26 pectinate setae diminishing in size proximally, distally one longer robust seta.

Left mandible with short bladelike incisor, lacinia mobilis crownlike with 17 cusps longer on both ends, accessory blades in spine row with five blades, all slightly serrate on inner margin, molar process well developed with 14 rows of triturative teeth. Right mandible with three bladelike incisors, two setose accessory blades, molar process well developed with 12 rows of triturative teeth and lateral plumose setae. Maxillule well developed, outer plate with 14 apical spines and five subapical setae, middle inner margin setose, inner plate globose with four pectinate spinules, four simple setae and one hooked serrated spine on distal margin, seven plumose setae subdistally and two simple setae on lateral process. Maxillae (not figured) typical of the genus, exopod elongate with 22 plumose setae on distolateral margin. Paragnath typical of the genus with inner and outer lobe shoulders setose, mandibular process short, setose. Labrum tyical of the genus with apical margin setose.

Thoracic endopod 1 (Fig. 2E), short, robust, carpopropodus with six marginal setae and eight dorsodistally; dactylus rounded with nine pectinate setae.

Thoracic endopod 2 (Fig. 3A), ischium with 10–11 simple setae on anterior margin, merus anterior margin with seven setae; carpopropodus distally expanded with 10 spines on posterior margin, three distal setae, and four robust setae distally on anterior margin; dactylus small, rounded mitten-shaped, setose all around.

Thoracic endopod 3 (Fig. 3B), strong, short, merus and carpopropodus inflated, lacking spines characteristic of genus; dactylus ending in terminal claw.

Thoracic endopod 4 (Fig. 3C), carpopropodus with six segments, distal one with two serrated flexible spines; dactylus small with long terminal setae and ending in curved clawlike spine.

Thoracic endopod 5 (Fig. 3D) to 8, carpopropodus with five segments, increasing slightly in size distally.

Female with oostegites in thoracic segments 6, 7 and 8 well developed, increasing in size distally.

Pleopods 1 to 5 (Fig. 3E–H) not sexually dimorphic. Well developed, similar in form, unsegmented, increasing in size distally. Pleopod 1, five setae and one terminal spine on anterior surface, five plumose setae on lateral margin, five setae on pseudobranchial lobe. Pleopod 2, six setae on anterior surface, one setae on distal margin, three setae on pseudobranchial lobe, four setae on lateral margin. Pleopod 3 with 11 setae on anterior surface, two setae on distal margin, four setae on pseudobranchial lobe, four on lateral margin. Pleopod 4, 13 setae on anterior surface, three setae on distal margin, three setae on pseudobranchial lobe, four setae on lateral margin, one distally.

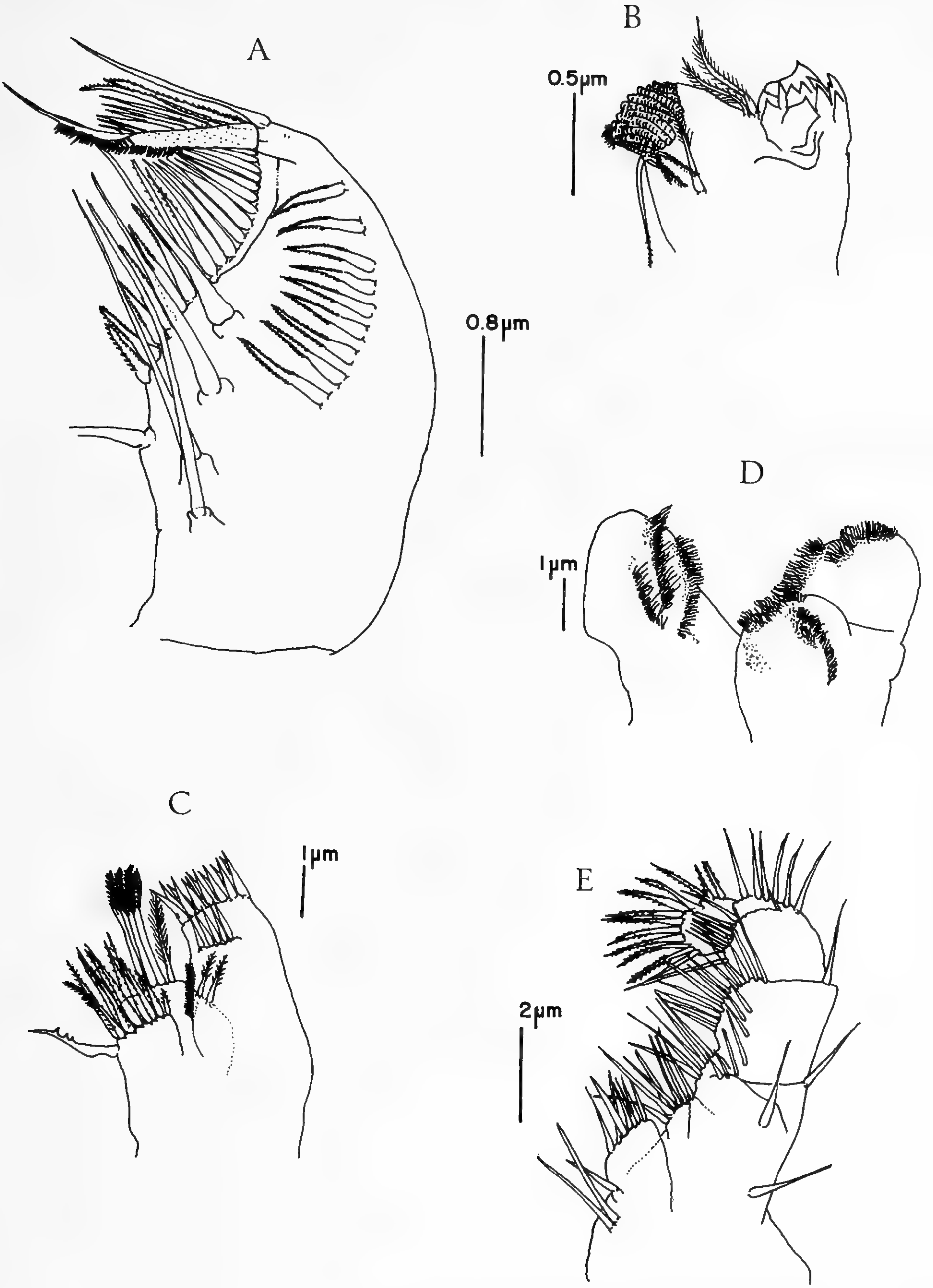


Fig. 2. *Heteromysis mexicana* (male 10.2 mm). A. Mandibular palp third segment; B. right mandible; C. maxillule; D. paragnath; E. thoracic endopod 1.

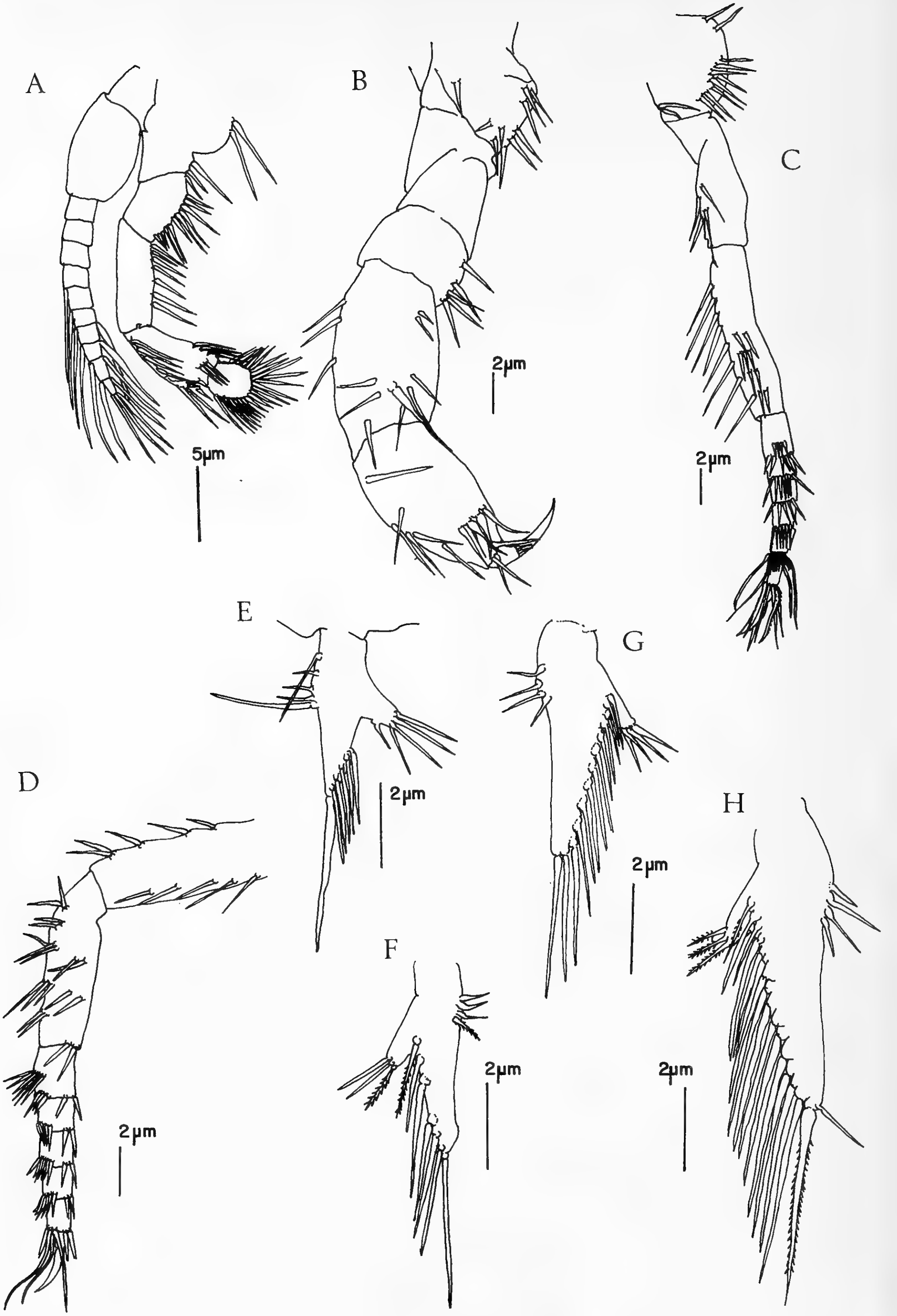


Fig. 3. *Heteromysis mexicana* (male 10.2 mm). A. Thoracic endopod 2; B. thoracic endopod 3; C. thoracic endopod 4; D. thoracic endopod 5; E. pleopod 1; F. pleopod 2; G. pleopod 3; H. pleopod 4.

Pleopod 5, 16 setae on anterior surface, four setae on distal margin, three setae on pseudobranchial lobe, four setae on lateral margin.

Uropods (Fig. 4A), exopod subequal in length to endopod, lateral margin straight, apex rounded, medial margin slightly convex, setose all around. Endopod lateral margin straight, medial margin concave with 23 stout spines, equal in size along entire margin, apex rounded, both margins with plumose setae.

Telson (Fig. 4B) 1.7 times longer than wide at base, lateral margins straight, distal half of lateral margins with 14–15 spines increasing slightly in length posteriorly; one longer apical spine on each side. Telsonal cleft completely lined with 22–23 small spines, increasing slightly in size distally; depth 0.17 times length of telson.

Remarks.—The new species closely resembles the eurytopic species *Heteromysis formosa* Smith (1873) and can be distinguished from it by morphological differences listed in Table 3 from which the most important features that separate them are the well developed male lobe on antennular peduncle segment 3; the absence of three pairs of spines on the carpopropodus of the thoracic limb 3; medial margin of uropodal endopod with 20–23 spines (14–19 in *H. formosa*) and 22–23 spines in the cleft of the telson (8–20 in *H. formosa*). Both species have in common well developed but not sexually dimorphic pleopods (Modlin, pers. comm.).

Ecological notes.—This species was an occasional component of the macrocrustacean epibenthic community from the inner continental shelf. Specimens were obtained associated with empty *Strombus gigas* shells between 19°31′N, 92°37′W and 19°33′N, 92°37′W at 168 m depth. Bottom salinity was 36.28‰ and temperature was 23.08°C. The sediment at the site was fine sand mud with an organic matter content of 23% and carbonates 11%. The behavior of hiding in gastropod shells closely resembles that reported for *Heteromysis formosa* (Clarke 1955, Brattegard 1969) and other species morphologically dissimilar, e.g., *H. bermudensis, H. mayana, H. tuberculospina* (Modlin, 1987a).

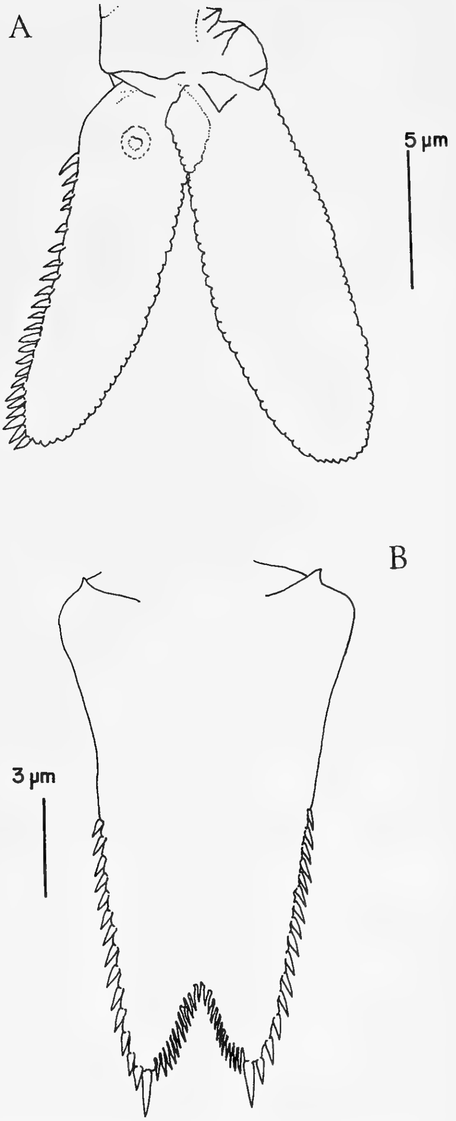


Fig. 4. *Heteromysis mexicana* (male 10.2 mm). A. uropodal endopod and exopod; B. telson.

Etymology.—Named for the country in which it was found, Mexico.

Table 3.—Comparison of *Heteromysis formosa* Smith (1873) and *H. mexicana* n. sp.

Character	*H. formosa*	*H. mexicana*
Antennular peduncle, male lobe	rudimentary[1]	well developed
Antennular peduncle segment 3	with 2 plumose setae[4]	with 1 plumose seta
Antennal scale length/breadth ratio	3[4]	2.3
Third thoracic limb carpopropodus	with 3 pairs of spines[3–5]	without spines
Uropodal endopod	with 14–16 spines[3] with 17–19 spines[4] with 16–19 spines[5]	with 20–23 spines
Telson lateral margin	with 12–14 spines[1] with 14–16 spines[2,3] with 11 spines[4] with 10–18 spines[5]	with 14–17 spines
Telson cleft	with 20 spines[2,3] with 8–10 spines[4] with 16–13 spines[5]	with 22–23 spines

[1] Smith, 1873.
[2] Sars, 1882.
[3] Tattersall, 1951.
[4] Brattegard, 1969.
[5] Stuck et al., 1979a.

Discussion

This new species is the first report of Heteromysini for the southwestern Gulf of Mexico. The peracaridean shelf fauna in this region is largely unknown. Knowledge of it is limited to the investigations of epibenthic macroinvertebrates in Laguna de Términos (Escobar & Soto 1988) and Alvarado (Soto et al. 1986).

Twenty-six species of Heteromysids have been described in the West Tropical Atlantic (Băcescu 1968, 1970, 1986; Brattegard 1969, 1970, 1973, 1974a, b; Clarke 1955; Modlin 1982, 1984, 1987a, b, c; Sars 1885; Smith 1873; Stuck et al. 1979a, b), of which 11 have been reported from the northern and southeastern parts of the Gulf of Mexico (Table 1), and 13 have been reported from the Caribbean and the Western Tropical Atlantic (Table 2). At least 12 species are cryptic and are associated with sponges and corals. Heteromysids mostly inhabit shallow waters, but the present report of *Heteromysis mexicana* from the Campeche Bank at 168 m is among the deepest. Reports for the closely related species, *H. formosa,* reach up to 203 m in the Gulf of Mexico and 227 m in the southeastern coast of the United States (Tattersall 1951).

Acknowledgments

The authors wish to express their appreciation to Dr. Thomas Bowman of the Smithsonian Institution, Dr. Mihail Băcescu from the Musee D' Histoire Naturelle "Grigore Antipa," Rumania and Dr. Richard F. Modlin of the University of Alabama in Huntsville for their critical reviews on an earlier version of this manuscript. For their support in the field gratitude is expressed to the team of the Benthic Ecology Lab. This is Contribution #587 from the Instituto de Ciencias del Mar y Limnologia, UNAM.

Literature Cited

Băcescu, M. 1968. Heteromysini nouveaux des eaux cubaines: trois especes nouvelles de *Heteromysis* et *Heteromysoides spongicola* n.g. n. sp.—Revue Roumaine de Biologie–Zoologie 13:221–237.

———. 1970. New spongicolous *Heteromysis* of the Caribbean sea (*H. gomezi* n. sp. and *H. mariani*

n. sp.).—Revue Roumaine de Biologie–Zoologie 15:11–16.

———. 1986. *Heteromysis mureseanui* n. sp. and *Kalliapseudes viridis,* ssp. *brasiliensis* n. ssp., from the Brazilian littoral waters.—Revue Roumaine de Biologie–Biologie Animale 31:93–97.

Brattegard, T. 1969. Marine biological investigations in the Bahamas. 10. Mysidacea from shallow water in the Bahamas and southern Florida. Part I.—Sarsia 39:17–106.

———. 1970. Mysidacea from shallow water in the Caribbean Sea.—Sarsia 43:111–154.

———. 1973. Mysidacea from shallow water on the Caribbean coast of Colombia.—Sarsia 54:1–66.

———. 1974a. Additional Mysidacea from shallow water on the Caribbean coast of Colombia.—Sarsia 57:47–86.

———. 1974b. Mysidacea from shallow water on the Caribbean Coast of Panama.—Sarsia 57:87–108.

Clarke, W. D. 1955. A new species of the genus *Heteromysis* (Crustacea, Mysidacea) from the Bahama Islands, commensal with a sea-anemone.—American Museum Novitates 1716:1–13.

Escobar, E., & L. A. Soto. 1988. Mysidacea from Términos Lagoon, Southern Gulf of Mexico, and description of a new species of *Taphromysis.*—Journal of Crustacean Biology 8:335–367.

Folk, R. L. 1969. Petrologia de las rocas sedimentarias. Universidad Nacional Autónoma de México, Mexico, 405 pp.

Modlin, R. F. 1982. Contributions to the ecology of the mysid crustaceans in the shallow waters of Dauphin Island, Alabama.—Northeast Gulf Science 5:45–49.

———. 1984. Mysidacea from the Florida Middle Ground, northeast Gulf of Mexico, with descriptions of three new species of *Heteromysis* and a key to the Heteromysini of the western Atlantic.—Journal of Crustacean Biology 4:287–297.

———. 1987a. Mysidacea from shallow waters in the vicinity of Carrie Bow Cay, Belize, Central America, with descriptions of two new species.—Journal of Crustacean Biology 7:106–121.

———. 1987b. *Heteromysis kensleyi* and *H. coralina,* new species from the shallow waters off Looe Key, Florida (Mysidacea:Heteromysini).—Proceedings of the Biological Society of Washington 100:653–658.

———. 1987c. Heteromysini from Grand Bahama Island: description of *Heteromysis agelas,* new species, first description of male *H. floridensis,* and notes on *H. guitarti* (Crustacea:Mysidacea).—Proceedings of the Biological Society of Washington 100:296–301.

Sars, G. O. 1882. Oversight af Nerges Crustaceer med forelobige Bemaerkninger over de nye eller mindre bekjendte Arter. I Podophthalmata-Cumacea-Isopoda-Amphipoda.—Christiania Videnskabsselskabs Forhandlinger 18:54–55.

———. 1885. Reports on the Shizopodda collected by H.M.S. Challenger during the years 1873–1876.—Challenger Reports–Zoology 13:1–225.

Smith, S. I. 1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters.—Report of the Commission of Fisheries and Fish 1871–1872:295–747.

Soto, L. A., et al. 1986. Ecología poblacional de los camarones peneidos de los principales sistemas lagunares del Golfo de México. Segundo Informe Técnico. CONACyT-PCEBNA 021436, 65 pp.

Stuck, K. C., H. M. Perry, & R. W. Heard. 1979a. An annotated key to the Mysidacea of the north central Gulf of Mexico.—Gulf Research Reports 6:225–238.

———, ———, & ———. 1979b. Records and range extensions of Mysidacea from coastal and shelf waters on the eastern Gulf of Mexico.—Gulf Research Reports 6:239–248.

Tattersall, W. M. 1951. A review of the Mysidacea of the United States National Museum.—Bulletin of the United States National Museum 201: 1–292.

Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, A.P. 70-305, 04510 Mexico City, Mexico.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 140–150

REDESCRIPTION AND NEW RECORDS OF *TRICHODIAPTOMUS CORONATUS* (G. O. SARS) (COPEPODA; CALANOIDA; DIAPTOMIDAE) FROM BRAZIL

Janet W. Reid

Abstract.—*Trichodiaptomus coronatus* (G. O. Sars), originally described from São Paulo, Brazil, has been recorded recently only from Brazilian Amazonia and the Orinoco Delta. This article reports new records from four localities in the Brazilian highlands, including the first record from the Rio São Francisco Basin. A redescription of representatives from these populations is furnished. Morphological variations reported for this species in Amazonia were not observed in the southern populations examined. *T. coronatus* inhabits clear or blackwater, extremely oligotrophic rivers, ponds and reservoirs.

G. O. Sars (1901) described a distinctive freshwater calanoid copepod, *Diaptomus coronatus,* from cultures of dried mud from the State of São Paulo, Brazil. Wright furnished additional morphological details of populations of this species from Santarém, State of Pará (1927), and the State of São Paulo (1937). Thomasson (1954, 1955) reported *Diaptomus melini* as a new, similar species from Manaus, State of Amazonas. Noting morphological variability in Amazonian populations of *D. coronatus,* Brandorff (*in* Brandorff et al. 1982) synonymized *D. melini* with Sars' species and proposed the new genus *Trichodiaptomus* for it. Although *T. coronatus* has been recorded several other times from Brazilian Amazonia (Andrade & Brandorff 1975, Brandorff 1972, Cipólli & Carvalho 1973, Matsumura-Tundisi 1986) and once from the Orinoco Delta, Venezuela (Dussart 1984), it has not been encountered again in southeastern Brazil. This article reports new records from the Distrito Federal, Goiás, and Minas Gerais in the central Brazilian highlands, including the first record from the Rio São Francisco Basin; redescribes the species; and summarizes knowledge of its ecological requirements.

Genus *Trichodiaptomus* Brandorff (*in* Brandorff et al., 1982)

Trichodiaptomus coronatus (G. O. Sars, 1901)

Figs. 1–21

Diaptomus coronatus G. O. Sars, 1901:14–16, pl. III, figs. 9–17.—Daday, 1905: 151.—Tollinger, 1911:66, fig. A2.—Pesta, 1927:80.—Wright, 1927:74, 75, 90–91, 100, pl. VI, figs. 7–9; 1937:66, 77–79, pl. III, figs. 5–8; 1938:562.—Brandorff, 1972:8, 9, 20–23, 50, figs. 19–22.—Cipólli & Carvalho, 1973:95, 97, 98, 100, 101, 108.

"*Diaptomus*" *coronatus* G. O. Sars.—Andrade & Brandorff, 1975:97, 103.—Brandorff, 1976:618, 619, 622, fig. 3; 1978: 1201.

Diaptomus melini Thomasson, 1954:193–194, fig. III 1 a–c; 1955:214.—Brandorff, 1972:20–21, 48.

"*Diaptomus*" *melini* Thomasson.—Andrade & Brandorff, 1975:102.

Trichodiaptomus coronatus (G. O. Sars).—Brandorff et al., 1982:76, 104–106, figs. 104–110.—Dussart & Defaye, 1983: 134.—Arcifa, 1984:143.—Dussart, 1985: 201.—Reid, 1985:78–79, fig. 1.—Matsumura-Tundisi, 1986:547, 551, figs. 89–94, 100.

Notodiaptomus coronatus (G. O. Sars).—Dussart & Defaye, 1983:134.—Dussart, 1984:34, 39.

Rhacodiaptomus Melini (Thomasson).—Brehm, 1965:15.

Rhacodiaptomus Mileni (Thomasson).—Brehm, 1965:15.

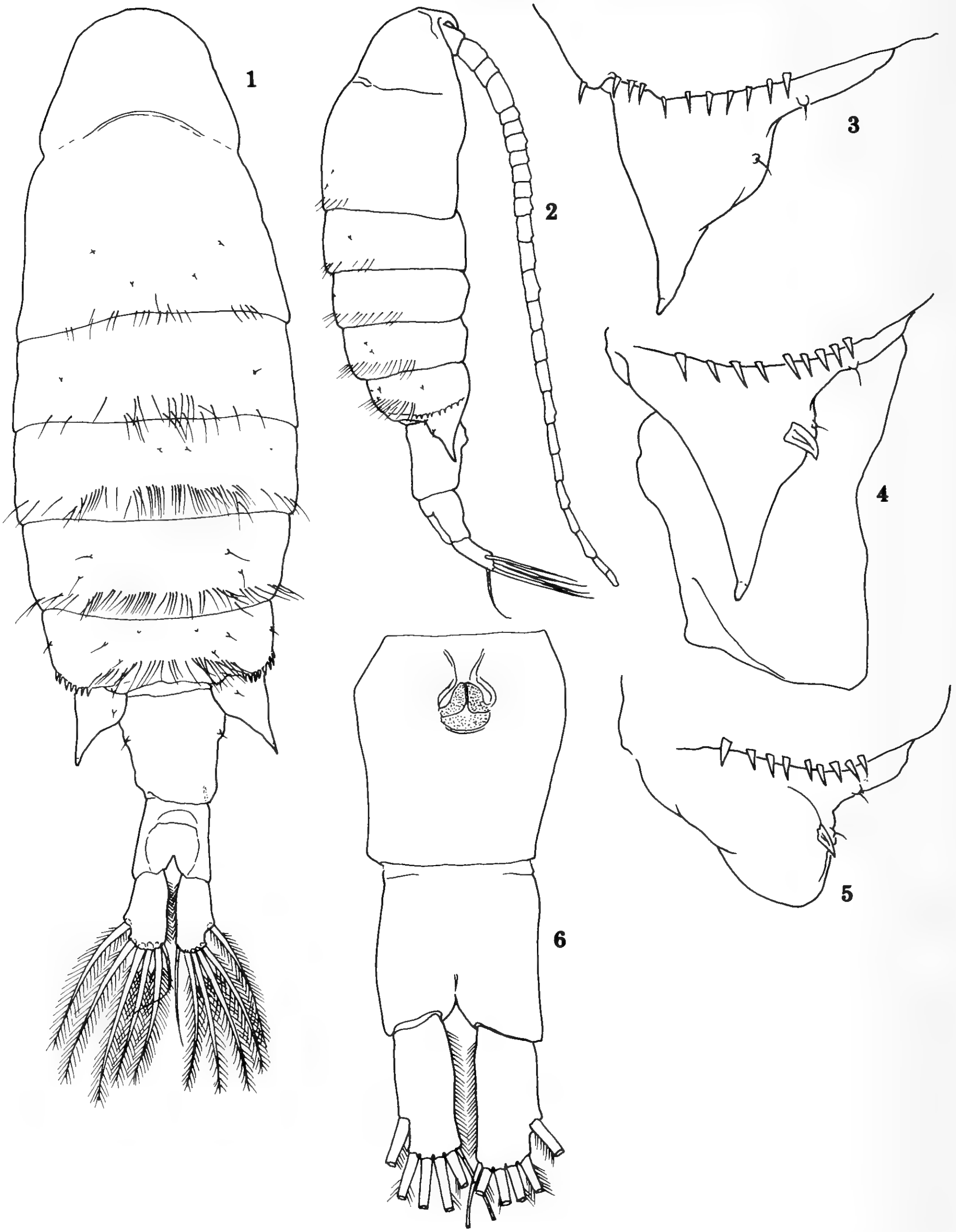
Material.—Brazil: 1 ♂ and 1 ♀, Santarém, Pará (undated), USNM 58920, 58921, col. S. Wright. 100+ adults, Lagoa Bonita (Lagoa Mestre d'Armas), Distrito Federal, 15°34'S, 47°10'W, 19 Jan 1979, 24 Jan 1979, 9 Sep 1980, 23 Sep 1980, 21 Oct 1980, 4 Nov 1980; 15 adults, Lagoa Formosa, Goiás, 15°30'S, 47°36'W, 26 Oct 1980, 4 Jul 1982; 100+ adults, Represa (Rep.) Santo Antônio do Descoberto, Distrito Federal/Goiás, 15°44'S, 48°10'W, 25 Oct 1980, 8 May 1982, all USNM 241951; 200+ adults, Lagoa Bonita, 23 Sep 1980, Museu de Zoologia da Universidade de São Paulo (MZUSP) 9651; 200+ adults, Lagoa Bonita, 9 Sep 1980, MZUSP 9652; 200+ adults, Rep. Santo Antônio do Descoberto, 8 May 1982, MZUSP 9653; 16 adults, Lagoa Formosa, 4 Jul 1982, MZUSP 9654; col. J. W. Reid and/or L. El-Moor Loureiro. 12 ♀, Lagoas Tacho, Paiano, and Cipó (combined samples), Pirapora, Minas Gerais, 17°20'55"S, 44°57'00"W, 1988; M. B. G. e S. Dabés collection.

Female.—Median lengths (and ranges), excluding caudal setae, of specimens from Lagoa Bonita 1.13 mm (1.05–1.28 mm; n = 40); from Rep. Descoberto 1.20 mm (1.12–1.28 mm; n = 14); from Lagoa Formosa 1.20 mm (1.08–1.30 mm; n = 18); from Pirapora ponds 1.28 mm (1.22–1.35 mm; n = 12). Body widest at pedigers 1–2 in dorsal view (Fig. 1). Pedigers 4 and 5 (Figs. 1–3) separated; pediger 5 produced on each side into posteriorly directed, pointed wing reaching past midlength of genital segment. Few females with one wing bearing large dorsally directed spine, wing sometimes also not fully pointed (Figs. 4, 5); opposite wing always normally pointed. Prosomites with 1–5 pairs of papillae each tipped with fine hair, and rows of hairs near posterior margins, hairs on pedigers 2–4 coarser. Pediger 4 (Figs. 1–5) with lateral row of 5–13 large spines, usually a similar number on each side. Urosome (Figs. 1, 2, 6) of 2 segments; anterior portion of genital segment slightly expanded laterally; lateral sensillae on genital segment similar to prosomal ones. Genital field as in Fig. 6. Inner margins of caudal rami hairy.

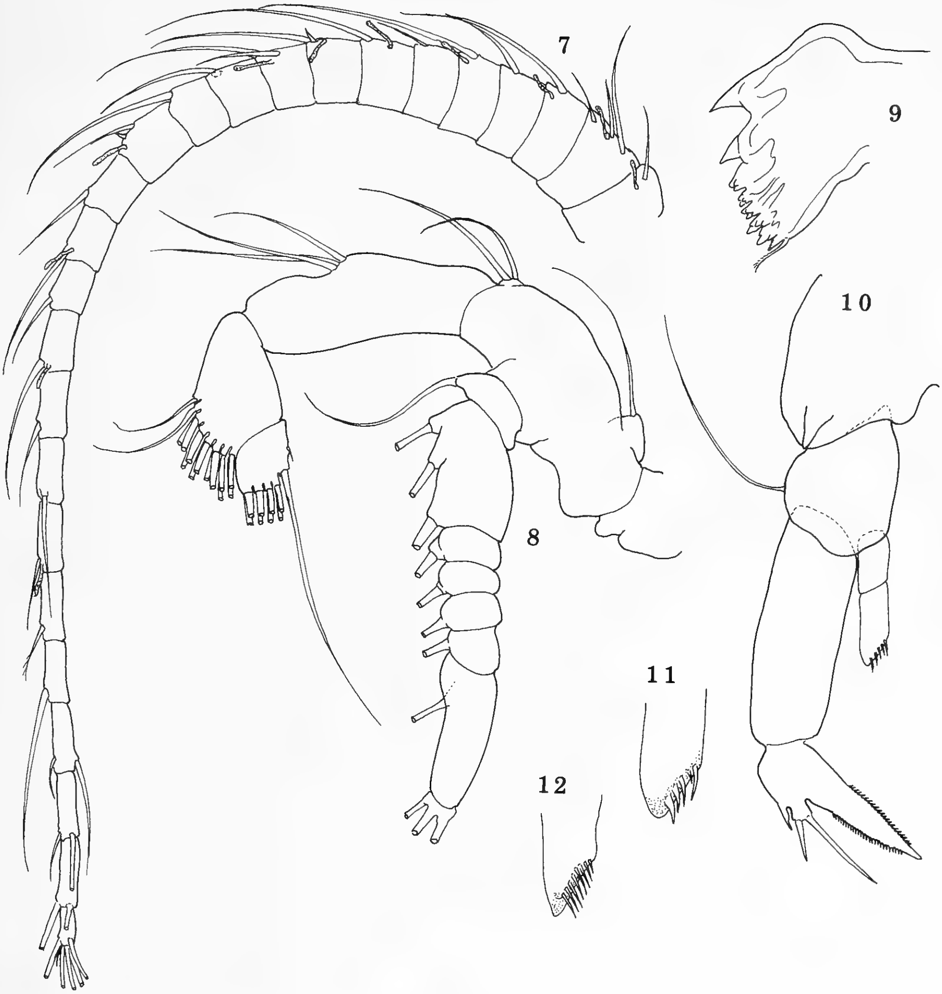
Rostral points acute. Antennule (Figs. 2, 7) reaching past end of caudal rami; armament similar to that of *Scolodiaptomus corderoi* (Wright) as redescribed by Reid (1987), particularly in having only 1 seta on article 11. Antenna (Fig. 8) with 2–3 setae on anterior margin of endopod 1, posterior margin of this article lacking ornament; antenna otherwise normal for family. Gnathal lobe of mandible (Fig. 9) with acute apical and subapical teeth, dentition otherwise similar to that of *S. corderoi.* Remaining mouthparts and legs 1–4 also similar to those of *S. corderoi* and typically diaptomid; Schmeil's organ present on posterior surface of leg 2 endopod article 2.

Leg 5 (Figs. 10–12) slender; exopod article 3 continuous with article 2. Endopod of 2 distinct articles, reaching slightly beyond midlength of exopod article 1; endopod 2 with subterminal oblique row of 5–8 spinules.

Male.—Median lengths of specimens from Lagoa Bonita 0.85 mm (range 0.82–1.00 mm; n = 24); Rep. Descoberto 0.90 mm (0.72–0.95 mm; n = 20); Lagoa Formosa 0.90 mm (0.88–1.06 mm; n = 3). Habitus (Fig. 13) as in female, except urosome 5-segmented, pediger 4 with 4–8 spines on each side, wings of pediger 5 short. Left antennule, mouthparts, and legs 1–4 as in female. Right antennule (Figs. 14–16) with articulated spines on articles 8 and 12; spine on article 11 longer than spine on article 10; spine on article 13 equal to or longer than



Figs. 1–6. *Trichodiaptomus coronatus,* females (1 and 2 from Pirapora ponds; 3–6 from Lagoa Bonita): 1, Habitus, dorsal; 2, Habitus, right lateral; 3, Pedigers 4-5 of normal specimen; 4, Pedigers 4–5 and genital segment of specimen with abnormal spine on left wing; 5, Pedigers 4–5 of specimen with abnormal spine on rounded left wing; 6, Urosome and caudal rami, ventral.

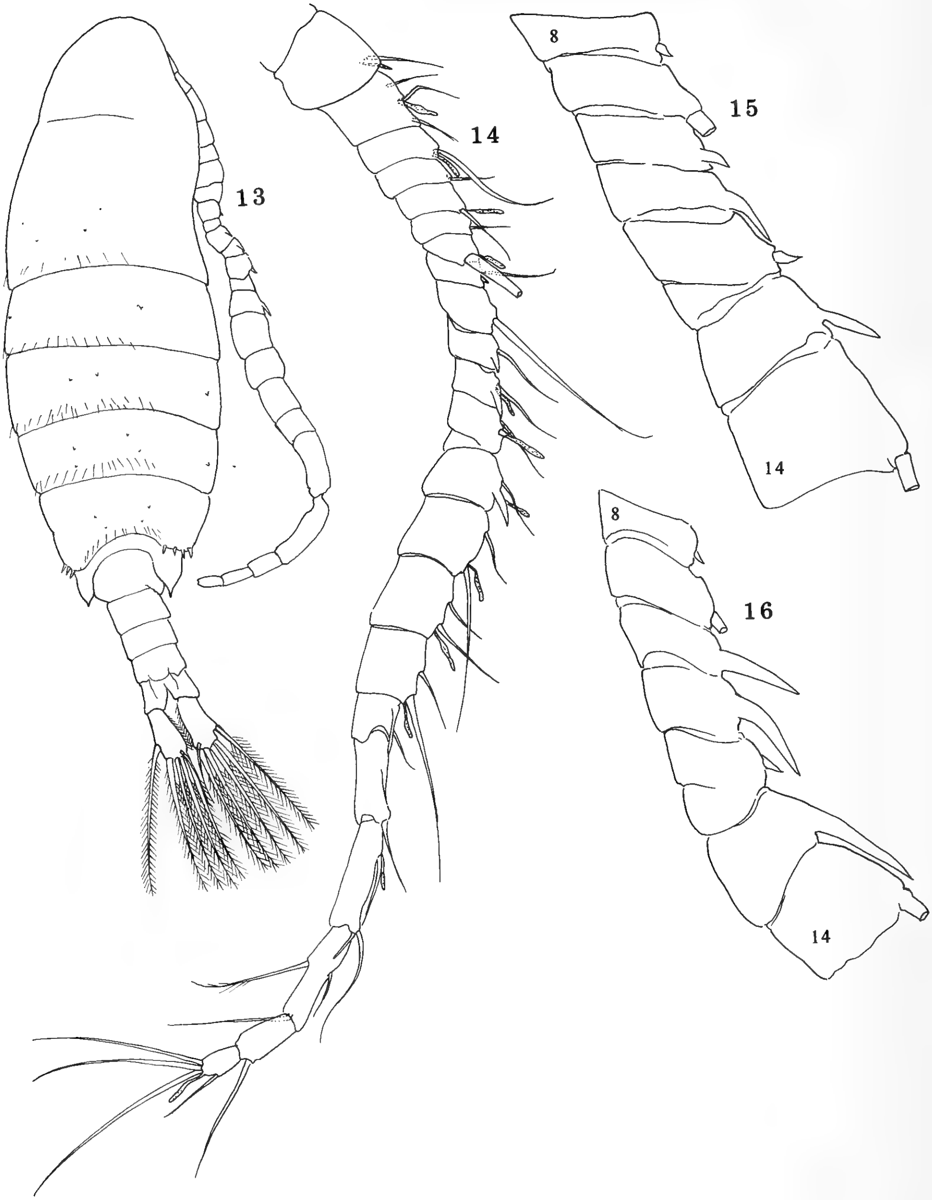


Figs. 7–12. *Trichodiaptomus coronatus,* females from Lagoa Bonita: 7, Antennule; 8, Antenna; 9, Gnathal lobe of mandible; 10, Leg 5; 11 and 12, Detail of end of leg 5 endopod 2 from different specimens.

spine on article 11. Spines on articles 10, 11, and 13 more developed in specimen from Amazonia (Fig. 16). Articles 14–16 without spines. Antepenultimate article without distal process.

Left leg 5 (Figs. 17–21) slender; posterior mammiform process on basipod 1 small, ending in short spine. Margins of basipod 2 nearly straight. Endopod of 2 indistinctly separated articles, distal article with few hairs near conical tip. Exopod of 2 articles, each with hairy pad on anteromedial surface, proximal pad slightly developed. Article 2 rotated inward, bearing acute, finely pectinate digital process, and slender spine with fine hairs.

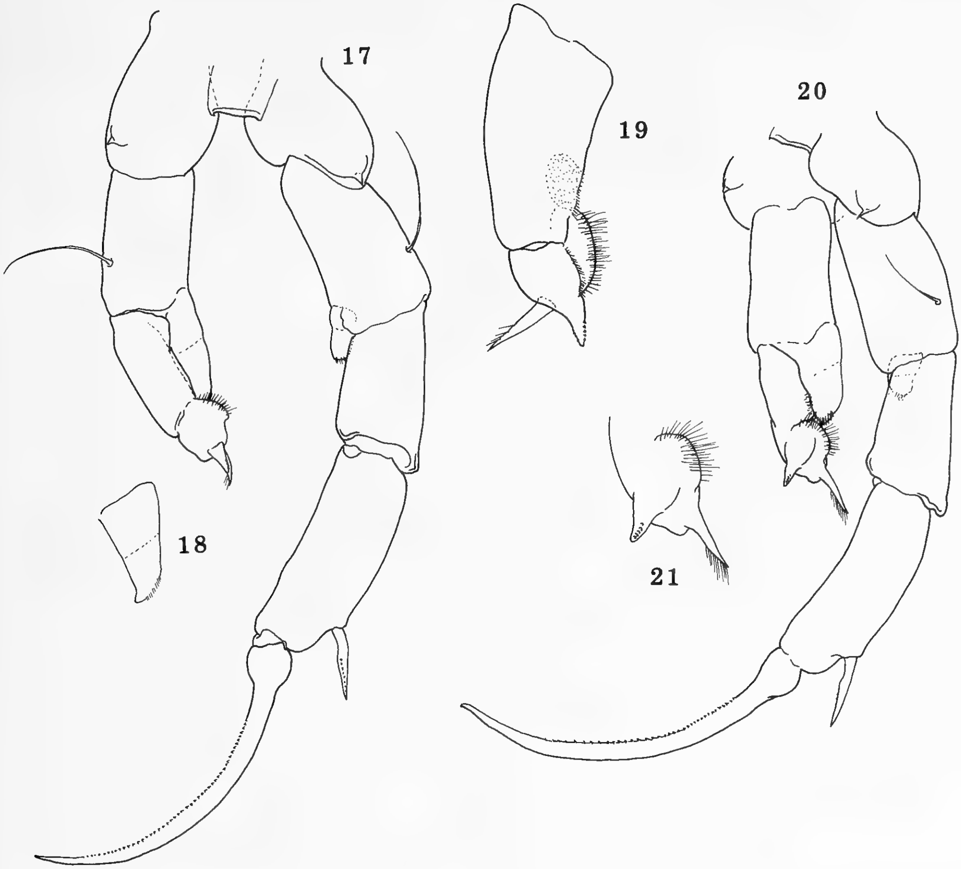
Right leg 5 (Figs. 17, 20), with basipods 1 and 2 similar to basipod of left leg; endopod of 2 indistinctly separated articles, oblique terminal surface hairy. Exopod 1 with inner and outer distal corners slightly extended. Exopod 2, lateral spine shorter



Figs. 13–16. *Trichodiaptomus coronatus,* males (13–15 from Lagoa Bonita; 16 from Santarém): 13, Habitus, dorsal; 14, Right antennule; 15 and 16, Articles 8–14 of right antennule (most setae and esthetascs not indicated).

than breadth of exopod; terminal claw equal in length to exopod, tip of claw slightly recurved in some specimens.

Variation.—Lengths of females from southern Brazil are less than lengths (1.19–1.46 mm) reported by Brandorff et al. (1982) for Amazonian populations. Wright (1937) gave the length of the female as 1.28 mm and of the male as 0.97 mm; Sars (1901) as 1.30 mm for females. The southern popu-



Figs. 17–21. *Trichodiaptomus coronatus,* males (17, 18, 20, 21 from Lagoa Bonita; 19 from Represa Descoberto): 17, Leg 5, posterior; 18, Detail of left endopod, posterior; 19, Detail of left exopod, posterior (stippling indicates area of proximal hairy pad); 20, Leg 5, right-lateral; 21, Left exopod 2, medial.

lations did not include individuals with short thoracic wings and/or prominences on the left side of the genital segment, originally named *D. melini* by Thomasson (1954) and termed "Females II–IV" by Brandorff (Brandorff et al. 1982). All southern females observed, both by Wright (1937) and in the present study, correspond to Brandorff's "Female I," with symmetrical genital segment and long, posteriorly directed, pointed wings; except for the few anomalous individuals noted here.

Brandorff *in* Brandorff et al. (1982) noted that Type I females tended to have more lateral spines on pediger 4 than did other morphs. Among the southern populations, females from Lagoa Formosa had significantly ($P \leq 0.01$; $t = 5.5$, $df = 114$) fewer spines on each side (4–10, mean 7.1) than females from Lagoa Bonita (6–13, mean 8.8). Lagoa Formosa females also had fewer, although not significantly fewer spines than females from Rep. Descoberto (7–11, mean 8.6) and Pirapora (9–11, mean 9.3). These latter three populations did not differ significantly among themselves in spine number. Males from the three populations examined (Bonita, Descoberto, Formosa) did not differ significantly in spine number, having 4–8 spines on each side. In both sexes, spine number tended to be about equal on each side, differing by no more than 4. On females from São Paulo, Sars (1901) observed "about 12 denticles," while Wright (1937) noted 8–12 spines.

Matsumura-Tundisi (1986, Amazon) figured the antennule of the female as reaching only to midlength of the genital segment; Wright (1927, Amazon) and Sars (1901, São Paulo) to midlength of the anal somite.

Brandorff (1972), Matsumura-Tundisi (1986), and Wright (1927) figured the exopod 3 of leg 5 of the female as distinct from exopod 2. Matsumura-Tundisi (1986) and Thomasson (1954) figured the endopod of leg 5 of the female as a single article. These are probably lapses of observation.

It appears that the unarticulated spines on articles 10, 11, and 13 of the right antennule of males are more prominently developed in Amazonian populations. Wright (1937:78) mentioned differences "particularly in the spination of the right antenna of the male" between São Paulo and Amazonian specimens. His figure of a male from São Paulo (op cit.: pl. III, fig. 6) shows relatively short spines on articles 10, 11 and 13, similar to those from the southern highlands (Fig. 15). Sars (1901: pl. III, fig. 15) also figured a short spine on article 13. Although Wright did not figure these spines from Amazonian males, he mentioned (1927:90) that the process of "the fifteenth segment" (probably article 13, since more distal articles have no processes) extends well past the middle of the succeeding article, similar to the structure of the male from Santarém deposited at NMNH (Fig. 16). Figures of Amazonian specimens by Brandorff (1972) and Matsumura-Tundisi (1986) also show long unarticulated spines similar to Fig. 16.

Distribution and ecology.—Brandorff (1976) noted the broad distribution of *T. coronatus* from the Brazilian Amazon to São Paulo State, a range further enlarged northwards by Dussart's (1984) record from the Orinoco Delta (Fig. 22). In spite of this unusual latitudinal distribution, *T. coronatus* seems to be a species of narrow habitat requirements (Table 1). Although it has been found in both lentic and lotic waters, available habitat data clearly indicate that it is restricted to warm, acid waters of low conductivity and extreme oligotrophy. Thus it has been most frequently collected from, but is not limited to Amazonian "black" waters (high in humic acids). Most of the localities, particularly in Amazonia, have been shallow streams and floodplain (várzea) lakes; similarly, Lagoas Bonita and Formosa are small, shallow ponds less than 10 ha in area, with extensive macrophyte beds. The ponds at Pirapora are also shallow, with much macrophyte coverage (M. B. G. e S. Dabés, pers. comm.). Santo Antônio do Descoberto and Guarapiranga seem to be unusual habitats for this species, being large reservoirs; at least the former, in which *T. coronatus* was the only diaptomid species at the time of collection, has no significant macrophytes. Possibly *T. coronatus* is a more littoral than pelagic species, particularly when in competition with other diaptomids.

Occurring only in Guarapiranga Reservoir out of 41 water bodies examined in eastern São Paulo in 1935 (Wright 1937), the species appears to have disappeared from Guarapiranga and has been recorded recently from none of the now mainly eutrophic reservoirs in that state (Sendacz et al. 1985). São Paulo reservoirs are now characterized by, among other species, *Scolodiaptomus corderoi* and *Thermocyclops decipiens* (Kiefer), which are typical inhabitants of highly productive systems (Reid 1987, 1988, 1989; Sendacz et al. 1985). Of numerous water bodies examined in the central Brazilian highlands, those in which *T. coronatus* is present include several of the most oligotrophic but none of the more productive systems. Therefore, it seems to be a useful indicator species, and

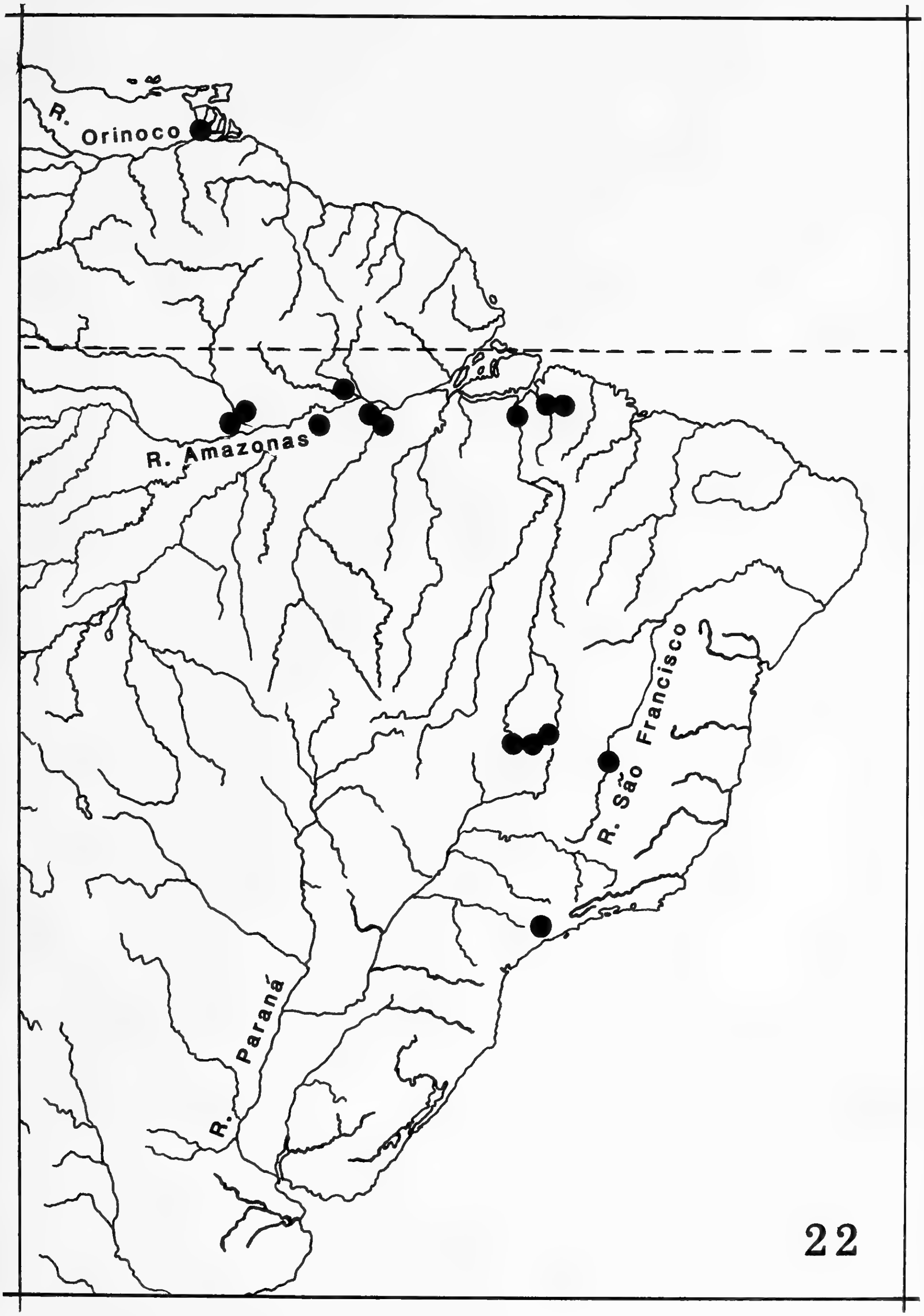


Fig. 22. Records of *Trichodiaptomus coronatus* (G. O. Sars) in eastern South America.

Table 1.—Environmental parameters recorded for collections of *Trichodiaptomus coronatus* (Sars).

Locality (Reference)[a]	Water body	Depth (m)	T (°C)	pH	Cond. (μS)	Color	Bottom
SP[b] (1)	—	—	—	—	—	—	mud
Santarém, PA (2)	bayou	—	—	—	—	—	—
Rep. Guarapiranga, SP (3)	reservoir	—	—	—	—	—	—
Rio Negro, Manaus, AM (4)	lagoon	—	28	—	—	—	—
Lago Jurucuí, PA (5)	lake	3.1	28.9	5.5	—	yellow	—
Rio Apocoitana, AM (5)	river	1.5	30.0	4.8	—	clear/green	—
Igarapé Jari, Ariacana, Rios Guamá/Capim, PA (6)	stream	—	—	5	—	black	—
Lago Timbiras, Caranandeua, PA (6)	flooded area	—	—	—	—	—	—
Igarapé S. Lourencinho, Rio Tocantins, PA (6)	stream	—	—	5	—	black	—
Tarumã-Mirim, Rio Negro, AM (7)	river	—	—	5.0[c]	9[c]	black	—
Lago da Terra Santa, Rio Nhamundá, AM/PA (8)	várzea lake	5.5	—	5.6	16	black	—
Terra Santa Village, AM/PA (8)	flooded meadow	1.4	—	5.4	12	black	—
Rio Xuedá, AM/PA (8)	igapó	—	—	5.2	9.5	black	—
Rio Nhamundá, AM/PA (8)	flooded meadow	—	—	5.0	9	black	sand
Caño Guara, Orinoco Delta, Venezuela (9)	stream	—	—	—	—	—	—
Lago Cristalino, AM (10)	lake	—	—	"low"	3–8	black	—
Rep. Santo Antônio do Descoberto, GO/DF (11)	reservoir	10	17.2	—	10	turbid	clay
Lagoa Bonita, DF (11)	pond	2	—	6.5	10	clear	organic
Lagoa Formosa, GO (11)	pond	2	25	—	10	clear	sand/clay
Lagoas Tacho, Paiano, Cipó, Pirapora, MG (11)	floodplain ponds	shallow	28	6.0	—	—	organic

[a] 1, Sars (1901); 2, Wright (1927); 3, Wright (1937); 4, Thomasson (1954, 1955); 5, Brandorff (1972); 6, Cipólli & Carvalho (1973); 7, Brandorff (1978); 8, Brandorff et al. (1982); 9, Dussart (1984); 10, Matsumura-Tundisi (1986); 11, present report (environmental data for Pirapora ponds supplied by M. B. G. e S. Dabés).

[b] Brazilian state abbreviations: AM, Amazonas; DF, Distrito Federal; GO, Goiás; MG, Minas Gerais; PA, Pará; SP, São Paulo.

[c] Means from Furch (1984).

its biological requirements merit further investigation.

Acknowledgments

I thank Mestres Lourdes El-Moor Loureiro and Maria Beatriz Gomes e Sousa Dabés for collecting and lending specimens, and Dr. Gerd-Oltmann Brandorff for valuable discussions of the Amazonian populations.

Literature Cited

Andrade, E. R. de, & G.-O. Brandorff. 1975. Uma nova espécie de Diaptomidae (Crustacea, Copepoda) "*Diaptomus*" *negrensis* das águas pretas perto de Manaus.—Acta Amazonica 5(1): 97–103.

Arcifa, M. S. 1984. Zooplankton composition of ten reservoirs in southern Brazil.—Hydrobiologia 113:137–145.

Brandorff, G.-O. 1972. Ein Beitrag zur Calanidenfauna (Crustacea Copepoda) des Amazonasgebietes, mit einem Überblick über die Diaptomiden (Crustacea, Copepoda) Südamerikas. Diplomarbeit, Universität Kiel, 57 pp.

———. 1976. The geographic distribution of the Diaptomidae in South America (Crustacea, Copepoda).—Revista Brasileira de Biologia 36(3): 613–627.

———. 1978. Preliminary comparison of the crustacean plankton of a white water and a black water lake in Central Amazonia.—Verhandlungen der Internationale Vereinigung für Limnologie 20:1198–1202.

———, W. Koste, & N. N. Smirnov. 1982. The composition and structure of rotiferan and crustacean communities of the lower Rio Nhamundá, Amazonas, Brazil.—Studies on Neotropical Fauna and Environment 17:69–121.

Brehm, V. 1965. Bericht über eine unvollendet gebliebene Untersuchung der Argentinischen Kopepodenfauna.—Sitzsungsberichte der österreichischen Akademie der Wissenschaften, Abteilung I, 174:1–15.

Cipólli, M. N., & M. A. J. de Carvalho. 1973. Levantamento de Calanoida e Cyclopoida (Copepoda, Crustacea) das águas da Região do Guamá, Capim e Tocantins, com nota sobre a fauna acompanhante.—Papéis Avulsos de Zoologia, São Paulo 27(8):95–110.

Daday, E. V. 1905. Untersuchungen über die Süsswasser-Mikrofauna Paraguays.—Zoologica 1–375 + pl. 23.

Dussart, B. H. 1984. Some Crustacea Copepoda from Venezuela.—Hydrobiologia 113:25–67.

———. 1985. Sur quelques copépodes d'Amérique du Sud V. Diaptomidae.—Archiv für Hydrobiologie 103(2):201–215.

———, & D. Defaye. 1983. Répertoire Mondial des Crustacés Copépodes des Eaux Intérieures. I.—Calanoïdes. Bordeaux, Éditions du C. N. R. S., 224 pp.

Furch, K. 1984. Water chemistry of the Amazon basin: the distribution of chemical elements among freshwaters. Pp. 167-199 *in* H. Sioli, ed., The Amazon: limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publishers, Dordrecht.

Matsumura-Tundisi, T. 1986. Latitudinal distribution of Calanoida copepods in freshwater aquatic systems of Brazil.—Revista Brasileira de Biologia 46(3):527–553.

Pesta, O. 1927. Ein Beitrag zur Kenntnis der Copepodenfauna von Argentinien.—Zoologischer Anzeiger 73(3/4):67–80.

Reid, J. W. 1985. Chave de identificação e lista de referências bibliográficas para as espécies continentais sulamericanas de vida livre da ordem Cyclopoida (Crustacea, Copepoda).—Boletim de Zoologia, Universidade de São Paulo 9:17–143.

———. 1987. *Scolodiaptomus,* a new genus proposed for *Diaptomus* (sensu lato) *corderoi* Wright, and description of *Notodiaptomus brandorffi,* new species (Copepoda: Calanoida) from Brazil.—Journal of Crustacean Biology 7(2):364–379.

———. 1988. *Thermocyclops decipiens* (Copepoda Cyclopoida): exemplo de confusão taxonômica.—Acta Limnologica Brasiliensia 2:479–499.

———. 1989. The distribution of species of the genus *Thermocyclops* (Copepoda, Cyclopoida) in the western hemisphere, with description of *T. parvus,* new species.—Hydrobiologia 175:149–174.

Sars, G. O. 1901. Contributions to the knowledge of the fresh-water Entomostraca of South America, as shown by artificial hatching from dried material. Part II.—Archiv for Mathematik og Naturvidenskab 24(1):3–50 + pl. I–VII.

Sendacz, S., E. Kubo, & M. A. Cestarolli. 1985. Limnologia de reservatórios do sudeste do Estado de São Paulo, Brasil. VIII. Zooplancton.—Boletim do Instituto de Pesca 12(1):187–207.

Thomasson, K. 1953 [1954]. Studien über das südamerikanische Süsswasserplankton 2. Zur Kenntnis des südamerikanischen Zooplanktons.—Arkiv för Zoologi 6(10):189–194.

———. 1955. Studies on South American fresh-water plankton 3. Plankton from Tierra del Fuego and Valdivia.—Acta Horti Gotoburgensis 19:193–225.

Tollinger, M. A. 1911. Die geographische Verbreitung der Diaptomiden und anderer Süss- und Brackwasser-Gattungen aus der Familie der

Centropagiden.—Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 30(1-3):1–301.

Wright, S. 1927. A revision of the South American species of *Diaptomus.*—Transactions of the American Microscopical Society 46(2):73–121.

———. 1937. A review of some species of *Diaptomus* from São Paulo.—Annais da Academia Brasileira de Ciencias 9:65–82, pls. I-III.

———. 1938. Distribuição geographica das especies de *Diaptomus* na America do Sul.—Livro Jubilar do Prof. Travassos, Rio de Janeiro, 3:561–566 + pl. 1.

Department of Invertebrate Zoology, NHB-163, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 151–156

ACHELIA ASSIMILIS (HASWELL, 1884) IN THE *HETEROZOSTERA* BED OF PUERTO ALDEA, COQUIMBO: FIRST RECORD FROM THE NORTHERN CHILEAN COAST (PYCNOGONIDA: AMMOTHEIDAE)

Sergio A. González and Mario E. Edding

Abstract.—This work describes individuals of *Achelia assimilis* (Haswell) collected in a bed of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog from Puerto Aldea (Coquimbo, Chile), extending its geographical range from Chiloé north to Coquimbo. Latitudinal variations in size and *A. assimilis* body proportions are suggested. The distribution and dispersal of *A. assimilis* along the southeast Pacific is briefly discussed.

In spite of the pycnogonid species richness found in the northeast Pacific (Nakamura & Child 1983), the pycnogonid southeast Pacific fauna is scarcely known (Child 1977). In the South American Pacific, few pycnogonid collections have been gathered. Hedgpeth (1961) found the only known pycnogonids in the north of Chile. This work documents the finding of a new record for pycnogonid fauna from the northern Chilean coast and describes its morphology with the purpose of contributing to *A. assimilis* recognition.

During August, 1987, six adult (1 ♀ with eggs, 5 ♂) of *Achelia assimilis* (Haswell) were found. The pycnogonids were collected in the Puerto Aldea intertidal (30°16′S), Tongoy Bay (Fig. 1), grasping the leaves of *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog. The *Heterozostera* bed in Puerto Aldea is the only seagrass site reported along the South American Pacific coast (Santelices 1982, Phillips et al. 1983).

Puerto Aldea is an area with particular conditions; shallow and protected from wave action, and to the prevalent Southwest Wind of the Coquimbo region (Alarcón 1975). *Heterozostera tasmanica* hosts a very diverse fauna, especially juvenile stages of species with commercial and ecologic importance.

Achelia assimilis (Haswell)
Fig. 2

Ammothea assimilis Haswell, 1884:1026–1027; pl. 55, figs. 5–9.
Achelia assimilis Flynn, 1919:87–89; pl. 22, figs. 22–26.
Achelia (Ignavogriphus) assimilis Fry & Hedgpeth, 1969:104–106; figs. 157, 163.

Description.—Trunk circular, compact, hardly segmented excepting one neck suture, lateral processes and neck contiguous. Neck with one small spine over each palp insertion. Lateral processes with dorsodistal tubercles, one on posterior process and two on other lateral processes; each tubercle armed with one spine. Trunk with three dorsal spines. Ocular tubercle short, conical, tip pointed. Proboscis long, length close to trunk length. Abdomen elongate, extending into first coxa, upward, armed with one dorsomedian spine, two dorsal and two lateral spines near tip.

Chelifores longer than second palp segment, with one dorsoproximal spine and one dorsomedian spine, with a low dorsodistal tubercle armed with two spines and one laterodistal spine. Chela reduced, slender, globe-shaped, with small spine.

Palp 8-segmented. First segment with one dorsal and lateral tubercle. Segment 2 lon-

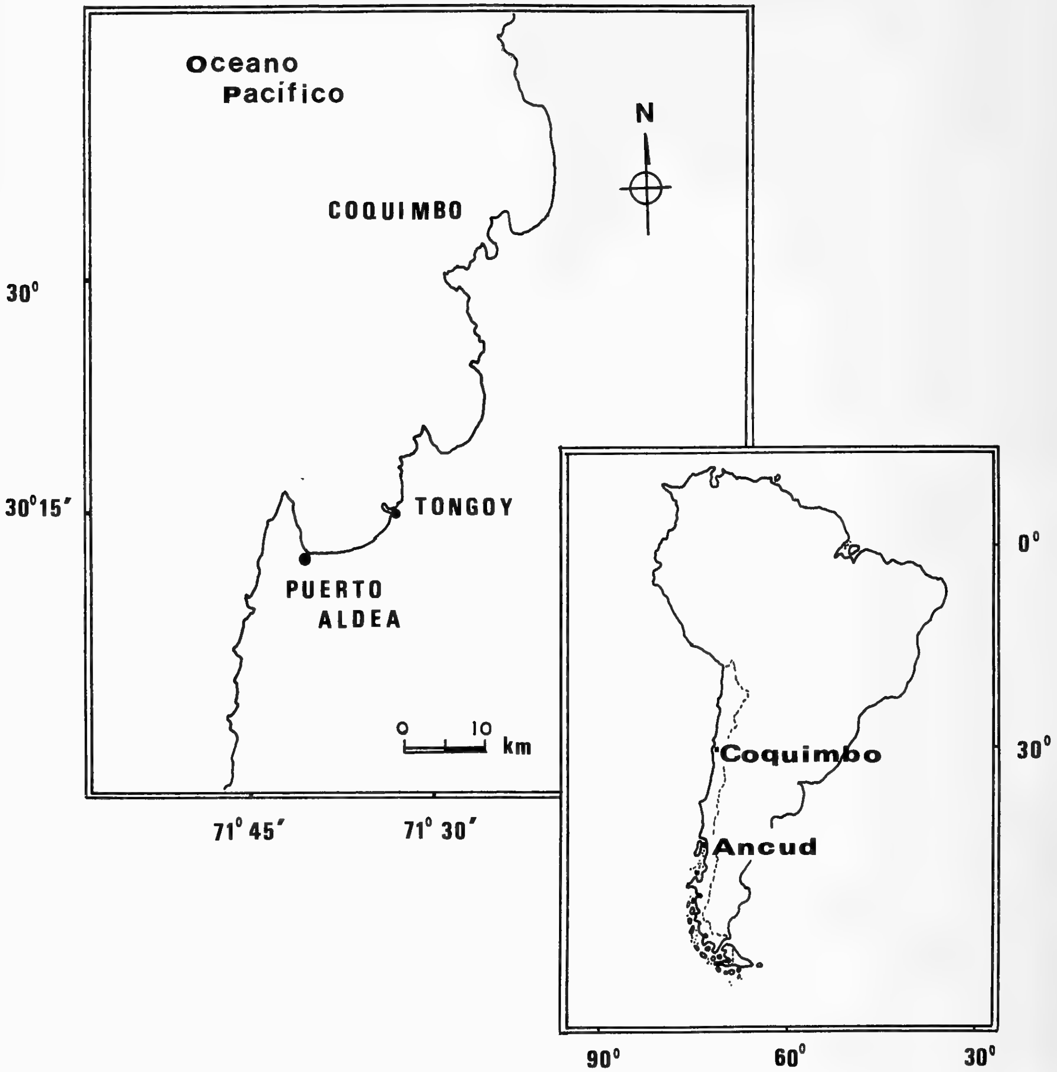


Fig. 1. Map of South America indicating the Chilean distributional limits of *Achelia assimilis* (Haswell) (bottom). Coquimbo coastal zone showing location of the collecting site on the *Heterozostera* bed in Puerto Aldea, Bahía Tongoy (top).

gest, equipped with two dorsodistal spines. Third segment broad, with one dorsal spine. Fourth segment shorter than second segment, equipped with two ventrodistal spines. Sixth and seventh segments widened ventro-distally forming a low process. Last segment with a rounded tip. Four terminal segments with several ventral setae.

Oviger 10-segmented. First and second segments without spines; third segment with one dorsal spine; fourth and fifth segments subequal, with lateral row of five to six setae; fifth segment with two dorsodistal spines; sixth segment with one ventrodistal spine, one dorsal spine and two lateral spines; seventh segment with five spines around dorsal border and two lateral small spines, and two ventral denticulate spines;

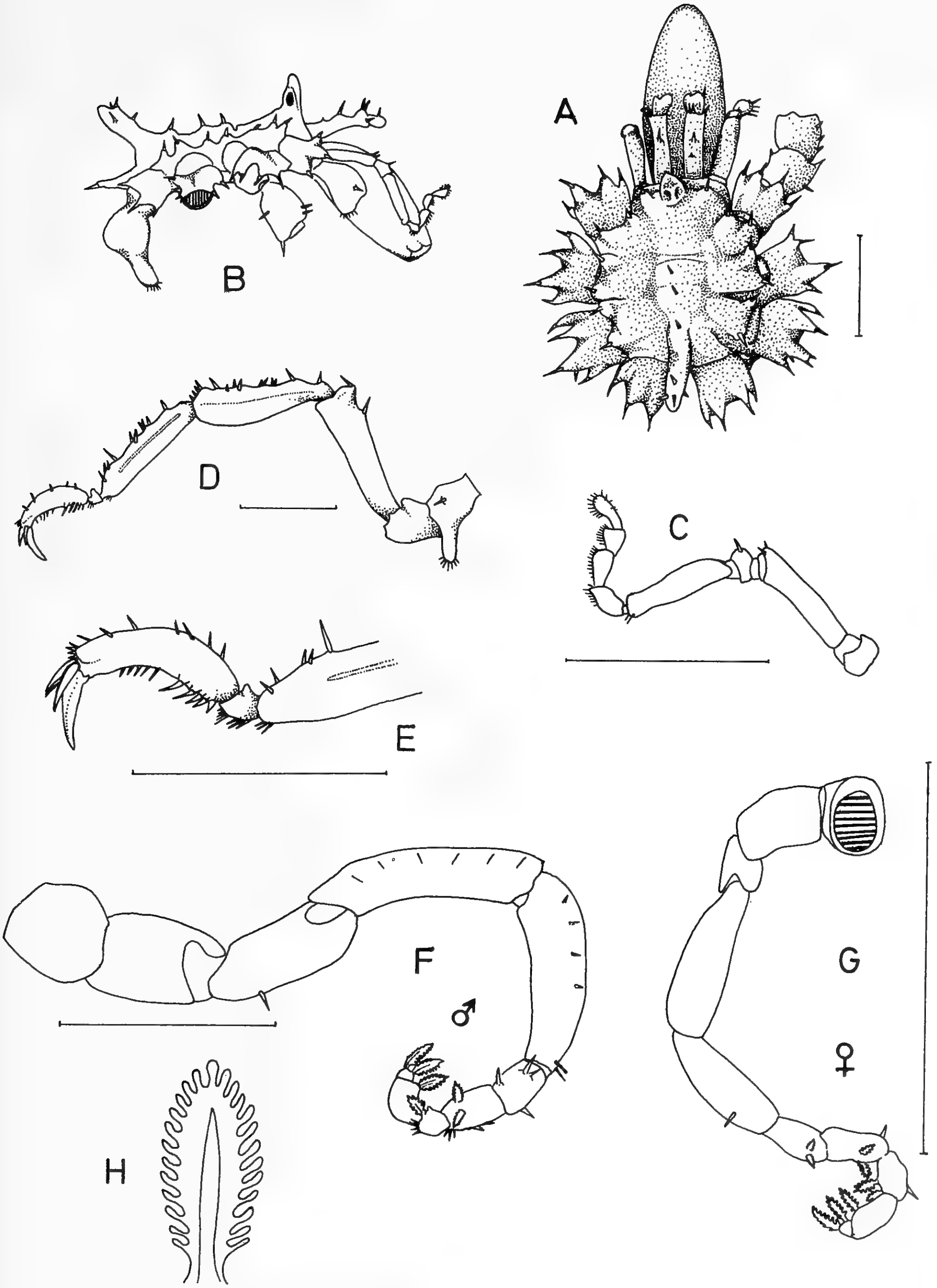


Fig. 2. *Achelia assimilis.* A, Body (dorsal); B, Body (lateral); C, Palp; D, Third leg; E, Terminal segments of third leg; F, Male oviger; G, Female oviger; H, Denticulate spine. (Bar = 1 mm, excepting drawing F = 0.5 mm.)

eighth segment broad, with four dorsodistal spines and one ventral denticulate spine; ninth with one denticulate spine, and tenth with two terminal denticulate spines. Denticulate spines with 12 serrations per edge. Terminal segment disposed synaxially. Female oviger smaller than male, fourth segment longest, five terminal segments each equipped with two denticulate spines.

Legs long; coxa 1 with four distal tubercles, each bearing a single spine except third tubercle armed with one to three spines; coxa 2 with ventrodistal genital process, as long as width of segment, equipped with several setae; coxa 3 with one dorsal tubercle and two lateral tubercles, bearing single short spine. Femur slightly shorter than tibia 1, broad distally, with two low dorsodistal tubercles, each bearing one spine; tibia 1 inflated medially but reduced distally, with five or six low tubercles in two dorsal rows, with single spines, with one distal and proximal long spine, and a lateral suture. Tarsus with small dorsal tubercle without spine, three delicate ventral spines and several distal setae. Propodus longer than tibia, curved, without heel, with five large basal spines and five pairs of small sole spines, seven or eight dorsal spines and several distal setae. Claw long, over two-thirds of propodal length. Auxiliary claws about half length of terminal claw. Female coxa 1 with two distal tubercles and without genital process in coxa 2.

Measurements (♂, in mm):

Trunk length (neck to tip 4th lateral process)	1.77
Trunk width (across 2nd lateral processes)	1.89
Proboscis length (ventral)	1.55
Abdomen length	0.66
Ocular tubercle height	0.43
Chelifore length	0.80
Third leg:	
Coxa 1	0.34
Coxa 2	0.57
Coxa 3	0.40
Femur	1.46
Tibia 1	1.49
Tibia 2	1.34
Tarsus	0.14
Propodus	0.66
Claw	0.40
Auxiliary claws	0.23

Remarks on identification.—The specimens collected in Puerto Aldea, differ from Stock's (1953, large form) individuals by having a body nearly circular; more compact and lateral processes juxtaposed; femur without dorsomedial spines; 4th and 5th oviger segments similar. The present pycnogonid agrees in all essentials with Hedgpeth's (1961) description from southern Chile. But, the latter bears only three or four basal spines on the propodus.

The size of the *A. assimilis* male found in Puerto Aldea is the greatest among literature reports. An interesting latitudinal sequence is observed in *Achelia assimilis* size and in the several terminal segments of characteristic locomotor appendages (Table 1). Although the evidence is limited, Table 1 suggests an inverse relation between trunk size, claw size, number of propodal spines, and latitude. To verify the effect of a latitudinal-dependence factor (e.g., temperature) on *Achelia assimilis* growth and development, it would be essential to have a more complete sampling program along the latitudinal gradient.

Remarks on distribution and dispersal.—*Achelia assimilis* has been previously found in the south and west Australian coasts (Stock 1973, Child 1975), New Zealand and Auckland Islands (Stock 1954), New Caledonia (Child 1977) and in the South American coast (Hedgpeth 1961, Fry & Hedgpeth 1969). The present work extends the actual *A. assimilis* distribution from Ancud, Chiloé (41°44′S) to Puerto Aldea, Bahía Tongoy (30°16′S) in the Chilean northern coast (Fig. 1).

Table 1.—Body measurements (mm) and proportions of third leg of male *Achelia assimilis* (Haswell) from different latitudes.

Characters	Locality and latitude Auckland Island (50°S)	 Chile south (40°S)	 Chile north (30°S)
Trunk length	1.09	1.44	1.77
Trunk width	1.00	1.33	1.89
Abdomen length	0.38	0.65	0.66
Locomotor appendage total length	4.16	3.64	6.40
Propodus/Claw	1/3–1/2	1/2	2/3
Claw/Auxiliary claw	2/3	2/3–1/2	1/2
Number of propodal spines	3	3–4	5
Source:	Stock (1954)	Hedgpeth (1961)	Present work

Pycnogonids can disperse into new areas clinging to drifting plants, by marine currents (Fage 1949) or, parasitizing ambulatory organisms (Fry & Hedgpeth 1969). The specific food associations and sedentary habits of *Achelia* (Bamber & Davis 1982) generate a reduced dispersal power over great distances. In general, disjointed distribution of *A. assimilis* could be explained through the same hypotheses which explain the presence of *Heterozostera tasmanica* in Chile: a) a transoceanic dispersal from South Pacific to central-northern Chile, via West Wind Drift and Humboldt current; or b) a South American-Antarctic-Australian continuous distribution in the Gondwanian paleocontinent (Edgar 1986). On the other hand, an antropic introduction cannot be discarded (Carlton 1987).

The *Achelia assimilis* and other species distribution—e.g., *Xenosiphon mundanum* (Selenka, de Man & Büllow) (Sipunculida; Tarifeño & Tomicic 1973), *Pyura preapuçialis* Heller (Chordata; Paine 1986), as with several marine algae listed by Santelices (1980)—confirms the biogeographical relationship between the South American and Australian coast. The finding of species with reduced dispersal capacity and species distributed in the Australian region, would confirm a Gondwanian origin for this disjoint distribution.

Acknowledgments

The authors gratefully acknowledge Prof. Nibaldo Bahamondes who encouraged them to publish this work, and C. Allan Child of the Natural History National Museum in Washington (USA), who confirmed the pycnogonid identification. This work was partly financed by the Dirección General de Investigación of Universidad del Norte (Programa Biologia y Cultivo de Algas Marinas). This publication is part of the Thesis requirements of the first author.

Literature Cited

Alarcón, E. 1975. Oceanographic conditions in coastal waters of the Coquimbo zone. International Symposium of Coastal Upwelling Proceedings, Coquimbo, Chile, pp. 149–161.

Bamber, R. N., & M. H. Davis. 1982. Feeding of *Achelia echinata* Hodge (Pycnogonida) on marine algae.—Journal of Experimental Marine Biology and Ecology 60(2–3):181–187.

Carlton, J. T. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean.—Bulletin of Marine Science 41(2):452–465.

Child, C. A. 1975. Pycnogonida of Western Australia.—Smithsonian Contributions to Zoology 190: 1–29.

———. 1977. On some pycnogonida of French Oceania.—Proceedings of the Biological Society of Washington 90(2):440–441.

Edgar, G. J. 1986. Biogeographical processes in the southern hemisphere marine environment.—Actas II Congreso de Algas Marinas Chilenas: 29–46.

Fage, L. 1949. Classe des Pycnogonides. Pp. 906-941 *in* P-P. Grassé, ed., Traité de Zoologie, VI. Masson et Cie., Paris.

Flynn, T. T. 1919. A re-examination of Professor Haswell's types of Australian Pycnogonida.—Papers and Proceedings of the Royal Society of Tasmania 1919:70–92.

Fry, W. G., & J. W. Hedgpeth. 1969. The fauna of the Ross Sea, 7: Pycnogonida, 1: Colossendeidae, Pycnogonidae, Endeidae, Ammotheidae.—New Zealand Oceanographic Institute Memoirs 49:9–139.

Haswell, W. A. 1884. On the Pycnogonida of the Australian coast, with descriptions of new species.—Proceedings of Linnean Society of New South Wales 9(4):1021–1034.

Hedgpeth, J. W. 1961. Pycnogonida. Reports of the Lund University Chile Expedition 1948-49, no. 40, Lunds Universitets Arsskrift N. F. Avd. 2, 57(3):3–18.

Nakamura, K., & C. A. Child. 1983. Shallow-water Pycnogonida from the Izu Peninsula, Japan.—Smithsonian Contribution to Zoology 386:1–71.

Paine, R. T. 1986. Old problems and new perspectives in marine community ecology.—Estudios Oceanológicos 5(1):9–18.

Phillips, R. C., B. Santelices, R. Bravo, & C. P. Mc Roy. 1983. *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Chile.—Aquatic Botany 15(2):195–200.

Santelices, B. 1980. Phytogeographic characterization of the temperate coast of Pacific South America.—Phycologia 19:(1):1–12.

———. 1982. Caracterización fitogeografica de la costa temperada del Pacífico de Sudamérica. Verificación de hipótesis y consecuencias ecológicas.—Archivos de Biologia y Medicina Experimental 15(3):513–524.

Stock, J. H. 1954. Pycnogonida from Indo-West-Pacific, Australian and New Zealand waters. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-1916, LXXVII.—Videnskabelige Meddelelser Fra Dansk Naturhistorisk Forening, Kobenhavn 116:1–168.

———. 1973. *Achelia shepherdi* n. sp. and other Pycnogonida from Australia.—Beaufortia 21(279): 91–97.

Tarifeño, E., & J. Tomicic. 1973. Primer registro en el Pacífico sur oriental para *Xenosiphon mundanum* (Selenka, de Man & Büllow, 1883). (Sipunculida, Sipunculidae).—Revista de Biología Marina 15(1):107–110.

Universidad del Norte, Facultad de Ciencias del Mar, Departamento de Biología Marina, Casilla 117, Coquimbo, Chile.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 157–160

PROTOTRYGAEUS JORDANAE, A NEW SPECIES OF PYCNOGONID FROM MONTEREY BAY, CALIFORNIA

C. Allan Child

Abstract.—A new species of Pycnogonida, *Prototrygaeus jordanae,* is described and illustrated from soft sediments in Monterey Bay, California. The new species is compared with the only other known species of the genus, *P. ammothelloides* Stock, from Guyana, South America, and their relationship and distribution are discussed.

While studying the biology and life history of two species of pycnogonids taken by epibenthic sleds from Monterey Bay, California, the new species described herein was discovered in large numbers inhabiting soft sediments at depths of 50–70 meters. Attempts were made to identify the species in question and it was then that their collector, Roxanne Jordan of Moss Landing Marine Laboratory, Monterey Bay, kindly sent specimens to me for examination. A second species, *Anoplodactylus erectus* Cole, was taken in large numbers from muddy sediments at 70–90 meters, but also occurred in some 70 meter sled hauls with the new species. This second species is known from British Columbia, Canada, to at least Panama, and probably occurs south of there, but it is usually taken in shallower water down to about 40 meters.

Systematics

Genus *Prototrygaeus* Stock, 1975

Emended diagnosis.—With the characters of the type genus except for palps of six or seven segments, ovigers of nine or ten segments, and female oviger terminal segment with claw or paired simple spines.

Prototrygaeus jordanae, new species

Fig. 1

Material examined.—California: Monterey Bay, 36°49.6′N, 121°50.8′W, epibenthic sled in soft sediment with hydroids on molluscs and wood, 50–70 m, collected on mixed dates, 1988 (1 m, holotype, USNM 234509). Same locality, 55 m, 22 Sep 1988 (1 f, 1 juv, paratypes, USNM 234510).

Other material.—Same locality, 60 m, 21 Apr 1988, epibenthic sled in soft sediment as above (250+ m, f, j).

Description.—Size moderately small, leg span 9.7 mm. Trunk and lateral processes moderately slender, trunk segmentation incomplete but suture lines partly present. Neck very short, broad. Lateral processes very long, separated by about twice their diameters distally, about 3.5 times longer than their diameters, armed with broad dorsodistal tubercles, as tall as segment diameters, glabrous. Ocular tubercle slender, about 2.5 times longer than basal diameter, directed obliquely anterior, tapering to rounded apex. Eyes large, darkly pigmented, anterior pair slightly more distal than posterior pair. Abdomen very slender, longer than ocular tubercle, almost erect, armed with few short lateral and distal setae.

Proboscis a swollen cylinder, tapering proximally and distally to rounded lips.

Chelifore scapes of two segments, first segment only 0.6 length of second which is swollen distally. Second scape segment armed with 2–3 setae as long as distal diameter of segment, chela with single similar seta. Chela with moderately large palm having only hint of finger buds.

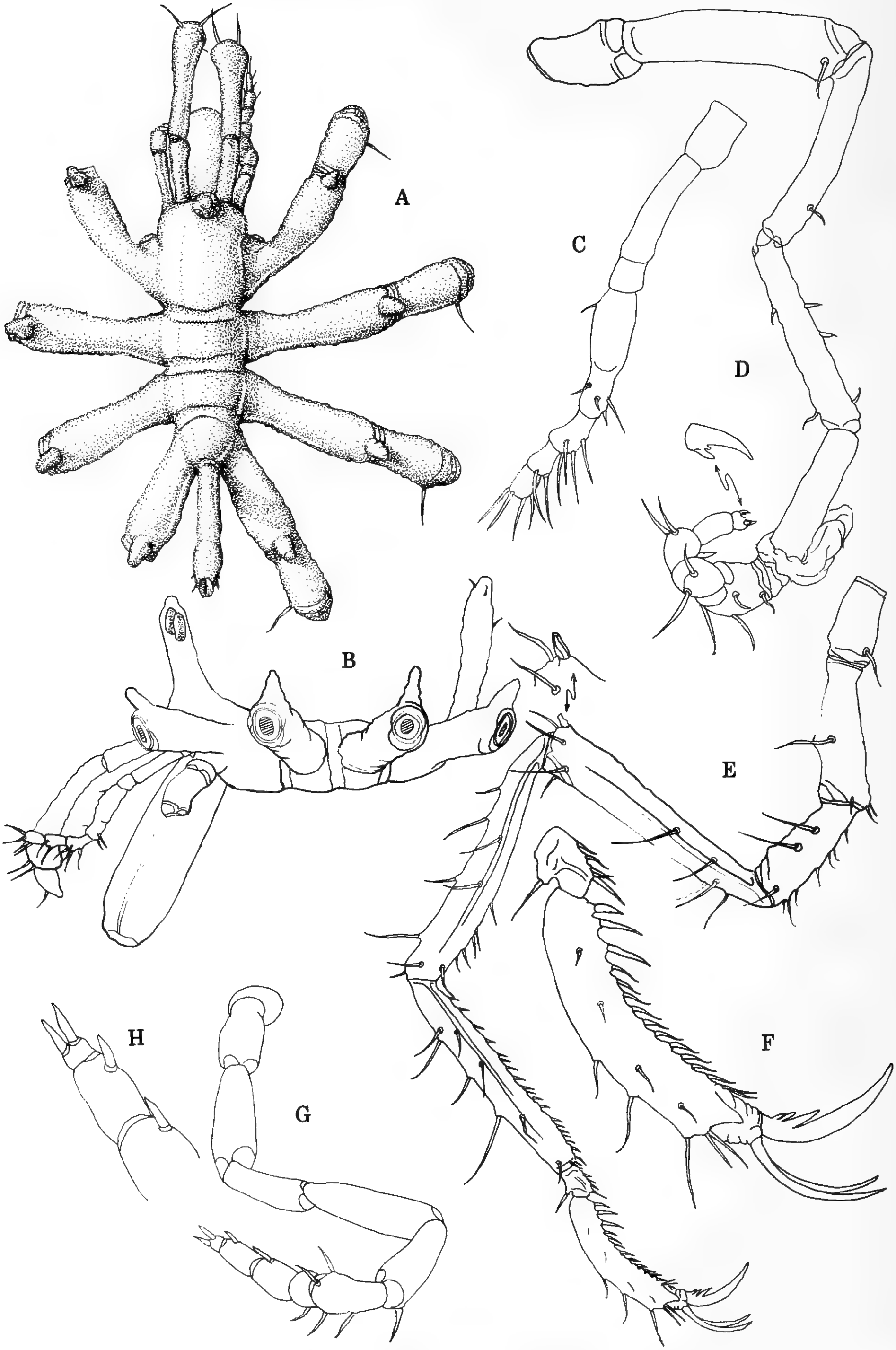


Fig. 1. *Prototrygaeus jordanae,* holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Palp; D, Oviger, with enlarged terminal claw; E, Third leg, with enlarged cement gland tube; F, Terminal segments of third leg, enlarged. Paratype female: G, Oviger; H, Oviger terminal segments, enlarged.

Palp with seven segments, second slightly shorter than fourth, terminal three segments decreasing in size only slightly, fourth and terminal three segments armed with few setae each longer than segment diameter.

Oviger with ten segments, elongate, second and third segments subequal, fourth and fifth each slightly shorter than last, strigilis very short, sixth, seventh and eighth segments with 2–4 ectal setae longer than segment diameter and 1–2 short endal spines. Terminal two segments short, tenth no longer than wide and armed with two curved sharply pointed spines bearing two lateral teeth, the proximal larger tooth followed by a very tiny second pointed tooth. Ninth segment cylindrical, glabrous.

Legs moderately long, segments increasingly setose distally. First coxae with long posterodistal seta each, second coxae with one long medianlateral seta per side, third coxae with two similar setae per side. Major leg segments with few lateral, ventral and distal long setae, first tibiae with few ventrodistal short setae, second tibiae with ventral row of very short setae. Femoral cement gland a small dorsodistal sac with a very short distal tube, much shorter than segment diameter. Tarsus short, semirectangular, armed with single dorsal seta and several ventral setae. Propodus slender, long, moderately curved, without marked heel but with three large heel spines. Sole with 12–13 curved spines. Claw long, well curved, with three endal teeth increasing in size from short proximal to broad distal tooth. Auxiliary claws very slender, as long as main claw.

Female: Dorsodistal tubercles on lateral processes not as robust or tall as those of male. Palp 7-segmented and oviger 10-segmented. Oviger with shorter segments; second, fourth and fifth subequal, strigilis of increasingly short segments, eighth and ninth armed with single lateral simple spine, terminal segment wider than long, armed with pair of simple spines but without a curved claw. Legs slightly less setose than those of male, gonopores prominent, ventrodistal on all second coxae. Juvenile with fully chelate chelae.

Measurements (of holotype) in mm.—Trunk length (chelifore insertion to tip fourth lateral processes), 1.04; width across 2nd lateral processes, 1.24; abdomen length, 0.49; proboscis length, 0.64; third leg, coxa 1, 0.27; coxa 2, 0.44; coxa 3, 0.38; femur, 0.82; tibia 1, 0.8; tibia 2, 0.74; tarsus, 0.11; propodus, 0.45; claw, 0.22.

Distribution.—The new species is only known from Monterey Bay, California, in 50–70 meters.

Etymology.—I take pleasure in naming this species after its collector, Ms Roxanne Jordan of the Moss Landing Marine Laboratory, Monterey Bay, California.

Remarks.—The most striking difference between this new species and the only other one known in this genus, *Prototrygaeus ammothelloides* Stock (1975:979–981, fig. 9), is the presence of prominent lateral process tubercles on *P. jordanae.* The legs, except for the longer cement gland tube in Stock's species, the ocular tubercle, and the chelifores are all very similar in the two species.

The other prominent differences are only evident under close examination: the increased number of palp and male oviger segments in the new species. The palp of Stock's species apparently has a coalesced or fused terminal segment giving it one less segment than the generally longer palp of *P. jordanae.* Possibly one of the two terminal oviger segments of the male of Stock's species has fused from an original count of three, although it is not apparent in his figure 9h. Such fusion would account for the reduction of palp and oviger segment counts and no other explanation seems appropriate for this discrepancy in numbers, particularly since the female of his species has the full number of oviger segments.

Stock's species also has a few anterior and posterior papillae on the lateral processes which are absent in the male and female of this species, and the abdomen is notably shorter in *P. jordanae.*

The occurrence of the two known species

of this genus on either side of the Western Hemisphere is noteworthy and suggests a pre-Panamanian emergence distribution with subsequent speciation from a parent species. There can be little doubt with the close morphological similarities between these species that they are near relations. It will be interesting to learn the degree of restriction in the distribution of both species when more specimens of each are collected in other localities. Both are apparently found in subtidal habitats of shallow depth. There is mention (Jordan, pers. comm.) of probable epifaunal forage in the form of hydroids on the soft sediments where the new species lives. This is in keeping with what is known of pycnogonid feeding habits and where the hydroid forage is heavy as it apparently is in this locality, the number of specimens can be extremely large as shown by the single sled haul of over 250 specimens.

Acknowledgments

I am grateful to the collector, Ms Roxanne Jordan, for the opportunity to examine and describe this interesting new species from an area believed to have been well collected in the past. Its occurrence suggests that careful collecting in almost any area can produce unexpected fauna of interest to the systematist.

I thank both the invertebrate editor and the Proceedings editor for their care and suggestions for improving manuscript.

The types and other material are deposited in the collections of the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., under the numbering system of the old U. S. National Museum (USNM).

Literature Cited

Stock, J. H. 1975. Pycnogonida from the Continental Shelf, Slope, and Deep Sea of the Tropical Atlantic and East Pacific. *In* Biological Results of the University of Miami Deep-Sea Expeditions, 108.—Bulletin of Marine Science 24(4):957–1092, 59 figs.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 161–178

FABRICINUDA, A NEW GENUS OF FABRICIINAE (POLYCHAETA: SABELLIDAE)

Kirk Fitzhugh

Abstract.—*Fabricinuda,* a new genus of the polychaete family Sabellidae, is described. The genus is unique in lacking a collar on the anterior peristomial ring; having an anterior peristomial ring as long as wide, or longer, and generally longer than the posterior peristomial ring; and having inferior thoracic pseudospatulate notosetae present on setigers 3–8. Two new species are described (*F. pseudopalpa* and *F. pseudocollaris*) and three species, *Fabriciola limnicola* (Hartman), *Fabricia bikinii* Hartman, and *Fabriciola trilobata* Fitzhugh, are assigned to this genus and redescribed. *Fabriciola mossambica* (Day) may be referable to this genus. *Fabricinuda* is more heterogeneous morphologically than other fabriciin genera but is still monophyletic. A key to species is provided.

As part of a cladistic revision of the Sabellidae-Caobangiidae-Sabellongidae complex (Fitzhugh 1988, 1989), an extensive reexamination of the genera *Fabricia* Blainville, *Fabriciola* Friedrich, and *Augeneriella* Banse was undertaken. These three genera commonly have been regarded as a monophyletic group by nature of the character combination of pygidial eyes and three pairs of radioles (e.g., Banse 1957). Generic diagnoses have implied that the three taxa are quite distinct. For example, species of *Fabricia* are stated to lack ventral filamentous appendages, but have an anterior peristomial ring collar (sensu Fitzhugh 1988, 1989) that is reduced dorsally and laterally, and developed ventrally as a lip-like extension (see also Banse 1956). *Fabriciola* has been distinguished by the presence of unbranched, nonvascularized ventral filamentous appendages (sensu Fitzhugh 1988, 1989) and a membranous, anterior, peristomial ring collar that is relatively well developed all around (Banse 1956, 1957). *Augeneriella* has been differentiated from the other two genera by the presence of paired, vascularized, ventral filamentous appendages that are branched to some degree, whereas the anterior peristomial ring collar is stated to be similar to that seen in *Fabricia* (Banse 1957, Gitay 1970).

Diagnoses for these genera have, however, changed over the years as new species have been described. Species in these genera now form very heterogeneous assemblages that cannot be adequately represented in only three genera. Currently, *Fabricia, Fabriciola,* and *Augeneriella* contain some of the smallest sabellid species. For this reason, the group is difficult to study, and there seems to have been a great deal of confusion as to what characters to use to distinguish species, and, in some instances, genera. This problem was recognized in the cladistic analyses by Fitzhugh (1988, 1989), in which two undescribed, monophyletic genera, "Genus A" and "B," were included as part of a revision of the sabellid subfamily Fabriciinae. The present paper is a formal description of "Genus B."

Generic and specific characters, and terminology (e.g., use of the term anterior peristomial ring collar or pseudospatulate setae) used in the present paper are explained and justified by Fitzhugh (1989). Additional setal terminology has been adopted from Perkins (1984). Results of methyl green staining for species discussed below follow the procedures outlined in Banse (1970) and Fitzhugh (1983). Specimens are available for study from the following institutions: Allan Hancock Foundation, University of Southern California (AHF) and the U.S. National Museum of Natural History, Smithsonian Institution (USNM).

Fabricinuda, new genus

Type species.—*Fabricia limnicola* Hartman, 1951.

Diagnosis.—Slender, small-bodied fabriciin species with 8 thoracic and 3 abdominal setigers. Branchial crown with 3 pairs of radioles; distal ends filamentous, about same width as pinnules. All pinnules terminating at same height, extending to same height as radioles or slightly shorter. Dorsal lips well developed or absent; ventral lips absent. Ventral filamentous appendages vascularized, slender, unbranched, or absent. Branchial hearts present. Branchial lobes attached in typical sabellid fashion or with very narrow attachment near dorsal margin of anterior peristomial ring. Mouth in typical sabellid position between branchial lobes or shifted dorsal to attachment point of branchial lobes. Anterior margin of anterior peristomial ring a low, even ridge all around or slightly oblique; rounded lobe present or absent on either side of dorsal midline. Anterior peristomial ring as wide as long or longer; as long as posterior peristomial ring or longer (e.g., Fig. 1B, C); anterior part of anterior peristomial ring may be narrower in lateral view. Annulation between anterior and posterior peristomial rings only distinct ventrally and laterally. Peristomial eyes black, rounded to crescentic; pygidial eyes black, rounded. Inferior thoracic notosetae of setiger 2 short, elongate, narrowly hooded; setigers 3–8 with pseudospatulate setae. Thoracic uncini acicular, with large tooth above main fang; hood present. Abdominal uncini rasp-shaped plates; manubrium about same length as dentate region; dentate region with several teeth per row. Abdominal neurosetae modified, elongate, narrowly hooded. Body wall pigmentation variable.

Etymology.—The first component of a compound word, *Fabricio-*, refers to similarity this genus has with *Fabriciola*; specifically, the presence of ventral filamentous appendages (in most species). The suffix, *-nuda,* derived from the Latin *nudus,* refers to the absence of the anterior peristomial ring collar, typical in one form or another in all other fabriciin genera (sensu Fitzhugh 1989).

Remarks.—The definition of *Fabricinuda* points out a number of variable characters, especially with regard to position of the branchial crown and mouth, and shape of the anterior peristomial ring. This is the most morphologically diverse genus within the revised Fabriciinae (Fitzhugh, in prep.).

The informal diagnosis for this genus in Fitzhugh (1989, as "Genus B") is not as complete as the one given here since this original diagnosis was based only on specimens of *Fabricinuda bikinii* (Hartman; described below) from the Aldabra Atoll. Some of the character states (e.g., absence of dorsal lips, presence of vascularized, ventral filamentous appendages) originally assumed invariant are no longer considered synapomorphies for the genus in the present diagnosis.

Fabricinuda is monophyletic on the basis of 1) reduction of the anterior margin of the anterior peristomial ring to a low ridge, 2) the anterior peristomial ring being at least as wide as long, and 3) the occurrence of pseudospatulate setae in setigers 3–8. The genus contains three previously described species and three new species. In general, species display a longer and more slender body form than seen in other fabriciins.

Key to Species of *Fabricinuda*

1a. Branchial crown attachment to peristomium shifted dorsally to some extent (Figs. 2F, 3B, 5B) . . 4

b. Branchial crown attachment to peristomium not shifted dorsally . . . 2
2a. Vascularized ventral filamentous appendages present; dorsal lips absent . . . 3
b. Ventral filamentous appendages absent; dorsal lips present . . . *F. pseudopalpa,* n. sp.
3a. Ventrum of anterior peristomial ring with paired, membranous lappet-like processes . . . *F. pseudocollaris,* n. sp.
b. Ventrum of anterior peristomial ring smooth, without processes . . . *F. limnicola* (Hartman, 1951)
4a. Mouth in typical sabellid location (Fig. 5B) . . . *F. trilobata* (Fitzhugh, 1983)
b. Mouth shifted more dorsally, above branchial lobe attachment (Figs. 2F, 3F) . . . *F. bikinii* (Hartman, 1954)

Fabricinuda limnicola (Hartman, 1951), new combination

Fig. 1

Fabricia limnicola Hartman, 1951:384–386, pl. 1, figs. 1–9; 1959:545; 1969:695–696, figs. 1–6.—Rullier, 1954:24–25.
Fabriciola limnicola.—Banse, 1956:430.

Material examined.—California: Holotype (AHF 209), Newport, northeast of Highway 101 bridge, between 33°36′58″N, 117°54′12″W, and 33°37′12″N, 117°53′25″W, intertidal sand flats, 18 Dec 1941. 17 specimens (AHF 3387), Anaheim Slough, near Long Beach, along shore, in sand, mud, *Zostera,* 5 Dec 1938. 7 specimens (USNM 41525), Southern California, 13 Jan 1933.

Description.—Holotype complete with 8 thoracic and 3 abdominal setigers; length 7.60 mm (branchial crown comprising 1.20 mm), maximal width 0.28 mm. Branchial crown one-third to one-eighth total body length, attached to peristomium in typical sabellid fashion. Three pairs of radioles; distal ends filamentous, same width as pinnules. Radioles each with 7–10 pairs of pinnules, all terminating at same height as radioles or up to one-third shorter. Dorsal and vental lips absent. Pair of unbranched, vascularized ventral filamentous appendages (Fig. 1E) distinctly wider than pinnules; width of each uniform except proximal one-fourth slightly wider; distal ends blunt. Surface of ventral filamentous appendages with numerous minute transverse wrinkles; length variable, one-half total radiole length to one-fourth longer than radioles. Body cylindrical, slender. Peristomial eyes black, crescentic to rounded; pygidial eyes black and rounded, situated in posterior fourth of pygidium. Anterior margin of anterior peristomial ring of even height or slightly oblique, as long ridge all around (Fig. 1A–C). Anterior peristomial ring 2 to 4 times longer than posterior ring; annulation distinct ventrally and laterally; posterior three-fourths of ventrum of anterior ring appearing glandular, swollen (Fig. 1B, C). Setigers 1–3 shortest, usually wider than long; following setigers longer; setigers 7–8 each 2 to 3 times longer than anterior setigers, much longer than wide. Setiger 9 about same length as 8 or slightly shorter; setigers 10 and 11 successively shorter, setiger 11 about as long as wide. Pygidium about as long as setiger 11; distinctly tapered, conical (Fig. 1D). Superior thoracic notosetae elongate, narrowly hooded; 4–5 per fascicle. Inferior thoracic notosetae of setiger 2 short, elongate, narrowly hooded; 2 per fascicle. Setigers 3–8 with pseudospatulate setae; 2–3 per fascicle (Fig. 1F). Abdominal neurosetae modified, elongate, narrowly hooded, 3–4 per fascicle. Thoracic acicular uncini in single, sometimes irregular rows; 6–9 per fascicle (Fig. 1G). Abdominal uncini with 9–10 teeth in profile, 3–4 teeth per row; manubrium slightly contricted below dentate region, expanded somewhat proximally to quadrangular base (Fig. 1H); manubrium slightly longer than dentate region; 25–30 uncini per fascicle. All specimens examined pigmented; radioles uniformly light to dark brown,

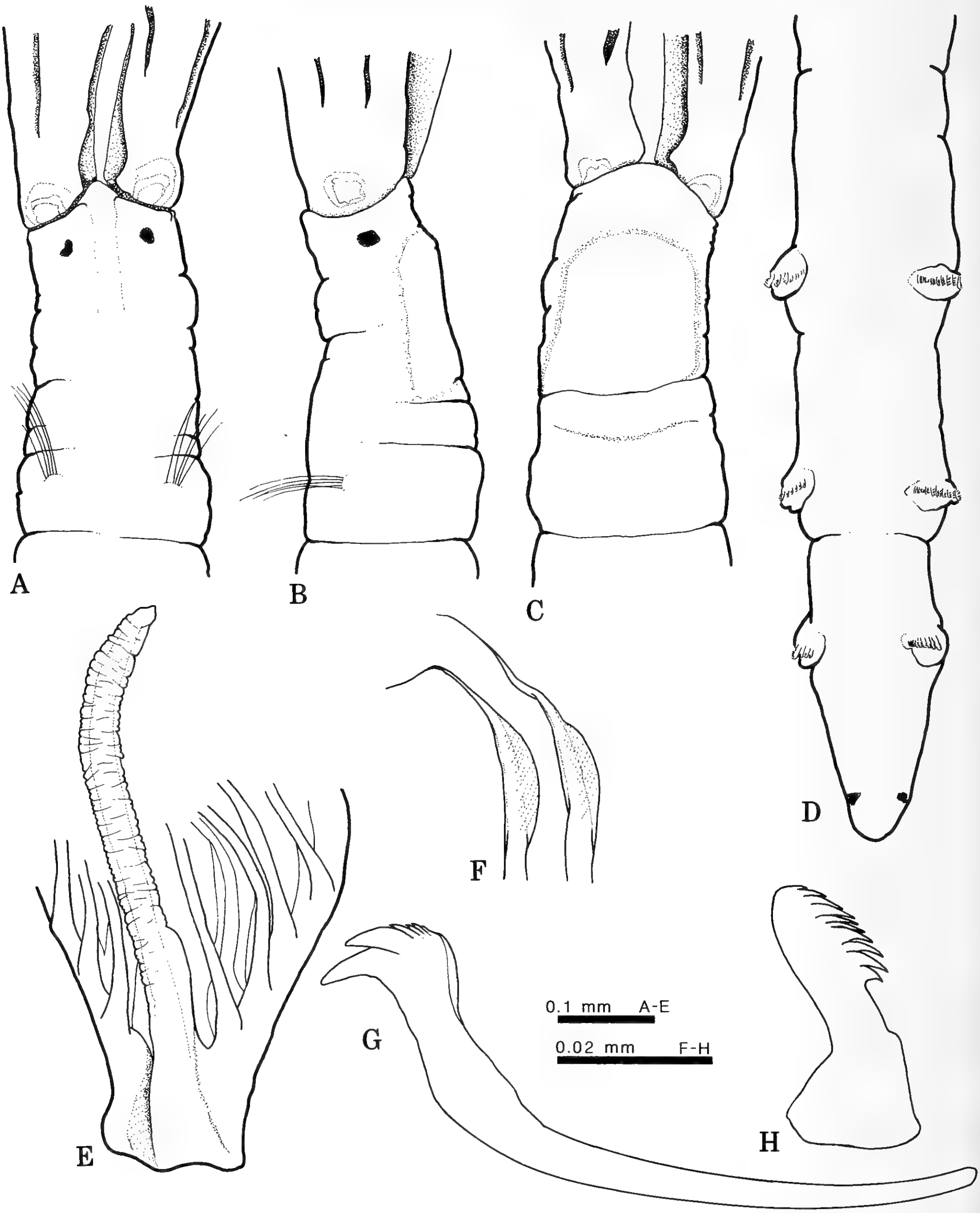


Fig. 1. *Fabricinuda limnicola* (AHF 3387): A–C, Dorsal, lateral (right side) and ventral views, respectively, of the anterior end; D, Posterior end, dorsal view; E, Right half of branchial crown, inner margin; F, Pseudospatulate setae from setiger 8; G, Thoracic uncinus from setiger 7; H, Abdominal uncinus from setiger 9.

some with darker pigmentation along inner dorsal and ventral margins of branchial lobes; ventral filaments light to dark brown; conical structure above mouth dark brown; pigment commonly extending posteriorly along middorsal groove on peristomium; ventrum of anterior peristomial ring, anterior to glandular area, dark brown, quadrangular or triangular in shape, remainder of peristomium light brown; thoracic and abdominal setigers unpigmented, cream colored. Tubes loosely constructed of quartz sand grains and fine mud. Methyl green staining (AHF 3387 material) darkest on anterior midventral margin of setiger 1, uniformly light staining on ventrum from setiger 2 to pygidium; uptake of stain less in crown and peristomium.

Remarks.—*Fabricinuda limnicola* is a very long, slender species that is distinguished from other species in the following characters: 1) the anterior peristomial ring margin does not have lobes to either side of the dorsal midline; 2) there is a glandular-like area on the ventrum of the anterior peristomial ring; and 3) there is a distinctive pigment pattern on the ventral side of the anterior end, accentuating the glandular region. Characters 2 and 3 are illustrated in Hartman (1951: fig. 2).

The figure of an abdominal uncinus in Hartman (1951: fig. 5; compare with Fig. 1H herein) incorrectly depicts a very long, slender manubrium, about four to five times longer than the dentate region. The uncinus was probably drawn while still within the fascicle, which usually gives the impression of the manubrium being longer and narrower than what is seen in true profile.

Fabricinuda bikinii (Hartman, 1954), new combination
Figs. 2–4

Fabricia bikinii Hartman, 1954:641, fig. 178; 1959:544.

Material examined.—Pacific Ocean: Holotype (USNM 24725) and 18 paratypes (AHF 207), Bikini Island, Bikini Atoll, reef flat, white coralline sand, coll., K. O. Emery, 26 Sep 1950. Indian Ocean: Picard Island, Aldabra Atoll. Station Q1-83: replicates 1–11, sand flat with *Thalassia* in front of wet lab, 31 Mar 1983; Q1-83-2, 1 specimen (USNM 121977); Q1-83-3, 1 specimen (USNM 121978); Q1-83-5, 1 specimen (USNM 121979); Q1-83-6, 1 specimen (USNM 121980); Q1-83-9, 1 specimen (USNM 121981). Station Q1A-83: replicates 1-5, same locality as Q1-83, 1 Apr 1983; Q1A-83-1, 7 specimens (USNM 121982); Q1A-83-3, 1 specimen (USNM 121983); Q1A-83-4, 5 specimens (USNM 121984). Station Q5-83: replicates 1–5, *Halodule* flat off beach in front of wet lab, 7 Apr 1983; Q5-83-3, 1 specimen (USNM 121985). Station Q6-83: replicates 1–15, *Thalassodendron* seagrass bed in front of wet lab, Apr 1983; Q6-83-2, 1 specimen (USNM 121986); Q6-83-13, 2 specimens (USNM 121987). Station Q7-83: replicates 1–5 (9 Apr 1983), 6–10 (10 Apr 1983), lagoon, *Caulerpa* on limestone pavement; Q7-83-1, 22 specimens (USNM 121988); Q7-83-3, 6 specimens (USNM 121989); Q7-83-6, 3 specimens (USNM 121990); Q7-83-7, 15 specimens (USNM 121991); Q7-83-8, 15 specimens (USNM 121992); Q7-83-9, 9 specimens (USNM 121993); Q7-83-10, 10 specimens (USNM 121994). Station Q8-83: replicates 1–5, *Thalassia* seagrass bed in lagoon just inside Passe Femme, 16 Apr 1983; Q8-83-3, 143 specimens (USNM 121995); Q8-83-5, 62 specimens (USNM 121996). Coll., K. Fauchald, B. Kensley, P. Hutchings, M. Schotte. Station 85-Q1: replicates A–E, *Thalassia* seagrass bed 120 m from shore, 20 cm depth, 12 Mar 1985; replicates F–K, *Thalassodendron* seagrass bed 120 m from shore, 20 cm depth, 13 Mar 1985; 85-Q1A, 4 specimens (USNM 121997); 85-Q1B, 17 specimens (USNM 121998); 85-Q1C, 3 specimens (USNM 121999); 85-Q1D, 4 specimens (USNM 122000); 85-Q1G, 4 specimens (USNM 122001); 85-Q1H, 10 specimens (USNM

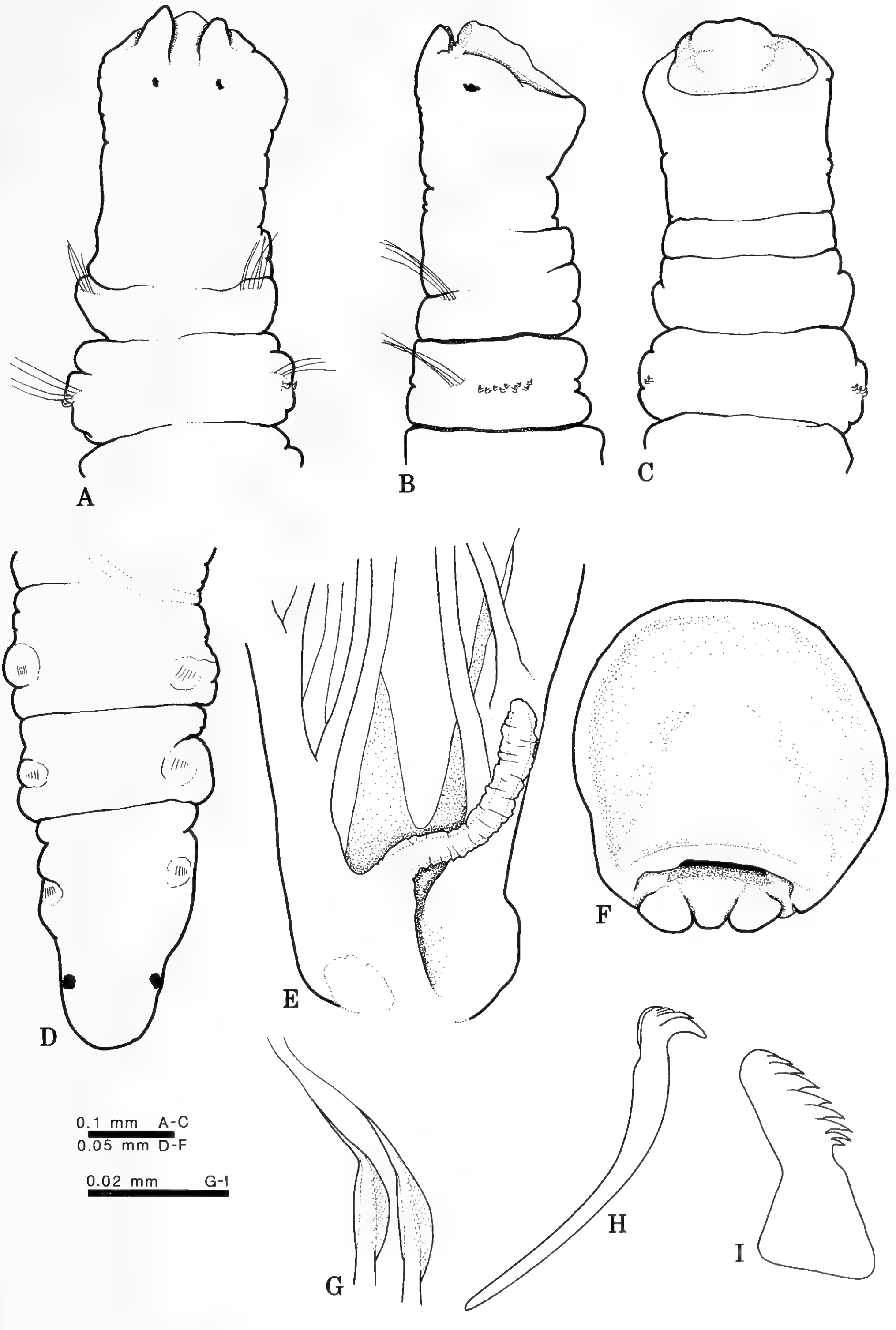
122002); 85-Q1K, 35 specimens (USNM 122003). Station 85-Q2: replicates A-E (15 Mar 1985) and F-K (22 Mar 1985), *Thalassia* bed in lagoon, inside Passe Femme, 10 cm depth; 85-Q2A, 10 specimens (USNM 122004); 85-Q2B, 104 specimens (USNM 122005); 85-Q2C, 16 specimens (USNM 122006); 85-Q2D, 11 specimens (USNM 122007); 85-Q2E, 14 specimens (USNM 122008); 85-Q2H, 80 specimens (USNM 122009); 85-Q2J, 85 specimens (USNM 122010); 85-Q2K, 56 specimens (USNM 122011). Station 85-Q3: replicates F–K, core sample, *Thalassodendron* seagrass bed, 21 Mar 1985; 85-Q3K-Core, 1 specimen (USNM 122012). Coll., K. Fauchald, B. Kensley, K. Fitzhugh, M. Schotte. Station ALD-BC: Bassin Lebine, 1 m depth, 13 March 1985; replicates 1–5 from "*Codium*"-like algal scrapings from undercut sides of bassin; replicates 6–9 from "*Bryopsis*"-like algal scrapings from undercut sides of bassin; replicate 10 from "*Caulerpa*"-like algal scraping from undercut side of bassin; ALD-BC-Bottom: thin veneer of flocculent sediment over smooth rock bottom, 1.5 m depth; ALD-BC-1, 1 specimen (USNM 122013); ALD-BC-2, 10 specimens (USNM 122014); ALD-BC-5, 7 specimens (USNM 122015); ALD-BC-6, 2 specimens (USNM 122016); ALD-BC-10, 125 specimens (USNM 122017); ALD-BC-Bottom, 28 specimens (USNM 122018). F5-85: station data unavailable; 2 specimens (USNM 122019). F9-85: station data unavailable; 89 specimens (USNM 122020). Coll., K. Fauchald, B. Kensley, K. Fitzhugh, M. Schotte.

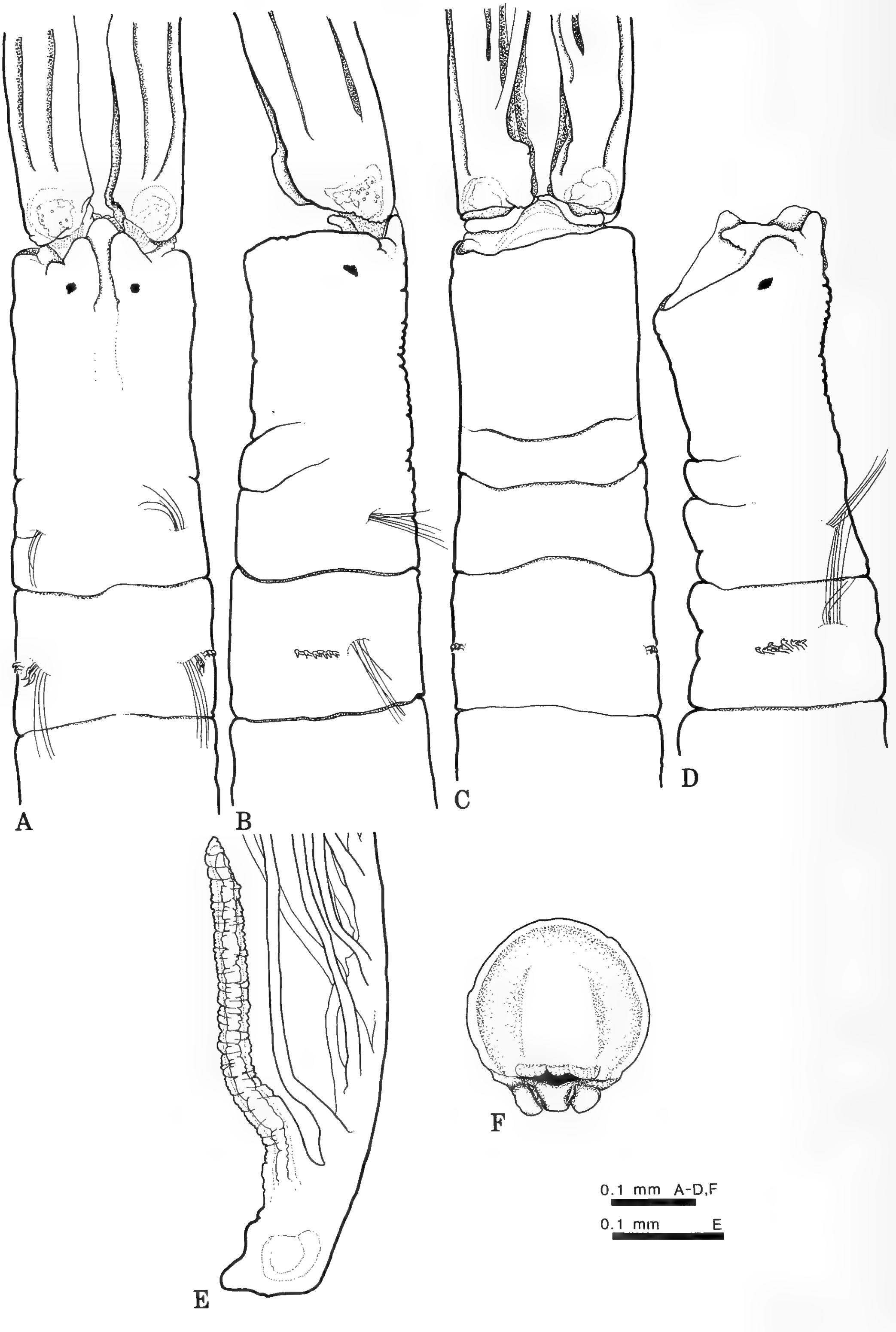
Description (based on type material).—Holotype incomplete (left half of branchial crown missing) with 8 thoracic and 3 abdominal setigers; length 3.4 mm (branchial crown comprising 1.00 mm); maximal width 0.28 mm. Branchial crown one-half to one-third total length. Three pairs of radioles; distal ends filamentous, same width as pinnules. Radioles each with 6–7 pairs of pinnules, all terminating at same level, or proximalmost pair slightly longer, ending at same height as radioles or slightly below. Dorsal and ventral lips absent. Ventral filamentous appendages vascularized, unbranched (Fig. 2E); one-half to one-fifth total radiole length; width uniform, slightly wider than pinnules; distal ends blunt; surface with minute, transverse wrinkles. Body cylindrical, tapering slightly posteriorly. Branchial crown attachment limited to narrow transverse ridge near dorsal peristomial margin (Fig. 2B, F); mouth located just dorsal to ridge. Peristomial surface ventral to mouth and crown attachment ridge an oblique or horizontal shelf-like process, sometimes slightly raised along dorso-ventral midline. Anterior margin of anterior peristomial ring a low ridge except for rounded lobe to either side of dorsal midline (Fig. 2A–C); slightly overlapping middorsal conical lobe above mouth; all lobes same height. Anterior peristomial ring 2–3 times longer than posterior peristomial ring; annulation between rings distinct ventrally and laterally. Peristomial eyes rounded to crescentic, black; pygidial eyes rounded, black. Anterior thoracic setigers each of similar length, wider than long; length increasing in posterior thoracic setigers, setigers 6–7 longer than wide, setiger 8 similar to anterior setigers. Setiger 9 about same length as 8; setigers 10–11 successively shorter; all wider than long. Pygidium same length as setiger 11; tapered, bluntly rounded (Fig. 2D). Superior thoracic notosetae

---

⟶

Fig. 2. *Fabricinuda bikinii* from the Bikini Atoll (AHF 207): A–C, Dorsal, lateral (right side) and ventral views, respectively, of the anterior end; D, Posterior end, dorsal view; E, Left half of branchial crown, inner margin; F, Frontal view of anterior peristomial margin, dorsal margin at bottom; G, Pseudospatulate setae from setiger 7; H, Thoracic uncinus from setiger 3; I, Abdominal uncinus from setiger 9.


A
B
C
D
E
F
G
H
I
0.1 mm A-C
0.05 mm D-F
0.02 mm G-I


A
B
C
D
E
F
0.1 mm A-D,F
0.1 mm E

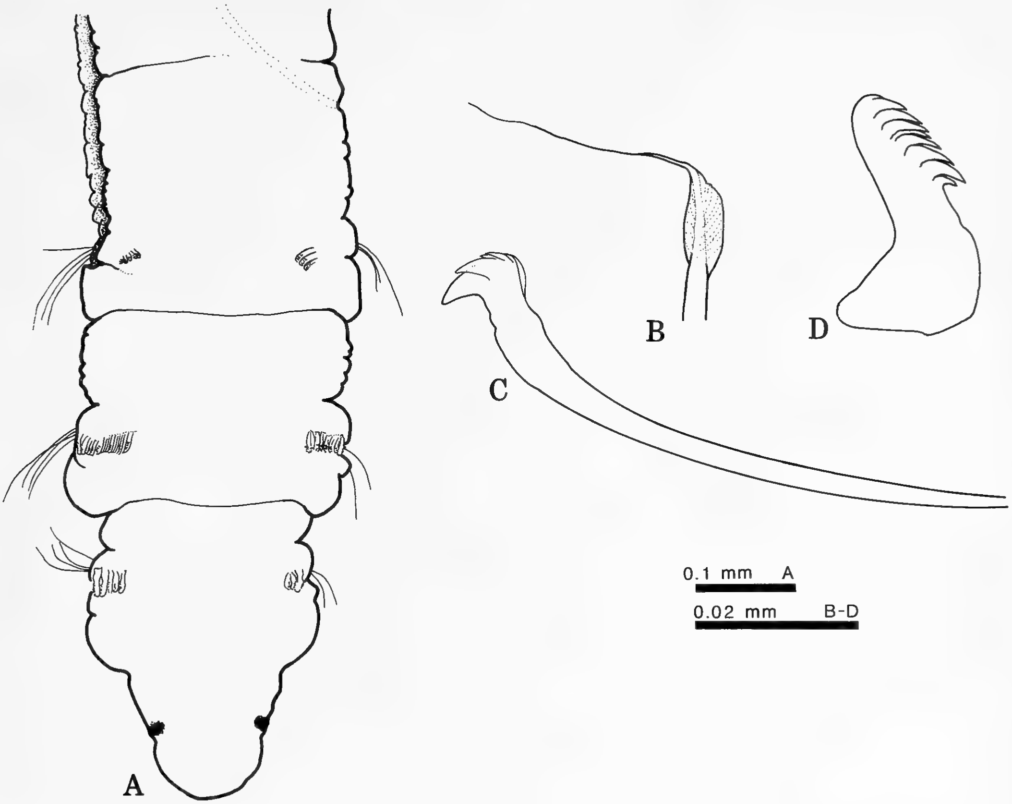


Fig. 4. *Fabricinuda bikinii* from the Aldabra Atoll (USNM 121995): A, Posterior end, dorsal view; B, Pseudospatulate seta from setiger 6; C, Thoracic uncinus from setiger 5; D, Abdominal uncinus from setiger 10.

elongate, narrowly hooded; 4–5 per fascicle. Inferior thoracic notosetae of setiger 2 short elongate, narrowly hooded; 2 per fascicle. Setigers 3–8 with pseudospatulate setae; 2 per fascicle (Fig. 2G). Abdominal neurosetae modified, elongate, narrowly hooded; 3–4 per fascicle. Thoracic acicular uncini in straight or irregular rows; 5–11 per fascicle (Fig. 2H). Abdominal uncini with 8–9 teeth in profile, 3–4 teeth per row; manubrium slightly expanded proximally, base quadrangular, about same length as dentate region (Fig. 2I). All specimens examined unpigmented; body opaque. Tubes loosely constructed of calcareous sand grains; about same length as animals. Methyl green staining darkest on ventrum of posterior peristomial ring, ventral anterior margin of setiger 1, ventrally and laterally on setigers 2–5; staining distinctly increasing on setigers 6–8; abdominal setigers and pygidium staining darkest; all other areas staining very lightly.

Remarks.—The material of *Fabricinuda bikinii* examined here extends the species distribution from the Bikini Atoll in the Pa-

---

⟵

Fig. 3. *Fabricinuda bikinii* from the Aldabra Atoll (USNM 121995): A–C, Dorsal, lateral (left side) and ventral views, respectively, of the anterior end; D, Lateral view (left side) of slightly contracted specimen; E, Proximal region of dorsalmost radiole, inner margin; F, Frontal view of anterior peristomial ring margin, dorsal margin at bottom.

cific Ocean to the Aldabra Atoll in the Indian Ocean. Because there are minimal differences between specimens from both areas (cf., Fig. 2, based on type material, and Figs. 3, 4, based on Aldabra material), I am reluctant to view them as separate species.

In general, specimens from the Aldabra Atoll tend to be more slender and elongate than what is seen in the type material. Similarly, the branchial crown of specimens from Aldabra may be relatively shorter, comprising only one-fifth the total body length. The number of individuals in the type series is, however, considerably fewer.

The only marked difference between specimens from both areas is seen with methyl green staining: there are no distinct staining patterns on the anterior peristomial ring in the type material, whereas in the Aldabra material there are a pair of dark rectangular patches laterally and a dark patch ventrally on the anterior peristomial ring. This condition in the Aldabra material is similar to what has been seen in some specimens of *Fabricinuda trilobata* (Fitzhugh 1983; see below). While differences in staining patterns may be indicative of regional, populational, or species-specific variation, the differences seen in the present material may also be a function of age and preservation.

Facricinuda bikinii is unique in that the mouth has been shifted dorsally and in front of the attachment point of the branchial lobes to the peristomium. In addition, the point of attachment for the branchial lobes is reduced to a narrow, transverse ridge just behind the mouth. As a result of this latter condition, the branchial lobe bases sit largely unattached over the anterior end; only the dorsal margins of the lobes are connected to the peristomium. An intermediate condition is seen in *F. trilobata* (Fitzhugh 1983; see below) in that the crown attachment has been shifted dorsally to a lesser degree but with lobes completely attached to the peristomium and the mouth in the typical sabellid position. As a result of this shift in crown attachment in these two species, the anterior margin of the anterior peristomial ring is exposed ventrally to some extent as a horizontal or oblique shelf. This shelf-like condition was described in part by Hartman (1954) for *F. bikinii.*

The abdominal uncinus figured by Hartman (1954: fig. 178B; compare with Figs. 2I and 4D herein) is unusual in that the manubrium is slender and gently curved back, similar to the handle of thoracic uncini. This misinterpretation of the manubrium was probably due to examining only uncini which were still lying side by side in the fascicle and not in true profile.

Fabricinuda trilobata (Fitzhugh, 1983), new combination
Fig. 5

Fabriciola trilobata Fitzhugh, 1983:276–284, figs. 1, 2, 3a–c.—Uebelacker, 1984a: 54-20, 54-22, figs. 54-15, 54-16.

Additional description.—Dorsal and ventral lips absent. Ventral filamentous appendages vascularized, unbranched (Fig. 5A), slightly wider than pinnules; width uniform except for basal swelling of margin adjacent to dorsal radiole; distal end blunt; surface with minute transverse wrinkles. Anterior peristomial ring margin available for branchial lobe attachment reduced in size, attachment shifted dorsally (Fig. 5B). Branchial lobes completely attached to peristomium. Mouth in usual sabellid position relative to branchial lobes. Narrow, exposed shelf-like region present below crown attachment area. Inferior thoracic notosetae of setiger 2 short, elongate, narrowly hooded; 1 per fascicle. Inferior thoracic notosetae of setigers 3–8 pseudospatulate setae (Fig. 5C); 1–2 per fascicle.

Remarks.—*Fabricinuda trilobata* is distinctive in the partial shifting dorsally of the branchial crown and mouth, resulting in an exposed, narrow shelf. As noted in Remarks under *F. bikinii,* this condition in *F. trilobata* is intermediate to what is seen in *F. bikinii* on the one hand and remaining species on the other. This suggests a possible

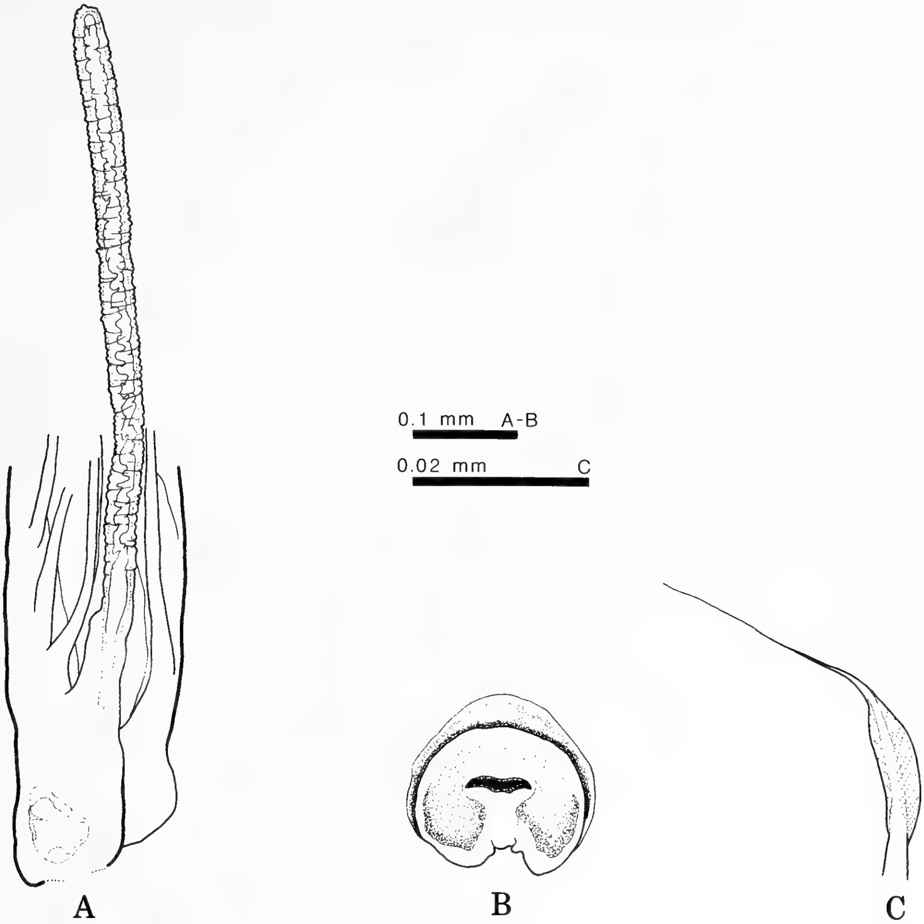


Fig. 5. *Fabricinuda trilobata* (paratypes, A, C from USNM 74689, B from USNM 74691): A, Left half of branchial crown, inner margin; B, Frontal view of anterior peristomial ring margin, dorsal margin at bottom; C, Pseudospatulate seta from setiger 7.

transformation series in which dorsal shifting of the branchial crown occurred prior to the mouth being displaced above the branchial lobes.

Together with various workers in the past, Fitzhugh (1983) erroneously referred to the ventral filamentous appendages as "palps."

Fabricinuda pseudopalpa, new species
Figs. 6, 7

Material examined.—California: Holotype (USNM 122021) and 24 paratypes (USNM 122022), Dutch Harbor, San Nicolas Island, Channel Islands, low intertidal, among roots of *Phyllospadix* and rocks, coll., R. Seapy, 5 May 1977.

Description.—Holotype complete with 8 thoracic and 3 abdominal setigers; length 3.10 mm (0.70 mm comprising branchial crown), maximal width 0.23 mm. Branchial crown one-fourth to one-sixth total body length. Three pairs of radioles; distal ends filamentous, same width as pinnules. Radioles each with 8–10 pairs of pinnules, all terminating at same height as radioles. Dorsal lips erect (Fig. 6E), longer than wide, slightly tapered, distally blunt. Ventral filamentous appendages absent. Branchial crown broadly attached to peristomium. Body cylindrical, elongate, tapering slightly in abdomen. Peristomial eyes black, rounded to crescentic; pygidial eyes black, rounded. Anterior rim of anterior peristomial ring with lobe on either side of dorsal midline; length and thickness of lobes variable; lobes on most specimens small (Fig. 6A), about same size as conical lobe-like structure above mouth (located between lobes); with vascular loops visible in peristomium below paired lobes; specimens with slightly longer lobes (Fig. 7A) with vascular loops extending through most of length, lobes slightly thicker, surface smooth; less commonly, lobes very long, digitiform (Fig. 7B–D), with vascular loops extending most of length, surfaces relatively smooth, width uniform, distal ends rounded. Remainder of anterior peristomial ring margin a low ridge, slightly higher ventrally, smooth. Anterior and posterior peristomial rings of equal length or anterior ring slightly longer; each ring about as long as wide. Annulation between rings distinct ventrally and laterally. Setiger 1 slightly shorter than posterior peristomial ring, less than one-half length of setiger 2; setigers 3–7 successively longer, setigers 4–7 each about 2–2.5 times longer than setiger 2; setiger 8 shorter, same length as setiger 3. Setiger 9 about one-half length of 8, about as long as wide; setigers 10–11 successively shorter, narrower. Pygidium about same length as setiger 11; conical, bluntly rounded (Fig. 6D). Superior thoracic notosetae elongate, narrowly hooded; 4–5 per fascicle. Inferior thoracic notosetae of setiger 2 short, elongate, narrowly hooded; 2 per fascicle. Setigers 3–8 with pseudospatulate setae; 1–3 per fascicle (Fig. 6F). Abdominal neurosetae modified, elongate, narrowly hooded; 4–6 per fascicle. Thoracic acicular uncini in straight single or irregular rows; 6–13 per fascicle (Fig. 6G). Abdominal uncini with 11–12 teeth in profile, proximal tooth slightly larger (Fig. 6H); 4–5 teeth per row; 17–22 uncini per fascicle; manubrium slightly expanded proximally. Branchial crown unpigmented; anterior peristomial ring light to dark brown, anterior margin of posterior peristomial ring similar; pigment diminishing posteriorly; posterior thoracic setigers and abdomen unpigmented, cream colored. Tubes loosely constructed with quartz sand grains, about same length as animals. No distinct methyl green staining patterns.

Etymology.—The specific name refers to the extensible, palp-like quality of the dorsal, anterior peristomial ring lobes.

Remarks.—*Fabricinuda pseudopalpa* is very distinctive in that the vascular loops can extend into the dorsal lobes of the anterior peristomial ring, with the lobes lengthening to varying degrees, resembling ventral filamentous appendages or palps. It is not known to what extent this condition might be a preservation artifact. Specimens with vascular loops not extending into the lobes resemble *F. limnicola* (Hartman, 1951) and *F. pseudocollaris,* new species, with regard to the branchial crown not being shifted dorsally. *Fabricinuda pseudopalpa* differs from these and other species of the genus in lacking ventral filamentous appendages but in having dorsal lips.

Fabricinuda pseudocollaris, new species

Figs. 8, 9

Material examined.—Florida: Holotype (USNM 122023) and five paratypes (USNM 65903), entrance to East Lagoon, Seahorse Key, silty sand, coll., J. H. Taylor, 24 Apr 1960.

Description.—Holotype complete with 8 thoracic and 3 abdominal setigers; length 10.00 mm (branchial crown comprising 1.00 mm), maximal width 0.24 mm. Branchial crown one-ninth to one-tenth total body length. Crown broadly attached to peristomium, not displaced dorsally (Fig. 8B); with mouth between branchial lobes. Three pairs of radioles; distal ends filamentous, same width as pinnules. Radioles each with

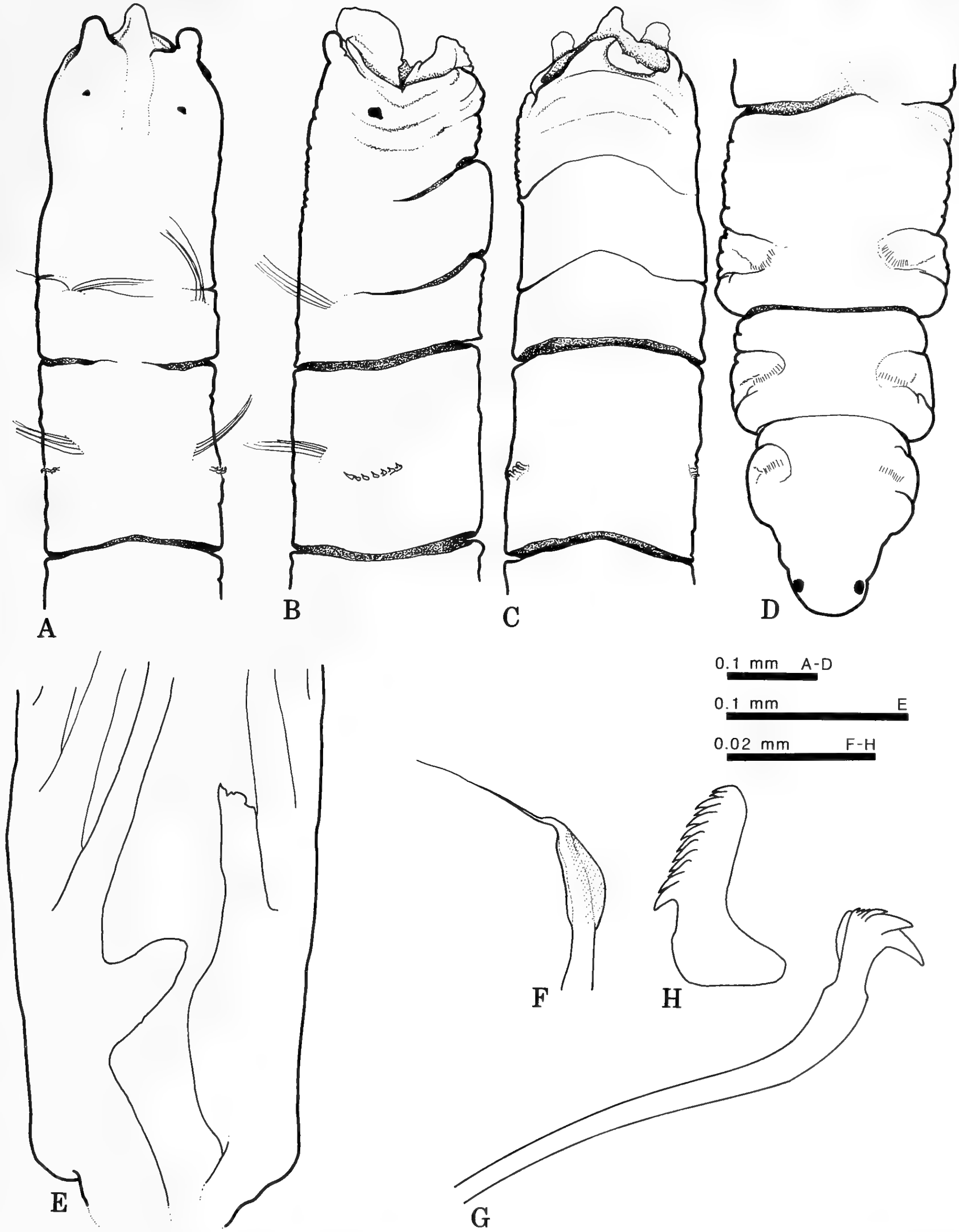


Fig. 6. *Fabricinuda pseudopalpa* (paratypes, USNM 122022): A–C, Dorsal, lateral (right side) and ventral views, respectively, of anterior end; D, Posterior end, dorsal view; E, Left half of branchial crown, inner margin; F, Pseudospatulate seta from setiger 4; G, Thoracic uncinus from setiger 4; H, Abdominal uncinus from setiger 9.

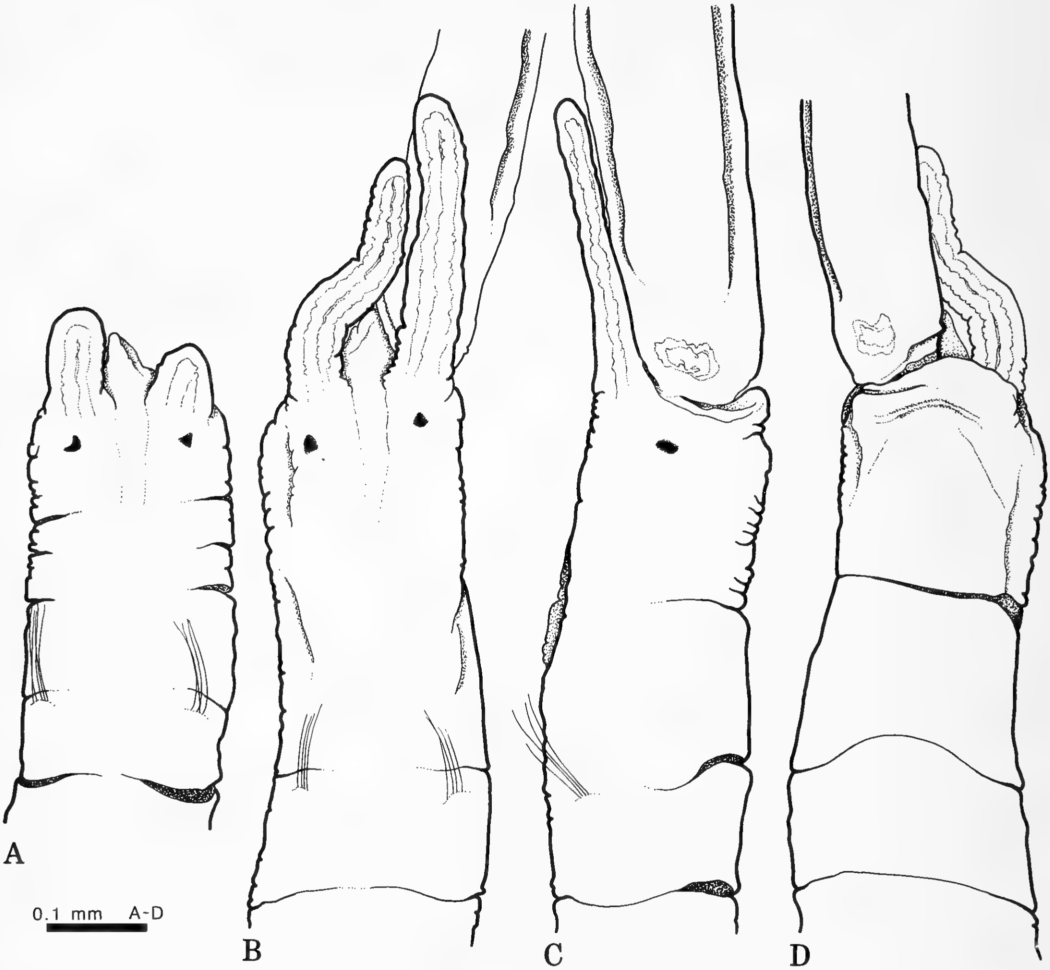


Fig. 7. *Fabricinuda pseudopalpa* (paratypes, USNM 122022): A, Dorsal view of anterior end of specimen with dorso-lateral lobes partially expanded due to extension of vascular loops; B–D, Dorsal, lateral (right side) and ventral views, respectively, of anterior end of specimen with extreme extension of vascular loops into dorso-lateral lobes.

6–7 pairs of pinnules, all terminating at same height; longest about two-thirds total radiole length. Dorsal and ventral lips absent. Ventral filamentous appendages vascularized, unbranched (Fig. 9A); distinctly wider than pinnules, width uniform throughout except for slight basal swelling along margin adjacent to dorsal radiole; distally blunt; same length as radioles or slightly shorter. Ventral filament surface relatively smooth or with minute transverse wrinkles; blood vessel very large. Body cylindrical, uniformly slender, thread-like, tapering slightly posteriorly. Peristomial eyes black, rounded to crescentic; pygidial eyes black, rounded. Anterior margin of anterior peristomial ring a low ridge all around except for low rounded lobe to either side of dorsal midline (Fig. 8A–C); dorsal lobes smaller than median conical lobe above mouth; ridge of same height ventrally and dorsally, concave laterally (Fig. 8B). Anterior peristomial ring

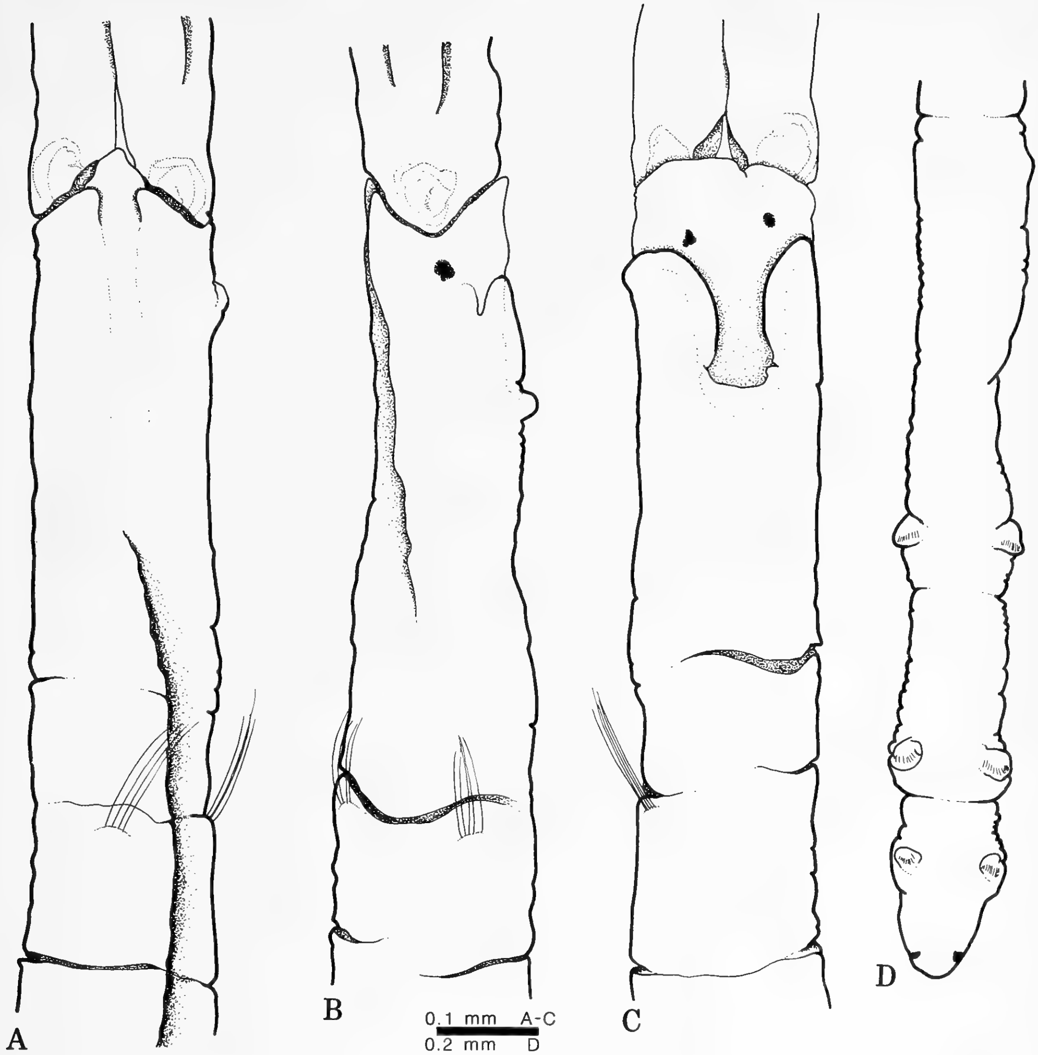


Fig. 8. *Fabricinuda pseudocollaris* (holotype, USNM 122023): A–C, Dorsal, lateral (right side) and ventral views, respectively, of the anterior end; D, Posterior end, dorsal view.

about 4 times longer than posterior ring; annulation between rings visible ventrally and laterally. Large pair of membranous lappets on ventrum of anterior peristomial ring (Fig. 8C), originating ventro-laterally on anterior half of ring; separated by wide gap, with posterior margin of gap developed as narrow shelf. Lappets directed anteriorly with distal margins broadly rounded; terminating below anterior rim of anterior peristomial ring; area of ring anterior to lappets slightly narrower in lateral view (Fig. 8B). Setiger 1 as wide as long, slightly longer than posterior ring; setigers 2–3 each about twice as long as setiger 1; setigers 4–5 each twice as long as 3; setigers 6–7 each twice as long as 4 or 5; setiger 8 slightly longer than 6 or 7. Setiger 9 about one-half length of setiger 8; setigers 10–11 successively shorter. Pygidium same length as setiger 11,

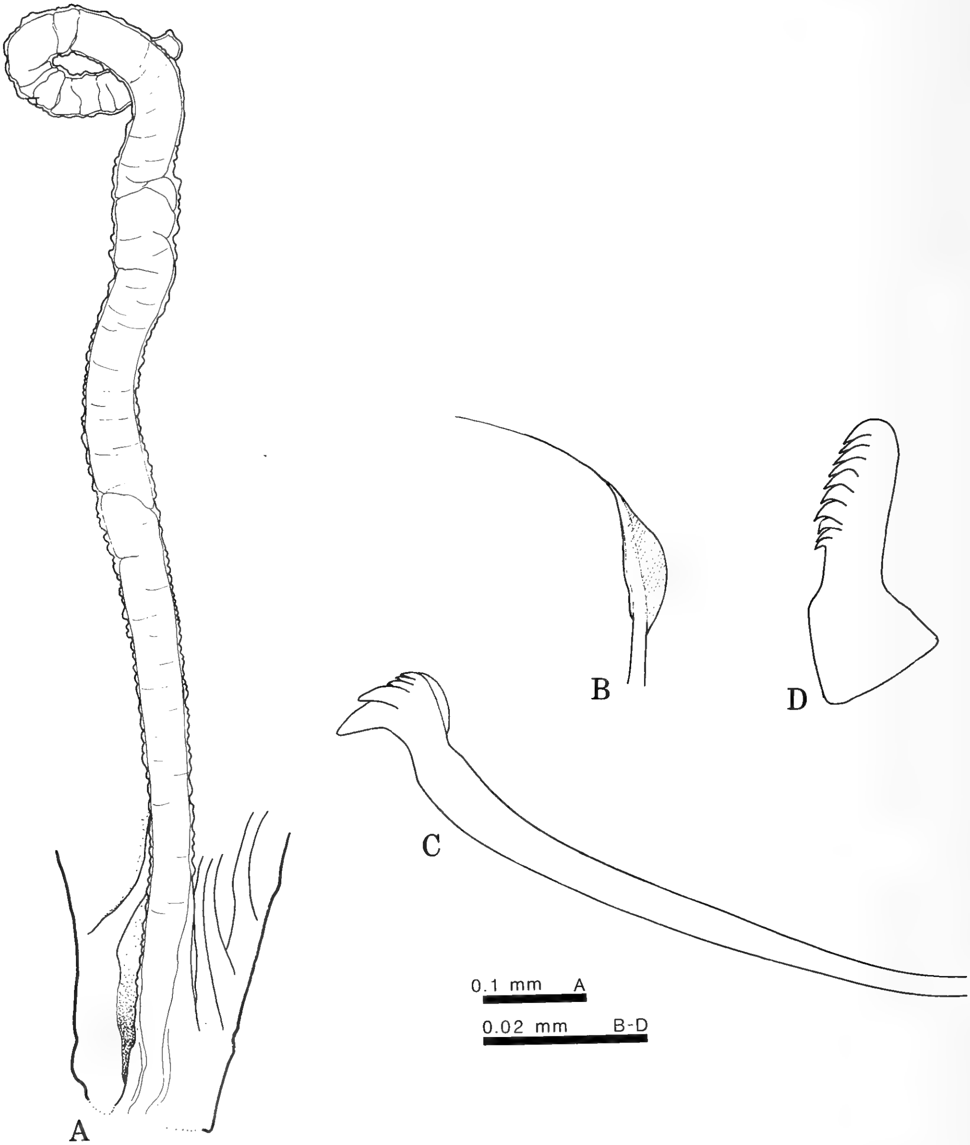


Fig. 9. *Fabricinuda pseudocollaris* (paratypes, USNM 65903): A, Proximal region of right half of branchial crown, inner margin; B, Pseudospatulate seta from setiger 5; C, Thoracic uncinus from setiger 5; D, Abdominal uncinus from setiger 9.

tapering to rounded end (Fig. 8D). Superior thoracic notosetae elongate, narrowly hooded; 4–6 per fascicle. Setiger 2 inferior thoracic notosetae short, elongate, narrowly hooded; 2 per fascicle; setigers 3-8 with pseudospatulate setae; 2 per fascicle (Fig. 9B). Abdominal neurosetae modified, elongate, narrowly hooded; 3–4 per fascicle. Thoracic acicular uncini in irregular double rows; 8–12 per fascicle (Fig. 9C). Abdominal uncini with 9–10 teeth in profile, 3–4 teeth per row; manubrium constricted below dentate region, expanded proximally with quadrangular base (Fig. 9D); 20–25 uncini per fascicle in setigers 9–10; 18 per fascicle in setiger 11. Ventral filamentous appendages yellowish to light brown; remainder of branchial crown unpigmented or dark brown on inner lobe margins. Conical lobe above mouth dark brown, pigment extending posteriorly along dorsal midline of anterior peristomial ring; region between ventral lappets of anterior ring dark brown; remainder of body cream colored. Tubes loosely constructed with quartz sand grains; same length as animals. Methyl green staining greatest in ventral rectangular area of anterior peristomial ring below lappets, through posterior peristomial ring to anterior margin of setiger 1; ventrum of setigers 2–4 or 5 uniformly dark, remaining thoracic setigers lightly stained; abdominal setigers and pygidium dark.

Etymology.—The specific name refers to the ventro-lateral anterior peristomial ring lappets, which give the impression of a collar.

Remarks.—*Fabricinuda pseudocollaris* is very distinctive with its paired, ventral, membranous lappets on the anterior peristomial ring. The concomitant narrowing of this ring anterior to these structures appears somewhat similar to the more pronounced narrowing of the far anterior region seen in *F. trilobata* and *F. bikinii.* At this time I do not consider the two conditions to be homologous. Relative to other species in the genus, *F. pseudocollaris* also has the longest anterior peristomial ring.

Species Possibly Referable to *Fabricinuda*

Day (1957) described the species, *Fabricia mossambica,* later referred to as *Fabriciola mossambica* by Day (1963, 1967), from South Africa. In the original description, Day (1957: fig. 8k) noted that contracted specimens have a truncated anterior end. The figure shows the anterior end of a specimen lacking the branchial crown and with the anterior peristomial ring margin smooth. The attachment area for the crown is displaced dorsally somewhat and the anterior peristomial ring is indicated as longer than the posterior ring. Day's figures of relaxed specimens (Day 1957: fig. 8g–j), however, show a rounded ventral lobe and no dorsal lobes on the anterior peristomial ring margin; ventral filamentous appendages are present, but degree of vascularization is not mentioned. Unlike typical *Fabriciola,* this species lacks the membranous anterior peristomial ring collar and the manubrium of abdominal uncini is the same length as the dentate region. The general features described by Day (1957) for *F. mossambica* suggest that it is a species of *Fabricinuda.*

Acknowledgments

I gratefully acknowledge the following individuals for comments on earlier drafts of this paper: Kristian Fauchald, Robert E. Knowlton, Diana L. Lipscomb, Meredith L. Jones, and Vicki A. Funk.

I thank Brian Kensley and Kristian Fauchald for supplying material collected from the Aldabra Atoll, and for allowing me to participate in the 1985 expedition. Leslie H. Harris, Collections Manager, Allan Hancock Foundation, kindly provided loans of specimens. I thank Thomas H. Perkins for bringing the specimens of *Fabricinuda pseudocollaris* to my attention and for his very thorough review of the manuscript.

Literature Cited

Banse, K. 1956. Beiträge zur Kenntnis der Gattungen *Fabricia, Manayunkia* und *Fabriciola* (Sabellidae, Polychaeta).—Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 84:415–438.

———. 1957. Die Gattungen *Oriopsis, Desdemona* und *Augeneriella* (Sabellidae, Polychaeta).—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, København 119:67–105.

———. 1970. The small species of *Euchone* Malmgren (Sabellidae, Polychaeta).—Proceedings of the Biological Society of Washington 83:387–408.

Day, J. H. 1957. The polychaete fauna of South Africa. Part 4: New species from Natal and Moçambique.—Annals of the Natal Museum 14: 59–129.

———. 1963. The polychaete fauna of South Africa. Part 8: New species and records from grab samples and dredgings.—Bulletin of the British Museum (Natural History) Zoology 10:383–445.

———. 1967. A monograph on the Polychaeta of southern Africa. Part 2: Sedentaria.—British Museum of Natural History Publications 656: 459–878.

Fitzhugh, K. 1983. New species of *Fabriciola* and *Fabricia* (Polychaeta: Sabellidae) from Belize.—Proceedings of the Biological Society of Washington 96:276–290.

———. 1988. A phylogenetic systematic analysis of several hierarchical levels within the Order Sabellida (Polychaeta: Annelida). Unpublished Ph.D. Dissertation, George Washington University, Washington, D.C., xxvi + 604 pp.

———. 1989. A systematic revision of the Sabellidae-Caobangiidae-Sabellongidae complex (Annelida: Polychaeta).—Bulletin of the American Museum of Natural History 192:1–104.

Gitay, A. 1970. A review of *Augeneriella* (Polychaeta: Sabellidae) and a new species from Northern Sinai.—Israel Journal of Zoology 19:105–109.

Hartman, O. 1951. Fabricinae (feather-duster polychaetous annelids) in the Pacific.—Pacific Science 5:379–391.

———. 1954. Marine annelids from the northern Marshall Islands.—Professional Papers of the U.S. Geological Survey 260-Q:619–644.

———. 1959. Catalogue of the polychaetous annelids of the world. Part 2.—Allan Hancock Foundation Occasional Paper 23:355–628.

———. 1969. Atlas of sedentariate polychaetous annelids from California.—Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.

Perkins, T. H. 1984. Revision of *Demonax* Kinberg, *Hypsicomus* Grube, and *Notaulax* Tauber, with a review of *Megalomma* Johansson from Florida (Polychaeta: Sabellidae).—Proceedings of the Biological Society of Washington 97:285–368.

Rullier, F. 1954. Essai de révision du genre *Fabricia* (Annélides Polychètes).—Bulletin Société Zoologique de France 79:14–29.

Uebelacker, J. M. 1984. Chapter 54. Family Sabellidae Malmgren, 1867, pp. 54-1, 54-43 *in* J. M. Uebelacker and P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Vol. VII. Final Report to the Mineral Management Service, contract 14-12-001-29091. Barry A. Vittor & Associates, Inc., Mobile, Alabama.

Department of Invertebrates, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 179–186

DIPLOCARDIA KANSENSIS, A NEW EARTHWORM FROM KANSAS, WITH REDESCRIPTIONS OF *D. RIPARIA* SMITH AND *D. FUSCULA* GATES (ANNELIDA: OLIGOCHAETA: MEGASCOLECIDAE)

Samuel W. James

Abstract.—The definition of *Diplocardia riparia* is changed to include an intestinal origin in the seventeenth segment. Consequently *D. prosenteris* is synonymized with *D. riparia. Diplocardia fuscula* is now understood to have genital markings in the male field and a variable circulatory system. *Diplocardia kansensis,* closely related to *D. riparia* and *D. fuscula,* is described from Kansas and Arkansas material. It is proposed to refer to the posterior extension of the extra-esophageal vessels of Megascolecidae as clitellar vessels, rather than as posterior latero-parietals.

Diplocardia riparia F. Smith was described from material collected in the floodplain of the Illinois River near Havana, Illinois. It has since been recorded from several locations around the American Midwest, from Ohio to Oklahoma and Nebraska (Olson 1928; Gates 1955, 1977; McNab & McKey-Fender 1955; Teotia et al. 1950). It is of minor economic importance in southern Kansas and western Missouri, where it is collected and sold for bait. There have been questions about the status of certain specimens (see Gates 1955). In the course of examining material identified by the late W. R. Murchie and deposited in the National Museum of Natural History (USNM), it became clear that the original description (F. Smith 1895a) and Eisen's (1899) additions contained information that was incorrect or misleading. Further, there were three distinct taxa represented in the USNM lots labelled *Diplocardia riparia,* one of which was clearly that species.

One lot labelled *D. riparia* actually belongs to *D. fuscula* Gates. In the course of examining these specimens and paratypes of *D. fuscula,* it was determined that the definition of *D. fuscula* needed to be altered.

Another group is similar to worms previously identified as *Diplocardia prosenteris* McNab & McKey-Fender in James (1984, 1988) and James & Cunningham (1989). These worms are described here as *D. kansensis. Diplocardia prosenteris* was described as a subspecies of *D. riparia* (McNab & McKey-Fender 1955) and was elevated to specific rank in Gates (1977).

The species described below was determined to be new based on Gates (1977) and examination of *D. riparia* collected by F. Smith. A complete description of *D. riparia* is included to provide a single source for morphological characteristics of this species. No other museum collections were searched for representatives of this or any related species.

In placing these earthworms in subfamily Acanthodrilinae of the Megascolecidae, I follow the classification of Jamieson (1971) and Brinkhurst & Jamieson (1971).

Diplocardia kansensis, new species
Fig. 1A–C

Diplocardia prosenteris.—James, 1982:38.—James, 1984:91.—James, 1988:479.—James & Cunningham, 1989:79.

Material.—USNM 42137, limestone quarry east of Myron, Izard Co., Arkansas, 16 Apr 1962, W. R. Murchie; Konza Prairie

Research Natural Area, 1 km north of Interstate 70 in Geary Co., Kansas, 25 May 1981, S. W. James; West Kimball Road, Manhattan Riley Co., Kansas, 12 May 1986, S. W. James; Schoolyard at Browning and Dickens Sts., Manhattan, Riley Co., Kansas; 27 May 1987; upland tallgrass prairie in Fort Riley, Geary Co., Kansas, 16 Sep 1986, S. W. James; Big Basin, Clark Co., Kansas, 7 Oct 1986, S. W. James.

Description.—External characteristics: 55 to 100 by 2 to 3.5 mm, width at segment xxx, body cylindrical in cross section throughout, widest at segments vi to ix, segments 120 to 145. Setae closely paired throughout; setal formula AA:AB:BC:CD = 3:1:3.5:1.5. Prostomium tanylobous, peristomium smooth, biannulate segments iv plus one of iii or v, triannulate posterior to iv or v. Medium to dark brown anterior pigmentation, sometimes present along mid-dorsal line and on hindmost dorsal segments, nephridiopores near D. First dorsal pore 9/10 or 10/11, spermathecal pores on small bumps on leading edges of viii and ix, just lateral to setae a. Ovipores in xiv, presetal; male pores in xix in male grooves which are in AB in xviii to xx; prostatic pores and penial setae at ends of grooves. Clitellum 1/2 xii, xiii to xviii or xix, saddle-shaped to annular. Unpaired mid-ventral genital markings viii, ix or ix, x; rarely x, xi or all of viii to xi; unpaired mid-ventral genital markings xvii, xx; paired genital markings postsetal in xvii, xx (all), paired, postsetal in one or more of xx to xxii, presetal in some of xviii, xxi, xxii; some paired 20/21. Penial setae bowed, 750 to 850 μm by 12 to 17 μm, tips tapering to a point slightly flattened around the edges (Fig. 1C).

Internal characteristics: Septum 5/6 faintly muscled, 6/7 to 12/13 muscular, thickest in 7/8 to 9/10; last set of transseptal muscles originating in xiii. Alimentary canal with gizzards in v, vi; esophagous smooth externally with some chloragogen, vascularized in xii to xiii, internal texture pebbly changing to low longitudinal folds in xv, xvi; no calciferous lamellae. Small glands on dorsal and lateral surfaces of esophagus in vii–ix. Intestinal origin at 16/17 or within xvii, intestinal constriction usually present just anterior to origin of simple typhlosole in xxi or xxii; typhlosole half to one-third of lumen diameter.

Nephridia 2 per segment, stomate, without bladders, duct meeting body wall near D. Ascending tubule from nephrostome with blind "caecum."

Vascular system with subintestinal trunk, single dorsal trunk, these connected by lateral trunks in v to ix, lateral-esophageal hearts in x to xiii. Lateral trunks have lateral and septal branches from a point above attachment to subintestinal trunk, in ix a large vessel from lateral trunk to body wall of segments ix to xii. Supra-esophageal vessel x to xiii, extra-esophageal v to xiii, in xiii branching out as clitellar vessel over xii to xvii. Small vessels from extra-esophageal to septa and body wall in v to xii.

Male sexual system holandric, testes and funnels free, coagulum usually filling x and xi; vasa deferentia from funnels under peritoneum, entering body wall in xvii; seminal vesicles of ix divided into 2 to 4 lobes, of xii divided into numerous small ovoid lobes, vesicles of xii larger. Paired prostates in xviii and xx, slender, 2 to 3 times longer than the delicate kinked ducts, extending through several segments.

Ovaries and funnels in xiii, free, ovaries fan-shaped or globular cluster of numerous strings. Spermathecae (Fig. 1B) in viii, ix, variable ampulla and diverticular shape. Diverticulum 4 to 5 lobed internally, or lobes slightly incised, sessile or ectal end free, diverticulum attached to duct below base of ovoid ampulla.

Holotype.—USNM 122285. Konza Prairie Research Natural Area, 1 km north of Interstate 70 in Geary Co., Kansas, 25 May 1981, S. W. James.

Paratypes (3).—USNM 122286. Konza

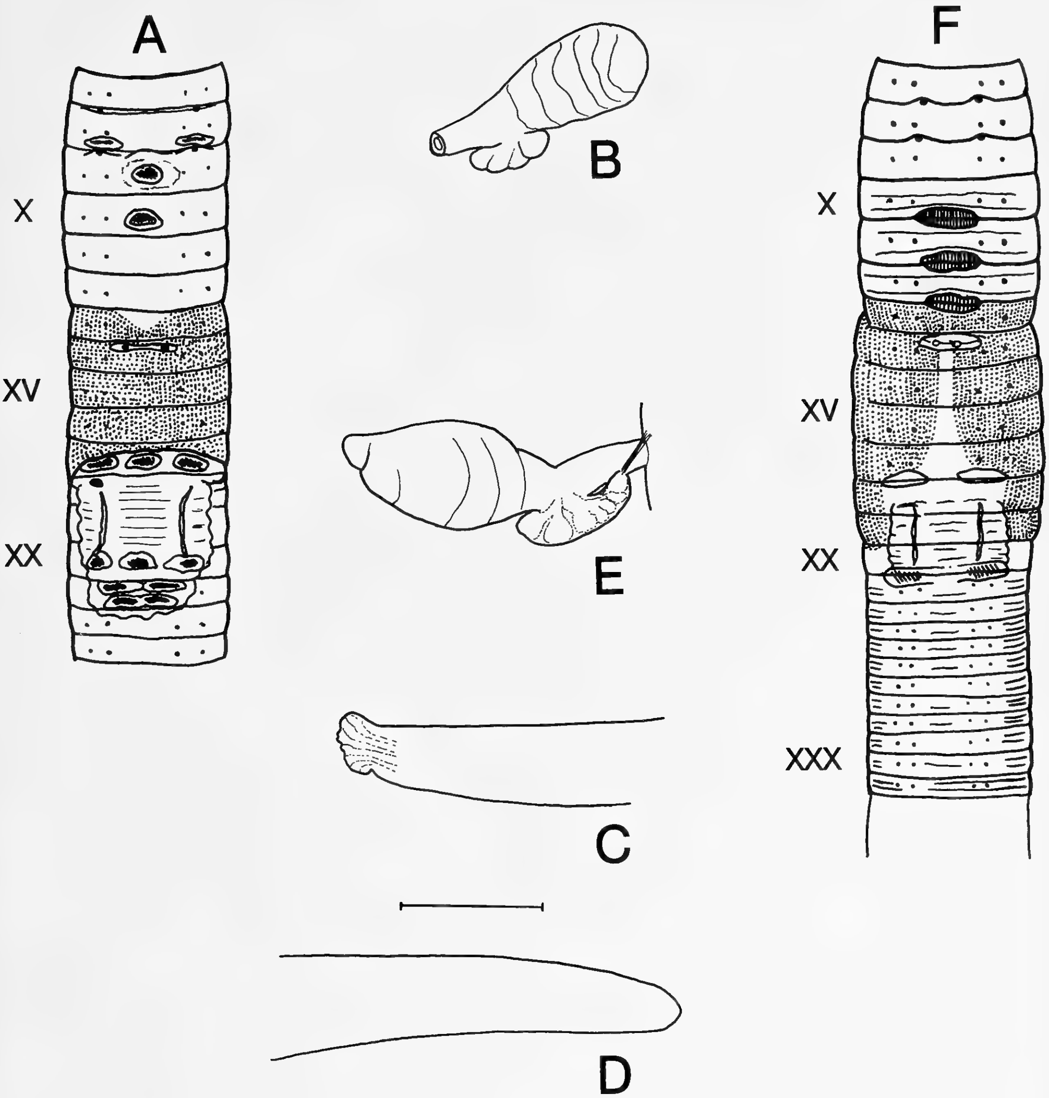


Fig. 1. *Diplocardia kansensis* new species: A, Ventral view of segments vii–xxiii; B, Spermatheca; C, Tip of penial seta, scale line equals 10 μm. *D. riparia*: D, Tip of penial seta, same scale as C. *D. fuscula*: E. Spermatheca; F, Ventral view of segments vii to xxxi.

Prairie Research Natural Area watershed 1D, eroded waterway, 8 Oct 1988, S. W. James.

Remarks.—Diplocardia kansensis differs from *D. riparia* in the slightly spatulate tip of the penial setae, smaller body size, presence of pre-clitellar genital markings, the large number of genital markings, the presence of unpaired mid-ventral genital markings, greater typhlosolar development and a more anterior typhlosolar origin. This species can be distinguished from other members of the genus by the following set of characters: spermathecae in vii, ix; last hearts in xiii, no calciferous lamellae, genital markings pre- and post-clitellar, a typhlosolar origin in or before xxii, and a tanylobous prostomium. In Gates (1977) or James (1990) it will key to *D. fuscula* Gates, from which it differs in size, disposition of genital markings, typhlosole, presence of clitellar vessels, and prostomium characteristics.

Diplocardia kansensis inhabits upland areas rather than river banks, though on Konza Prairie it is only abundant in eroded areas at the upper ends of water courses. However, none of the drainages along which it has been collected bear water except after heavy rains. The Big Basin material was obtained on prairie ridgetops under *Bison bison* dung pats. The nature of the habitat of Murchie's Arkansas material is unknown. James & Cunningham (1989) give the dietary habits of this species, under the name *D. prosenteris.*

Diplocardia riparia F. Smith, 1895
Fig. 1D

Diplocardia riparia.—Smith, 1895a:138.—Smith, 1895b:286.—Eisen, 1899:166.—Eisen, 1900:175, figs. 143, 144.—Michaelsen, 1900:325.—Smith, 1900:442.—Gates, 1955:242.—McNab & McKey-Fender, 1955:128.—Murchie, 1967:534.
Diplocardia riparia prosenteris.—McNab & McKey-Fender, 1955:128.

Material.—Section 23, Range 18&19, Ohio Twp., Franklin Co., Kansas, in cattle feedlot near spring, 17 Apr 1987, S. W. James; bank of the Le Moine River near Ripley, Brown Co., Illinois, 6 Sep 1987, S. W. James; bank of the Chariton River near U.S. Hwy. 136, Schuyler Co., Missouri, 9 Apr 1988, S. W. James; bank of the Walnut River at fairgrounds, Winfield, Cowley Co., Kansas, 19 Sep 1987, S. W. James; bank of Cedar Creek, SW of Fairfield, Jefferson Co., Iowa, 11 Oct 1987, S. W. James; River Rat bait shop, Manhattan, Kansas (allegedly from SE Kansas), 16 May 1987; bank of Grand River, near Freeman, Cass Co., Missouri, 12 Jun 1987, S. W. James; Minnesota Bait and Fly shop, Kansas City, Kansas, 12 Jun 1987; Angler's Market, Harrisonville, Missouri, 12 Jun 1987; bank of Stranger Creek at Kansas Hwy 92, Leavenworth Co., Kansas, 22 Jun 1987, S. W. James; USNM 42142, Newlight, Tensas Parish, Louisiana, 16 Apr 1966, R. E. Tandy; USNM 42139, Illinois Hwy 149 W of Murphysboro, Jackson Co., Illinois, 19 Apr 1963, W. R. Murchie; USNM 42143, Beaucoup Creek, N of Murphysboro, Jackson Co., Illinois, 11 Apr 1967, W. R. Murchie; USNM 42144, Prairie Creek, Benton Co., Iowa, 15 Apr 1963, W. R. Murchie; USNM 42145, Osage Fork at Rt. 5, Laclede Co., Missouri, 18 Apr 1963, W. R. Murchie; USNM 26409, Dirty Creek Bottoms, near Warner, Oklahoma, Apr 1954, V. L. Rounds; USNM 47995, Kansas, "various localities," Nov 1917, Mr. Harrah (F. Smith collection); USNM 48035, Havana, Mason Co., Illinois, 24 May 1894, F. Smith; USNM 47993, Havana, Mason Co., Illinois, Apr 1895, F. Smith; USNM 47994, bottomlands near Rankin Crossing Bridge, White Heath, Piatt Co., Illinois, 10 Apr 1915, F. Smith. Types lost.

Description.—External characteristics: 85 to 170 by 4 to 6 mm, width at segment xxx, body cylindrical in cross section throughout, widest at segments vi to ix, segments 126 to 206. Setae closely paired throughout; setal formula AA:AB:BC:CD = 3:1:4:1.4. Prostomium tanylobous, numerous longitudinal furrows in peristomium, biannulate iii or v, triannulate posterior to iv or v. Medium to dark brown segments iv plus one of anterior dorsal pigmentation, sometimes present along mid-dorsal line and on hindmost segments, nephridiopores near D. First dorsal pore 9/10 to 12/13, spermathecal pores on small bumps on leading edges of viii and ix, just lateral to setae *A*. Ovipores in xiv, presetal; male pores in xix in male grooves which are in AB in xviii to xx; prostatic pores and penial setae at ends of grooves. Clitellum xii to xviii or xix, saddle-shaped or interrupted at mid-ventral line, paired genital markings postsetal in xvii (all), paired, postsetal in one or both of xx–

xxi. Penial setae bowed, 700 to 900 μm by 22 to 28 um, tips tapering to a conical, unsculptured point (Fig. 1).

Internal characteristics: Septa 5/6 to 12/13 muscular, thickest in 7/8 to 9/10; last set of trans-septal muscles originating in xiii. Alimentary canal with gizzards in v and vi, esophagous smooth externally with some chloragogen, vascularized in xi to xiii, internal texture pebbly changing to low longitudinal folds by xv, xvi; no calciferous lamellae. Intestinal origin at 16/17 or within xvii, intestinal constriction usually present just anterior to origin of simple low to rudimentary typhlosole in xxii to xxv.

Nephridia 2 per segment, stomate, without bladders, duct meeting body wall near D.

Vascular system with subintestinal trunk, single dorsal trunk, these connected by lateral trunks in v to ix, lateral-esophageal hearts in x to xiii. Lateral trunks have lateral and septal branches from a point above attachment to subintestinal trunk, in ix a large vessel from lateral trunk to body wall of segments ix to xii. Supra-esophageal vessel ix or 9/10 to xiii, extra-esophageal iii to xiii, in xiii branching out to body wall over xii to xvi. Small vessels from extra-esophageal to septa and body wall in v to ix.

Male sexual system holandric, testes and funnels free, coagulum usually filling x and xi; vasa deferentia from funnels, under peritoneum, entering body wall in xvii. Seminal vesicles of ix divided into two or three lobes, of xii divided into numerous small ovoid lobes; vesicles of xii larger. Paired prostates in xviii and xx, long and slender, several times longer than the kinked ducts, extending through several segments. Stout ducts lacking muscular sheen, meeting body wall just posterior to penial setal follicles.

Ovaries and funnels in xiii, free, ovaries fan-shaped or globular cluster of numerous strings. Spermathecae in viii, ix, variable ampulla and diverticular shape. Diverticulum 3 to 6 lobed internally, slightly incised, ental end sessile, ectal end free, diverticulum attached to thickened portion of duct below base of ampulla.

Remarks.—Types of *D. riparia* are not mentioned in Reynolds & Cook (1976:163).

The most important difference between the material examined here and earlier descriptions is the intestinal origin in xvii, rather than xviii. It was repeatedly observed that relaxed specimens and those that had been starved prior to preservation appeared to have an intestinal origin posteriorly in xvii or apparently in xviii. Specimens fixed with full guts, as were all of Murchie's and mine, clearly showed an intestinal origin within xvii or at 16/17, which is commonly interpreted as in xvii. Sections made by F. Smith and now at USNM have collapsed intestines, the first segments of which have longitudinal furrows resembling the valvular condition of the last portions of the esophagus.

McNab & McKey-Fender (1955) used the segment of intestinal origin and spermathecal characters to define *Diplocardia riparia prosenteris,* but spermathecal variation within individuals and within populations is equal to that deemed of subspecific rank. This is not to say that consistent geographic variations in spermathecal details do not exist. However, the consistency of somatic morphology within the material examined argues against naming subspecific variants.

Since *D. riparia prosenteris* McNab & McKey-Fender was distinguished from *D. riparia* primarily on the basis of an intestinal origin in xvii, I suggest that this subspecies, elevated to specific rank by Gates (1977), be synonymized with *D. riparia. Diplocardia riparia prosenteris* is also unrepresented by types.

Diplocardia fuscula Gates 1968
Fig. 1E, F

Diplocardia fuscula.—Gates, 1968:22.—Gates, 1977:21.

Material.—USNM 42134, Greenwood, Caddo Parish, Louisiana, 16 Nov 1954, D.

Brumfield coll. USNM 38789, Negreet, Sabine Parish, Louisiana, 28 Mar 1965, R. E. Tandy, G. E. Gates, and J. M. Byrd, coll. (paratypes).

Description (Greenwood material).—External characteristics: 154 to 193 by 5 to 7 mm, width at segment xxx, body cylindrical in cross section throughout, widest at segments vi to ix, segments 120 to 145. Setae closely paired throughout; setal formula AA:AB:BC:CD = 4:1:5:2. Prostomium proepilobous, peristomium furrowed, segments biannulate iii, iv or iv only, triannulate posterior to iv. Traces of medium brown anterior dorsal pigmentation (bleached by preservative?), sometimes present along mid-dorsal line and on posterior segments, nephridiopores near D. First dorsal pore 10/11, spermathecal pores on small bumps on leading edges of viii and ix, just in the line of or median to setae a. Ovipores in xiv, presetal; male pores in xix in male grooves which are in AB in xviii to xx; prostatic pores at ends of grooves. Clitellum 1/2 xii, xiii to xix, interrupted at mid-ventral line. Unpaired mid-ventral sucker-like genital markings 10/11, 11/12, 12/13; paired genital markings postsetal in xvii (all), sometimes in xx (Fig. 1). Penial setae vestigial, sigmoid, not markedly different from ambulatory setae.

Internal characteristics: Septum 5/6 faintly muscled, 6/7 to 12/13 muscular, thickest in 7/8 to 9/10; last set of transseptal muscles originating in xiii or xiv. Alimentary canal with gizzards in v, vi; esophagous smooth externally, covered with brown chloragogen, vascularized in xii to xv, internal texture pebbly changing to low longitudinal folds by xv, xvi; ventral esophageal typhlosole viii to xiv; no calciferous lamellae. Intestinal origin in xviii, intestinal constriction anterior to origin of simple typhlosole in xxiv or xxv; typhlosole one quarter of lumen diameter or less.

Nephridia 2 per segment, stomate, without bladders, duct meeting body wall near D. Ascending tubule from nephrostome with blind "caecum" at point of joining with main nephridial tubule.

Vascular system with subintestinal trunk, single dorsal trunk, these connected by lateral trunks in v to ix, lateral-esophageal hearts in x to xiii. Segmental vessels of xiv to xvi not connected to ventral trunk; posterior latero-parietal vessels lacking. Lateral trunks of vi to viii have body wall and septal branches from a point above attachment to subintestinal trunk, of v, vi with body wall branches and vessels to gizzard; in ix a large vessel from lateral trunk to body wall of segments ix to xii. Supra-esophageal vessel x to xiii, extra-esophageal v to xii, originating as small sub-pharyngeal vessels in i or ii. Small vessels from extra-esophageal to septa and body wall in vi to xii, to gizzards in v, vi.

Male sexual system holandric, testes and funnels free, coagulum usually filling x and xi; vasa deferentia from funnels superficial, passing lateral to prostatic ducts, entering body wall at 18/19; seminal vesicles of ix divided into 2 to 4 lobes, of xii divided into numerous small ovoid lobes, vesicles of xii larger. Paired prostates in xviii and xx, slender, 2 to 5× longer than stout, muscular ducts, glands in segments of origin or also extending into one or two adjacent segments; duct diameter increasing ectally.

Ovaries and funnels in xiii, free, ovaries fan-shaped or globular cluster of numerous strings. Spermathecae (Fig. 1E) in viii, ix, ovoid ampulla, variable diverticular shape. Diverticula 1 to 5 lobed internally, attached at middle by a short, broad stalk to lateral or anterior face of spermathecal duct, a muscle attaching ectal diverticular end to base of the preceding septum.

Remarks.—These worms were identified as *Diplocardia riparia* by W. R. Murchie, probably on the basis of pigmentation and intestinal origin. Since *D. riparia* is now understood to have an intestinal origin in xvii, placing these specimens in *D. riparia* is inappropriate. There are other differences, such as the locations of genital markings and the size of penial setae.

One specimen of *D. fuscula* reported by Gates (1968) has the same location and date as the material described herein, but the collector is (erroneously?) listed as "D. Brumble." No mention was made of variation that may be related to location of collection, and the holotype was chosen from the Negreet specimens. Differences between the Greenwood specimens and the paratypes are (characteristics of the former are given): an intestinal origin in xviii, extra-esophageal trunks not extending to xiv and, segmental vessels of xiv to xvi not meeting the ventral trunk. However, the three paratypes were variable in several characteristics, and two disagreed with the description given by Gates (1968): These two have posterior latero-parietal trunks in xiii and supra-esophageal vessels terminating in xiii. The third lacks posterior latero-parietals and its supra-esophageal vessel ended in xiv, and agrees with the species description in these and most other particulars. However it has post-clitellar genital markings, a characteristic shared with the other paratypes, but not with Gates' description.

The great majority of characteristics usually considered of systematic importance in this genus are similar in the Greenwood and Negreet lots. The major difference—and in view of the vascular system variability in the *D. fuscula* paratypes—the only consistent difference, is the segment of intestinal origin. The collection locations are approximately 100 km apart and in separate river drainages. The two lots may be considered subspecifically distinct, but until more data can be collected on geographic variation in *D. fuscula,* they should be considered the same variable species.

In view of the change in the definition of *D. riparia* proposed above, and the new data on *D. fuscula, D. fuscula* is now to be distinguished from *D. riparia* by reduction or loss of penial setae, frequent replacement of posterior latero-parietal vessels with large segmental connections from the dorsal vessel to the body wall and the ventral vessel, presence of unpaired pre-clitellar genital markings and a greater number of segments. Contrary to the original description, *D. fuscula* are not characterized by lack of genital markings in segments xvii and xx, and variability in intestinal origin and the blood circulation in clitellar segments are to be expected.

For the sake of clarity in future discussions of the vascular system in megascolecids, I propose to replace the cumbersome term "posterior latero-parietal vessel" with "clitellar vessel." This pair of vessels is the posterior extension of the extra-esophageal vessels. The posterior extent of branches of the clitellar vessel coincides closely with the termination of the clitellum. In the Puerto Rican *Trigaster longissimus* (Borges & Moreno 1990), the clitellum begins in xx and the clitellar vessel in xviii. This clearly indicates a functional connection between external and internal characteristics, and nomenclature should reflect this.

Acknowledgments

This research was supported by a short-term visiting fellowship at the Division of Worms, National Museum of Natural History, Smithsonian Institution. The assistance of Meredith Jones and Cheryl Bright was essential to the project. The Maharishi International University Department of Engineering generously made its scanning electron microscope available for my use.

Literature Cited

Borges, S., & A. G. Moreno. 1990. Nuevas especies del genero *Trigaster* Benham 1886 (Annelida: Oligochaeta) para Puerto Rico.—Bolletino del Museo Regionale de Ciencia Naturale de Torino (in press).

Brinkhurst, R. O., & B. G. M. Jamieson. 1971. Aquatic

Oligochaeta of the world. University of Toronto Press, Toronto, xi + 860 pp.

Eisen, G. 1899. Notes on North American earthworms of the genus *Diplocardia.*—Zoological Bulletin 2:161–172.

———. 1900. Research in American Oligochaeta, with especial reference to those of the Pacific coast and adjacent islands.—Proceedings of the California Academy of Sciences, Third Series 2:85–276.

Gates, G. E. 1955. Notes on several species of the earthworm genus *Diplocardia* Garman 1888.—Bulletin of the Museum of Comparative Zoology at Harvard 113:229–259.

———. 1968. Louisiana earthworms. V. *Diplocardia fuscula,* n. sp., an addition to an American genus (Acanthodrilidae, Oligochaeta, Annelida).—Proceedings of the Louisiana Academy of Sciences 31:22–26.

———. 1977. More on the earthworm genus *Diplocardia.*—Megadrilogica 3:1–47.

James, S. W. 1982. Effect of fire and soil type on earthworm populations in a tallgrass prairie.—Pedobiologia 24:37–40.

———. 1984. New records of earthworms from Kansas (Oligochaeta: Acanthodrilidae, Lumbricidae, Megascolecidae).—Prairie Naturalist 16:91–95.

———. 1988. The postfire environment and earthworm populations in tallgrass prairie.—Ecology 69:476–483.

———. 1990. Oligochaeta: Megascolecidae and other earthworms from southern and midwestern North America. *in* D. L. Dindal, biology guide. Wiley, New York (in press).

———, & M. R. Cunningham. 1989. Feeding ecology of some earthworms in Kansas tallgrass prairie.—American Midland Naturalist 121:78–83.

Jamieson, B. G. M. 1971. A review of the megascolecoid earthworm genera (Oligochaeta) of Australia. Part I—Reclassification and checklist of the megascolecoid genera of the world.—Proceedings of the Royal Society of Queensland 82:75–86.

McNab, J. A., & D. McKey-Fender. 1955. Studies in the genus *Diplocardia* (Oligochaeta: Megascolecidae).—The Wasmann Journal of Biology 13: 113–143.

Michaelsen, W. 1900. Oligochaeta. Das Tierreich 10. R. Friedlander and Son, Berlin. xxix + 575 pp.

Murchie, W. R. 1967. Chromosome numbers of some Diplocardian earthworms (Megascolecidae–Oligochaeta).—American Midland Naturalist 78: 534–537.

Olson, H. W. 1928. The earthworms of Ohio.—Ohio Biological Survey 4:47–90.

Reynolds, J. W., & D. G. Cook. 1976. Nomenclatura Oligochaetologica. University of New Brunswick Press, Fredericton, New Brunswick, x + 217 pp.

Smith, F. 1895a. A preliminary account of two new Oligochaeta from Illinois.—Bulletin of the Illinois State Laboratory of Natural History 4:138–148.

———. 1895b. Notes on species of North American Oligochaeta.—Bulletin of the Illinois State Laboratory of Natural History 4:285–297.

———. 1900. Notes on species of North American Oligochaeta. III. List of species found in Illinois, and descriptions of Illinois Tubificidae.—Bulletin of the Illinois State Laboratory of Natural History 5:441–459.

Teotia, S. P., F. L. Duley, & T. M. McCalla. 1950. Effect of stubble mulching on number and activity of earthworms.—Nebraska Agricultural Experimental Station Research Bulletin 165, 20 pp.

Department of Biology, Maharishi International University, Fairfield, Iowa 52556.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 187–196

REDESCRIPTION AND SYNONYMY OF *NEPHTYS IMBRICATA* GRUBE, 1857 (POLYCHAETA: NEPHTYIDAE)

Takashi Ohwada

Abstract.—The polychaets *Nephtys imbricata* Grube, 1857, *Nephtys serratifolia* Ehlers, 1897 and *Nephtys serrata* Hartman, 1953 are synonymized. The holotype of *N. imbricata* is redescribed.

Nephtys imbricata was originally described by Grube (1857) as *Nephtys,* appearing like polynoids due to the scale-like structures on the dorsum. These structures are exceptional in the family Nephtyidae, and *N. imbricata* has been known only by its short original Latin description which lacked a figure. Although its possible synonymy with *Nephtys squamosa* Ehlers, 1887 was suggested by Hartman (1950, 1959), its identity remained obscure until now. The holotype of *N. imbricata,* however, was found in the Zoological Museum, University of Copenhagen by Dr. Mary E. Petersen, and she kindly provided me an opportunity to examine that specimen.

Nephtys imbricata Grube, 1857
Figs. 1–4

Nephthys imbricata Grube, 1857:11.
Nephthys serratifolia Ehlers, 1897:24–25, tab 1, fig. 13.—Ehlers, 1901:68.—Monro, 1930:114–115, fig. 41a, b.—Monro, 1936:139–140.—Wesenberg-Lund, 1962: 89–94, figs. 35–39.—Hartman, 1964:106, pl. 32, fig. 7.—Hartmann-Schröder, 1965: 141–145, figs. 110–113.—Rozbaczylo & Castilla, 1974:202–203, fig. 7.
Nephtys serratus Hartman, 1953:33–34, fig. 10a–g.—Hartman, 1964:106, pl. 32, figs. 5, 6.
Nephtys imbricata Wesenberg-Lund, 1962: 95.—Rozbaczylo & Castilla, 1974:195.

Material examined.—Holotype of *Nephtys imbricata*: Valparaiso, Chile, 18.ix.1841, H. Kröyer, coll. (Zoological Museum, University of Copenhagen = ZMC unnumbered; for measurement see the description below). Syntypes of *Nephtys serratifolia*: Between Falkland Islands and Argentina (49°35′S, 64°43′W), 113 m, Rophaniel coll., 2 specimens (Zoological Museum, University of Hamburg = ZMH V-1198; both incomplete posteriorly, 15.1 mm long for 44 setigers, 2.9 mm wide with parapodia, and 16.2 mm long for 51 setigers, 2.5 mm wide with parapodia). Holotype of *Nephtys serrata*: Port William, Falkland Islands (51°40′S, 57°41′W), 40 m, sand, small stones and algae, 4.vii.1902, Swedish Antarctic Expedition 1901–1903, (Swedish Museum of Natural History = SMNH 620; 53-setiger anterior fragment, 47.3 mm long, 5.8 mm wide with parapodia, and 11-setiger middle fragment, 11.7 mm long).

Description.—Holotype of *Nephtys imbricata* incomplete posteriorly, 48.1 mm long for 95 setigers; 3.2 mm wide with parapodia, 1.5 mm wide without parapodia at widest part of the body, about setiger 17, narrowing gradually to setiger 26. Body brown, lacking pigmentation in alcohol. Proboscis partly everted. Eyes absent (Fig. 1a).

Anterior margin of prostomium nearly straight, thin, spatulate (Fig. 2a); lateral margins rounded, broadest between second antennae, extending into setiger 1 to nuchal organs; posterior margin with V-shaped middorsal projection extending to near posterior border of setiger 1; posterolateral

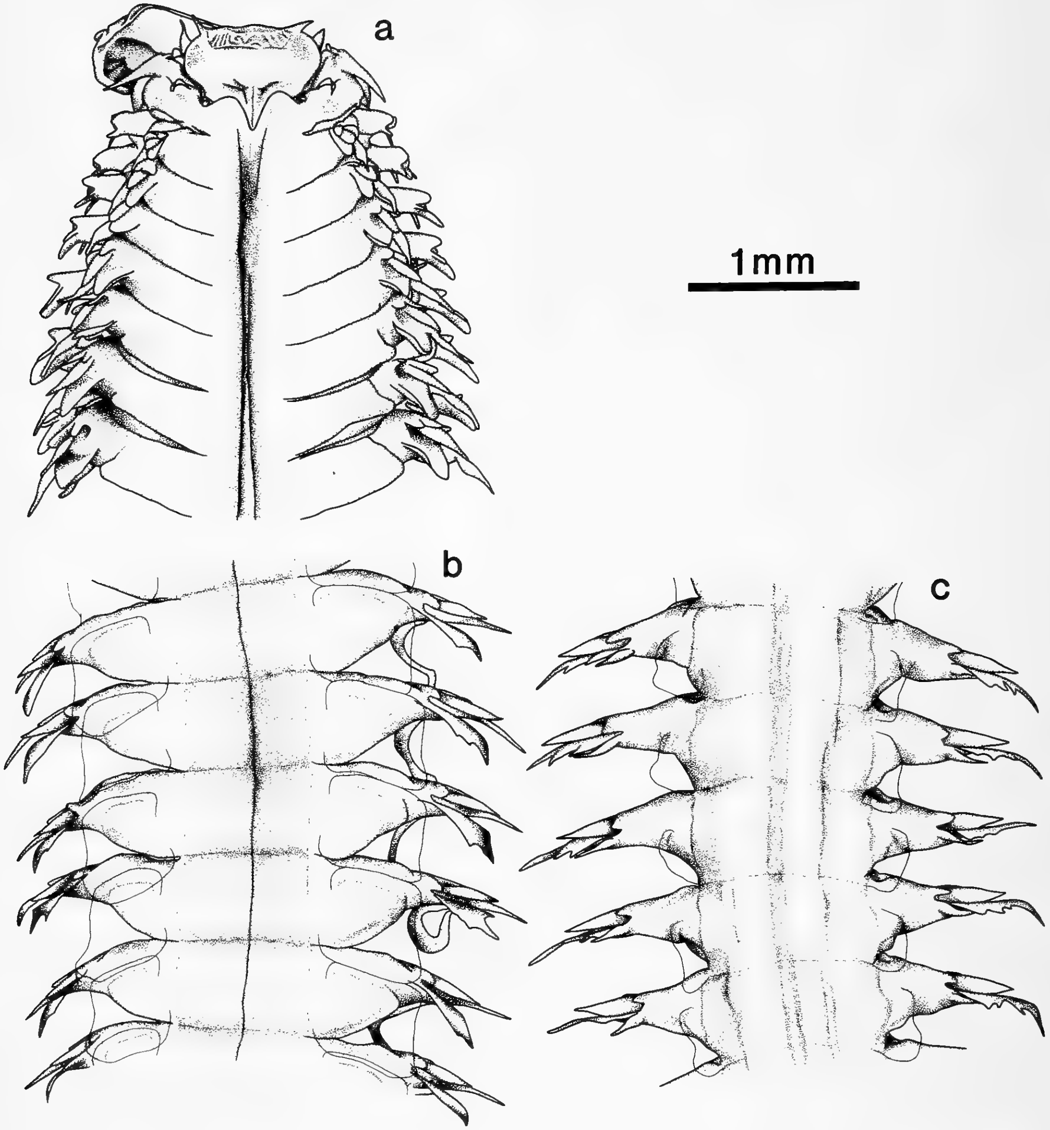


Fig. 1. *Nephtys imbricata,* holotype (ZMC unnumbered; setae omitted; b, c, translucent scale-like lamellae only outlined): a, Anterior part, dorsal view (anterior end stretched laterally due to partially everted proboscis); b, 85th to 89th setiger, dorsal view (neuropodia omitted); c, Same, ventral view (notopodia omitted).

margins joining lateral margins behind nuchal organs. Anterior part between first antennae somewhat translucent, marked by intricate pattern (Fig. 2a) of opaque tissue. First antennae tapered, pointed, continuous with frontal margin of prostomium, directed anterolaterally. Second antennae, stout, conical, pointed, much stouter than first ones, nearly twice as long, well behind 1st antennae and halfway on ventral surface of prostomium near lateral margins, directed anterolaterally. Nuchal organs everted at posterolateral corners of prostomium.

Proboscis (on the basis of the holotype of

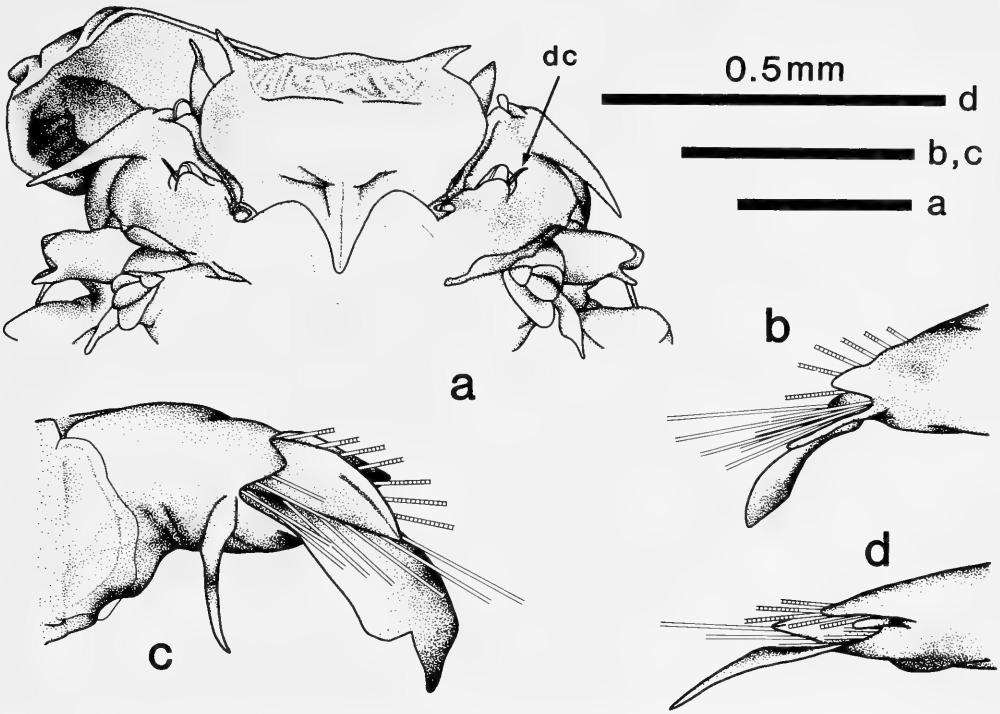


Fig. 2. *Nephtys imbricata,* holotype (ZMC unnumbered; a, setae omitted; b–d, tips of setae omitted): a, Anterior end, dorsal view (stretched laterally due to partially everted proboscis; anterior part of prostomium bending downward. dc—dorsal cirrus); b, Left neuropodium, setiger 7, dorsolateral view; c, Same, setiger 15, ventral view; d, Same, setiger 90, dorsolateral view.

Nephtys serrata) terminally with 20 bifid papillae and single small triangular middorsal and midventral papillae. Subterminal papillae rapidly decrease in size towards base of proboscis, distalmost 2 or 3 arranged in 22 longitudinal rows, longer than or similarly long as bifid papillae, thereafter reduced to 14 rows proximally, 3–5 in each row. No middorsal or midventral papilla. Proximal surface smooth.

Setiger 1 modified (Fig. 2a); notopodia reduced, with short rounded postacicular lobe in front of, and rounded preacicular lobe behind rather rounded acicular lobe; acicular lobe supported by acicula whose tip curves outward. Dorsal cirri tiny, slender, pointed, arising anterolaterally from outer side of acicular lobes near base between preacicular and postacicular setal fascicles (Fig. 2a—dc), hardly recognizable. Neuropodia of setiger 1 on anterior margin, lateral to prostomium, with thin rudimentary acicular lobes projecting anteriorly; left acicular lobe supported by thin acicula whose tip curves inward. Ventral cirri large, long, tapered, pointed, lateral to neuropodia, continuous with anterior setigerous margin, directed posterolaterally. Notosetae of setiger 1 include preacicular barred (laddered) capillaries and postacicular very finely serrated slender capillaries; neurosetae long, thin, smooth capillaries, surrounding acicular lobes.

Parapodia generally similar throughout from setiger 2 (Figs. 1, 3) except that branchiae (interramal cirri) lacking on setiger 2. Both rami with preacicular and postacicular setal fascicles (Fig. 3). Both notopodial and neuropodial acicular lobes conical and pointed (Figs. 1, 2b–d, 3). Acicula termi-

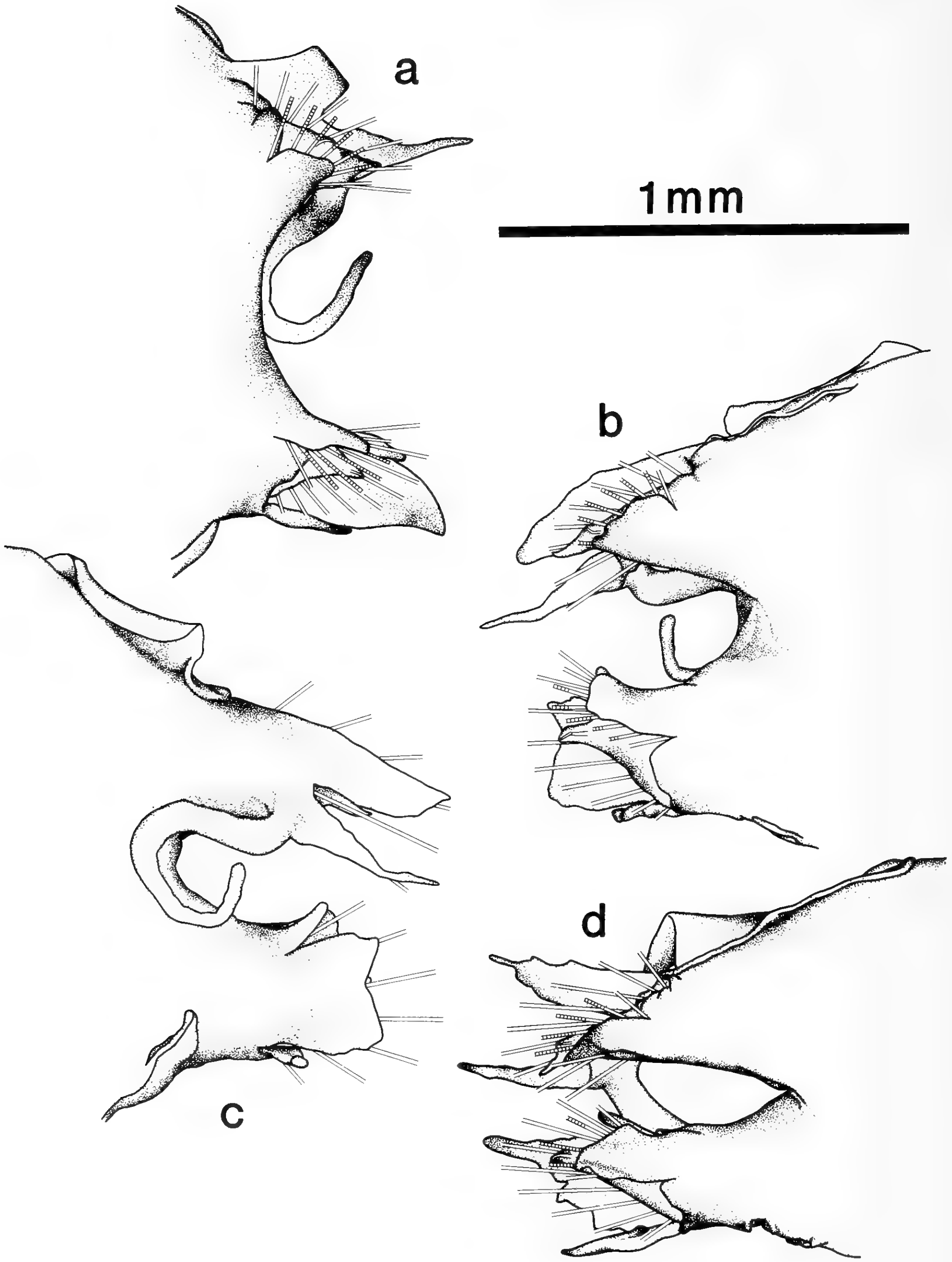


Fig. 3. *Nephtys imbricata,* holotype (ZMC unnumbered; tips of setae omitted): a, Left parapodium, setiger 7, anterior view (tip of notopodial postsetal lamella bending posteriorly); b, Right parapodium, setiger 28, anterior view (neuroacicula broken near its tip); c, Same, posterior view (preacicular setae omitted); d, Right parapodium, setiger 78, anterior view.

nates dorsal to the tip of acicular lobe in notopodia, and in the tip of acicular lobe in neuropodia. Notopodial presetal lamellae thin and broad, extending from lower margins of notopodia, shorter than acicular lobes, projecting almost to the level of the tip of notoacicula, distally rounded on anterior parapodia (Fig. 3a, b), triangularly pointed on posterior parapodia (Fig. 3d). Small lamellae dorsal to notopodial presetal lamellae (Figs. 1a, 3a, b), thin and rounded, posteriorly reduced and becoming much smaller and hardly recognizable (Figs. 1b, 3d). Preacicular setae appear mostly beyond dorsal margins of presetal lamellae, usually slightly cover small suprapreacicular lamellae (Fig. 3a, b, d). Neuropodial presetal lamellae thin, extending from upper margins of neuropodia, rather triangularly on anterior parapodia (Figs. 2b, 3a) and rather truncately on middle and posterior parapodia (Fig. 3b, d), similarly long as acicular lobes on anterior neuropodia (Figs. 2b, 3a) and shorter than acicular lobes posteriorly (Figs. 2d, 3b, d). Inconspicuous thin broad lamellae ventral to neuropodial presetal lamellae (Figs. 1c, 2c, 3a, b, d), much shorter than presetal lamellae. Preacicular setae appear mainly beyond ventral margins of presetal lamellae on anterior and middle neuropodia (Figs. 2c, 3a, b), partly cover infrapreacicular lamellae on anterior parapodia (Fig. 3a).

Notopodial postsetal lamellae thin, extending further than acicular lobes from segmental wall above and behind acicular lobes; small on setigers 2–5 or 6 following the small size of parapodia, increasing in size on anterior setigers (Fig. 3a–c), thereafter becoming smaller and narrower posteriorly (Fig. 3d). Notopodial postsetal lamellae ligulate with rather rounded tip on setigers 2–10 on right side and setigers 2–13 on left side (Figs. 1a, 3a), especially rounded on setigers 2–4 (Fig. 1a); ligulate with triangular tip from setiger 11 on right side and setiger 14 on left side (Fig. 3b, c); becoming tapered posteriorly as lamellae becoming narrower (Fig. 3d). On ligulate notopodial postsetal lamellae with triangular tip, often a few (mostly one, sometimes two, rarely three) incisions on dorsal margin and/or one (rarely two) incision on ventral margin (Fig. 3d); postsetal lamellae with incision(s) occurring more often posteriorly among entire ones (Fig. 1b); no clear regularity in the change of the number of incisions along body. Neuropodial postsetal lamellae thin, larger than notopodial ones, extending from behind acicular lobes. Neuropodial postsetal lamellae ligulate, entire with rather triangular tip on setigers 2–11 on right side and setigers 2–14 on left side (Fig. 3a); one incision develops from setiger 12 on right side and setiger 15 on left side (Figs. 2c, 3b, c); second incision occurs from setiger 36 on right side and setiger 43 on left side (Fig. 3d), incisions more conspicuous posteriorly; third incision appears from setiger 87 on right side and setiger 83 on left side (Fig. 1c); incisions, however, inconspicuous thereafter. Although the number of incisions tends to increase along the body, postsetal lamellae without incision and with two incisions among those with one incision, and postsetal lamellae with one incision and with three incisions among those with two incisions. Small lobe on superior edge of neuropodia (Figs. 1a, 2b, d, 3a–d). Dorsal cirri thin, long and narrow, triangularly elongate, extending laterally from basal part of branchiae behind acicular lobes, no longer than neuropodial postsetal lamellae on anterior setigers (Figs. 1a, 3a), longer than any lamella on middle and posterior setigers (Figs. 1b, 3b–d).

Branchiae first present on setiger 3, fully developed by setiger 8 (Fig. 3a), thereafter not reduced (Fig. 3b, c) even on last segment of the incomplete holotype (Fig. 3d). On right side, branchia appears as short process on setiger 3, elongates on setiger 4, begins to recurve on setiger 5, and completely recurves on setiger 6, thereafter gradually in-

Fig. 4. *Nephtys imbricata,* holotype (ZMC unnumbered): a, Tip of rather short finely serrated neuropodial preacicular capillary seta, 78th right parapodium, anterior view; b, Subdistal part of long finely serrated notopodial postacicular capillary seta without spur, same, anterior view; c, Basal part of long finely serrated notopodial postacicular capillary seta with spur, same, anterior view.

creases in size to setiger 8. On left side, branchia emerges as very small, conical process on setiger 3, elongates but still very short on setiger 4, abruptly develops into recurved form on setiger 5, thereafter gradually increases in size to setiger 8.

Scale-like thin translucent lamellae (Figs. 1a, b, 3) on dorsolateral surface of body from setiger 6, not fully developed until middle setigers where lamellae extend mainly posterolaterally over notopodia and partly overlap successive segments in imbricate arrangement (Fig. 1b). Similar but smaller lamellae (Figs. 1c, 3b, c) on ventrolateral surface of body from setiger 4, not fully developed until middle setigers where lamellae extend somewhat posterolaterally and slightly cover neuropodia and successive segments (Fig. 1c).

Both preacicular and postacicular setae occur in spreading fascicles, with postacicular fascicles wider than preacicular ones (Fig. 3a, b, d); preacicular setae much fewer than postacicular setae; postacicular setae mostly thicker than preacicular ones. Preacicular setae mostly consist of barred capillaries; a few finely serrated capillaries (Fig. 4a) also occur at upper and lower end of preacicular fascicles (Fig. 3a, b, d), usually as thick as barred setae and similarly long or longer than barred setae. Postacicular setae consist of very long finely serrated capillaries (Fig. 4b), and in addition, on middle and posterior setigers, are several equally long finely serrated capillaries with spur on basal one-third to one-fourth (Fig. 4c) in middle of setal fascicles, and some short finely serrated capillaries on anterior side of ventral half of neuropodial postacicular setal fascicles, thick as barred setae and similarly long or slightly longer than barred setae. No lyrate setae found.

Remarks.—*Nephtys imbricata* is closely related to *N. acrochaeta* Hartman, 1950 and *N. squamosa* Ehlers, 1887. *Nephtys imbricata,* however, differs from *N. acrochaeta* in that branchiae are present from setiger 3 in the former and setigers 9–10 in the latter. Neuropodial postsetal lamellae are laciniate in *N. acrochaeta* and *N. imbricata* whereas they are entire in *N. squamosa.* The capillary setae with basal spur are present in the postacicular fascicles both in *N. acrochaeta* and *N. imbricata,* but absent in *N. squamosa.*

Nephtys glossophylla Schmarda, 1861 from Chile also resembles *N. imbricata* in the possession of scale-like dorsal lamellae, laciniate neuropodial postsetal lamellae and finely serrated capillary setae with basal spur. Although it is probable that *N. glossophylla* is synonymous with *N. imbricata,* the former is known only by its original description (Schmarda 1861:90) and that is insufficient to distinguish it from other species.

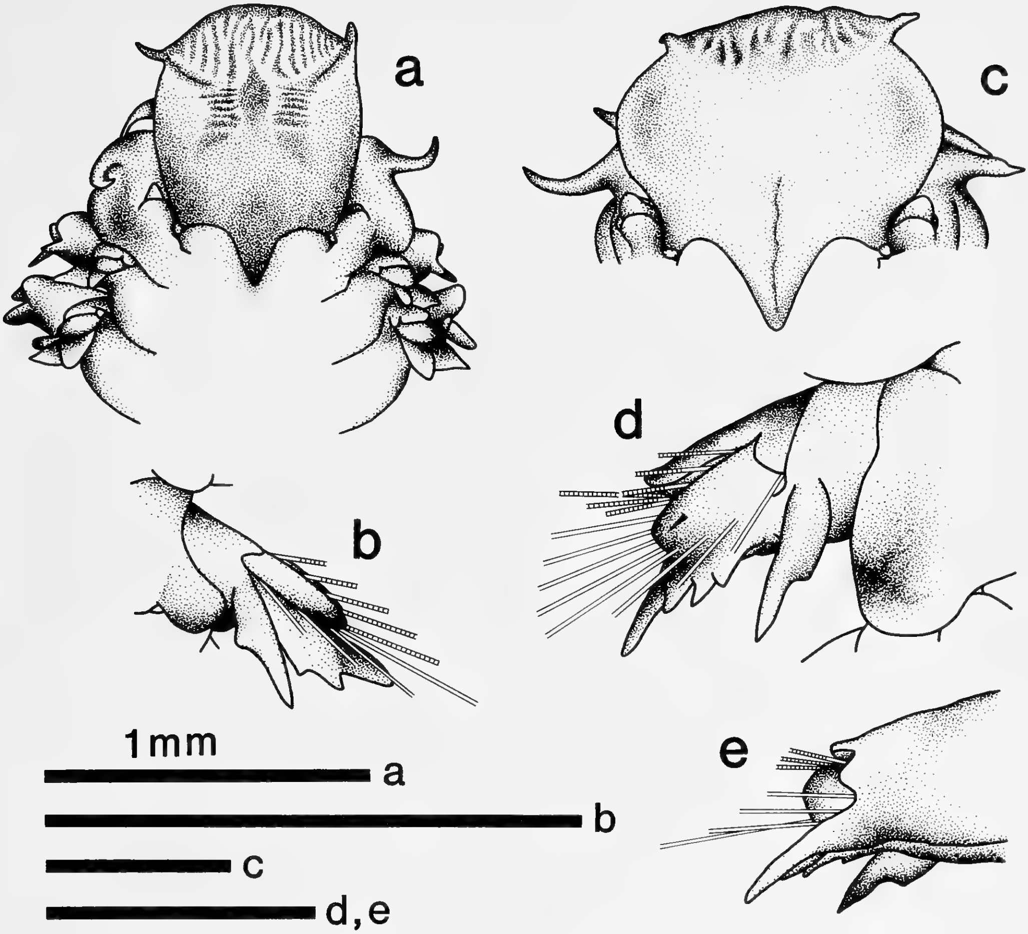


Fig. 5. Anterior end and neuropodia of *Nephtys serratifolia* and *N. serrata* (a, b, *N. serratifolia,* syntypes (ZMH V-1198), c–e, *N. serrata,* holotype (SMNH 620); tips of setae omitted): a, Anterior end, dorsal view; b, Left neuropodium, setiger 26, ventral view; c, Anterior end, dorsal view; d, Right neuropodium, setiger 46, ventral view; e, Left neuropodium, middle setiger, dorsal view.

The type of *N. glossophylla* is deposited in the British Museum (Natural History), but the specimen has collapsed and its identity could not be clarified.

Distribution.—Southern part of South America (both Atlantic and Pacific Coasts), 20–309 m, fine sand (Fig. 6).

Synonymy of *Nephtys imbricata*

Examination of the type specimens of *Nephtys imbricata, N. serratifolia,* and *N. serrata* revealed that all of them have scale-like lamellae, laciniate neuropodial postsetal lamellae, and postacicular capillary setae with basal spur. Branchiae occur from setiger 3 in all type specimens, although *N. serrata* was originally described to have branchiae from setiger 4 (Hartman 1953: 33). Geographically, *N. serratifolia* has been reported from both Pacific and Atlantic Coasts of southern South America, and the only known occurrences of *N. imbricata* and *N. serrata* (their type localities) are within

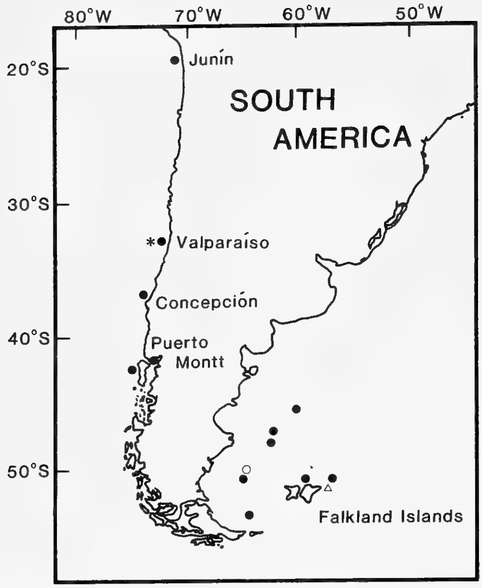


Fig. 6. Geographical occurrence of *Nephtys imbricata* (asterisk—type locality of *Nephtys imbricata,* open circle—type locality of *N. serratifolia,* solid circle—occurrence reported as *N. serratifolia,* triangle—type locality of *N. serrata*).

the range of distribution of *N. serratifolia* (Fig. 6).

There are few differences between the type specimens of the three species (Table 1). While the presence of the tiny dorsal cirri on the 1st notopodia has been found in the holotype of *N. imbricata* (Fig. 2a), they have not been recognized in the syntypes of *N. serratifolia* or the holotype of *N. serrata.* This type of tiny dorsal cirri is barely recognizable and is supposed to be easily broken off (Ohwada 1989). Their apparent absence in the syntypes of *N. serratifolia* and the holotype of *N. serrata* does not necessarily imply their absence in live animals.

The most distinct difference between the type specimens examined lies in the morphology of the erect lobes on the superior edge of neuropodia. While these small lobes extend further than presetal lamellae on the anterior neuropodia of the holotype of *N. imbricata* (Fig. 2b), they are short throughout the length of the holotype of *N. serrata* (Fig. 5e), and they are apparently absent in the syntypes of *N. serratifolia.* The previous descriptions of *N. serratifolia* show that the erect lobes develop to various extent in this species, and the degrees of their developments in the type specimens of *N. imbricata* and *N. serrata* are within the range of their variations reported for *N. serratifolia.* This indicates that the difference in the morphology of the erect lobes between *N. imbricata* and *N. serrata* has no specific importance. Their apparent absence in the syntypes of *N. serratifolia* is also explained

Table 1.—Differences among the type specimens of *Nephtys imbricata, N. serratifolia,* and *N. serrata.*

	N. imbricata	*N. serratifolia*	*N. serrata*
1st dorsal cirri	tiny, slender, pointed (Fig. 2a)	not recognized	not recognized
Erect lobes on neuropodia	small, ligulate, extending beyond presetal lamellae in the anterior setigers (Fig. 2b, d)	not recognized	small, short throughout the body (Fig. 5e)
Ventral cirri	cirriform on anterior parapodia, thereafter foliaceous with tapered tip (Figs. 1c, 2c)	cirriform on anterior parapodia, thereafter rather flattened in basal half, decreasing in width to varying extent, distally becoming conical, tips pointed (Fig. 5b)	rather flattened in basal half, suddenly decreasing in width to about ½, distally becoming conical, terminating in fine columnar tip (Fig. 5d)

by the small size of the specimens. There appear to be some differences in the morphology of the ventral cirri among the type specimens examined (Table 1), but they are thought to be nothing more than intraspecific variations.

Based on the close agreement among the type specimens of *N. imbricata, N. serratifolia,* and *N. serrata* in the other characters, and the geographically overlapping ranges of these three species (Fig. 6), it is appropriate to synonymize *N. serratifolia* and *N. serrata* with *N. imbricata,* the latter the senior synonym. The similarity in the prostomium morphology has been suggested to reflect phylogenetic closeness (Ohwada 1985), and the possession of the similar patterns of opaque tissue in the anterior translucent part of prostomium in these three species (Figs. 2a, 5a, c) denies the possible morphological convergence between the species of different phylogenetic origins.

Acknowledgments

I am grateful to Dr. J. B. Kirkegaard and Dr. M. E. Petersen, Zoological Museum, University of Copenhagen, Dr. G. Hartmann-Schröder, Zoological Institute and Zoological Museum, University of Hamburg, and Dr. R. Oleröd, Swedish Museum of Natural History, for the loan of the type specimens. Mr. A. I. Muir, British Museum (Natural History) kindly permitted me to examine the specimens in that museum. The manuscript benefited from the helpful suggestions by Dr. M. E. Petersen, and Dr. T. H. Perkins, Florida Department of Natural Resources, U.S.A. This work was supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan.

Literature Cited

Ehlers, E. 1887. Report on the annelids of the dredging expedition of the U.S. coast survey steamer *Blake.* Memoirs of the Museum of Comparative Zoology of Harvard College 15:vi + 335 pp., 60 pls.

———. 1897. Polychaeten. Hamburger Magelhaenische Sammelreise. Hamburg, Friedrichsen & Co., 148 pp., 9 pls.

———. 1901. Die Polychäeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. Festschrift zur Feier des Hundertfünfzigjährigen Bestehens des Königlichen Gesellshaft der Wissenschaften zu Göttingen (Abh. Math.-Phys.). Berlin, Wiedmannsche Buchhandlung, 232 pp., 25 pls.

Grube, E. 1857. Annulata Örstediana. Enumeratio Annulatorum, quae in itinere per Indiam occidentalem et Americam centralem annis 1845–1848 suscepto legit cl. A. S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinere ad Americam meridionalem collectis.—Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn 1857:1–29.

Hartman, O. 1950. Polychaetous annelids. Goniadidae, Glyceridae, Nephtyidae.—Allan Hancock Pacific Expeditions 15:1–181.

———. 1953. Non-pelagic Polychaeta of the Swedish Antarctic Expedition 1901–03.—Further Zoological Results of the Swedish Antarctic Expedition, 1901–03 4(2):1–83, 21 figs, 1 chart.

———. 1959. Catalogue of the polychaetous annelids of the world. Part 1.—Allan Hancock Foundation Publications, Occasional Paper 23:1–353.

———. 1964. Polychaeta Errantia of Antarctica.—Antarctic Research Series 3:1–131.

Hartmann-Schröder, G. 1965. Die Polychaeten des Sublitorals. Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtung der Polychaeten und Ostracoden.—Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 62 (Suppl.):59–305.

Monro, C. C. A. 1930. Polychaete worms.—Discovery Report 2:1–222. 91 figs.

———. 1936. Polychaete worms. II.—Discovery Report 12:59–198, 34 figs.

Ohwada, T. 1985. Prostomium morphology as a criterion for the identification of nephtyid polychaetes (Annelida: Phyllodocida), with reference to the taxonomic status of *Aglaophamus neotenus.*—Publications of the Seto Marine Biological Laboratory 30(1/3):55–60.

———. 1989. Redescription of *Nephtys squamosa* Ehlers (Polychaeta: Nephtyidae).—Proceedings of the Biological Society of Washington 102(1): 124–130.

Rozbaczylo, N., & J. C. Castilla. 1974. La familia Nephtyidae en Chile (Annelida, Polychaeta).—Studies on the Neotropical Fauna 9:179–206.

Schmarda, L. K. 1861. Untersicht der Ordnung Abranchia. Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. 1. Turbellarien, Rotatorien und Anneliden, Part 2, 164 pp., 22 pls., Leipzig.

Wesenberg-Lund, E. 1962. Polychaeta Errantia. Reports of the Lund University Chile Expedition 1948–1949.—Lunds Universitets Årsskrift, N.F. Afdelning [2] 57(12):1–137.

Ocean Research Institute, University of Tokyo, 15-1, 1-Chome, Minamidai, Nakano-ku, Tokyo, 164 Japan.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 197–204

ANTRORBIS BREWERI, A NEW GENUS AND SPECIES OF HYDROBIID CAVESNAIL (GASTROPODA) FROM COOSA RIVER BASIN, NORTHEASTERN ALABAMA

Robert Hershler and Fred G. Thompson

Abstract.—An aquatic cavesnail from Coosa River Basin, Alabama, representing a monotypic genus, is described (*Antrorbis breweri,* new genus, new species). Diagnostic features of the genus include a minute, planispiral to low-trochoid shell with apical microsculpture of spirally arranged low tubercles; blind, unpigmented animal; few ctenidial filaments; intestine with coils on lateral surface of style sac and in pallial roof; simple penis; capsule gland with ventral channel; and two sperm pouches. *Antrorbis* and three other North American cavesnail genera that also have a simple penis and capsule gland with ventral channel herein are placed in the Lithoglyphinae.

Among the numerous discoveries of North American nonmarine mollusks made by Leslie Hubricht is a minute planispiral snail from subterranean stream in Manitou Cave, northeastern Alabama, which he assigned (Hubricht 1940:35) to *Horatia* Bourguignat, 1887. Hubricht did not describe the snail, and its affinities were uncertain in light of the determination by Hershler & Longley (1986) that other putative North American *Horatia* are not congeneric with this European group. As part of ongoing review of North American cavesnails, the senior author recently collected live examples of the Manitou cavesnail which we describe below as a new genus and species of Hydrobiidae.

Antrorbis, new genus

Diagnosis.—A minute-sized (2.7–3.0 mm) North American group characterized by a planispiral–low-trochoid shell with apical microsculpture of spirally arranged low tubercles. Operculum paucispiral, without ventral peg. Animal blind, unpigmented. Ctenidial filaments few (7–10). Central radular teeth with single pair of basal cusps. Intestine coiling on right-lateral style sac and in pallial roof. Male with a simple penis. Females oviparous. Oviduct entering capsule gland, which has a ventral channel. Two sperm pouches present.

Type species.—*Antrorbis breweri,* new species (by monotypy).

Etymology.—Masculine, from the Classical Greek, *antrum,* a cave, and *orbis,* a circle, and referring to subterranean habitat and discoidal shell of the snail.

Discussion.—Among North American freshwater hydrobiids, the Lithoglyphinae group of epigean genera (Thompson 1984) and three subterranean forms (*Pterides* Pilsbry, 1909; *Phreatodrobia* Hershler & Longley, 1986; *Holsingeria* Hershler, 1989) share with *Antrorbis* the simple penis and capsule gland with ventral channel. *Antrorbis* resembles some *Phreatodrobia* which have planispiral to low-trochoid shells, but a number of other highly unusual features (i.e., wrinkled protoconch sculpture, absence of basal cusps on the central radular teeth, presence of an anterior coil of the capsule gland) occur among this group of Texas endemics, mitigating against a close relationship with *Antrorbis* or any other known genus. *Holsingeria* and *Pterides,* local endemics from the Powell River Basin in southwestern Virginia and Panuco River Basin in northeastern Mexico, respectively, share with *Antrorbis* the spirally arranged, tubercular protoconch sculpture; and although these three genera are well differentiated by various combinations of features from shell, operculum, intestinal coiling, and pallial oviduct complex, they appear to represent a natural group.

The heterogeneous assortment of unusual character-states exhibited by these cavesnails makes it difficult to assess affinities among them, or with other hydrobiid groups, but nevertheless we are placing them in the Lithoglyphinae, the only subfamily that agrees with them in general soft anatomical features.[1] The lithoglyphines, as previously conceived (Davis & Pons da Silva 1984, Thompson 1984), were a morphologically compact group of genera characterized by a squat shell with large aperture, which accomodates a broad foot required for holding onto hard substrate in swift current. In light of recent studies on the anatomy of hydrobiid snails, and the discovery of additional new genera, shell shape (reflecting specialization for a particular habitat) no longer can be considered a defining feature of the Lithoglyphinae. In the wake of the taxonomic changes proposed herein, the Lithoglyphinae now parallels the hydrobiid subfamilies Nymphophilinae and Littoridininae in that included genera vary from nearly planispiral to broadly trochoidal to elongate-slender in shell shape. The Lithoglyphinae are represented in South America and Europe, and are widely deployed on the North American continent where they inhabit lentic and lotic epigean habitats as well as subterranean streams. No lithoglyphines are known from brackish-water habitats. We suspect that the Lithoglyphinae are an ancient freshwater group, but the fossil record offers no useful information in this regard because the subfamily is not identifiable on the basis of shell features.

Antrorbis breweri, new species
Manitou cavesnail
Figs. 1–5

Horatia sp.—Hubricht 1940:35.
Horatia micra.—Stein 1976:21.
"*Horatia.*"—Burch 1982:270.—Hershler & Longley 1986:153, figs. 23k, 1, 28a.

Material examined.—USNM 860429, holotype; University of Florida (UF) 135984 (4 specimens), USNM 860430 (9), paratypes, RH and party coll., 6 Jun 1988.—USNM 860431 (16), RH coll., 16 Sep 1988.—USNM 860432 (10), L. Hubricht coll., 19 Jun 1957. All material from Manitou Cave (Fig. 1), Little Wills Valley, Coosa River Basin, Fort Payne, AL (7.5 minute series), T. 7S, R. 9E, NE ¼ section 18.

Description.—Shell (Fig. 2; Table 1) discoidal, clear, transparent, 1.5–1.7 mm wide; height about half of width. Surface usually covered by moderately thick, yellow-orange periostracum. Whorls, 2.5–3.0, well rounded, sutures deeply indented. Whorl expansion rate moderate. Translation of protoconch and first teleoconch whorl highly variable, yielding impressive diversity of spire development. Aperture near-circular in outline, often slightly longer than wide, with adapical edge advanced. Inner lip thin, less curved than outer, adnate to small portion of body whorl, very slightly flared. Umbilicus broadly open. Protoconch (Fig. 3a–d), 1.25 whorls, sculptured with raised tubercles arranged in numerous spiral rows. Tubercular sculpture weak or absent on teleoconch. Teleoconch having strong collabral growth lines.

Operculum (Fig. 3e) thin, paucispiral, with 4.5 whorls. Ventral surface of operculum slightly convex, lacking peg development.

Animal with 2.5 whorls. Pigment absent, except for some small black granules scat-

---

[1] The Hydrobiinae differ anatomically from this group in having a small pallial tentacle; a penial lobe; and a complex, pigmented renal oviduct.

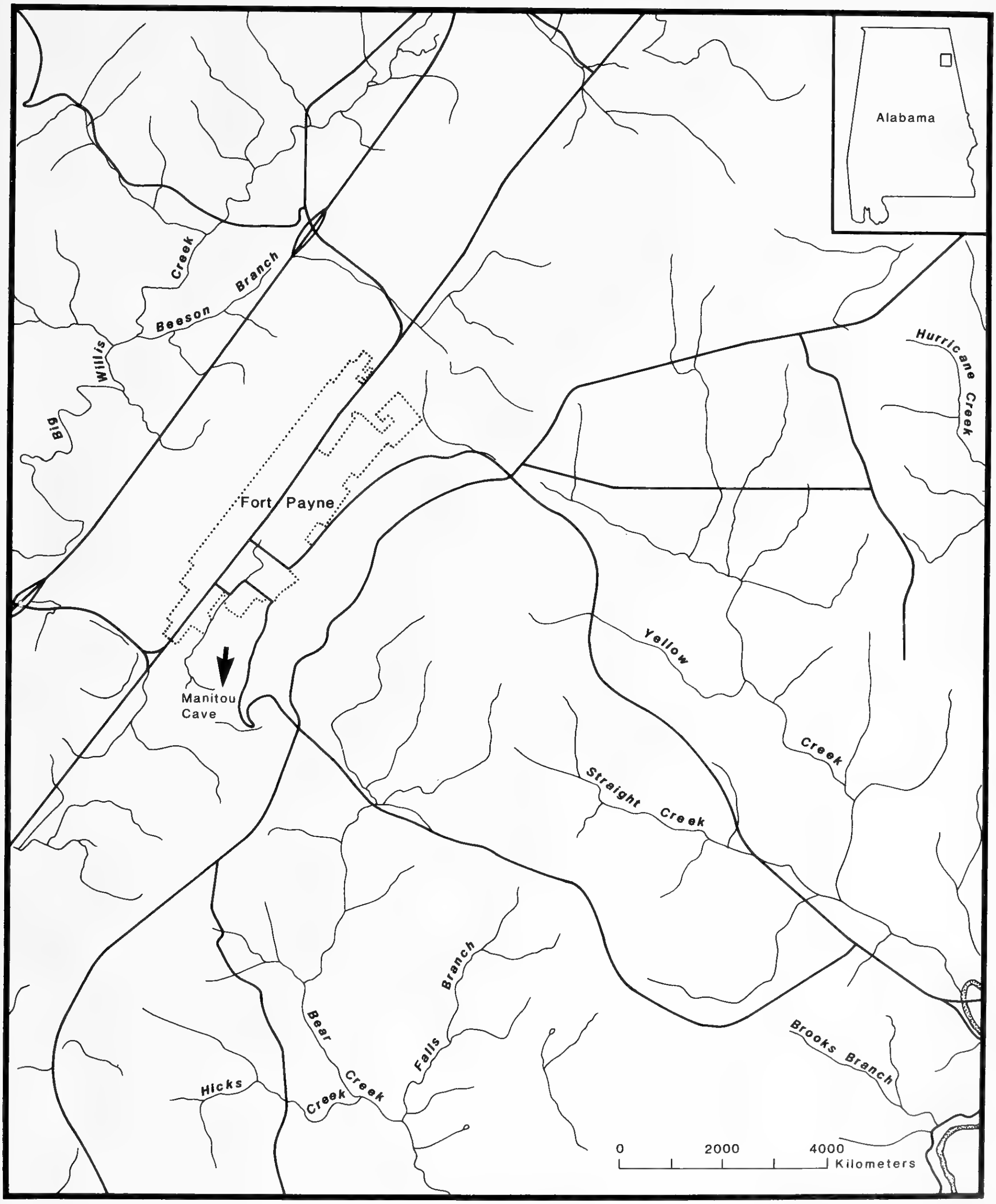


Fig. 1. Map (from Fort Payne Quadrangle, USGS 7.5 minute series, 1946 [revised 1983]) showing location of Manitou Cave.

tered on stomach and digestive gland posterior to gonad. Ctenidium with 7–10 small, triangular filaments. Osphradium filling about a third of ctenidium length.

Radular (Fig. 4) formula: 5-1-4(5)/1-1, 4-1-4(5), 20, 13-15 (from SEM micrographs of paratypes). Central teeth (Fig. 4a) broadly trapezoidal with deeply excavated basal

Fig. 2. SEM micrographs of shells of *Antrorbis breweri,* new species: shell at upper left, USNM 860429, holotype (shell width, 1.53 mm); all others, USNM 860430, paratypes (printed to same scale).

processes. Basal cusps of central teeth elongate, arising from edges of lateral angles. Style sac and stomach about equal in length (Fig. 5c). Stomach chambers poorly distinguishable externally; posterior caecal chamber absent. Digestive gland of 0.5–0.75 whorls, consisting of two elongate masses covered with small, lobate swellings. Posteriormost lobe terminates slightly proximal to tip of animal. Intestinal (In) coil on right lateral style sac surface a simple, "U-shape." Coil in anterior pallial roof a more complex, "reversed-S shape" (when viewed dorsally).

Testis a single, unlobed mass filling 0.5 whorl, slightly overlapping posterior stom-

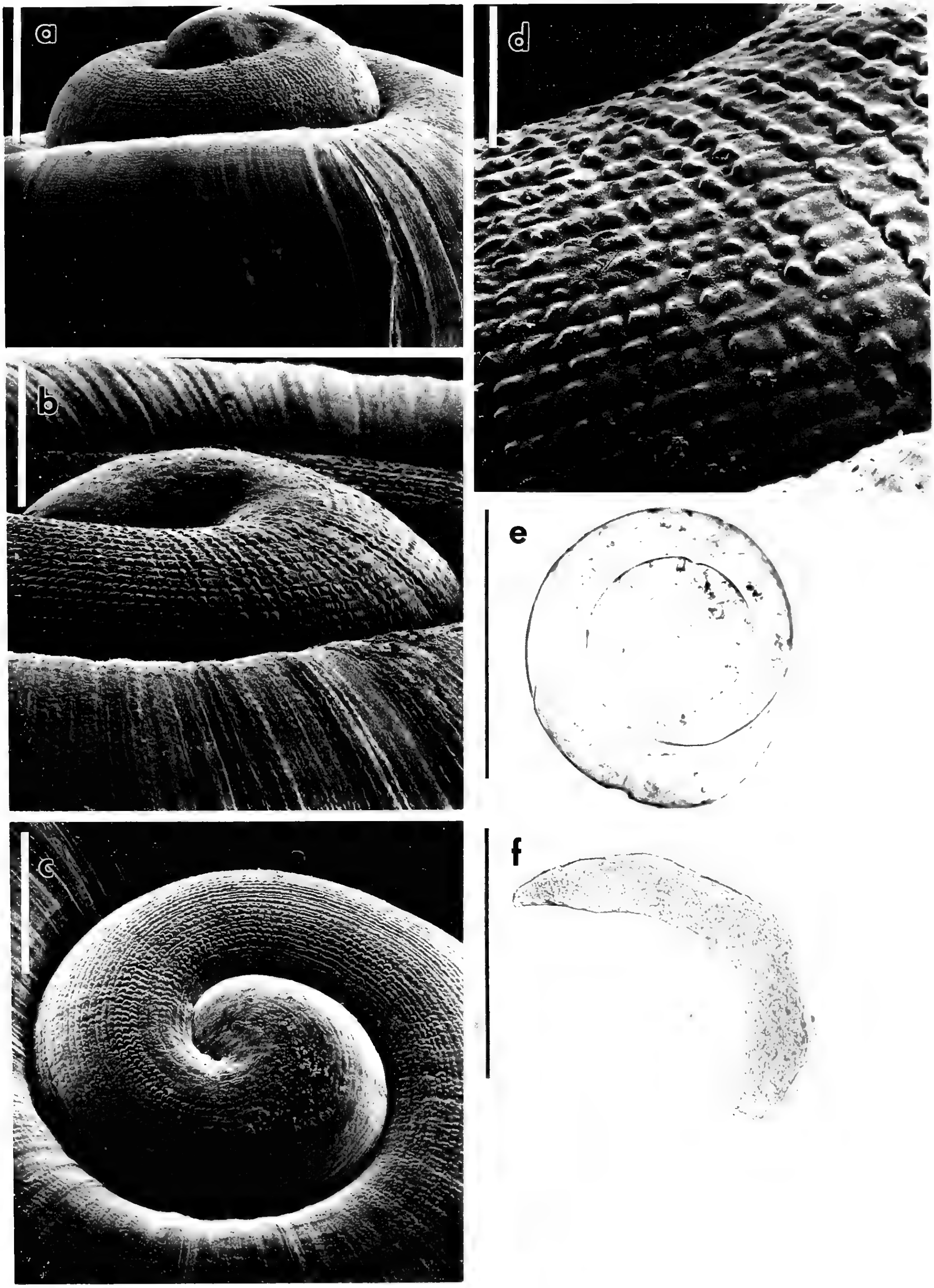


Fig. 3. Shells, operculum, penis of *Antrorbis breweri,* USNM 860430: a–d, SEM micrographs showing shell apex and microsculpture (scale bars = 200 μm, 86 μm, 176 μm, 27 μm); e, operculum (bar = 0.5 mm); f, penis (bar = 0.5 mm).

Fig. 4. Radula of *Antrorbis breweri,* USNM 860431: a, Centrals (scale bar = 6.0 μm); b, Laterals (bar = 3.8 μm); c, Inner marginals (bar = 4.3 μm); d, Outer marginals (bar = 4.3 μm).

ach. Seminal vesicle short, largely anterior to testis; connected just proximal to anterior tip of testis. Prostate gland elongate, largely pallial (ca. 80% of length); anterior vas deferens exits from prostate tip. Penis (Fig. 3f) simple, blade-like, with terminal papilla; specialized penial glands absent.

Ovary a single, unlobed mass (usually wholly posterior to stomach) filling <0.25 whorl, orange in color. Pallial oviduct (Fig. 5a) bipartite, overlapping style sac. Capsule gland (white) slightly smaller than albumen gland (clear). Oviduct (Ovi) with single, small coil on posterior left-lateral surface of albumen gland. Bursa copulatrix (Bu, Fig. 5b) pear-shaped, large, pressed against and partly posterior to albumen gland. Seminal receptacle (Sr) smaller, narrower, posi-

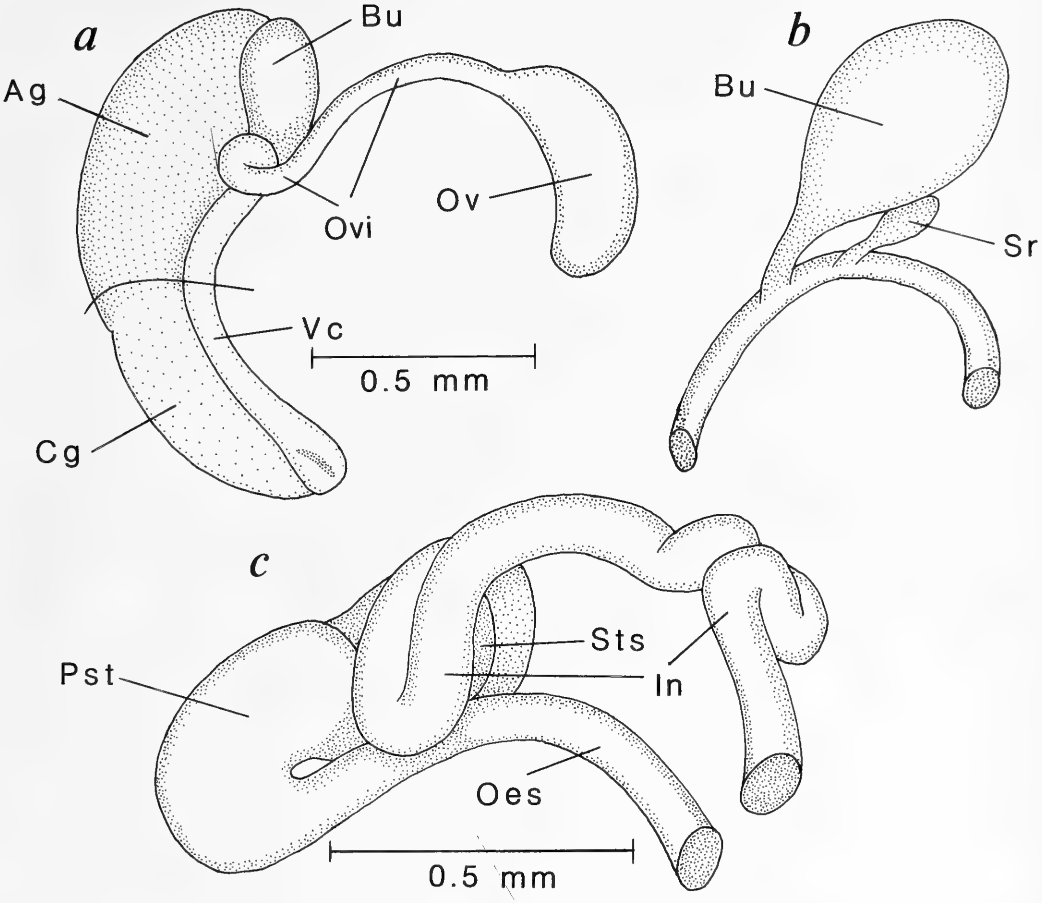


Fig. 5. Morphology of *Antrorbis breweri,* USNM 860431: a, Left lateral aspect of female reproductive system; b, Left lateral aspect of bursa copulatrix and seminal receptable (rotated and slightly enlarged relative to "a"); c, Right lateral aspect of stomach and associated structures. Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; In = intestine; Oes = oesophagus; Ov = ovary; Ovi = oviduct; Pst = posterior stomach; Sr = seminal receptacle; Sts = style sac; Vc = ventral channel of pallial oviduct.

tioned along posterior edge of bursa copulatrix. Ducts of sperm pouches short, entering oviduct just distal to coil. Ventral channel narrow relative to capsule gland width; opening of capsule gland broad, subterminal.

Etymology.—Named after Dr. Stephen Brewer, the current owner of Manitou Cave, in recognition of his cooperation with and interest in this study.

Habitat.—Manitou Cave, formerly a commercial cave, has been closed to the public since 1980. A large opening fitted with a metal door serves as the entrance to the cave on the side of a small hill. On ground level below the door a small (<1 m across), cool stream emerges amongst limestone rubble. *Antrorbis breweri* was absent from the epigean spring, but was collected from the uppermost portion of cave stream. Snails were found at a point where water cascaded from several narrow openings into a shallow (1–2 cm) pool in a small (ca. 4 m^2), cement-lined, rectangular structure (which formerly served as the municipal water source for Fort Payne). Snails were collected (rarely)

Table 1.—Shell measurements (mm) of adults of *Antrorbis breweri*. WH = number of whorls; SH = shell height; SW = shell width; LBW = length of body whorl; WBW = width of body whorl; AL = aperture length; AW = aperture width.

	WH	SH	SW	LBW	WBW	AL	AW
USNM 860429 (holotype)	2.75	0.98	1.53	0.83	1.07	0.68	0.53
USNM 860430 (paratypes)	3.0	0.85	1.69	0.72	1.19	0.62	0.63
	2.75	0.88	1.67	0.77	1.15	0.61	0.61
	2.75	0.80	1.66	0.68	1.17	0.59	0.57
	2.75	0.80	1.79	0.63	1.22	0.62	0.62

from bottoms of loose bricks and natural breakdown littering the pool bottom. Other accessible reaches of cave stream were not searched. Scarcity of the snail also was mentioned by Stein (1976).

Acknowledgments

We thank Dr. Brewer of Fort Payne for permission to collect in Manitou Cave. The assistance of staff of the Scanning Electron Microscopy Laboratory at National Museum of Natural History (NMNH) also is appreciated. Ms. M. Ryan, Department of Invertebrate Zoology, NMNH, drafted the map.

Literature Cited

Burch, J. B. 1982. North American freshwater snails: identification keys, generic synonomy, supplemental notes, glossary, references, index.—Walkerana No. 4:217–365.

Davis, G. M., & M. C. Pons da Silva. 1984. *Potamolithus*: morphology, convergence, and relationships among hydrobioid snails.—Malacologia 25:73–108.

Hershler, R. 1989. *Holsingeria unthanksensis*, a new genus and species of aquatic cavesnail from eastern North America.—Malacological Review 22: 93–100.

———, & G. Longley. 1986. Phreatic hydrobiids (Gastropoda: Prosobranchia) from the Edwards (Balcones Fault Zone) Aquifer Region, south-central Texas.—Malacologia 27:127–172.

Hubricht, L. 1940. A subterranean snail from an artesian well.—Nautilis 54:34–35.

Stein, C. B. 1976. Gastropods. *In* H. Boschung, ed., Endangered and threatened plants and animals of Alabama.—Alabama Museum of Natural History, Bulletin Number 2:21–41.

Thompson, F. G. 1984. North American freshwater snail genera of the hydrobiid subfamily Lithoglyphinae.—Malacologia 25:109–141.

(RH) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (FGT) Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 205–228

A NEW ISIDID OCTOCORAL (ANTHOZOA: GORGONACEA) FROM NEW CALEDONIA, WITH DESCRIPTIONS OF OTHER NEW SPECIES FROM ELSEWHERE IN THE PACIFIC OCEAN

Frederick M. Bayer

Abstract.—The status of the genera *Isidella, Acanella,* and *Lepidisis* in the subfamily Keratoisidinae is discussed and the new species *Isidella trichotoma* and *Acanella dispar* are described and illustrated. New records of *Acanella sibogae* Nutting are presented and description of the species amplified and supported by new illustrations of colony, polyps and sclerites. *Orstomisis crosnieri,* a new genus and species of Keratoisidinae, is described and illustrated. A new key to genera of Isidinae and Keratoisidinae is presented.

Among the gorgonians from New Caledonia obtained by M. Georges Bargibant of ORSTOM, Nouméa, is a large isidid colony superficially resembling a robust *Keratoisis* but branched dichotomously from the nodes rather than laterally from the internodes. The characters usually considered "diagnostic" agree with those attributed to *Isidella,* but its growth form and other features are so divergent that assignment of the specimen to that genus must be considered questionable.

The first specimen of this species was received after a manuscript describing New Caledonian Isididae (Bayer & Stefani 1987a) had been submitted for publication. A description of it was prepared for inclusion in another paper on Isididae (Bayer & Stefani 1987b) but was withdrawn when six more specimens were discovered among numerous isidids in a rich collection of deep-water gorgonians from New Caledonian waters received from the Muséum National d'Histoire Naturelle, Paris. As it is now clear that lack of research funding precludes further study of that collection, the unpublished original description has been revised for publication with supplemental data from the additional specimens and comparative investigation of species of Isididae from elsewhere in the Pacific.

In order to ascertain a taxonomically justifiable position in the family Isididae for this unusual species, it was necessary to survey all the genera of the subfamily Keratoisidinae. These are: *Keratoisis* Wright, 1869; *Isidella* Gray, 1858; *Acanella* Gray in Wright, 1869; *Lepidisis* Verrill, 1883; and, possibly, *Tenuisis* Bayer & Stefani, 1987; the subfamilial affinities of *Australisis* Bayer & Stefani, 1987, remain to be determined and may not lie with the Keratoisidinae. The genera *Keratoisis* and *Tenuisis,* all species of which branch from the internodes, need no further consideration in the present context.

The genus *Isidella* Gray, represented by two nominal species in the North Atlantic and the Mediterranean Sea, shares many morphological features with other genera of the subfamily Keratoisidinae, including *Acanella* Gray, *Lepidisis* Verrill and *Keratoisis* Wright. *Keratoisis* differs by branching from the calcareous internodes, and *Lepidisis* by its unbranched, whiplike, often spiral growth form. *Acanella* differs from *Isidella* chiefly by its bushy colonial form that results from branching in whorls of 3–6 from the horny nodes. Both species of *Isidella* are characterized by flattened, openly flabellate growth form produced by sparse, distant, dichotomous branching from the horny nodes mostly in one plane.

Muzik (1978:737) refers all species of Keratoisidinae branched from the organic nodes to the genus *Isidella* Gray, 1858, thus synonymizing *Acanella* Gray, 1869, and incorporating the branched *Lepidisis longiflora* Verrill, 1883. This treatment is consistent with the comment made by Verrill (1883:18) that *Lepidisis* differs from *Acanella* "only in having the external layer of small scale-like spicula, both in the coenenchyma and on the calicles," as the development of the superficial layer of small scales is inconsistent. Deichmann (1936:242), in commenting about Verrill's type specimen of *L. longiflora,* does not even mention scales, reporting only "a large number of flat, short, blunt rods, especially in the tentacles," but does describe (p. 241) "small, flattened, narrow rods or scales with rounded ends" in both coenenchyme and polyps of *Lepidisis caryophyllia* Verrill, the unbranched type species. Therefore, it seems quite certain that Verrill's "scales" are the small, flat rods observed in the present material.

The polyps of all species of Keratoisidinae have large spindles and/or rods in the body wall, often conspicuously projecting between the bases of the tentacles, and small, more or less flattened and sometimes thorny rods and/or double stars in the pharyngeal walls. In some species of *Keratoisis* there is a superficial layer of small, flattened, scale-like rods in the polyps and coenenchyme, so this character does not reliably distinguish *Lepidisis* from *Keratoisis.*

The quality of retractability of the polyps has long been used as a primary character distinguishing the subfamily Isidinae from the Keratoisidinae and Mopseinae (Studer [& Wright] 1887; Kükenthal 1915, 1919, 1924; Bayer 1956). The polyps of *Keratoisis, Acanella, Isidella,* and *Lepidisis* (Keratoisidinae) form permanently protruding, often prominent, columnar or conical verrucae incapable of retraction into the thin intervening coenenchyme. Although the polyps of *Isis hippuris* can be completely retracted within the thick coenenchyme, leaving only minute pores in the coenenchymal surface, this is accomplished by folding the virtually sclerite-free tentacles inward over the mouth and closing the coenenchymal aperture over them. The polyps of *Chelidonisis,* the other genus comprising the Isidinae (sensu Kükenthal), cannot retract because the coenenchyme is very thin; the body wall, stiffened by numerous sclerites, forms a permanently projecting verruca. In contraction, the tentacles fold inward over the mouth, closing the verrucal aperture with the sclerite-filled bases of the tentacles (see Bayer & Stefani 1987b: fig. 30). In Kükenthal's system, both are treated as retractile, comprising the subfamily Isidinae.

The polyps of *Muricellisis* Kükenthal also are retractile, but are armed with sclerites arranged as a transverse crown (=collaret) and points (=operculum), hence "retractile" in the more restricted sense of withdrawal of anthocodia within anthostele (Bayer et al. 1983:11; Verseveldt & Bayer 1988:8). Because of this difference, Kükenthal (1915) proposed a separate subfamily Muricellisidinae to accommodate this one genus.

When the character of "retractility" is considered in light of the morphology of *Isis, Chelidonisis, Muricellisis,* and *Keratoisis* (+*Acanella, Isidella, Lepidisis*), it is clear that the subfamily Isidinae as so defined is artificial. However, the genera *Isis* and *Chelidonisis* share a different character that sets them apart from all other isidids and may, indeed, justify the subfamily Isidinae. Those two genera alone in the family have sclerites of basically radiate capstan form, with tubercular sculpture. In *Isis* they are 8-radiates, some larger at one end, forming clubs, some elongated to form spindles that may be coarse and pebble-like; in *Chelidonisis* they are typical 6-radiates.

At the risk of redundance in dealing with isidid classification, a revised subdivision of the family is proposed as follows:

Key to the Genera of Isidinae and Keratoisidinae

1(4). Sclerites in the form of 6- and 8-radiates, clubs, and tuberculate spindles .... ISIDINAE

2(3). Coenenchyme thick, polyps not projecting ..... *Isis* Linnaeus

3(2). Coenenchyme thin, polyps projecting as conical verrucae .... *Chelidonisis* Studer

4(13). Sclerites in the form of more or less prickly rods or spindles .... KERATOISIDINAE

5(6). Colonies unbranched .... *Lepidisis* Verrill

6(5). Colonies branched

7(8). Branches originate on internodes .... *Keratoisis* Wright

8(7). Branches originate on nodes

9(10). Polyps forming short, cylindrical verrucae into which tentacles and oral part can be fully retracted; branching dichotomous, internodes short (up to 2 cm but mostly 1 cm or less); colonies multiplanar, flabellate, compressed, trunk forming a massive calcified holdfast .... *Orstomisis,* new genus

10(9). Polyps forming cylindrical, conical or trumpet-shape verrucae, tentacles folding over the mouth but not retractile

11(12). Branching dichotomous, trichotomous, or lateral, predominantly planar, internodes hollow, long or very long (3.5–8 cm) .... *Isidella* Gray

12(11). Branching verticillate, at least in upper parts, colonies densely or openly bushy, internodes solid, shorter, up to 2 cm ... . *Acanella* Gray

13(4). Sclerites in the form of flat plates, sometimes elongate and spindle-like but never with complex tubercular sculpture .... MOPSEINAE. (See Bayer & Stefani, 1987a:51; 1987b: 941.)

Isidella Gray, 1858

Isidella Gray, 1858:283; 1870:14.—Studer [& Wright], 1887:44.—Kükenthal, 1915: 118; 1919:564; 1924:414.—Deichmann, 1936:239.—Bayer, 1956:F222; 1981:941 (in key).—Carpine & Grasshoff, 1975: 107.—Bayer & Stefani, 1987a:51 (in key); 1987b:941 (in key).

Isis.—G. von Koch, 1887:90.

Diagnosis.—Isididae sparsely branched dichotomously or trichotomously from the nodes, usually in one plane, forming spindly colonies often of candelabrum form; internodes long (up to 8 cm), hollow, longitudinally grooved, straight or nearly so; base of main stem forming a lobed, rootlike calcareous holdfast anchored in soft substrate. Polyps non-retractile, cylindrical, armed with stout, faintly prickly needles and/or rods longitudinally placed in body wall; wall of pharynx with abundant small prickly rods.

Type species.—*Isis elongata* Esper (by monotypy).

Remarks.—Gray's original (1858) and subsequent (1870) descriptions of *Isidella* do not provide sufficient detail for adequately defining the genus. Verrill (1883:13) considered the genus doubtful, but Studer [& Wright] (1887:44) accepted it on the basis of Koch's (1887) account of *Isis neapolitana* Koch (=*Isidella elongata* [Esper]) and defined it essentially as diagnosed above. Koch (1887), Verrill (1883), Studer [& Wright] (1887), Nutting (1910), and Bayer

(1956) maintained that the large rods or spindles of the polyps do not project between the bases of the tentacles as they do in *Acanella,* but Kükenthal (1924) stated that the large septally placed spindles can "ein klein wenig zwischen den Tentakeln vorragen," and Carpine & Grasshoff (1975: 108, 109, fig. 59) showed that the spindles may project conspicuously (even though this fact contradicted the generic characteristics stated on page 107).

Three lots of *I. elongata,* among them one from the Zoological Station at Naples, the authenticity of which can hardly be doubted, clearly show the distinctly projecting spindles described and illustrated by Carpine & Grasshoff. A fourth, received from Prof. C. C. Nutting without locality (but possibly from the Zoological Station at Naples, as the polyps were skilfully relaxed before fixation), shows strong, septally placed spindles that do not project between the tentacles—because the tentacles are fixed in more or less extended attitudes. It is difficult to reconcile these observations with Koch's careful illustrations (1887:text-fig. 51; pl. 5, fig. 8), which show polyps of *I. elongata* without such strong needles, so the identity of "*Isis elongata*" seems open to question. Nevertheless, the salient generic features of the genus, i.e., dichotomous branching from the horny nodes, more or less in one plane, with prominent, non-retractile polyps armed with rods and needles, are sufficiently distinctive that validity of the genus *Isidella* is not in question.

Distribution.—Heretofore, the genus *Isidella* has been reported only from the Mediterranean and eastern Atlantic.

Isidella trichotoma, new species

Figs. 1a, 2–4

Material.—Southeast of Hawaii: 18°33.1′N, 155°26.1′W, 6300 feet (=1920 m), coll. J. G. Moore, serial 1723b, 17 Oct 1962. One colony much broken and lacking holdfast, alcohol, USNM 56715 (holotype).

Diagnosis.—*Isidella* with dichotomous and trichotomous branching, internodes long (to 8 cm), hollow, nearly straight. Polyps uniserially placed at wide intervals, cylindrical, short, armed with longitudinally placed needles the largest of which may project slightly between bases of tentacles; pharyngeal walls with small, flat rodlets.

Description.—The colony (Fig. 1a) is sparingly branched from the nodes, trichotomous and dichotomous, the internodes snow white, smooth, not longitudinally ribbed, hollow, nearly straight, long, the longest intact internode 8 cm long and 1.15 mm in diameter about mid-length; an internode broken at one end is 8.5 cm long and only 0.8 mm in diameter. The stoutest internode is 2 mm in diameter. The nodes of the largest branches are about 2 mm long, brown, those of the thinner branches 1 mm or less, yellowish brown.

The polyps (Fig. 2) are uniserially placed, mostly about 8 mm apart, occasionally as close as 5 mm and as far as 10 mm. They stand vertically or obliquely slanted toward the branch tips, cylindrical, mostly about 4–5 mm tall with tentacles folded over the mouth, but a few smaller individuals occur in the spaces between larger ones, indicating that new polyps do not arise exclusively at the branch tips; they are about 3 mm in diameter at mid-height, widening toward the base and sloping into the coenenchyme. Slender, nearly smooth pointed needles (Fig. 3a) about 1.5 mm long are longitudinally arranged in groups of 2 or 3 along the mesenterial insertions, projecting little if at all between the tentacle bases; smaller needles are scattered among and between the mesenterial groups, mostly lying deep in the thick, translucent mesogloea of the polyp body. Converging groups of still smaller needles lie in the bases of the tentacles, becoming more or less longitudinal along the rachis; clusters of small, flat, blunt rods (Fig. 3d) lie longitudinally in the pinnules. The pharyngeal wall contains scattered small, flattened rodlets, with a median waist and

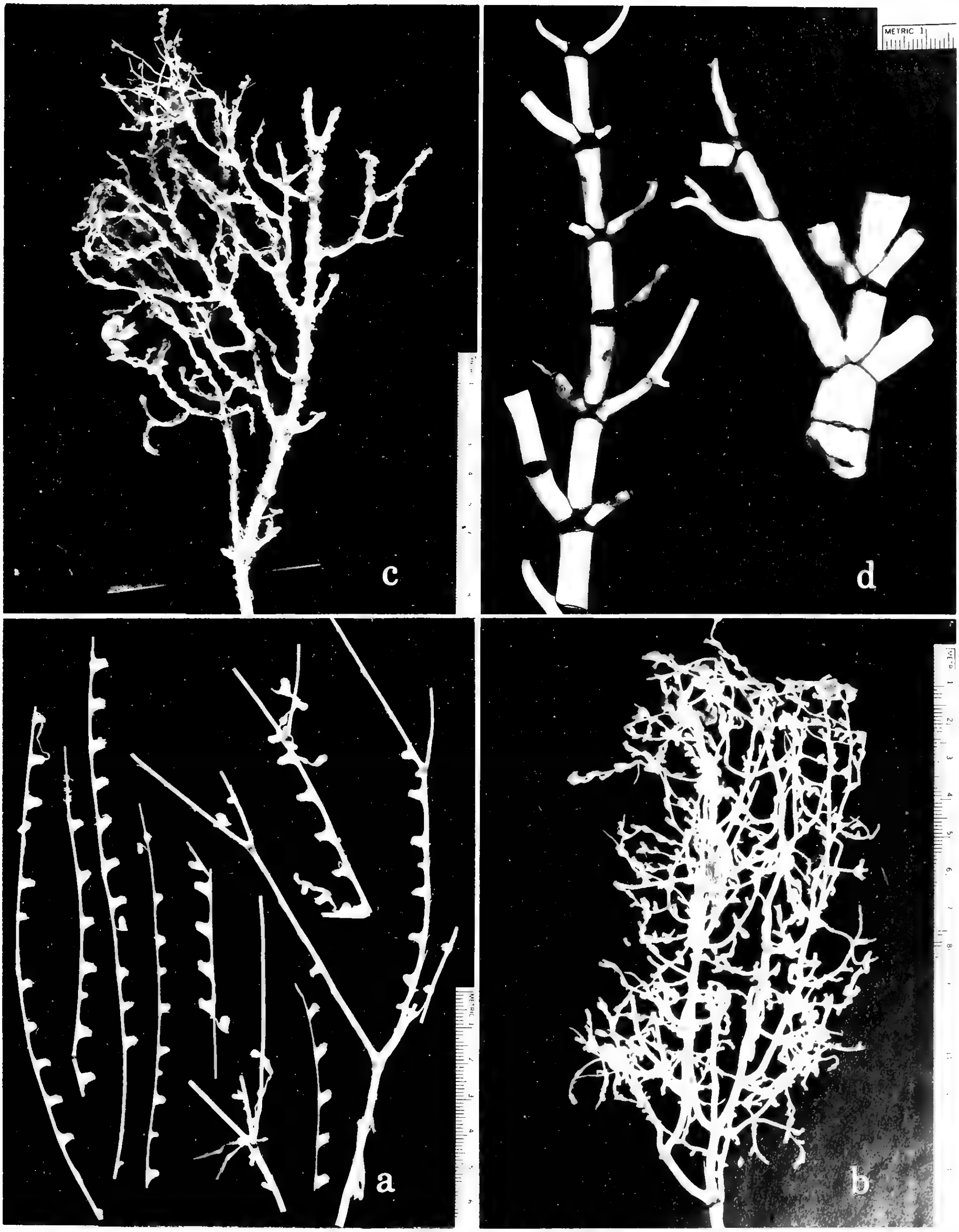


Fig. 1. a, *Isidella trichotoma* USNM 56715: branches. b, *Acanella sibogae* USNM 49969. colony. c, *Acanella dispar* USNM 56816: distal branches. d, *A. dispar* USNM 56816: axis.

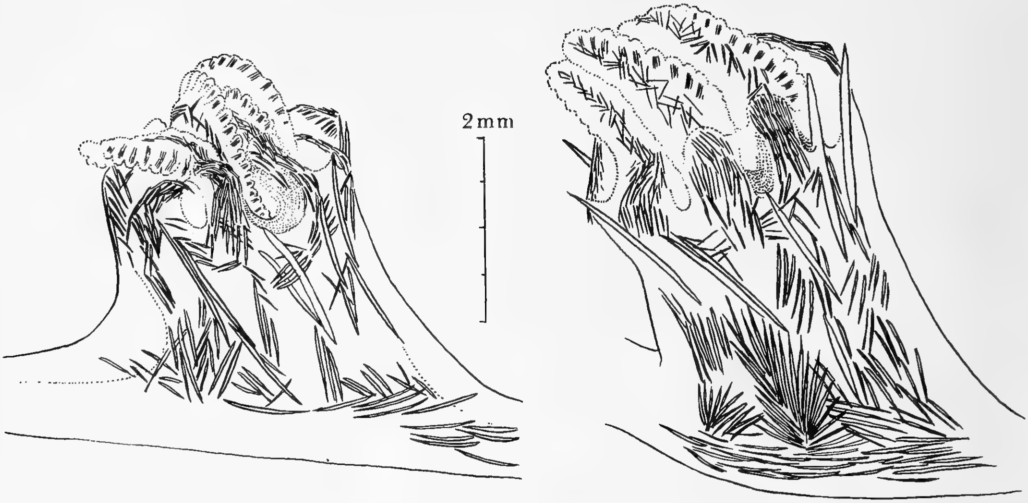


Fig. 2. *Isidella trichotoma* USNM 56715: polyps.

tapered to blunt ends, mostly 0.11 mm in length, with a few straight-sided flat rods up to 0.15 mm in length (Fig. 3d).

The extremely thin coenenchyme contains slender, delicate needles (Fig. 3b, c) up to 4 mm in length and 0.05 mm in diameter lying longitudinally along the axis. They are straight or slightly curved, not entirely uniform in diameter, and ornamented with scattered, low granules. There is clear evidence that their length is achieved by fusion of adjacent sclerites (Figs. 3c, 4).

The nature of the holdfast is unknown but, considering the shape of the colony and the depth of the habitat, it most likely was a lobate, rootlike structure similar to that of other species of *Isidella.*

Etymology.—From Greek *tricha* = in three parts + *tomos* = a cutting, in allusion to the manner of branching.

Remarks.—Even though the branching of this species is trichotomous in some cases and thus not uniplanar, it is not verticillate in the manner of *Acanella.* The very long, slender, nearly straight, hollow internodes and widely separated ramifications result in a spindly, openly branched colony of gross aspect closer to *Isidella* than to *Acanella* with its short, solid, more or less conspicuously curved internodes.

Acanella Gray, 1870

Acanella Gray, 1870:16.—Studer [& Wright], 1887:44.—Nutting, 1910:14.—Kükenthal, 1919:573; 1924:414.—Deichmann, 1936:243.—Bayer, 1956:F222; 1981:941 (in key).—Bayer & Stefani, 1987a:51 (in key); 1987b:941 (in key).
Isidella.—Muzik, 1978:737 (part).

Diagnosis.—Keratoisidinae branched in whorls from nodes, at least in upper parts of colonies, forming bush-like colonies of moderate size (rarely more than 20 cm) when anchored in soft substrate by lobate holdfast, larger and compressed (possibly to 1 m in height) when attached to hard bottom; internodes solid, short (to 2 cm). Polyps nonretractile, cylindrical, armed with sparsely prickly needles and/or rods longitudinally or obliquely placed in body wall; pharyngeal wall with small thorny stars or short rods.

Remarks.—The consolidation of *Isidella* and *Acanella* as a single genus of Keratoisidinae with branching originating at the nodes, as proposed by Muzik (1978) has practical advantages. However, the verticillate branching of *Acanella* is so distinctive that it seems preferable to retain it pending a thorough review of all species involved.

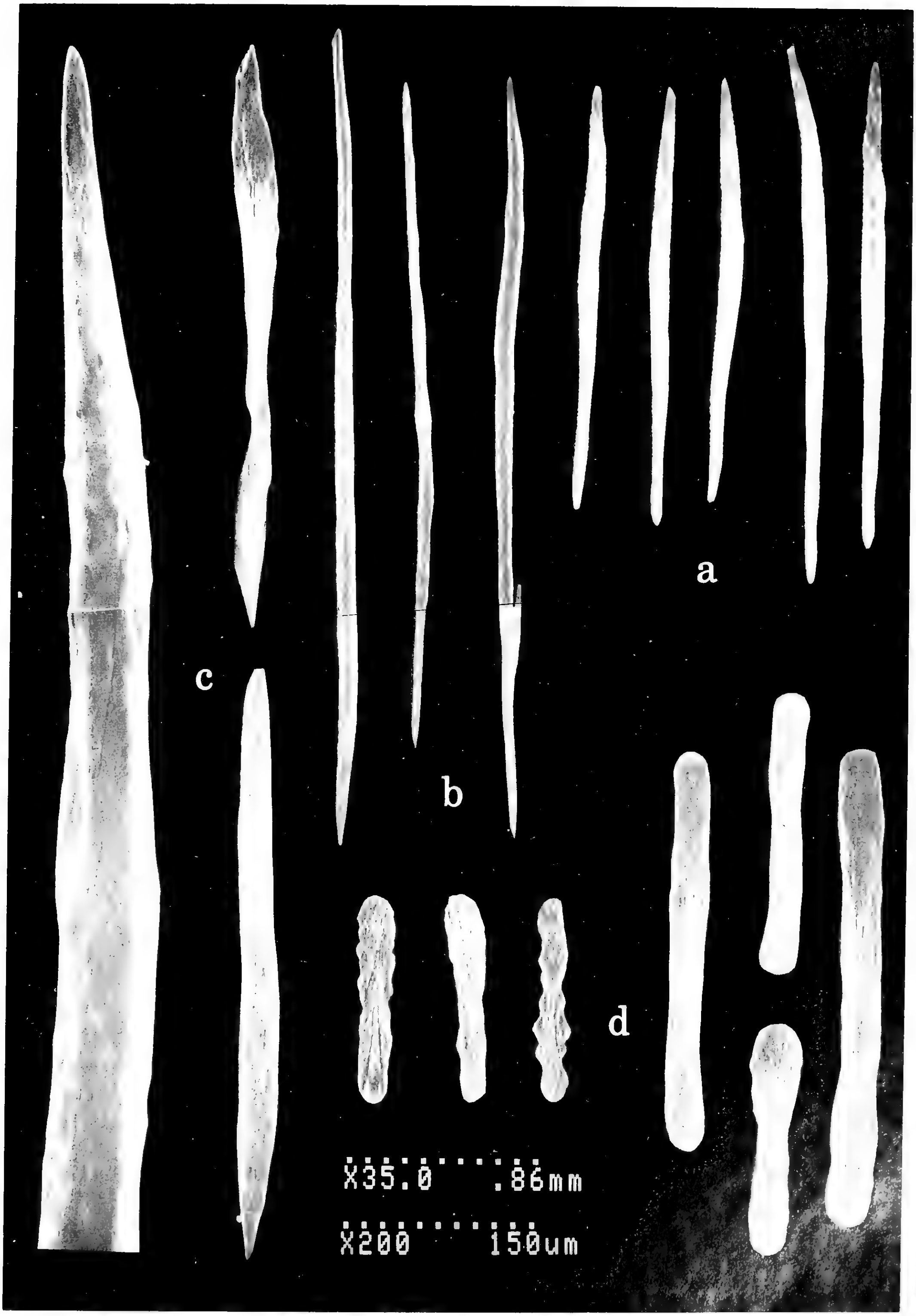


Fig. 3. *Isidella trichotoma* USNM 56715, sclerites: a, Body wall. b, c, Coenenchyme. d, Tentacles, pinnules, and pharynx. a, b, 0.86 μm scale; c–d, 150 μm scale.

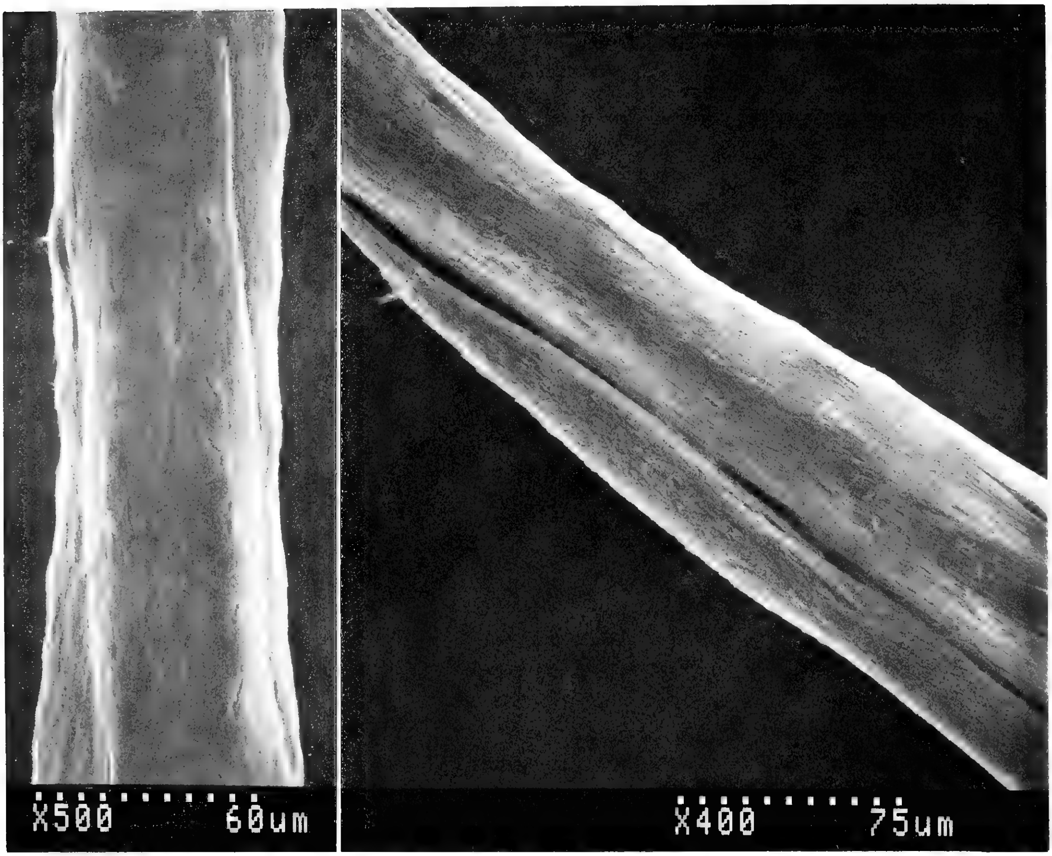


Fig. 4. *Isidella trichotoma* USNM 56715: Large coenenchymal needle produced by fusion of smaller sclerites.

Acanella sibogae Nutting, 1910
Figs. 1b, 5

?*Acanella rigida* Wright & Studer, 1889:31, pl. 9, fig. 4.—Thomson & Henderson, 1906:33.

?*Acanella robusta* Thomson & Henderson, 1906:33.

Acanella sibogae Nutting, 1910:14, pl. 3, fig. 2, 2a, pl. 5, fig. 4.—Kükenthal, 1919:575; 1924:419.

?*Acanella japonica* Kükenthal, 1915:120; 1919:582, pl. 44, fig. 76.

Material.—Japan, off Mizimoko-shima Light: 32°36′N, 132°23′E, 437 fathoms (=799 m), bottom greenish brown mud, fine grey sand and foraminifers, USFC steamer *Albatross* sta. D-4957, 23 Aug 1906. One large colony with holdfast, alcohol, USNM 49792.

Japan: off Shio Misaki Light: 33°25′20″N, 135°36′20″E, 244–290 fathoms (=446–530 m), bottom brown mud, sand and foraminifers, USFC steamer *Albatross* sta. D-4966, 29 Aug 1906. Two damaged colonies with holdfasts, alcohol, USNM 49619.

Japan: off Shio Misaki Light: 33°23′40″N, 135°33′E, 587 fathoms (=1074 m), bottom brown mud, sand and stones, USFC steamer *Albatross* sta. D-4969, 27 Aug 1906. Damaged branch, in alcohol, USNM 49468.

Japan: off Shio Misaki Light: 33°23′30″N, 135°34′E, 649 fathoms (=1187 m), bottom brownish green mud and foraminifers,

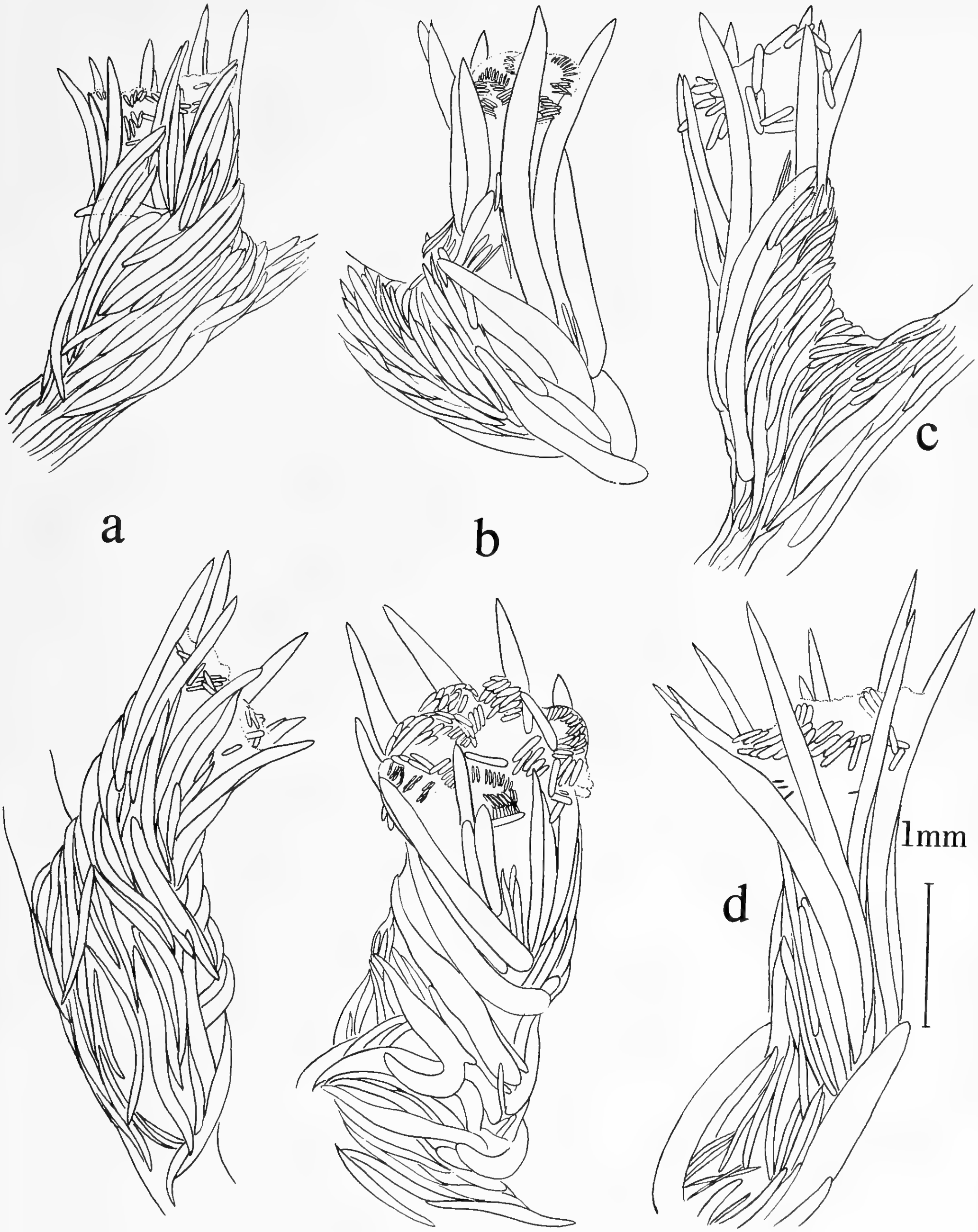


Fig. 5. *Acanella sibogae,* polyps: a, USNM 49917. b, 49969. c, 49619. d, 49468.

USFC steamer *Albatross* sta. D-4971, 30 Aug 1906. Two colonies, one with holdfast, in alcohol, USNM 49466.

Philippines: east coast of Luzon, off Batag I.: 12°44′42″N, 124°59′50″E, 383 fathoms (=700 m), green mud and sand, USFC steamer *Albatross* sta. D-5445, 3 Jun 1909. One colony with holdfast, in alcohol, USNM 50156.

Philippines: off Balicasag I. between Siquijor and Bohol Is.: 9°22′30″N, 123°42′40″E, 392 fathoms (=717 m), bottom globigerina ooze, USFC steamer *Albatross* sta. D-5527, 11 Aug 1909. Seven specimens more or less complete with holdfast, 3 lacking holdfast, and several fragmentary colonies, in alcohol, USNM 49917.

Molucca Passage, off Mareh I.: 0°37′00″N, 127°15′00″E, 417 fathoms (=763 m), bottom grey mud, USFC steamer *Albatross* sta. D-5618, 27 Nov 1909. Two colonies with holdfast, one nearly complete, alcohol, USNM 49896; 2 colonies, one with holdfast, alcohol, USNM 50147.

Buton Strait, off North I.: 5°35′00″S, 122°20′00″E, 559 fathoms (=1022 m), bottom green mud, USFC steamer *Albatross* sta. D-5648, 16 Dec 1909. Two colonies, alcohol, USNM 49969.

Indonesia: Flores Sea: 5°36′30″S, 120°49′00″E, 692 fathoms (=1266 m), grey mud and sand, bottom temperature 39.2°F, USFC steamer *Albatross* sta. D-5660, 20 Dec 1909. One verticillate branch, in alcohol, USNM 49959.

Diagnosis.—*Acanella* with tall, vertically or obliquely placed polyps armed with several very large spindles longitudinally or diagonally placed in the body wall, and projecting conspicuously as 8 strong points around the folded tentacles. Holdfast a lobed, rootlike structure; secondary branching commonly in whorls of 2.

Remarks.—Several colonies taken by the USFC steamer *Albatross* agree in all essential features with the original description of an incomplete colony obtained by the *Siboga* Expedition north of Ceram (2°40′S, 128°37.5′E, 835 m) (Nutting 1910:14) and provide data to supplement the description of the species.

One fully developed colony from Buton Strait southeast of Celebes (USNM 49969), lacking its basal holdfast, is about 15 cm tall (Fig. 1b); an immature specimen from the same station is 6 cm tall including the rootlike holdfast. Other specimens from Japan (USNM 49466, 48468, 49619, 49792), the Philippines (USNM 49917, 50156), Flores Sea (USNM 49959), and Molucca Strait (USNM 50147) are in close agreement in colonial form, and size and armature of polyps.

The type specimen (Nutting 1910:pl. 3, fig. 2, 2a), evidently a branch from a larger colony, branched in pairs from the nodes but two pairs showed evidence of a third branch. Whereas the present specimens show a tendency to branch in pairs (i.e., "whorls" of 2), whorls of 3 and 4 are common and some nodes produce as many as 6 branches in a whorl. The internodes are solid, white, smooth but weakly ribbed longitudinally, those of the principal branches 13–17 mm long, of the small side branches about 10 mm. The nodes are reddish brown, short, 1.5 mm to less than 1 mm in length. A few anastomoses between branches are present, as well as branchlets originating from internodes.

Although Nutting (1910:15) described the polyps as mostly columnar and vertically placed on the branches, his photographs of the type branch and a twig with 3 polyps clearly show that they tend to slant distad toward the twig tips. The same condition prevails in the present specimens, on which vertically placed polyps certainly occur, but oblique ones predominate.

The polyps (Fig. 5) generally conform in size with the dimensions given by Nutting, and show the "crown of eight well-marked points around the margin, each point consisting of the distal end of a single spicule"

(Nutting 1910:15). Several large, more or less obliquely placed, curved spindles about 3 mm long surround the body of the polyps, projecting between the bases of the tentacles to produce the crown.

Comparisons.—The polyps of *Acanella verticillata* Kükenthal, 1915, from off Siberut Island have strongly projecting marginal spines but are smaller (2 mm tall) than in the *Siboga* specimen and those reported here (4–5 mm). Moreover, according to Kükenthal's description and illustration (1919: 584, fig. 258), a layer of obliquely placed, curved spindles covers the proximal part of the vertically placed projecting spindles. The large number of branches in the whorls described for *verticillata* is present, if not common, also in some of the specimens of *sibogae* now reported.

Without a reexamination of type material, it is impossible to determine with certainty whether or not *Acanella rigida* Wright & Studer from off Banda, *A. robusta* Thomson & Henderson, 1906, from the Andaman Islands, and *A. verticillata* Kükenthal, 1915, from off Siberut Island west of Sumatra are identical with *sibogae,* but all characters mentioned in the original descriptions are consistent with that interpretation.

Distribution.—Japan south and west to the Philippines and Indonesia, 446–1266 m.

Acanella dispar, new species

Figs. 1c, d, 6–8

?*Lepidisis longiflora.*—Nutting, 1908:572.
Not *Lepidisis longiflora* Verrill, 1883:19.

Material.—Hawaiian Islands, off Makapuu: 21°18′N, 157°32′W, 1200 feet (=366 m), *Star II* submersible, dive 2, 1 Feb 1978, K. Muzik, coll. One large colony now much broken, of which 3 branches are preserved in alcohol, the main trunk and large branches as well as the greater part of the secondary branches dry, USNM 56816, holotype.

Hawaiian Islands, off Kaena Point: 21°35.85′N, 158°24.55′W, 275–445 m, "Sango XII" Haul 1, 27 Jul 1971, R. Grigg, coll. Damaged branches, identification uncertain, USNM 56719.

Hawaiian Islands, off French Frigate Shoal: 23°53.1′N, 165°31.9′W, 326–363 m, "Sango XIV" Haul 2, 27 Aug 1971, R. Grigg, coll. Damaged branches, identification uncertain, USNM 56726.

Hawaiian Islands, off NW coast of Oahu: Kahuku Point N. 79°, E. 10.1′, 216–251 fathoms (=395–459 m), USFC steamer *Albatross* sta. D-4121, 25 Jul 1902. Fragments, identification uncertain; reported as *Lepidisis longiflora* by Nutting (1908), USNM 25358.

Diagnosis.—*Acanella* with principal branching commonly in whorls of 2, roughly planar, secondary branching in whorls of 3 or more, bushy. Polyps with longitudinally placed needles of body wall developed asymmetrically, those of abaxial side stronger and more or less projecting between bases of tentacles; pharyngeal walls with thorny stars.

Description.—The intact colony was large, probably 1 m or more in height, in the shape of a profusely branched, strongly compressed bush. Branching arises from the nodes predominantly in one plane, singly and in opposite pairs, i.e., whorls of 2; branching becomes verticillate at several places in the colony resulting in branches of typical *Acanella* aspect; here the nodes may give rise to 3 or more branchlets as well as 1 or 2, and in some places are abnormally overgrown by internodal material, possibly induced by the presence of a small actinian.

The internodes of the principal branches are solid, cylindrical, slightly expanded at each end, weakly ribbed longitudinally, 15–20 mm long and up to 15 mm in diameter; all the subordinate branches bend upward so their proximal internodes are slightly curved. The distalmost internodes, straight or nearly so, are up to 20 mm in length but only 0.5–0.7 mm in diameter. The holdfast proper is not preserved, but the proximal

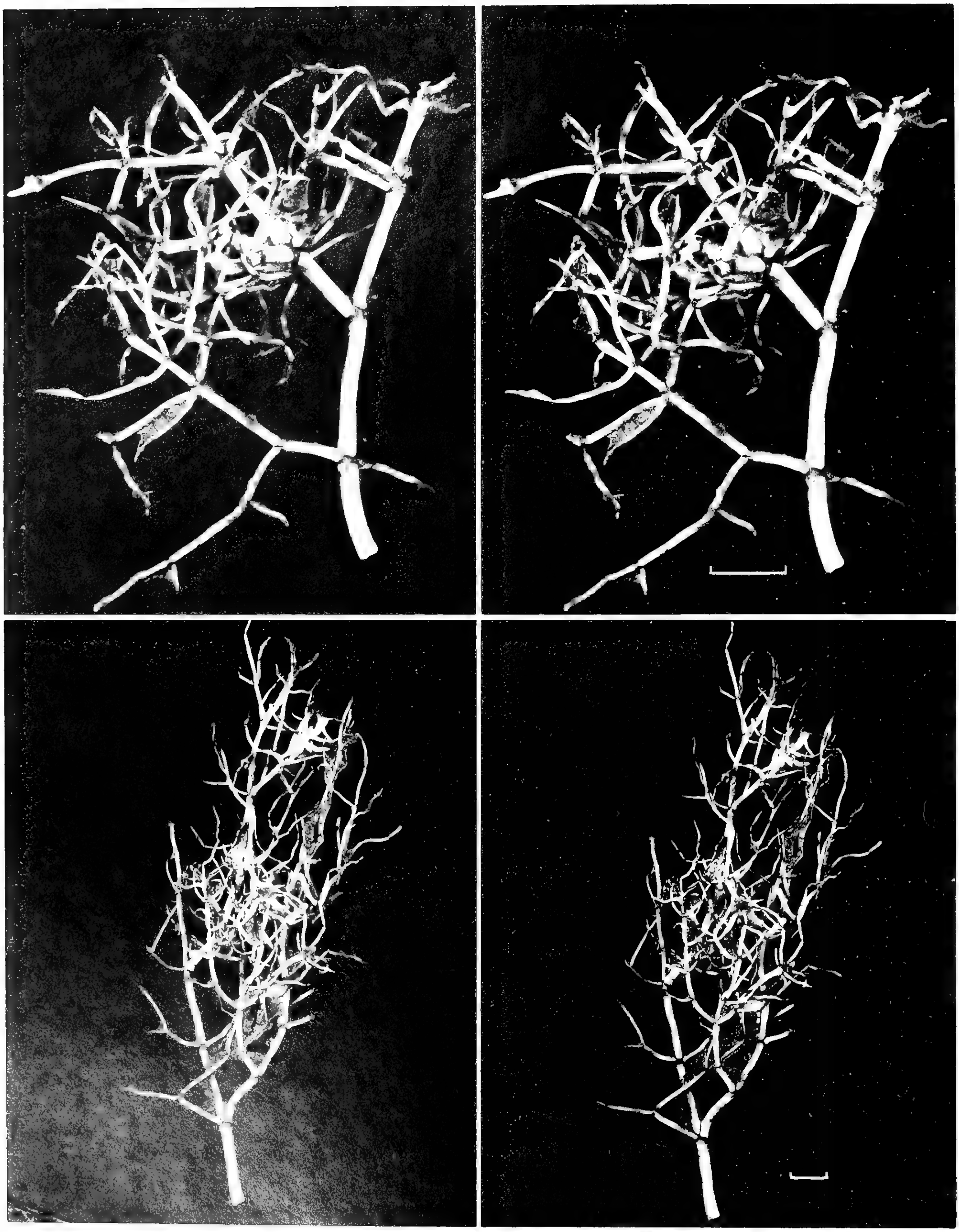


Fig. 6. *Acanella dispar* USNM 56816: Distal branches with twigs in whorls. Stereoscopic pairs. Scale bars = 1 cm.

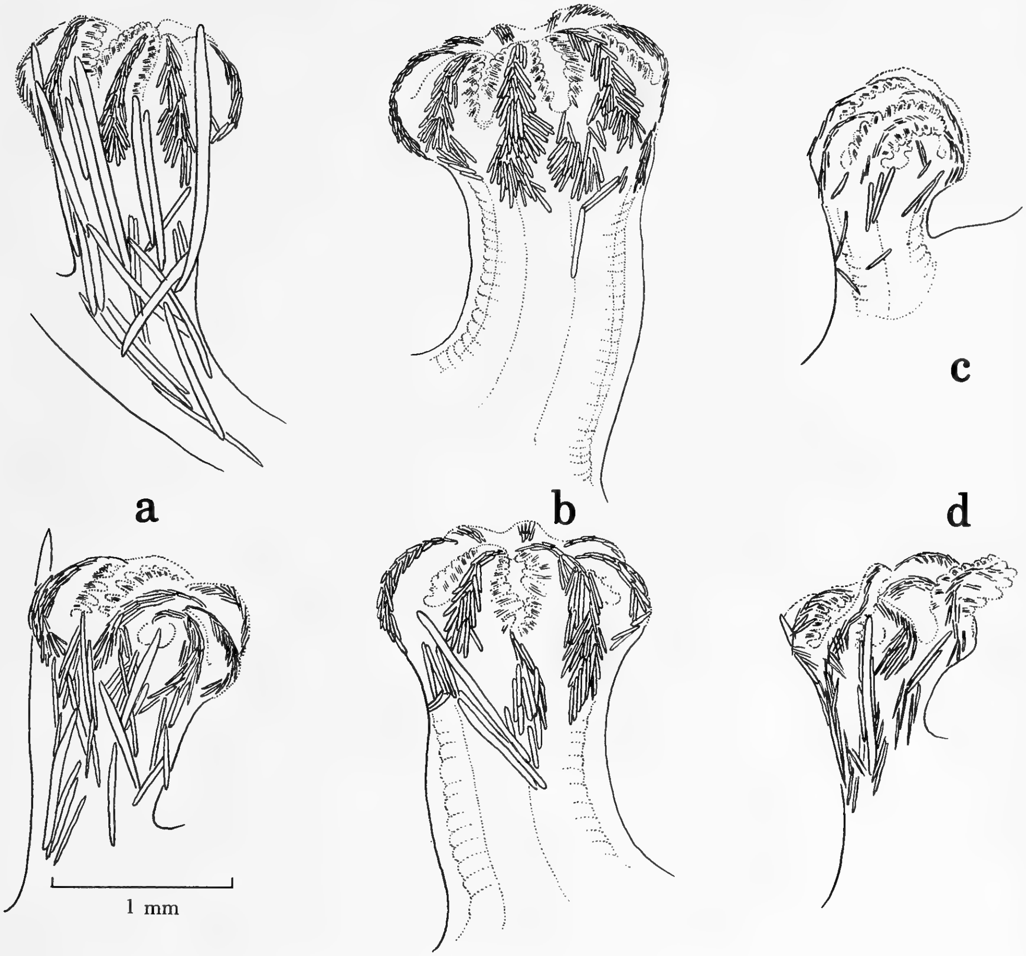
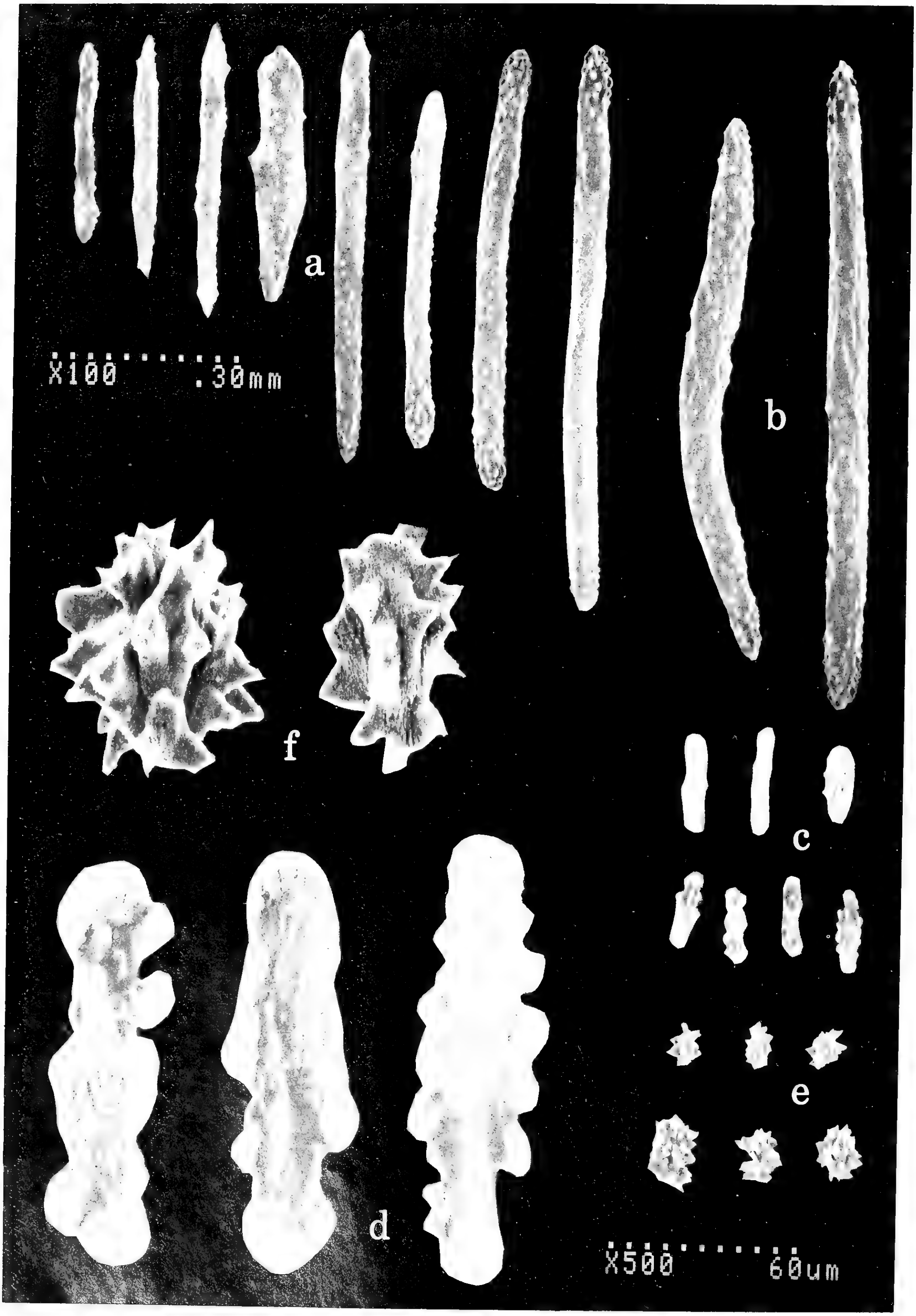


Fig. 7. *Acanella dispar,* polyps: a, b, USNM 56816. c, 56719. d, 56726.

10 cm of the main trunk is thickened by irregular massive deposits of internodal material that obscure many of the nodes and form a strong basal support about 2 cm in diameter.

The polyps are closely crowded on the smaller branches and twigs, concentrated on the two sides in the plane of branching but not in a strict biserial arrangement; on the major branches they are more distantly placed, commonly 4 mm apart or even more. They are cylindrical, weakly curved and directed more or less distally, somewhat wider apically across the bases of the infolded tentacles, about 2.25 mm tall and 1 mm in diameter, 1.5 mm across the bases of the tentacles.

Spiculation of the polyps varies with respect to size and number but the arrangement is generally consistent. Clusters of small needles lie along the mesenterial insertions, converging toward the margin of the tentacular crown (Fig. 8a); a few of the needles in one or more rows, sometimes only on the abaxial side, sometimes all around, are much larger than the rest (Fig. 8b). These project little, if at all, in some polyps, but in others one or more needles


a
X100 .30mm
b
f
c
e
d
X500 60um

may project conspicuously. Interseptal groups of small needles converge toward the base of each tentacle, extending upward along the rachis more or less longitudinally or obliquely; groups of much smaller rodlets extend into the pinnules (Fig. 8c, d). The walls of the pharynx contain numerous thorny [6-radiate?] stars (Fig. 8e, f), mostly about 0.06 mm long, but a few may reach 0.12 mm. The large needles of the polyps are about 1 mm long, the smaller ones about 0.5 mm.

The internodes are snow white, the distal nodes brown, the proximal ones nearly black; in the alcoholic material the polyps are light brown to dark brown, depending upon conditions of preservation; upon drying the soft tissue becomes dark brown, almost black.

Etymology.—Latin *dispar* = different.

Comparisons.—This is the only species of *Acanella* known so far that inhabits hard bottom and develops a stout trunk. It is also unique in its planar primary branching that in the smaller branches becomes bushy, forming a flattened colony with side branches of typical *Acanella* aspect. Its polyps are smaller and less strongly armed than in any species heretofore recorded. This combination of characters may eventually require generic reallocation of *A. dispar.*

Remarks.—It is probable, but not certain, that the fragments from Hawaii reported by Nutting (1908) as the western Atlantic *Lepidisis longiflora* Verrill are this species.

Orstomisis, new genus

Diagnosis.—Isididae dichotomously branched from the nodes, predominantly in one plane, forming compressed, multiplanar flabellate colonies; internodes solid, short (up to 10 mm), often strongly curved, not longitudinally grooved; base of main stem developed as a massive calcareous trunk attached to solid substrate. Polyps forming prominent, cylindrical verrucae invested by thick, skinlike epithelium into which tentacles can be retracted completely; calycular rods not projecting beyond the bases of the infolded tentacles; walls of pharynx with small, sparsely tuberculate rodlets.

Type species.—*Orstomisis crosnieri,* new species, here designated.

Etymology.—From the acronym "ORSTOM" for Office de la Recherche Scientifique et Technique Outre-Mer, now known as the Institut Français de Recherche pour le Développement en Coopération, the agency responsible for collection of the material here described.

Orstomisis crosnieri, new species
Figs. 9–14

Material examined.—South of New Caledonia: 22°59.5′S, 167°22′E, 542 m; N/O *Vauban,* ORSTOM, Georges Bargibant coll., 7 Feb 1986. HGP-49. One damaged, incomplete colony, USNM 78372 (syntype).

South of New Caledonia: 22°59′5S, 167°22′0E, 490–515 m, N/O *Vauban* sta. CP-216, 29 Sep 1985. Two colonies, MNHN Paris (syntypes).

Southeast of New Caledonia: 23°05′792S, 167°46′544E, 600 m, N/O *Jean Charcot,* ORSTOM, sta. CP-52, 31 Aug 1985. Two colonies MNHN Paris (syntypes), one USNM 84774 (syntype).

Loyalty Islands: 20°35′078S, 166°53′990E, 460 m, N/O *Jean Charcot* sta. DW-83, 6 Sep 1985. One colony MNHN Paris (syntype).

Diagnosis.—As for the genus.

Description.—The colonies (Figs. 9, 10a) are 20–45 cm in height, mostly not as wide as high but in two cases approximately so.

←

Fig. 8. *Acanella dispar* USNM 56816, sclerites: a, Small needles of body wall. b, Large needles of body wall. c, d, Flat rodlets from pinnules. e, f, Thorny stars from pharynx. a–c, e, 0.3 mm scale; d, f, 60 μm scale.

The main stem of all specimens forms a massive calcareous trunk (Fig. 10a), broken from the substrate so the holdfast proper is unknown. In the lower parts of the trunk, the thickening internodes grow over the nodes, ultimately obliterating all external evidence of their presence. Several primary branches arise from the main stem, subsequently branching from the nodes mostly in one plane from which the terminal twigs irregularly diverge; the resulting colonies consist of several roughly parallel planes forming a compressed, complex, multiplanar flabellum. Branching typically is dichotomous, two branches arising from a node at 90°–180°; the widely diverging branches usually curve upward producing conspicuously lyre-shaped bifucations (Fig. 10b).

The distal and intermediate internodes (Fig. 10c) are round in cross-section, not longitudinally grooved, the surface weakly granular and crowded with desmocyte pits clearly visible by SEM at low magnification; at higher power, vestiges of pits in various stages of infilling are abundant along with sharply defined pits where the desmocytes presumably were still functional at the time of collection (Fig. 10d). At the apex of the distalmost internodes the tubercles are more prominent and closely interspersed with desmocyte pits (Fig. 14). The thinnest internodes are only 0.5 mm in diameter. The lowermost internodes before the onset of secondary thickening are nearly straight, about 1 cm in diameter and 13–18 mm long, gradually decreasing in thickness distad where the narrower internodes are about 1 mm in diameter and 7–10 mm long.

On the larger branches, the nodes are very short, appearing as a dark brown line about 1 mm wide; those of the smaller branches may be up to 2.5 mm long. Although successive nodes may bifurcate, more commonly branches are separated by 2–4 unbranched internodes, i.e., they arise from every 3rd to 5th node. In some cases, three branches arise from a single node, one continuing the direction of the preceding internode, the others diverging to each side at about 90°; where three successive nodes produce two lateral and one axial branch a "pinnate" arrangement results. Rarely one node produces more than three branches, but this does not occur regularly to produce a bushy colony as in *Acanella.*

The polyps are cylindrical, about 0.9–1.3 mm in diameter and 1.5–2.0 mm tall, depending upon the degree of contraction (Fig. 11b). In contraction the tentacles are folded over the mouth and are withdrawn into the verrucal aperture. The verrucal margin may be closed more or less completely over the retracted tentacles. When undamaged, the verrucae are covered by a smooth, thick epithelium through which rodlike sclerites can be seen faintly or not at all. They have eight more or less distinct longitudinal furrows that distally divide the verrucal margin into low, rounded lobes. The smooth epithelium also covers the coenenchyme, in some places with faint longitudinal grooves following the course of the stem canals. Terminal branchlets may have two polyps opposed at the apex and the older polyps may be arranged approximately in pairs, but they become more or less widely separated by unequal growth of intervening coenenchyme on the more proximal internodes, where they are scattered on all sides. Cylindrical rods (Figs. 12a, 13a) reaching about 1 mm in length and 0.1 mm in diameter are placed longitudinally or diagonally in the verrucal wall, with smaller rods interspersed among them. The rachis of the tentacles contains smaller rods, decreasing in size in the pinnules (Figs. 12b, 13b). Twinned rods in the shape of crosses are not uncommon (Figs. 12a, 13a). The pharyngeal wall contains small, sparsely knobby or thorny rodlets of basically 8-radiate form (Fig. 12c).

The coenenchyme between the polyps is practically devoid of sclerites, although a few somewhat flattened rods occur widely

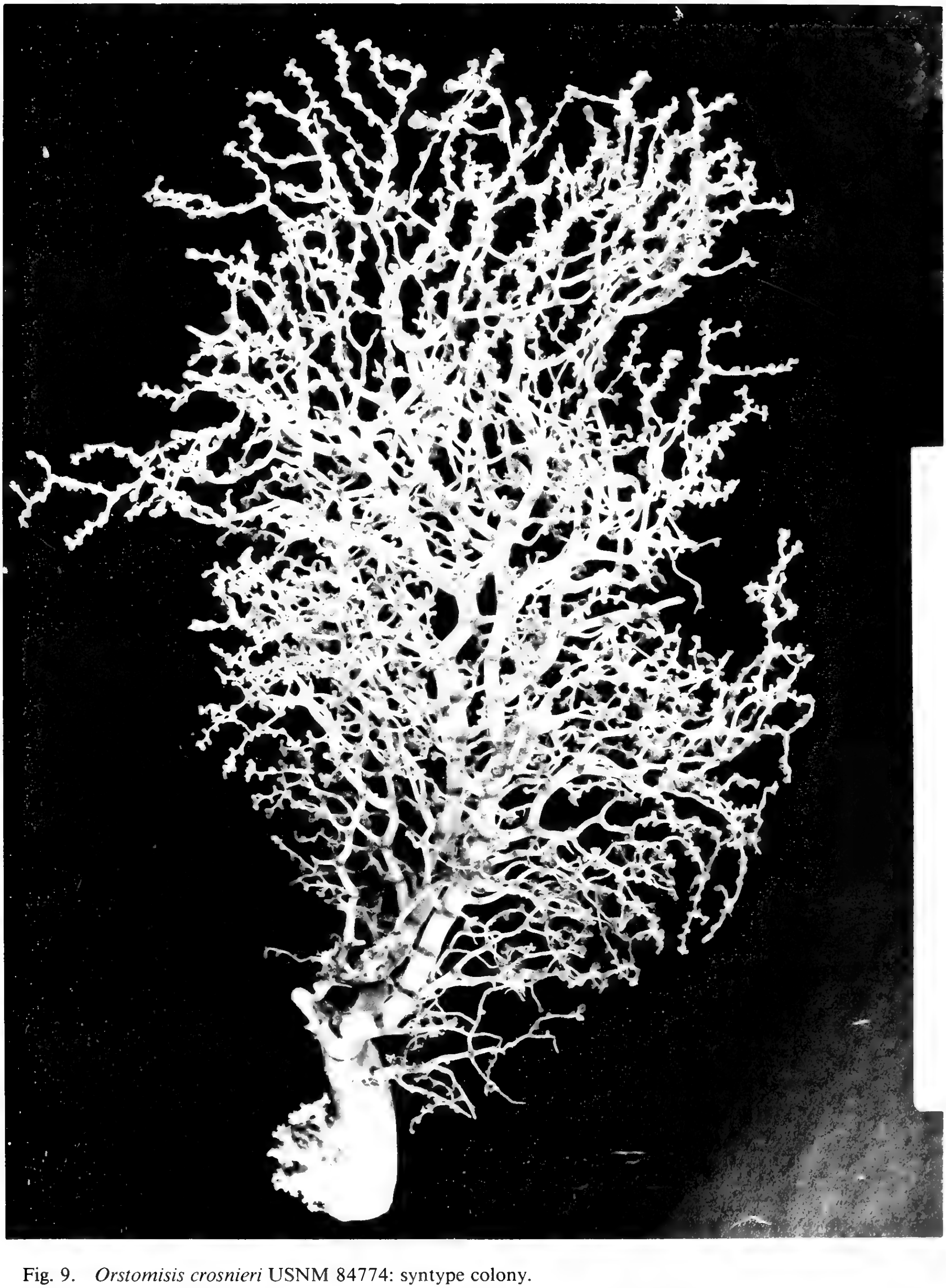


Fig. 9. *Orstomisis crosnieri* USNM 84774: syntype colony.

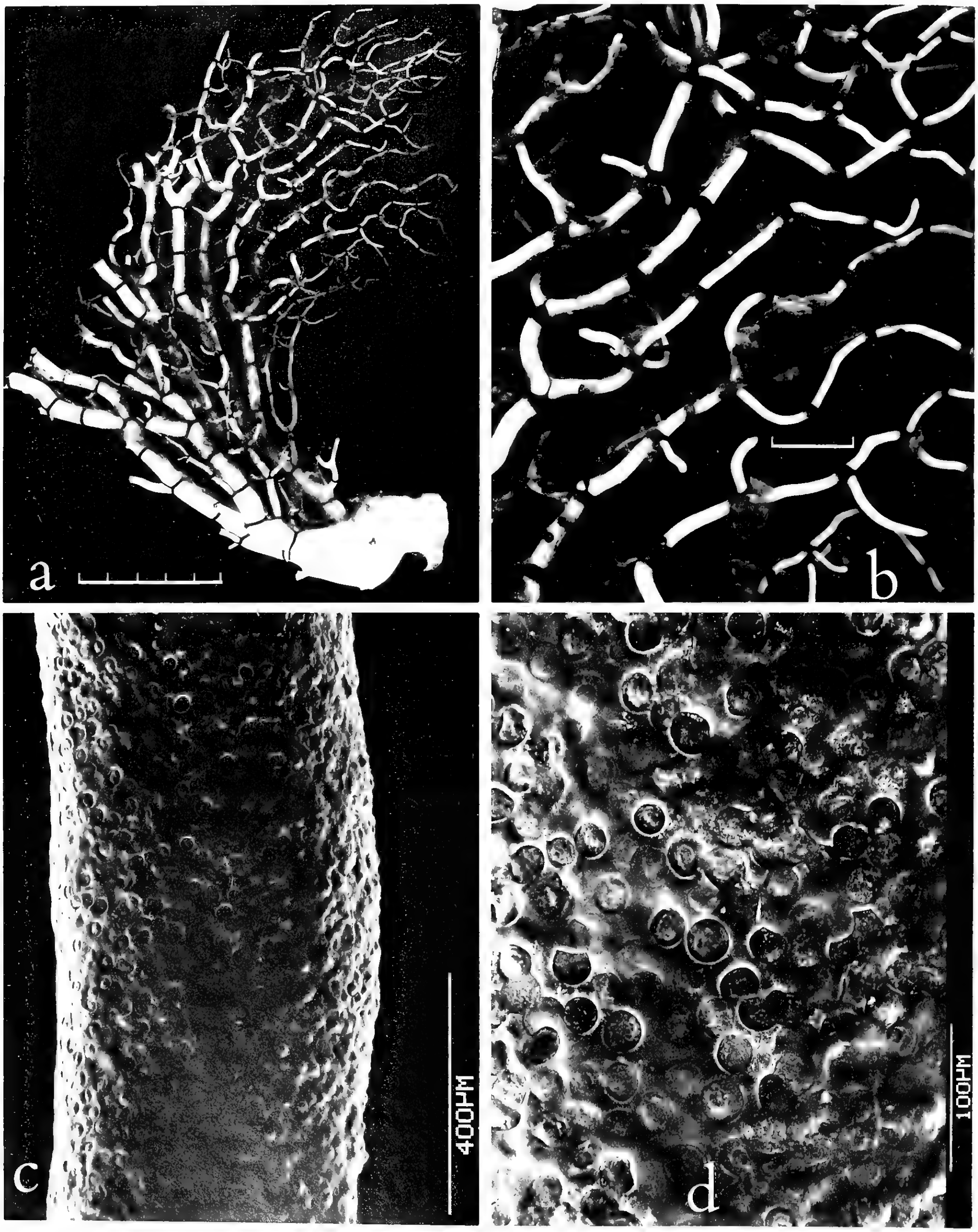


Fig. 10. *Orstomisis crosnieri* USNM 78372: a, Colony severely decorticated. b, Detail of branches. c, Part of axial internode. d, Surface of axial internode. Scale at a = 5 cm; b = 1 cm.

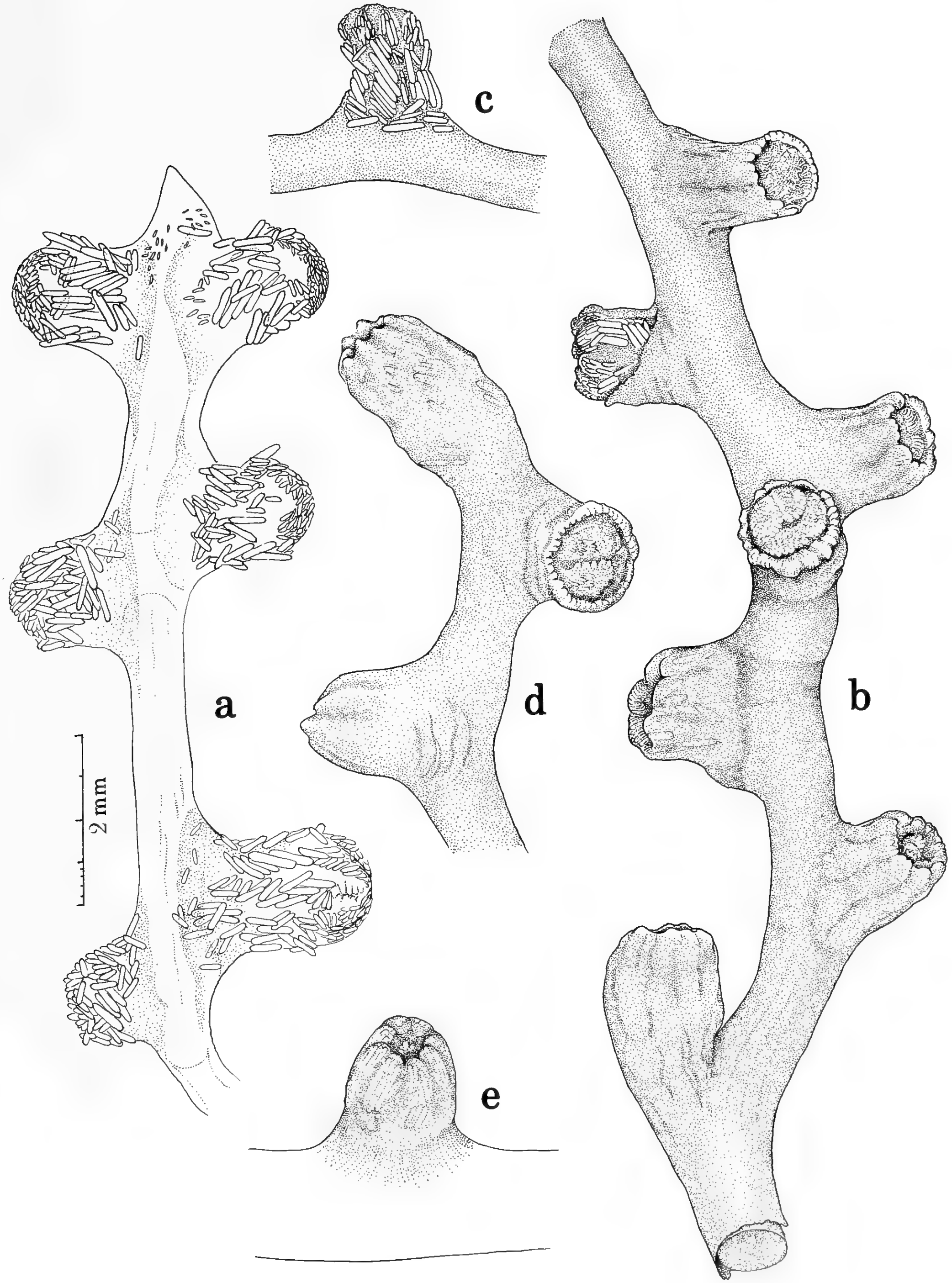


Fig. 11. *Orstomisis crosnieri,* terminal branchlets. a, USNM 78372, with verrucae flayed. b–e, USNM 84774: with verrucae intact or partly flayed.

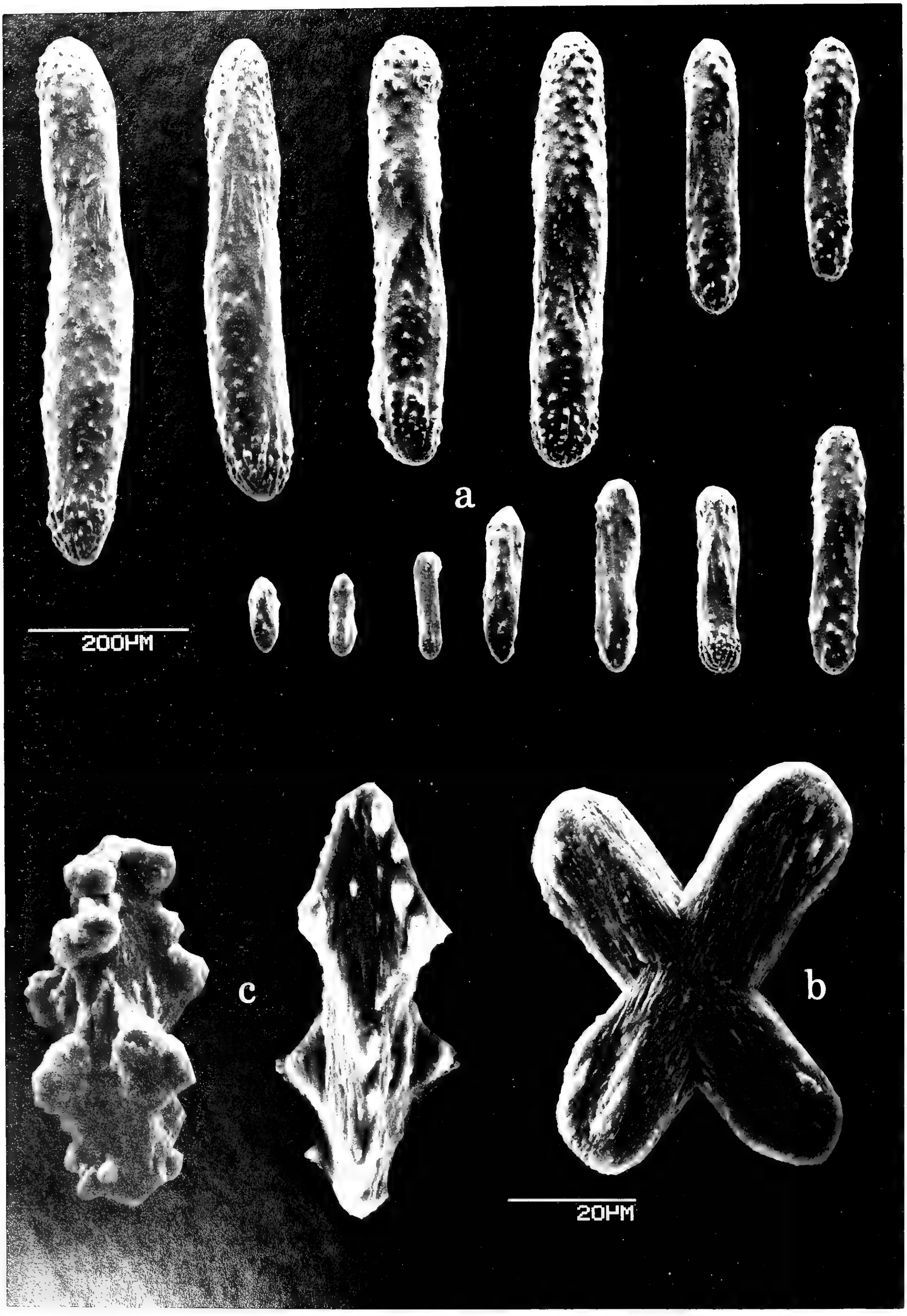


Fig. 12. [illegible] crosnieri USNM 78372, sclerites: a, Rods of verrucae. b, Twinned rodlet. c, Pharyngeal [illegible] 200 μm scale; b, c, 20 μm scale.

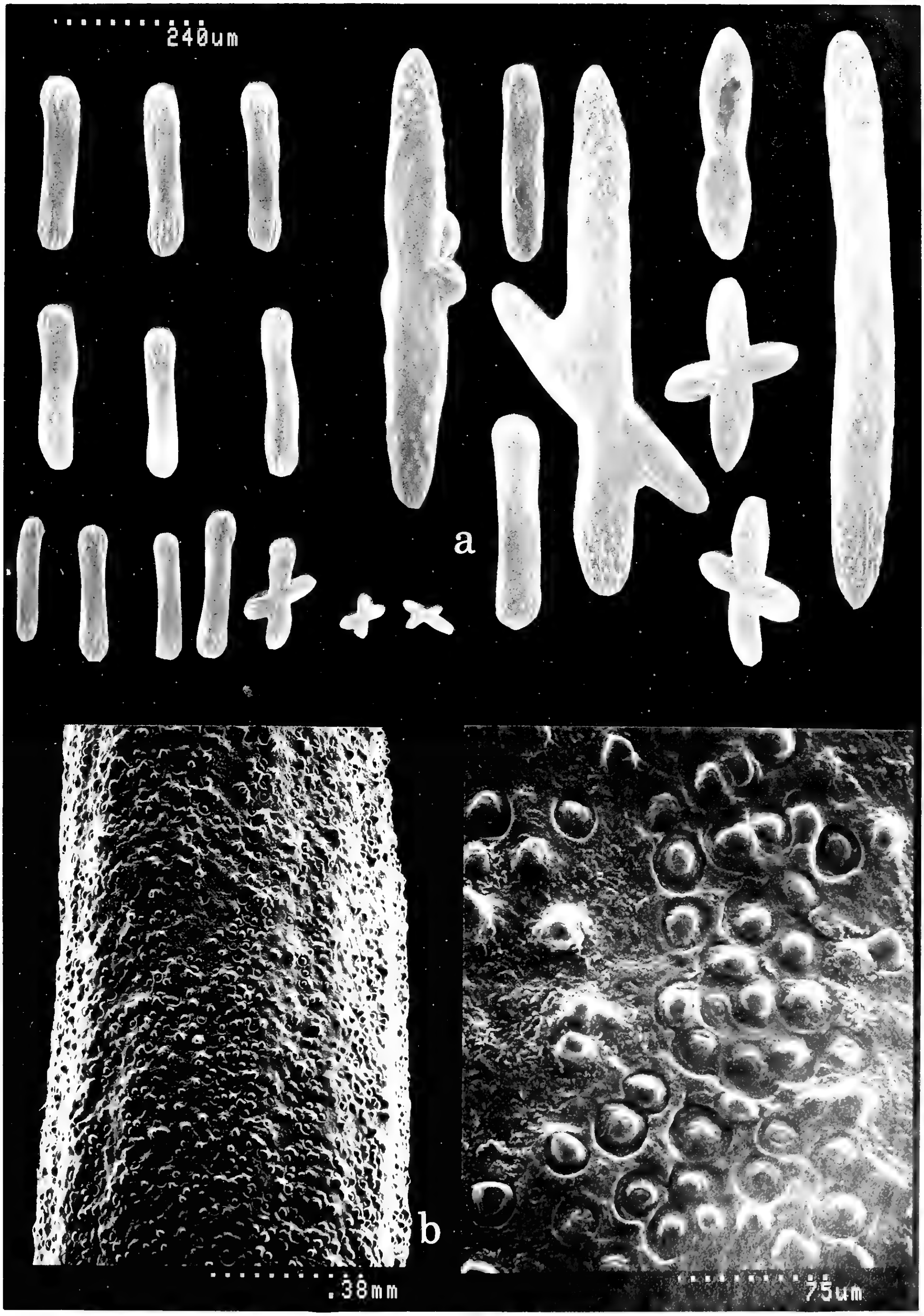


Fig. 13. *Orstomisis crosnieri* USNM 84774: a, Verrucal sclerites. b, Part of distal internode. c, Surface of distal internode.

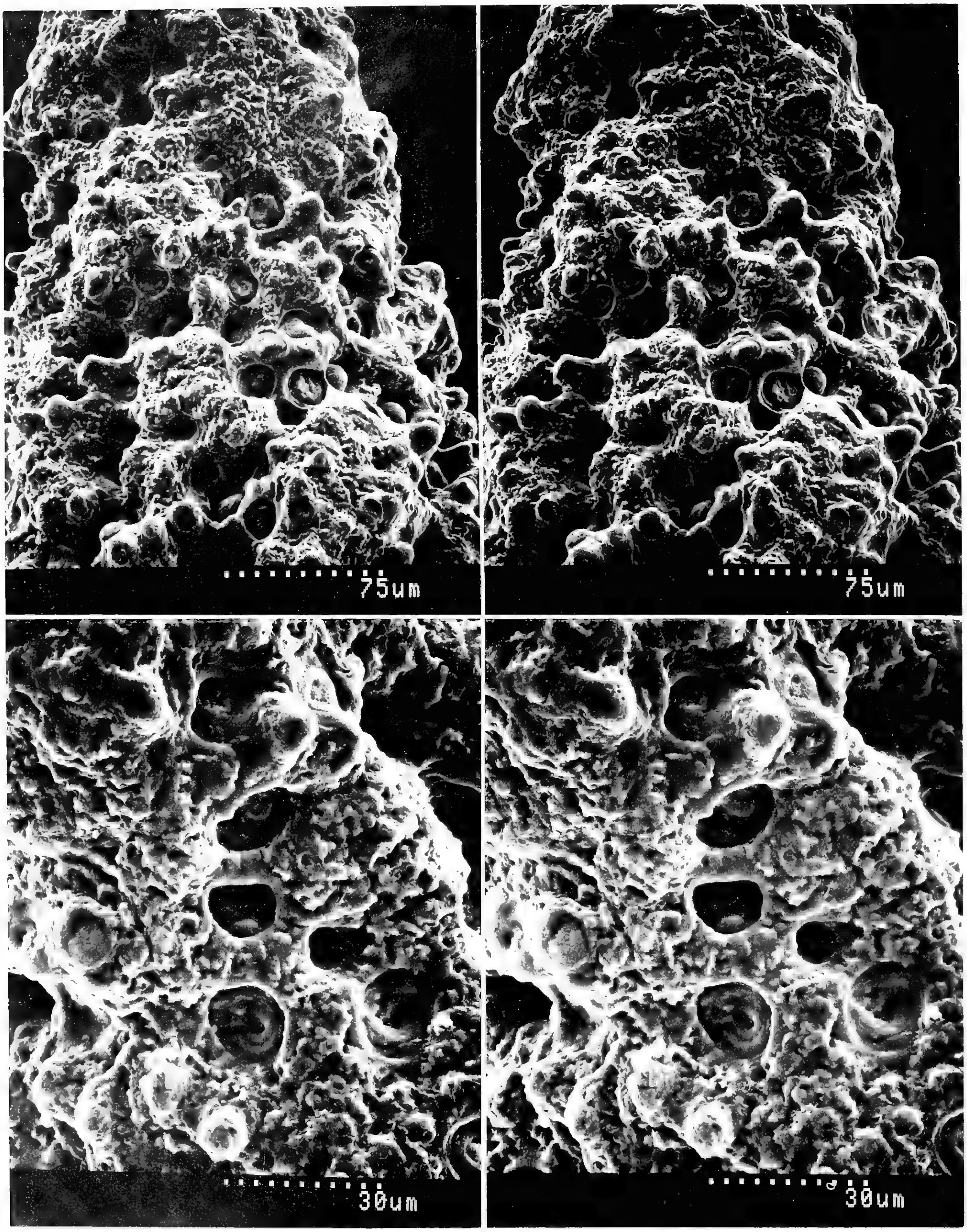


Fig. 14. *Orstomisis crosnieri* USNM 84774: Surface of distal internode immediately below tip. Stereoscopic pairs.

scattered, especially in the vicinity of polyps. Brownish pigmented streaks, usually discontinuous, mark the course of the stem canals.

Remarks.—Although thick, the smooth, skinlike epithelium seems to be very delicate, as it had been completely stripped off the first specimen received. This exposed the rod-shaped sclerites of the verrucae (Fig. 11a) and obscured the fact that the tentacles can be folded within a fleshy verrucal margin (Fig. 11b), leading to provisional classification of the specimen as a species of *Isidella* on the basis of its branching from the horny nodes, in spite of some morphological discrepancies. Specimens in better condition received later immediately revealed the unique nature of the verrucae (Fig. 11b–e), necessitating the establishment of a new genus.

This new genus cannot be accommodated in either of the subfamilies Isidinae and Muricellisidinae established by Kükenthal on the basis of retractability of the polyps. It provides evidence that retractability alone is an insufficient basis for subfamilial distinction. Among the Isididae, *Isis, Chelidonisis,* and *Muricellisis* are the only genera having non-scalelike sclerites with tubercular ornamentation; that they are "retractile" can only be regarded as coincidental, as the polyps of each retract in different ways. The polyps of *Isis* are virtually devoid of sclerites and retract into a thick coenenchyme by folding the tentacles over the mouth and closing the rim of the coenenchymal aperture. The polyps of *Chelidonisis* have blunt, conical or hemispherical verrucae filled with sclerites that extend onto the tentacles, which merely fold inward during contraction, and therefore are not "retractile" in the same sense. The polyps of *Muricellisis* are divided into a proximal, projecting anthostelar part into which the distal, anthocodial part armed with sclerites arranged as a crown and points can retract more or less completely—at least theoretically. The only character shared by these three genera is the tubercular ornamentation of the sclerites: capstans, clubs and spindles in *Isis,* sexradiates in *Chelidonisis,* and sharp spindles in *Muricellisis.*

Orstomisis, undeniably "retractile," does not share this spicular character. Its sclerites are definitely rods of the *Keratoisis* type. It does not clearly fit into either Isidinae or Muricellisidinae, but it does not justify still another subfamily. A solution to the subfamily problem is to define the Isidinae on the basis of tubercular ornamentation of sclerites, not retractability, and merge Muricellisidinae with it. Then Keratoisidinae can be defined on the basis of sparsely prickly or thorny rod-shaped sclerites, with *Orstomisis* the only genus with retractile polyps.

Etymology.—Dedicated to Dr. Alain Crosnier, in recognition of his tireless efforts to obtain financial support for a comprehensive study of the rich collection of Octocorallia obtained by expeditions of ORSTOM.

Comparisons.—This species is unlike any isidid heretofore described. The retractability of the tentacular part of the polyps into a firm, proximal calyx is unique in the Keratoisidinae and is paralleled only in *Muricellisis* in the Isidinae (Muricellisidinae of Kükenthal). The truly dichotomous manner of brancing predominant in this species occurs elsewhere only in *Chelidonisis* (Isidinae).

Acknowledgments

I here express thanks to Dr. B. Richer de Forges and Mr. Georges Bargibant of the Nouméa office of ORSTOM for making available the gorgonians from New Caledonia described in this paper. Dr. Manfred Grasshoff of the Natur-Museum Senckenberg, Frankfurt, West Germany, and Mr. Phil Alderslade of the Northern Territory Museum of Arts and Sciences, Darwin, Australia, kindly reviewed the manuscript and offered helpful comments. The scanning electron micrographs were made by Mr. W. R. Brown, chief of the SEM Laboratory, National Museum of Natural History, Smithsonian Institution. Ms. Molly Kelly Ryan provided lettering of the illustrations.

Literature Cited

Bayer, F. M. 1956. Octocorallia. *In* Treatise on Invertebrate Paleontology F:166–231. Lawrence, University of Kansas Press.

———. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa.—Proceedings of the Biological Society of Washington 94(3): 902–947, figs. 1–80.

———, M. Grasshoff, & J. Verseveldt, eds. 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. E. J. Brill/Dr. W. Backhuys, Leiden, 75 pp., 20 pls.

———, & J. Stefani. 1987a. Isididae (Gorgonacea) de Nouvelle-Calédonie. Nouvelle clé des genres de la famille.—Bulletin du Muséum National d'Histoire Naturelle Paris (4)9(A no. 1):47–106, figs. 1–4, pls. 1–30.

———, & ———. 1987b. New and previously known taxa of isidid octocorals (Coelenterata: Gorgonacea), partly from Antarctic waters.—Proceedings of the Biological Society of Washington 100(4):937–991, figs. 1–31.

Carpine, C., & M. Grasshoff. 1975. Les gorgonaires de la Méditerranée occidentale.—Bulletin de l'Institut Océanographique Monaco 71(1430): 1–140, figs. 1–62.

Deichmann, E. 1936. The Alcyonaria of the western part of the Atlantic Ocean.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 53:1–317, pls. 1–37.

Gray, J. E. [1858]. Synopsis of the families and genera of axiferous zoophytes or barked corals.—Proceedings of the Zoological Society of London 1857:278–294.

———. 1870. Catalogue of the lithophytes or stony corals in the collection of the British Museum. London, British Museum, [iv] + 40 pp.

Koch, G. von. 1887. Die Gorgoniden des Golfes von Neapel und der angrenzenden Meeresabschnitte.—Fauna und Flora des Golfes von Neapel 15: i–x + 1–99, pls. 1–10.

Kükenthal, W. 1915. System und Stammesgeschichte der Isididae.—Zoologische Anzeiger 46:116–126.

———. 1919. Gorgonaria.—Wissenschaftliche Ergebnisse der deutschen Tiefee-Expedition auf dem Dampfer "Valdivia" 1898–1899 13:1–946, pls. 30–89.

———. 1924. Gorgonaria.—Das Tierreich 47:i–xxviii + 1–478, figs. 1–209.

Muzik, K. 1978. A bioluminescent gorgonian, Lepidisis olapa, new species (Coelenterata: Octocorallia), from Hawaii.—Bulletin of Marine Science 28(4):735–741, figs. 1–4.

Nutting. C. C. 1908. Descriptions of the Alcyonaria collected by the U.S. Bureau of Fisheries steamer Albatross in the vicinity of the Hawaiian Islands in 1902.—Proceedings of the United States National Museum 34:543–601, pls. 41–51.

———. 1910. The Gorgonacea of the Siboga Expedition V. The Isidae.—Siboga-Expeditie Monographie 13b2:1–24, pls. 1–6.

Studer, T. [& E. P. Wright.]. 1887. Versuch eines Systemes der Alcyonaria.—Archiv für Naturgeschichte 53(1):1–74, pl. 1.

Thomson, J. A., & W. D. Henderson. 1906. An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. Part 1. The alcyonarians of the deep sea. i–xvi + 1–132 pp., pls. 1–10. Calcutta: Indian Museum.

Verrill, A. E. 1883. Report on the Anthozoa, and on some additional species dredged by the "Blake" in 1877–1879, and by the U.S. Fish Commission steamer "Fish Hawk" in 1880–82.—Bulletin of the Museum of Comparative Zoology at Harvard College 11:1–72, pls. 1–8.

Verseveldt, J., & F. M. Bayer. 1988. Revision of the genera Bellonella, Eleutherobia, Nidalia and Nidaliopsis (Octocorallia: Alcyoniidae and Nidaliidae), with descriptions of two new genera.—Zoologische Verhandelingen 245:i–vi + 1–131 pp., figs. 1–64.

Wright, E. P., & Th. Studer. 1889. Report on the Alcyonaria collected by H.M.S. Challenger during the years 1873–1876.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1973–76, Zoology 31 (part 64):i–lxxvi + 1–314, pls. 1–43.

Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 229–234

A NEW SPECIES OF *CLADOCARPUS* (CNIDARIA: HYDROIDA: PLUMULARIIDAE) FROM THE STRAITS OF FLORIDA

Mary Anna Bogle

Abstract.—*Cladocarpus delicatus,* a new species of plumulariid hydroid, is described, bringing to nine the number of species of *Cladocarpus* known from the Straits of Florida. The delicate appearance of the colony and spike-like projection from the medial abcauline wall of the hydrotheca distinguishes *C. delicatus* from other species of this genus. A key to the species of *Cladocarpus* known from the tropical western Atlantic is provided.

In May 1962, the staff of the Institute of Marine Sciences [now the Rosenstiel School of Marine and Atmospheric Sciences (RSMAS)] of the University of Miami began a faunal survey of the Straits of Florida and its approaches. During the course of the project, conducted intermittently over a 10-year period, a large number of thecate hydroids was collected, including many members of the family Plumulariidae. In this collection a new plumulariid species, *Cladocarpus delicatus,* belonging to the subfamily Aglaopheniinae was discovered. The holotype is described and illustrated in this paper. An unpublished account of the species appears elsewhere (Bogle 1975).

The holotype of *Cladocarpus delicatus* is deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). The paratype is located in the invertebrate museum of the Rosenstiel School of Marine and Atmospheric Sciences.

Subfamily Aglaopheniinae Stechow, 1911
Genus *Cladocarpus* Allman, 1874
Cladocarpus delicatus, new species
(Figs. 1–3)

Material examined.—Material in the USNM: Holotype, USNM 60212, 1 colony, R/V *Gerda* Sta. G-237, Straits of Florida (25°15′N, 79°14′W–25°17′N, 79°14′W), 393–397 m, 30 Jan 1964. Colony with phylactogonia and gonothecae present (Table 1); 18 mm high.

Material at RSMAS: Paratype, UMML 5: 151, one colony, R/V *Gerda* Sta. G-239, Straits of Florida (25°20′N, 79°15′W–25°22′N, 79°16′W), 256–348 m, 30 Jan 1964. Fragments of colony with phylactogonia and gonothecae present.

Description.—Trophosome: Holotype colony with unbranched hydrocaulus, attaining a height of 18 mm; anchored in the substrate by a tangle of rhizoidal filaments. Hydrocaulus slender and nonfascicled, carrying hydrocladia along the distal half. Hydrocauline nodes indistinct. Three very strong, oblique, hydrocauline constrictions just proximal to the first hydrocladium with one nematotheca present between successive constrictions. Proximal half of hydrocaulus with a single longitudinal row of nematothecae along the anterior face. Anterior face of distal half of hydrocaulus with two tubular nematothecae between successive hydrocladia, one in the axil of the apophysis and the other proximal to it.

Unmodified hydrocladia arranged alternately, few in number and distant (~0.75 mm apart); divided into long (~1 mm), sinuous, often weakly delineated internodes. Distal fourth of each internode arched

Table 1.—Measurements of nematothecae and hydrothecae of the holotype of *Cladocarpus delicatus.*

Measurements (in micrometers)	Range (mean)	Number*
Distance from apex of supracalycine nematotheca to apex of preceding supracalycine nematotheca	966–1092 (1016)	10
Hydrotheca, total depth	522–605 (574)	11
Maximum diameter	231–314 (298)	11
Diameter at margin	138–176 (162)	11
Mesial nematotheca, total length	132–165 (151)	11
Supracalycine nematotheca, total length	143–176 (164)	11
Length above hydrothecal margin	33–60 (44)	11
Gonotheca, length	396–418 (411)	2
Width	170–226 (209)	2

* Number of measurements made.

slightly over the hydrotheca of that internode.

Hydrothecae distant, located approximately midway along each hydrocladial internode. Each hydrotheca narrow at the proximal end, greatly inflated toward the middle and narrowing again slightly near the hydrothecal margin. Medial abcauline wall noticeably thickened and often protruding out and upward so as to form a spike-like projection originating approximately two-thirds up the hydrothecal face. Length of spike as much as 0.1 mm. Projection usually with a small cavity formed by the continuation of the hydrothecal cavity into it but without a terminal aperture. Hydrothecal margin with a single large medial tooth and 4 to 5 smaller lateral teeth on each side. Strong, posterior intrathecal ridge extending obliquely upward across one-third to one-half of both lateral faces of the hydrotheca. Number of internodal septa opposite hydrotheca usually 2, occasionally 3. Septa very short and weak; located proximal to the posterior intrathecal ridge. No other septa regularly present per internode except one at the base of the mesial nematotheca.

A single long, tubular mesial nematotheca springing from the hydrocladium as much as 100 μm below the base of the hydrotheca. Mesial nematotheca with an aperture running from the top to midway along the free upper surface.

A pair of long, tubular supracalycine nematothecae projecting obliquely outward and upward from their hydrocladial origin; slightly geniculate near their distal end.

Gonosome: Gonothecae narrow, lengthened, obovate sacs arising in small clusters near the base of the apophyses of unmodified and modified hydrocladia that bear phylactogonia. Gonothecae with oval terminal aperture.

Phylactogonia arising from the most distal hydrocladia, each of which is usually modified into a short, nematophorous spike bearing no hydrotheca. A single phylactogonium arises from an area lateral to the proximal nematothecae of each of these hydrocladia and arches medially over the front of the hydrocaulus, thus protecting the gonangia borne there. Phylactogonium usually composed of 3 to 4 very slender nematophorous branchlets formed by the bifurcation of alternate branchlets, with the entire structure resembling stag antlers. Phylactogonial nematothecae long and tubular, directed outward and upward away from the gonangia.

Etymology.—Delicatus (Latin) = delicate, alluding to the delicate appearance of the colony.

Geographic range.—*Cladocarpus delica-*

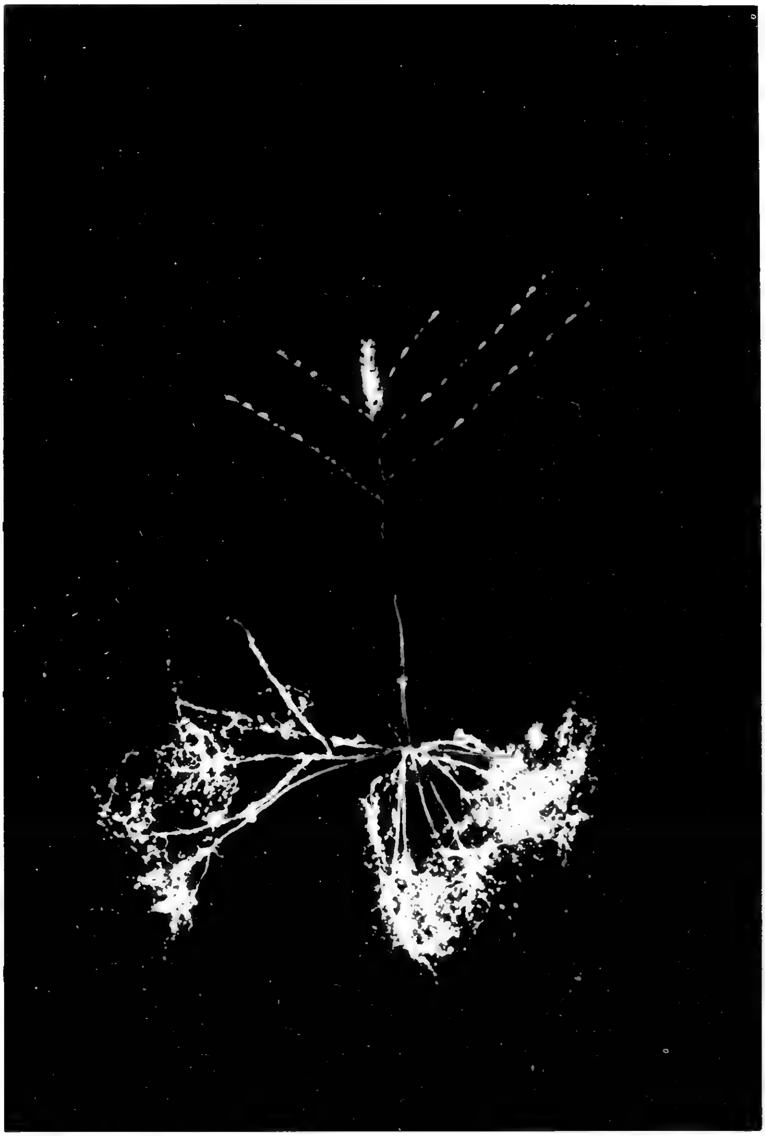


Fig. 1. *Cladocarpus delicatus,* new species: Holotype colony, USNM 60212, 18 mm high.

tus is known only from the northern Straits of Florida.

Discussion.—This small delicate hydroid closely resembles in size and in the general form of the trophosome and gonosome two other species of *Cladocarpus* reported from the Straits of Florida. They are *C. dolichotheca* Allman, 1977, and *C. tenuis* Clarke, 1879. The distinctive hydrotheca of *C. delicatus* with its inflated appearance and its unusual spine-like projection from the abcauline wall, however, readily distinguishes it from either *C. dolichotheca* or *C. tenuis* as well as from other members of the genus *Cladocarpus.* This new hydroid brings to nine the number of species of *Cladocarpus*

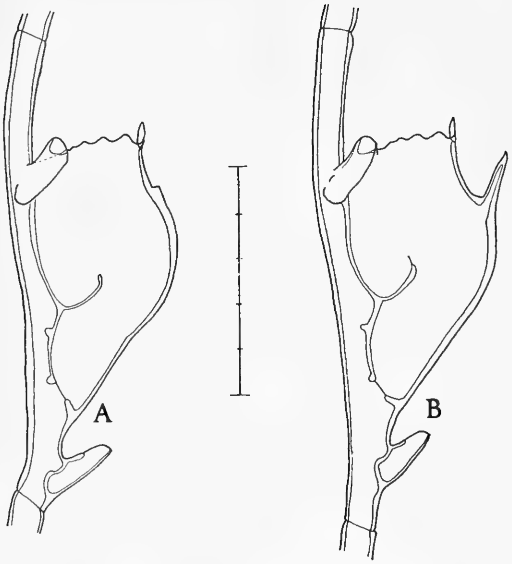


Fig. 2. *Cladocarpus delicatus,* new species: A, Hydrotheca of holotype, lateral view, USNM 60212 (northern Straits of Florida), scale 0.5 mm; B, Hydrotheca of holotype, lateral view showing spike-like projection from medial abcauline wall, USNM 60212 (northern Straits of Florida), scale 0.5 mm.

reported from the Straits of Florida and its approaches and to thirteen the number known from the tropical western Atlantic. Currently, approximately 60 species are assigned to the genus *Cladocarpus* (see Millard 1975, Rees & Vervoort 1987, Vervoort 1966) though several are questionably included in the genus since no gonosome has been described. The following key is to assist in the identification of species of *Cladocarpus* known from the tropical western Atlantic. Those species of *Cladocarpus* reported from the Straits of Florida and its approaches and treated in detail by the author (Bogle 1975) are indicated in the key with an "*".

A Key to the Tropical Western Atlantic Species of *Cladocarpus*

1a. Hydrothecal margin entire .... *C. carinatus* Nutting, 1900*

1b. One or more teeth on hydrothecal margin 2

2a. Hydrothecal margin with 1 or 2 prominent median teeth; others, if present, low 3

2b. Hydrothecal margin with several subequal teeth; none prominent 11

3a. Hydrothecal margin with 1 prominent median tooth 4

3b. Hydrothecal margin with 2 prominent median teeth 12

4a. Posterior (adcauline) intrathecal ridge absent 5

4b. Posterior (adcauline) intrathecal ridge present 7

5a. Hydrotheca obconic (like an inverted cone); face of hydrotheca straight .. *C. flexuosus* Nutting, 1900

5b. Hydrotheca long and slender, not cone-like; anterior profile of hydrotheca concave 6

6a. Anterior profile of hydrotheca weakly concave; hydrotheca not appreciably narrowed (ratio of lateral width of hydrotheca at its midpoint to the length approximately 1:4) .... *C. dolichotheca* Allman, 1877*

6b. Anterior profile of hydrotheca strongly concave; lateral and frontal aspect of hydrotheca appreciably narrowed (ratio of lateral width of hydrotheca at its midpoint to the length approximately 1:6) *C. tenuis* Clarke, 1879*

7a. Hydrocaulus fascicled .... *C. longipinna* Fraser, 1945

7b. Hydrocaulus nonfascicled 8

8a. Intrathecal ridge present but short and weak; anterior (abcauline) profile of hydrotheca slightly convex ..... *C. flexilis* Verrill, 1885

8b. Intrathecal ridge short but strong; anterior (abcauline) profile of hydrotheca convex or sinuous ... 9

9a. Hydrocladial internode with no

Fig. 3. *Cladocarpus delicatus,* new species: Phylactogonium of paratype, UMML 5:151 (northern Straits of Florida), height 1.3 mm.

more than 3 septa; mesial nematotheca not adnate to the hydrotheca but arising as much as 100 μm below the base of the hydrotheca *C. delicatus,* new species*

9b. Hydrocladial internode with 5 or more septa; mesial nematotheca adnate to or arising just below the base of the hydrotheca 10

10a. Anterior (abcauline) profile of hydrotheca sinuous .... *C. ventricosus* Allman, 1877*

10b. Anterior (abcauline) profile of hydrotheca convex .... *C. obliquus* Nutting, 1900*

11a. Hydrotheca with a conspicuous, sigmoid, posterior intrathecal ridge extending to anterior (abcauline) face .... *C. sigma* (Allman, 1877)*

11b. Hydrotheca with a very short and straight posterior intrathecal ridge .... *C. compressus* Fewkes, 1881

12a. Hydrotheca deep with 3 or more internodal septa opposite it; supracalycine nematothecae with

strong posterior constriction; nematothecal margin not noticeably serrate ....
...... *C. paradiseus* Allman, 1877*

12b. Hydrotheca relatively short and squat with usually only 1 or 2 internodal septa opposite it; supracalycine nematothecae lacking a strong posterior constriction and with a finely serrated margin .. *C. grandis* Nutting, 1900*

Acknowledgments

This paper is a result of research undertaken while at the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, and is part of a series resulting from the National Geographic Society–University of Miami Deep-Sea Biology Program.

I wish to thank Dr. Dennis M. Opresko and Dr. Richard B. McLean, both of Oak Ridge National Laboratory, for their suggestions and comments on the manuscript. I would also like to express my gratitude to Dr. Stephen D. Cairns of the National Museum of Natural History for his assistance in depositing the holotype in the collections of the USNM.

Oak Ridge National Laboratory is operated by Martin Marietta Energy Systems, Inc., under contract DE-AC05-840R21400 with the U.S. Department of Energy. Publication No. 3238, Environmental Sciences Division, Oak Ridge National Laboratory.

Literature Cited

Allman, G. J. 1874. Report on the Hydroida collected during the expedition of H.M.S. 'Porcupine.'—Transactions of the Zoological Society of London 8:469–481.

———. 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès.—Memoirs of the Museum of Comparative Zoology at Harvard College 5(2): 1–66.

Bogle, M. A. 1975. A review and preliminary revision of the Aglaopheniinae (Hydroida: Plumulariidae) of the tropical western Atlantic.—Unpublished M.S. Thesis, University of Miami, 307 pp.

Clarke, S. F. 1879. Report on the Hydroida collected during the exploration of the Gulf Stream and the Gulf of Mexico by Alexander Agassiz, 1877–1878.—Bulletin of the Museum of Comparative Zoology at Harvard College 5:239–252.

Fewkes, J. W. 1881. Report on the Acalephae, *in* Reports on the results of dredging, under supervision of Alexander Agassiz, in the Caribbean Sea, in 1878, 1879, and along the Atlantic coast of the United States during the summer of 1880, by the U. S. Coast Survey Steamer Blake.—Bulletin of the Museum of Comparative Zoology at Harvard College 8:127–140.

Fraser, C. M. 1945. Notes on some recently collected hyroids in the United States National Museum, with descriptions of three new species.—Journal of the Washington Academy of Sciences 35:21–23.

Millard, N. A. H. 1975. Monograph on the Hydroida of southern Africa.—Annals of the South African Museum 68:1–513.

Nutting, C. 1900. American hydroids. Part I. The Plumularidae.—Special Bulletin United States National Museum 4(1):1–285.

Rees, W. J., & W. Vervoort. 1987. Hydroids from the John Murray Expedition to the Indian Ocean, with revisory notes on *Hydrodendron, Abietinella, Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa).—Zoologische Verhandelingen 237: 1–209.

Stechow, E. 1911. Über Hydroiden der Deutschen Tiefsee-Expedition. Ein neues Genus thecater Hydroiden.—Zoologischer Anzeiger 37:193–197.

Verrill, A. E. 1885. Results of the explorations made by the Steamer Albatross off the northern coast of the United States in 1883.—Report of the United States Fish Commission 11:503–699.

Vervoort, W. 1966. Bathyal and abyssal hydroids.—Galathea Report 8:97–174.

Environmental Sciences Division, Oak Ridge National Laboratory, Building 1505 MS 6036, P.O. Box 2008, Oak Ridge, Tennessee 37831-6036.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 235–247

THE FOURTH ANNUAL RISER LECTURE: THE ROLE OF PHYSIOLOGY AND BIOCHEMISTRY IN UNDERSTANDING ANIMAL PHYLOGENY

Charlotte P. Mangum

Abstract.—On several occasions in the history of physiology and biochemistry, claims have been made of uniquely superior approaches to understanding animal phylogeny. Perhaps the most infamous episode was the putative dichotomy between the muscle phosphagens found in protostomes and deuterostomes, which later proved to be factually incorrect. I argue that physiology and biochemistry can be powerful tools in understanding animal evolution, and I give an example in which the common quaternary structure of the oxygen carrier hemocyanin in the three groups of living arthropods is strong evidence for a common origin and the integrity of the Phylum Arthropoda. The evidence is compelling, not because the character is molecular but because molecular structure can be interpreted in the context of its physiological setting in living, breathing animals. Thus the argument can be constructed in Darwinian terms and the evidence would be extremely difficult to interpret alternatively.

G. Evelyn Hutchinson has defined the phylum as a group of organisms which is not very clearly related to any other group. This definition may seem to be only humorous but in fact it is fairly accurate, both historically and conceptually. Throughout the modern history of zoology taxonomists have devised subsuming sets until they can no longer do so, and have then stopped and called the most general set a phylum. Thus it is the height of absurdity when we turn around and ask ourselves why we do not understand the relationships of the animal phyla. Ignorance has been cleverly built into the process (to keep ourselves in business?).

Nevertheless I, like many others, find the temptation irresistable. I believe that the quest makes us think about how animals work in ways that we would not if we fail to undertake it. And understanding how animals work is what physiological and biochemical zoology is all about.

Do physiology and biochemistry have anything to offer to understanding animal phylogeny that other subdisciplines do not? In one sense the answer must be affirmative because the logic is essentially tautologous. If physiology and biochemistry had nothing unique about them they would not be recognized as coherent disciplines. The more meaningful question is do physiology and biochemistry have anything especially cogent to offer because of their unique subject matter? My answer is yes, but my reasons may surprise the reader.

Historical Episodes of Physiological and Biochemical Inquiry into Animal Phylogeny

Muscle phosphagens.—First I must illustrate the reasons why physiology and bio-

---

In 1985 the annual Riser Lecture was initiated by members, alumni and friends of the Marine Science Center, Northeastern University of Nahant, Massachusetts. The occasion was the official retirement of Professor Nathan W. Riser. As teacher, biologist and founder of the facility, 'Pete' Riser endowed the laboratory with a legacy—the importance of considering the whole organism regardless of one's special focus. We dedicate these annual lectures to that principle.

chemistry have not lived up to their potential in contributing to phylogenetic knowledge. The most celebrated example of an attempt to use biochemical data in the study of animal evolution involves the distribution of the phosphagens, the guanidine derivatives found in muscle and a variety of other tissues that store high energy PO_4s. In the 1920s and 30s there was something of a revolution in thinking about animal phylogeny. The early metabolic biochemists were rapidly unravelling pathways of intermediary metabolism, concentrating on somatic muscle. A "dichotomy" was perceived to distinguish "vertebrates"[1] and "invertebrates"[1]: while the vertebrates contain creatine PO_4, it was said, the invertebrates contain the structurally distant compound arginine PO_4 (Needham et al. 1932, Kutscher & Ackermann 1933, Baldwin & Needham 1937). This theory also supposed that phosphoarginine was the original, now relict form and that phosphocreatine is a relatively new molecule that arose late in animal evolution. Even more excitement was generated by the first exceptions because they were found in the deuterostomes, some of which contain both phosphagens (e.g., Baldwin & Yudkin 1950). The coexistence was regarded as an example of transition from the relict to the modern form.

A number of reviews and monographs were written using these relationships to introduce the idea that biochemistry undertaken in a comparative framework can make important contributions to phylogenetic knowledge. When Baldwin published the 1949 edition of his essay entitled *Comparative Biochemistry,* the evidence cited in support of a phylogenetic distribution of the muscle phosphagens represented six of the several dozen animal phyla. Ten years later in the final edition of his textbook, the database included about 50 species representing 9 phyla, which was considered a large sample (Baldwin 1959).

By the middle 1950s van Thoai & Robin (1969) had begun to report a number of disturbing exceptions of phosphocreatine in the wrong (viz. protostomate) animals. Nonetheless the notion that these compounds are distributed along phylogenetic lines persisted for another decade. Of some 118 species of annelids and related groups examined by van Thoai & Robin (1969), for example, more than twice as many contain the wrong phosphagen as the right one (albeit an equally large number contains compounds closely related to phosphoarginine, which were unknown to the early workers). Phosphocreatine has been found in the Porifera as well.

Thomas Kuhn (1970) wrote a book on the heuristic role of what he called paradigms in advancing scientific knowledge. Paradigms are "universally recognized scientific achievements that for a time provide model problems and solutions to a community of practitioners" (p. viii). And if the communication facilitated by such widespread concurrence is fruitful, the truth of the paradigm matters very little. In support of his thesis Kuhn (1970) noted that he would use examples from physics and chemistry because he knew them best. But he also maintained that he could have used examples from biology had he so chosen.

I have always thought that Kuhn was wrong on that point, primarily because in biology we almost never concur so widely that we communicate without a lot of argument. But the phosphagen theory was about as close to a paradigm as biology ever gets.[2]

---

[1] I remain amazed by our persistence in employing, not only in our biological curricula but also in our original researches, this particular pseudo-dichotomy, the fallacy of which has been recognized for a century and a half!

[2] The only other examples that come to my mind of paradigms that proved to be incorrect are the biogenetic law and perhaps, insofar as the principles are regarded as generally true, *Drosophila* genetics.

As early as 1946 Greenwald had found the wrong phosphagen in annelids and echiuroids. Instead of concluding that something might be wrong with the theory, however, he concluded that the annelids and echiuroids are more closely related to the chordates than previously supposed! When later investigators failed to confirm his original report of both phosphagens in the hemichordate *Balanoglossus,* Baldwin (1953) acknowledged that the original finding might be wrong (the field had always been plagued by inadequate analytical methods). But, he also suggested, in the intervening 20 years perhaps a mutation has occurred and the relict compound has now been replaced by the modern form. Finally, in their 1958 review Ennor & Morrison wrote:

> "This suggestion (of a phylogenetic distribution) . . . had an unfortunate and inhibitory effect on biochemical thought in this field for many years, and was made in spite of the fact that there was evidence to show that some invertebrates possess creatine" (p. 664, parenthesis mine).

They then hedged by concluding that the theory might be valid within the deuterostomes!

It is difficult for those of us who were not around at the time to appreciate the impact made by the phosphagen theory. Consider, for example, the status of inquiry into animal phylogeny in the 1920s. The deuterostome grouping was by no means universally accepted, and the notion that acorn worms might be more closely related to vertebrates than to other Vermes was also distasteful to some. The phosphagen theory was welcomed by proponents of modern phylogeny as especially cogent evidence because it was biochemical. Evelyn Hutchinson has reminded me that the introduction of biochemical data irreversibly expanded zoological thinking about phylogeny and so, in that sense, it is a good example of Kuhn's (1970) heuristic though erroneous paradigm. But, I suggest, physiologists and biochemists would be remiss if we failed to conclude that there is a better way of thinking about phylogeny.

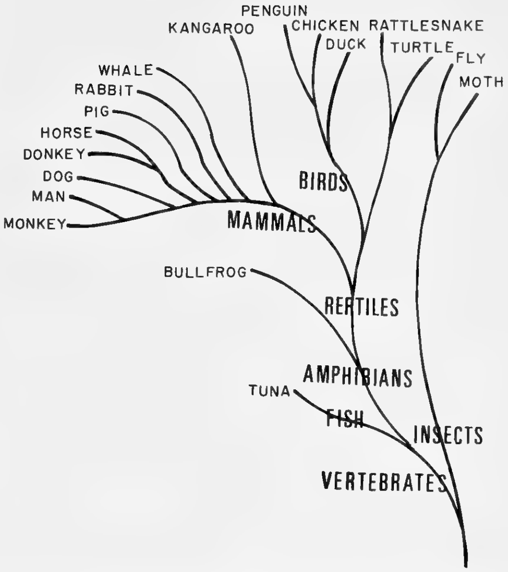


Fig. 1. Phylogenetic tree of the animal kingdom based on the primary structural similarities of cytochrome c. Redrawn from Dickerson & Geis (1969).

The theory has become a whipping boy for classical zoologists who do not want to be told that morphological data may not always take precedence. And biochemists have written a number of fairly messianic papers on how to go about the task in the right way. In my opinion, few have.

Alternative biochemical approaches.—In the 1960s the comparison of primary structure of proteins was advocated as a biochemical approach to phylogeny (e.g., Zuckerkandl & Pauling 1965). Indeed there have now been a number of such comparisons, perhaps the best known of which culminated in the phylogenetic tree based on the amino acid sequences of cytochrome c (Fig. 1). This approach, though certainly less simplistic than the phosphagen theory still has two major difficulties. One is technical and hopefully transient and the other epistemological and therefore more persistent.

Until recently, sequencing macromolecules has remained a formidable task. Cytochrome c was a good choice because it is

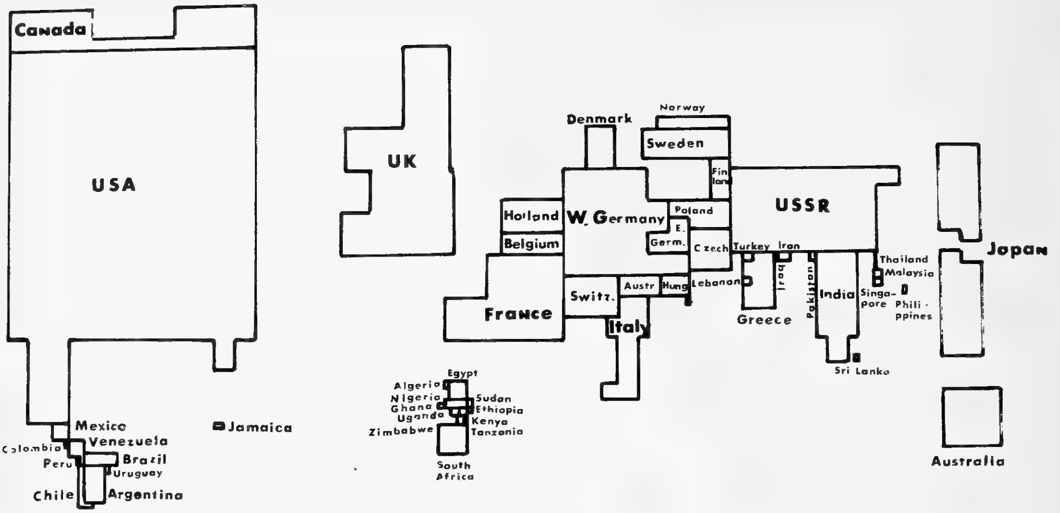


Fig. 2. A map of the world based on the frequency with which a nation's scientific journals are cited. Redrawn from Kidron & Segal (1984).

ubiquitous and it is at least not the biggest or most complex of proteins. But note the scope of the phylogenetic tree (Fig. 1). In no way does it truly depict the relationships of the animal phyla. If one were to map the nations of the world based not on their land masses but on the frequency with which their scientific journals are cited (Fig. 2), one would distort the geographic truth by a factor averaging about eight. In contrast, basing animal phylogeny on nine species of mammals, three birds, two reptiles, one amphibian, one teleost, and two insects distorts zoological truth by a factor of eighteen! Scarcity of information is no reason to reject an entire approach, but it does underscore the need to explore alternatives, unless one can suppress curiosity more than I can.

The second problem is that the nature of a putatively causal relationship between protein structure and phylogenetic relatedness is by no means clear. I will argue that the comparison of primary structures, made outside of a physiological context, tells us more about the evolution of the molecule than the evolution of the animal phyla. Once again the annelids, that perhaps most biochemically diverse of multicellular animals, can be used as an example. The primary structure of the monomeric hemoglobin in the red cells of the bloodworm *Glycera dibranchiata* has more in common with that of the hemoglobins of the distantly related vertebrates than it does with the monomeric hemoglobin in the red cells of the terebellid *Enoplobranchus sanguineus,* a member of the same class (Imamura et al. 1972, Weber et al. 1977)!

Still different molecular approaches have also been introduced. The technique of DNA pairing remains in limbo and at this writing the prospects do not appear to be good. Neither it nor immunological techniques promise to be very useful in understanding the relationships of higher taxa, for the simple reason that they require a minimum amount of relatedness that is essentially precluded by our definition of the phylum.

The very recent introduction of comparisons of sequences of nucleic acids rather than amino acids should prove to be useful. Only time and extensive validation of methodology will tell. I cannot resist the temptation to report a sense of the déjà vu, however, when I read sentences such as "the use of methods discussed here make it pos-

Table 1.—Phylogenetic relationships based on fractional structural similarity of 5S rRNA. Data from Lane et al. (1985). Mean ± SD.

	Sabellastarte japonica	*Perinereis brevicirrus*	*Solemya velum*	*Lingula anatina*
Sabellastarte japonica		0.87 ± 0.03	0.92 ± 0.03	0.88 ± 0.04
Perinereis brevicirrus	0.90 ± 0.03		0.93 ± 0.03	0.92 ± 0.03
Solemya velum	0.90 ± 0.03	0.92 ± 0.02		0.96 ± 0.02
Lingula anatina	0.86 ± 0.03	0.91 ± 0.03	0.96 ± 0.02	

sible to define the phylogenetic affiliations of any organism" (Pace et al. 1986). In fact the use of those very methods led to patently absurd conclusions, apparently unnoticed by Lane et al. (1985). The mean values for fractional "homology" (read: structural similarity) of 5S RNA indicate that the mollusc *Solemya velum* is more closely related to the annelids *Perinereis brevicirrus* and *Sabellastarte japonica* than the two annelids are to one another (Table 1)! To be more accurate by taking into account the error around the mean values, Table 1 suggests that *S. velum, P. brevicirrus, S. japonica* and *Lingula anatina* are all more or less equally related to one another.

(At this point I will confess parenthetically that I eagerly await further explication and application of the methods used in relating sequences of the 16–18S ribosomal RNA fractions, a better choice, by Field et al. (1988). The exact way in which the matrix analysis of the data was performed was unclear in the original, presumably due to space constraints specified by the journal, and consultation of the literature cited clarified only the general approach, not details that would help me understand discrepancies between the relationships depicted in the various figures. I hope that my enthusiasm for this work does not arise entirely from the agreement of the conclusions reached by Field et al. (1988) with my own phylogenetic predilections, but I am not sure.)

Why have we gone wrong?—I describe these historical incidents to illustrate what I believe are at best limited and at worst poor approaches to animal phylogeny. The databases remain small. But the comparison of muscle phosphagens and protein structures were also unsound because they lacked a Darwinian component. The practitioners never asked the question why a particular phosphagen or heme protein was selected in a particular group. The early metabolic biochemists noted that they really did not know why phosphocreatine appeared to have been selected over phosphoarginine in the deuterostomes, but there was so little discussion that they must not have regarded the point as serious. To this day the relative advantages of the various phosphagens remain a subject of speculation (Hird 1986, W. R. Ellington pers. comm.).

Centipedal Hemocyanin and Its Phylogenetic Implications

Finally, I arrive at my own subject, an example of biochemical data that are sufficiently large in number and clear in relation to physiological function that they can make a contribution in deciding a controversial question about animal phyla. The biochemical and physiological data pertain to the molecular structure and respiratory function of the hemocyanins (Hcs), the Cu-containing O_2 carriers; the phylogenetic question is the status of the Phylum Arthropoda.

Distribution and quaternary structures of the hemocyanins.—In contrast to the hemoglobins the Hcs have always been regarded as coherent in taxonomic distribution, being found only in arthropods and molluscs. Moreover, their higher order structure differs so fundamentally that there is little doubt that arthropod and molluscan Hcs had a separate origin.

Arthropod hemocyanins: Arthropod Hcs are built as multiples of anywhere from 6 to 48 monomeric subunits of about 67–80 × 10^3 d, each with a single active site (Van Holde & Miller 1982). The monomers are put together loosely. The first aggregate in assembly of the native polymer is a hexamer, which exists alone in the blood of some species. In the laboratory a hexamer can be made of only one kind of polypeptide chain, although in nature there are always two or more. If the 450 × 10^3 d hexamers contain an immunologically distinctive kind of chain that tends to dimerize, two hexamers pair to form 900 × 10^3 d dodecamers, the most common aggregate. The further formation of still larger aggregates remains somewhat unclear but some hypotheses suppose that a still different kind of chain is required to make the 1.5 × 10^6 d 24-mers (icosatetramers, found in a number of chelicerates and a single group of crustaceans) and another still must be present to make 3 × 10^6 d 48-mers (tessaracontaoctamers, found in *Limulus*).

In the arthropods especially, the progressive formation of higher order polymers is a physiologically important process because it lowers the number of osmotically active macromolecules without diminishing the O_2 carrying capacity of the blood, which allows the animal to maintain an excess of blood hydrostatic over colloid osmotic pressure and thus to form its primary urine (Snyder & Mangum 1982). Polymerization also makes more compact molecules, which minimizes viscosity and makes it easier for the animal to push its blood around.

Arthropod Hcs have a distinctive electron dense image. In high resolution micrographs hexamers look like 12.5 μm wide hexagons in top view and squares in side view. In lower resolution micrographs they appear more or less spherical. The hexagons are actually trigons of kidney-shaped monomers and there are two stacks of them in a hexamer. With only one exception the two hexamers in a dodecamer are rotated 45° with respect to one another, so they look like one hexagon and one square. 24-mers look like two pairs of spherical hexamers divided by a 2 μm cleft. The orientation of the 24-mers in a 48-mer is still somewhat uncertain. But a native 48-mer can dissociate to an aggregate that looks like a native 24-mer, which can dissociate to a native-looking dodecamer, etc. The dissociation products never include intermediate multiples, 18- or 36-mers. One would not expect to find 18-mers if the assembly process entails pairing first hexamers and then dodecamers. But there is no known structural constraint on putting a third dodecamer onto a 24-mer to make a triantahexamer.

Molluscan hemocyanins: Molluscan Hcs are built of very large (450–500 × 10^3 d) monomers that have been likened to a string of beads because each contains not one but 7–8 active sites (Van Holde & Miller 1982). The 7–8 O_2 binding domains are covalently linked to one another, although the giant monomers are loosely linked together in higher order aggregates. The native polymer exists in the blood as 10 (4.5 × 10^6 d), 20 (no less than 9 × 10^6 d) or sometimes even more of these chains. The blood of many gastropods is opaque, not because the Hc is so highly concentrated but because it scatters so much light. We routinely prepare these molecules, incidentally, by spinning them down in a not especially powerful ultracentrifuge. In electron micrographs they look like cylinders of various heights depending on degree of polymerization, and the ends of the cylinders have 'collars' and 'caps.'

Distribution of the hemocyanins: In the arthropods Hcs have long been known to occur in the crustaceans and chelicerates and several years ago I suggested that they might also have occurred in the trilobites, because trilobites inhabited the O_2 poor aquatic habitat (Mangum 1980). In the molluscs they have been found in four of the five classes examined (Polyplacophora, Bivalvia, Gastropoda and Cephalopoda), and my recent preliminary examination of the scaphopods was inconclusive (Mangum et al. 1987).

So a few years ago I was surprised to run across a report of Hc in a centipede, a member of the largely terrestrial uniramian arthropods. Sundara Rajulu (1969) had the interesting idea that an O_2 carrier might be needed in the relatively primitive scutigeromorph centipedes because it is the only group of Uniramia in which the tracheal system ends blindly in the blood rather than proceeding all the way to the tissues. His evidence was very suggestive but it did not include reversible O_2 binding, the critical property of an O_2 carrier. Perhaps for this reason the importance of the possibility had not been recognized by proponents of various points of view in the ongoing debate about arthropod phylogeny. At the time I was visiting Drs. Robert and Nora Terwilliger at the University of Oregon Institute of Marine Biology. We went out into the woods and picked up the first centipede we saw and performed an electrophoretic analysis of its blood. Sure enough the blood contained a Cu-binding polypeptide. But when we examined its absorption spectrum, it was totally different from that of a Hc. We had chosen a group of centipedes in which the tracheal system does terminate at the tissues, making a blood O_2 carrier redundant.

When I returned to Virginia I asked the resident expert where one must go to collect scutigeromorph centipedes and he pointed to the ceiling and I grabbed an individual of *Scutigera coleoptrata* and started working on it.[3]

Centipedal Hemocyanin

Structural and functional properties.—The blood of the common house centipede has the typical absorption spectrum of Hc, with a protein band at 280 and a Cu-O_2 maximum at 339 μm (Mangum et al. 1985). Following deoxygenation the absorption peak at the active site disappears and following re-oxygenation the peak reappears. Already this means that a Hc is present. Detailed measurements of O_2 binding revealed an exceptionally low oxygen affinity, which may prove to be related to high blood PO_2 in this terrestrial animal, and exceptionally great cooperativity that increases markedly with oxygenation state (Fig. 3). The Bohr shift is typically arthropod in magnitude and also normal, unlike that of some chelicerates. However, the direction of the Bohr shift varies within fairly closely related species so it cannot be regarded as taxonomically useful.

Centipedal Hc is fairly concentrated in the blood, which is typical of terrestrial arthropods, and the concentration almost certainly varies with hydration state in these desiccation-prone animals. In our original report I said that the blood, mercifully, fails to clot but this statement may slightly misrepresent the case. At least in small bore capillary tubes and at the termini of severed antennae, the blood becomes sticky and ceases to flow.

In electrophoretic procedures intended to estimate molecular size the centipede monomers co-migrate almost exactly with those of the blue crab *Callinectes sapidus* and slightly behind the smaller ones found in *Limulus.* Centipedal Hc has monomers of two different sizes, 72 and 80 × 10^3 d, figures very typical of the arthropod Hcs.

In our early electron micrographs of the native polymer we saw only four hexamers and we thought that the native polymer might be a 24-mer, which would also be very conventional. But in the meantime our collaborators Drs. K. E. Van Holde and K. I. Miller of Oregon State University performed sedimentation equilibrium measurements, and they arrived at a molecular weight estimate of 2.8 × 10^6 d, in between what we would expect for a 24- and a 48-mer. We had noticed on our gels that, unlike

---

[3] I later learned that my bathtub is a far better collecting site.

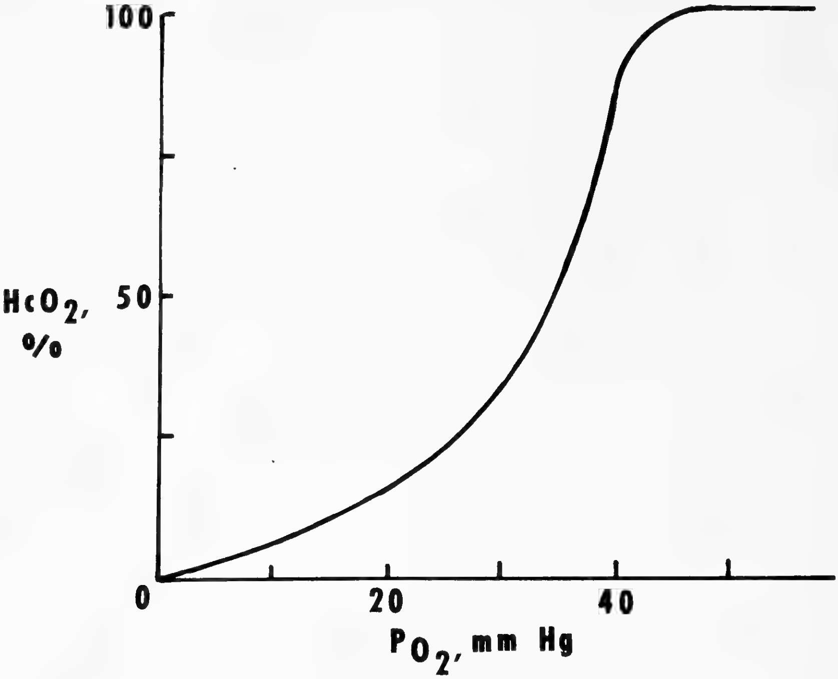


Fig. 3. O_2 binding of centipedal Hc at pH 7.5 and 25°C. 0.05 M Tris maleate buffered physiological saline. Data from Mangum et al. (1985).

C. sapidus and *Limulus,* centipede blood contains a lot of material that differs in size from typical arthropod monomers. The amount this material, 30–35% of the total, would be more than enough to bias the molecular weight estimates. We thought that centipedal Hc might consist of garden-variety arthropod monomers somehow complexed with a uniquely uniramian matrix. But when Dr. Miller purified the Hc (which was no mean feat; I feel fortunate when I collect as much as 10 μl blood from an individual, and I rarely find more than one or two animals per week and only from about May into October) and re-electrophoresed it, all of the extra material disappeared, leaving behind only the garden-variety arthropod monomers. By this time our micrographs fairly clearly showed more than four hexamers.

The centipede polymer is a triantahexamer, a multiple of 36 monomers. Initially we were quite excited about this result because, as indicated above, Hc triantahexamers had never before been found. But after contemplating it for just a little while we recognized that the aggregation of three dodecamers violates no known structural constraint. The real question is why there are not more of them.

There is one structural feature of persistent interest. The electrophoretic procedure to which I alluded above is useful in characterizing molecular weight but it is not the most sensitive. For example, *C. sapidus* Hc contains monomers of only two different sizes but it can have as many as six chains separable in the native conformation by charge (Mason et al. 1983, Mangum & Rainer 1988). But centipedal Hc still contains only two monomers when we separate the native chains by charge. So, according to some of the current models of assembly, it should not have enough different chains to

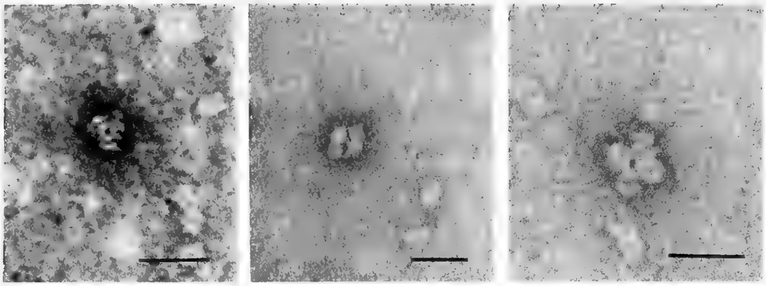


Fig. 4. Electron dense images of centipedal Hc. See text for explanation.

make the native polymer! This is of no phylogenetic interest but it does mean that the process of assembly must be rethought.

In electron micrographs we see nothing about centipedal Hc that fundamentally distinguishes it from other arthropod Hcs (Fig. 4). One image shows two pairs of spheres, each sphere measuring about 12 μm in diameter and each separated by a 2 μm cleft. Garden variety hexamers. One pair is in sharper focus than the other and one pair is slightly skewed with respect to the other. A second view shows two pairs of hexamers with a fifth in the middle. A third view shows a triangle of substructures surrounding a fourth. Two of the three peripheral units are in sharper focus than the third and, on closer inspection, additional material even more out of focus can be seen on the flat sides. More complex images, suggesting larger numbers of hexamers are also common.

All of these images can be produced by the model shown in Fig. 5. The six hexamers are arranged in an octahedral array. Two of the three pairs are lined up side by side and the third is located in an axis perpendicular to the other two. When viewed from the top or from one side only four hexamers can be seen. In this view the two pairs are not in exactly the same focus because one pair is on top and the other is underneath. When viewed from the other side five of the six can be seen. Slight tilt results in the virtual disappearance of the fifth and further tilting results in the virtual disappearance of a fourth. This is the most closed possible structure, permitting maximal interactions between the various subunits, which is consistent with the very great cooperativity of O_2 binding.

In an alternative, less closed arrangement all three pairs might be lined up side by side. But this arrangement cannot yield the image of five symmetrically placed hexamers and the image of four would show them unskewed and in the same focus. Finally, the

Fig. 5. Postulated arrangement of hexamers in centipedal triantahexamer. See text for explanation.

triangular image would not have additional material on the flat sides.

Arthropod phylogeny.—What is the phylogenetic significance of uniramian Hc? Again I must digress, to summarize briefly the various views of arthropod phylogeny.

For more than two decades Manton (e.g., 1973, 1979) argued forcefully that the so-called Phylum Arthropoda is in fact a polyphyletic assemblage of at least three and possibly four unrelated taxa. She considered the three extant groups to be of clearly different origins and noted that the extinct Trilobita may be so. Her conclusion was based on the functional morphology of the limbs, both locomotor and masticator. The sheer volume of morphological evidence she amassed in support of this inference was so formidable that few non-experts such as myself dared attempt to assess it. Her view of the living groups was supported by Anderson (1973), who compared their developmental morphology and concluded that features such as the fate map of the blastula are quite different. Because the developmental biologists among my colleagues usually decline comment on the fundamentality of blastular fate maps, I cannot assess this evidence either. The arguments were articulated so persuasively that they have even begun to appear in recent textbooks (e.g., Barnes 1987).

Recently, however, more conservative views have been revived, also persuasively. Hessler & Newman (1975) considered all of the living species of primitive crustaceans and mentally dissected away their specialized features, leaving behind only the primitive ones. From them they reconstructed a hypothetical primitive crustacean and concluded that it could have descended from a trilobite, which they also regarded as a viable candidate for the ancestral chelicerate. They argued that the Phylum Arthropoda is at most diphyletic and at least one reason for not favoring monophyly is that they did not even address the question of the origin of the Uniramia.

Most of the contributors to a volume on the subject (Gupta 1979) favored monophyly. While many of the arguments were based on a single character, taken together they are fairly cogent. Still more so are chapters by Clarke (1979), who broadly surveyed internal organ systems and came down in favor of monophyly, and Boudreaux (1979), who tried to show that 17 both derived and shared characters are not convergent. Boudreaux (1979), however, went to some lengths to emphasize that many of the 17 characters are the same ones used by Manton (1973, 1979) to support her case, which seems to me to indicate only the ease of alternative interpretation and thus to weaken his case.

The importance of Uniramian Hc in arthropod phylogeny.—By far the simplest interpretation of our findings is that the native arthropod Hc polymer is an 18th derived and shared character with a common, single origin. In each of the three living groups the native polymer is built of polypeptide chains of about the same size and linked to one another in the same way. In the uniramians, the crustaceans and all chelicerates except *Limulus,* the size of the chains is essentially identical; thus the monomers may be primitive features. In each group the hexamer, the basic functional unit that exhibits many of the critical respiratory features has the same size and the same appearance. The hexamer may also be a primitive character. But, the arrangement of hexamers in larger aggregates is distinctive and characteristic of the particular group. Recently, the homology (in the strict evolutionary sense) of the crustacean and chelicerate Hcs has been further documented by elegant and quite compelling structural evidence (Linzen et al. 1985, Markl 1986).

My inference does not clearly predict the condition of the blood in the onycophorans, which are variously regarded as more or less peripheral to the mainstream of uniramian evolution. H. D. Ellerton (Ellerton et al. 1983 and pers. comm.) could find none but he does not believe that his evidence is com-

Table 2.—The relationship of the respiratory properties of selected arthropod and molluscan Hcs. Data from Mangum & Lykkeboe (1979), Mangum (1983), Mason et al. (1983), Diefenbach & Mangum (1983), Mangum & Burnett (1986) and Mangum (unpubl.).

	Busycon canaliculatum	*Limulus polyphemus*	*Callinectes sapidus*
Bohr shift	reversed	reversed	normal
O_2 affinity at physiological pH	moderate	moderate	moderately low
Cooperativity	moderate	moderate	very great
Inorganic ion sensitivity	broad	broad	narrow
L-lactate sensitivity	none	none	great
Urate sensitivity	none	none	great
CO_2 sensitivity	indirect	indirect	direct

pletely decisive. Sundara Rajulu (pers. comm.) suspects that Hc may be there. If so, it will be most exciting to examine its quaternary structure.

My hypothesis does require the existence of Hc in the Trilobita. The elemental composition of trilobite fossils would be most interesting to learn, if it is technically possible.

The role of biochemical evidence in a physiological context.—Is this character more persuasive than others because it entails molecular structure and is therefore "closer to the gene"? Of course not—certainly not quaternary structure. But I suggest that it is more persuasive than Manton's and Boudreaux's morphological characters for two reasons. First, as I will show below, on good Darwinian principles this evidence cannot be interpreted alternatively. Second, we know a great deal about these molecules and how they work in living, breathing animals and so we know which features are and are not critical to respiratory function and hence subject to natural selection. The database on which my summary of structure is based consists of almost 200 Hcs. We have O_2 binding data obtained under fairly physiological conditions for about 150 arthropod and 80 molluscan Hcs. We have information on in vivo blood PO_2, pH and oxygenation state for probably several dozens of arthropods though, regrettably, only perhaps one dozen molluscs. We know how much oxygenation occurs at the gill and why, how much deoxygenation occurs at the tissues and why, and what environmental and physiolgical challenges perturb the system and how much and why. We know how big a role the Hc plays in total aerobic metabolism, that most fundamental process in life. We can make quantitative predictions of the hypothetical consequences of altering particular respiratory properties of the molecule.

Let us suppose for the moment that my conclusion is wrong, that the arthropod Hcs arose independently on three separate occasions and that their common quaternary structures are the products of convergence. If that were true, there must have been an overwhelming selection pressure for that particular structure, almost certainly to dictate particular respiratory properties. And yet no such selection pressure exists. It is very clear that the quaternary structure of a Hc does not constrain respiratory properties. I remind the reader once more that we have an actual example of a convergent Hc, the molluscan variety. And the O_2 binding properties of molluscan and arthropod Hcs, convergent molecules, can be more alike than those of two arthropod Hcs, homologous molecules (Table 2). So very similar respiratory properties can be associated with fundamentally dissimilar quaternary structures and one cannot argue that the arthropod structure was evolved repeatedly to preserve any particular respiratory properties because it simply does not do so. By far the more probable interpretation is that the arthropod structure arose only once and that it is an inherited feature that (along with others) unites at least the three living groups in a natural, monophyletic taxon.

There must be other examples of molecules understood so well at both structural and physiological levels. I shall welcome the time when physiologists and biochemists once again regard animal phylogeny as a proper subject of inquiry.

Acknowledgments

This essay was written while the author was supported by the National Science Foundation (DCB 88-16172, Physiological Processes).

Literature Cited

Anderson, D. F. 1973. Embryology and phylogeny of annelids and arthropods. Oxford, Pergamon Press, 495 pp.

Baldwin, E. 1949. An introduction to comparative biochemistry. Cambridge University Press, Cambridge, 164 pp.

———. 1953. Biochemistry and evolution.—Society for Experimental Biology, Symposium 7:22–30.

———. 1959. Dynamic aspects of biochemistry. Cambridge University Press, Cambridge, 526 pp.

———, & D. M. Needham. 1937. A contribution to the comparative biochemistry of muscular and electric tissues.—Proceedings of the Royal Society, London B 122:197–205.

———, & W. N. Yudkin. 1950. The annelid phosphagen, with a note on phosphagen in Echinodermata and Protochordata.—Proceedings of the Royal Society of London B136:614–631.

Barnes, R. D. 1987. Invertebrate zoology. W. D. Saunders & Co., Philadelphia, 893 pp.

Boudreaux, H. B. 1979. Significance of intersegmental tendon system in arthropod phylogeny and a monophyletic classification of Arthropoda. Pp. 551–556 *in* A. P. Gupta, ed., Arthropod phylogeny. Van Nostrand Reinhold Co., New York.

Clarke, K. U. 1979. Visceral anatomy and arthropod phylogeny. Pp. 467–549 *in* A. P. Gupta, ed., Arthropod phylogeny. Van Nostrand Reinhold Co., New York.

Dickerson, R. E., & I. Geis. 1969. Structure and action of proteins. Harper & Row, New York, 120 pp.

Diefenbach, C. O. da C., & C. P. Mangum. 1983. The effects of inorganic ions and acclimation salinity on hemocyanin-oxygen binding in the horseshoe crab *Limulus polyphemus.*—Molecular Physiology 4:197–206.

Ellerton, H. D., N. F. Ellerton, & H. A. Robinson. 1983. Hemocyanin—a current perspective.—Proceedings of Biophysics and Molecular Biology 41:413–248.

Ennor, A. H., & J. F. Morrison. 1958. Biochemistry of the phosphagens and related guanidines.—Physiological Reviews 38:631–674.

Field, K. G. et al. 1988. Molecular phylogeny of the animal kingdom.—Science 239:748–753.

Greenwald, I. 1946. The presence of creatine in the testes of various invertebrates.—Journal of Biological Chemistry 162:239–250.

Gupta, A. G. 1979. Arthropod phylogeny. Van Nostrand Reinhold Co., New York, 762 pp.

Hessler, R. R., & W. A. Newman. 1975. A trilobitomorph origin for the Crustacea.—Fossils and Strata 4:437–459.

Hird, F. J. R. 1986. The importance of arginine in evolution.—Comparative Biochemistry and Physiology 85B:285–288.

Imamura, T., T. O. Baldwin, & A. Riggs. 1972. The amino acid sequence of the monomeric hemoglobin component from the bloodworm *Glycera dibranchiata.*—Journal of Biological Chemistry 247:2785–2797.

Kidron, M., & R. Segal. 1984. The new state of the world atlas. Simon & Schuster, New York, no pagination.

Kuhn, T. S. 1970. The structure of scientific revolutions. University of Chicago Press, Chicago, 210 pp.

Kutscher, F., & D. Ackermann. 1933. The comparative biochemistry of vertebrates and invertebrates.—Annual Review of Biochemistry 2:355–390.

Lane, D. J., D. A. Stahl, G. J. Olsen, & N. R. Pace. 1985. Analysis of hydrothermal vent-associated symbionts by ribosomal RNA sequences.—Biological Society of Washington Bulletin 6:389–400.

Linzen, B. et al. 1985. The structure of arthropod hemocyanins.—Science 229:519–524.

Mangum, C. P. 1980. Respiratory function of the hemocyanins.—American Zoologist 20:19–38.

———. 1983. The effect of hypoxia on hemocyanin-oxygen binding in the horseshoe crab *Limulus polyphemus.*—Molecular Physiology 3:217–224.

———, & L. E. Burnett. 1986. The CO_2 sensitivity of the hemocyanins and its relationship to Cl^- sensitivity.—Biological Bulletin 171:248–263.

———, & G. Lykkeboe. 1979. The influence of inorganic ions and pH on the oxygenation properties of the blood in the gastropod mollusc *Bu-*

sycon canaliculatum.—Journal of Experimental Zoology 207:417–430.

———, K. I. Miller, J. L. Scott, K. E. Van Holde, & M. P. Morse. 1987. Bivalve hemocyanin: Structural, functional and evolutionary relationships.—Biological Bulletin 173:205–221.

———, & J. S. Rainer. 1988. The relationship between subunit composition and oxygen binding of blue crab hemocyanin.—Biological Bulletin 174:77–82.

———, J. L. Scott, R. E. L. Black, K. I. Miller & K. E. Van Holde. 1985. Centipedal hemocyanin: Its structure and its implications for arthropod phylogeny.—Proceedings of the National Academy of Science USA 82:3721–3725.

Manton, S. M. 1973. Arthropod phylogeny—a modern synthesis.—Journal of Zoology 171:111–130.

———. 1979. Uniramian evolution with particular reference to the pleuron. Pp. 317–343 *in* M. Camatini, ed., Myriapod biology. Academic Press., London.

Markl, J. 1986. Evolution and function of structurally diverse subunits in the respiratory protein hemocyanin from arthropods.—Biological Bulletin 171:90–115.

Mason, R. P., C. P. Mangum, & G. Godette. 1983. The influence of inorganic ions and acclimation salinity on hemocyanin-oxygen binding in the blue crab *Callinectes sapidus.*—Biological Bulletin 164:104–123.

Needham, D. M., J. Needham, E. Baldwin, & J. Yudkin. 1932. A comparative study of the phosphagens with some remarks on the origins of vertebrates.—Proceedings of the Royal Society of London B110:260–272.

Pace, N. R., D. A. Stahl, D. J. Lane, & G. J. Olsen. 1986. The analysis of natural microbial populations by rRNA sequences.—Advances in Microbial Ecology 9:1–56.

Snyder, G. K., & C. P. Mangum. 1982. The relationship between the size and shape of an extracellular oxygen carrier and the capacity for oxygen transport. Pp. 173–188 *in* J. Bonaventura, C. Bonaventura, & S. Tesh, eds., Physiology and biology of horseshoe crabs. Allan Liss Co., New York.

Sundara Rajulu, G. 1969. Presence of haemocyanin in the blood of a centipeded *Scutigera longicornis* (Chilopoda: Myriapoda).—Current Science 38:168–169.

Van Holde, K. E., & K. I. Miller. 1982. Haemocyanins.—Quarterly Review of Biophysics 15:1–129.

van Thoai, N., & Y. Robin. 1969. Guanidine compounds and phosphagens. Pp. 163–204 *in* M. Florkin & B. T. Scheer, eds., Chemical zoology Vol. IV, Academic Press., New York.

Weber, R. E., C. Mangum, H. Steinman, C. Bonaventura, B. Sullivan, & J. Bonaventura. 1977. Hemoglobins of two terebellid polychaetes: *Enoplobranchus sanguineus* and *Amphitrite ornata.*—Comparative Biochemistry and Physiology 56A:179–187.

Zuckerkandl, E., & L. Pauling. 1965. Molecules as documents of evolutionary history.—Journal of Theoretical Biology 8:357–366.

Department of Biology, College of William and Mary, Williamsburg, Virginia 23185.

PROC. BIOL. SOC. WASH.
103(1), 1990, pp. 248–253

SIX NEW COMBINATIONS IN *BACCHAROIDES* MOENCH AND *CYANTHILLIUM* BLUME (VERNONIEAE: ASTERACEAE)

Harold Robinson

Abstract.—Three species, *Vernonia adoensis* Schultz-Bip. ex Walp., *V. guineensis* Benth., and *V. lasiopus* O. Hoffm. in Engl., are transferred to the genus *Baccharoides* Moench, and three species, *Conyza cinerea* L., *C. patula* Ait., and *Herderia stellulifera* Benth. are transferred to the genus *Cyanthillium* Blume.

The present paper provides six new combinations of Old World Vernonieae that are known to belong to the genera *Baccharoides* Moench and *Cyanthillium* Blume. The applicability of these generic names to these species groups was first noted by the author almost ten years ago (Robinson et al. 1980), and it was anticipated that other workers more familiar with the paleotropical members of the Vernonieae would provide the necessary combinations. A recent study of eastern African members of the tribe by Jeffrey (1988) also cites these generic names as synonyms under his *Vernonia* Group 2 subgroup C and *Vernonia* Group 4, although he retains the broad concept of *Vernonia.* At this point it is not certain when anyone will undertake more detailed studies of these groups. However, the author does need to refer to a few members of these genera and does not intend to use older, incorrect names. Instead of making isolated combinations as needed, as was done with *Gymnanthemum coloratum* (Robinson & Kahn 1986), an effort is made here to place needed combinations together in one paper. Detailed monographic studies and the majority of the combinations are left to future workers. In spite of the limited scope of the present effort, some explanation is offered.

The summary of the Vernonieae by S. B. Jones (1977) showed that the Eastern Hemisphere species placed in the genus *Vernonia* were all chemically and cytologically distinct from the Western Hemisphere members of that genus. Although generic limits were not discussed by Jones, his study placed the Old World *Vernonia* in a group on the opposite side the basic division in the genus from typical *Vernonia* in the eastern United States. Subsequent studies by Jones (1979b, 1981) showed that certain pollen types also were restricted to Old World members of *Vernonia* s.l., types that are shared by some Old World members of the tribe traditionally placed in other genera. The characters noted by Jones have been treated by the present author as evidence of a basic division in the Vernonieae between groups that have included many genera in each hemisphere, and traditional *Vernonia* s.l. can be seen as an excessively paraphyletic core genus that is defined only by what "it is not" rather than by what "it is." In progressing toward definitive generic concepts in the Vernonieae, the pattern seen by Jones justifies removing at least all of the Eastern Hemisphere members of the tribe from *Vernonia.* This segregation of the Old World genera was partially put into practice by the use of the names *Baccharoides* Moench, *Gymnanthemum* Cass., and *Cyanthillium* Blume, by Robinson et al. (1980) and in the transfers made in the study of *Distephanus* Cass. (Robinson & Kahn 1986).

At present there is good reason not to transfer all the Old World species of *Vernonia* out of the genus. Morphological and anatomical studies show the problem is more complex than one Old World genus versus one New World genus. Several genera should be recognized in both the neotropical and paleotropical elements of *Vernonia* s.l. More detailed studies of the type under way in neotropical species (Robinson 1987a, b, c, 1988a, b, c, 1989; Robinson & Funk 1987) are needed before all transfers can be made properly. Nevertheless, the position of some of the species is fully resolved, especially of species belonging to older segregate genera such as *Baccharoides* and *Cyanthillium.*

The lack of total resolution of the tribe is not a reason to retain under *Vernonia* s.l. names and concepts known to be obsolete. The author believes that *Vernonia* will ultimately be restricted to Western Hemisphere species with non-lophate type A pollen and a chromosome number of N = 17 and will perhaps be restricted to only the eastern North American element of that group.

The detailed variations of pollen in the tribe are to be more fully compared and illustrated elsewhere. The generic synonymies follow mostly those of Jeffrey (1988), but some additional synonymy is provided under *Cyanthillium.*

Baccharoides Moench

Baccharoides Moench, Methodus. 528. 1794. Type: *Conyza anthelmintica* L. (=*B. anthelmintica* (L.) Moench).

Ascaricida Cass., Dict. Sci. Nat. 3, suppl. 38. 1817, nom. superfl. Type: *Conyza anthelmintica* L.

Candidea Tenore, Atti Reale Accad. Sci. Sez. Soc. Reale Borbon 4 (Cl. Botan.): 104, t. 1, 2. 1839. Type: *Candidea senegalensis* Tenore.

Vernonia subsect. *Stengelia* Schultz-Bip. ex Walp., Repert. Bot. Syst. 2: 946. 1843. *Vernonia adoensis* Schultz-Bip. ex Walp.

Stengelia Steetz in Peters, Naturw. Reise Mossambique, Bot. 360. 1864. Type: *Vernonia schimperi* DC.

Vernonia sect. *Stengelia* (Schultz-Bip. ex Walp.) Benth. in Benth. & Hook. f., Gen. Pl. 2: 127. 1873.

This group of species has been imperfectly recognized in the past, primarily on the basis of expanded foliose appendages on the involucral bracts. The character is well developed in the genus but is not a reliable basis for distinction. Smith (1971) studied a group titled the "stengelioid species" of *Vernonia,* but many species included in the study were not *Baccharoides.* Smith recognized the heterogeneity in the group he treated, especially in the form of the pollen and in the shape of the corolla, but these were not detailed for all of the species.

More recently, Kingham (1976), Jones (1981), Jeffrey (1988), and the present author have studied *Baccharoides* pollen in more detail. It is lophate and distinctive among Old World tricolporate Vernonieae by the presence of polar areoles. The grains fall into Jones' (1981) Type C, although pollens of all species studied in detail are different from most Type C pollen of the Neotropics by the 3 equatorial areoles of the intercolpi and the strong basal columellae under the crests of the exine.

Jeffrey (1988) emphasized the pollen, the flattened inner pappus bristles, and the corollas with long, slender, basal tubes and abruptly expanded cylindrical limbs and comparatively short erect lobes as definitive characters of *Baccharoides* within *Vernonia* s.l.

Ignoring some older counts, the genus seems to have a consistent chromosome number of N = 10 (Smith 1971, Jones 1979a). The group is also notable for the presence of epoxy resins and has been studied for possible commerical exploitation. Neither the chromosome number nor the chemistry is unique to the genus.

Many of the species are understood well enough to justify new combinations, but most of these, and others not known to the present author, are left for final resolution by other workers. The species listed by Smith

(1971) are an artificial group and the Smith paper should not be used without reference to the discussion by Jeffrey (1988). Except for its discussion of the Smith paper, the Jeffrey study itself is limited to East African species. It seems that a monograph of the genus would be comparatively simple for someone with better resources to study paleotropical plants, for most of the species occur in Africa. One species was described from Arabia, and the widely distributed type species was described from Sri Lanka.

The three species combinations needed at present are as follows:

BACCHAROIDES ADOENSIS
(Schultz-Bip. ex Walp.)
H. Robinson, comb. nov.

Vernonia adoensis Schultz-Bip. ex Walp., Repert. Bot. Syst. 2:946. 1843. For extensive synonymy see Smith (1971) and Jeffrey (1988). Distribution is subsaharan Africa with concentration in the east (Smith 1971, map p. 19).

BACCHAROIDES GUINEENSIS
(Benth. in Hook. f. & Benth.)
H. Robinson, comb. nov.

Vernonia guineensis Benth. in Hook. f. & Benth., Niger Fl. 427. 1849. For extensive synonymy see Smith (1971). Distribution is subsaharan Africa from Sierra Leone in the west eastward to western Tanzania and south to southwestern Angola and northern Zimbabwe (Smith 1971, map p. 48).

BACCHAROIDES LASIOPUS
(O. Hoffm. in Engl.)
H. Robinson, comb. nov.

Vernonia lasiopus O. Hoffm. in Engl., Pflanzew. Ost. Afrika 403. 1895. For extensive synonymy see Smith (1971). The species ranges from western Ethiopia to northeastern Angola and northeastern Zimbabwe (Smith, 1971, map p. 38).

Cyanthillium Blume

Cyanthillium Blume, Bijdr. Fl. Ned. Ind. 889. 1826. Lectotype (designated here): *Cyanthillium villosum* Blume.

Isonema Cass., Bull. Soc. Philom. Paris 1817:152. 1817, nom. illeg., non R. Br. (1810). Type: *Isonema ovata* Cass.

Cyanopis Blume ex DC., Prodr. 5:69. 1836, nom. illeg. et superfl., non Cass. (1817). Lectotype (Jones 1980): *Cyanthillium villosum* Blume.

Vernonia sect. *Tephrodes* DC., Prodr. 5:24. 1836. Lectotype (Jones 1981): *Conyza cinerea* L.

Claotrachelus Zoll. & Mortiz ex Zoll., Natuur-Geneesk. Arch. Ned Indië 2:263, 565. 1845. Type: *Claotrachelus rupestris* Zoll. & Moritz ex Zoll.

Seneciodes L. ex Post & O. Kuntze, Lex. Gen. Phan. 2:515. 1903. Type: *Conyza cinerea* L.

Triplotaxis Hutch., Bull. Misc. Inform. 1914:355. 1914. Lectotype: *Herderia stellulifera* Benth. in Hook.

Vernonia subsect. *Orbivestus* S. B. Jones, Rhodora 83:61. 1981. Lectotype (Jeffrey 1988): *Vernonia karaguensis* Oliv. & Hiern.

Vernonia subsect. *Hilliardianae* S. B. Jones, Rhodora 83:66. 1981. Lectotype (Jeffrey 1988): *Webbia oligocephala* DC.

Vernonia subsect. *Tephrodes* (DC.) S. B. Jones, Rhodora 83:70. 1981.

The designation of a new lectotype for *Cyanthillium* rejects the earlier choice of *C. moluccense* that seems to date from Jones (1980). Jones' selection was totally arbitrary, being the first species listed by Blume without any evident study of the group involved, and thus can be rejected under the Code. The lectotype cited by Jeffrey (1988) evidently follows Jones. Jones' lectotypification is unsuitable because the species is virtually unknown, being available to most botanists only as a microfiche of the fragment in the DeCandolle herbarium at Geneva. The fragment *C. moluccense* as seen in the microfiche may be a *Cyanthillium.* The choice in this paper brings the typification into conformity with those of the synonyms, the superfluous generic name *Cyanopis* Blume and the homonym *Isonema* Cass., which both equal *Cyanthillium patula.*

It is unfortunate that many Flora formats now require types to be selected for all generic names, even those treated as synonyms. Although the intention is noble, the result is too often poorly chosen lectotypes, made by unqualified investigators.

Any study of *Cyanthillium* should include a study of members of *Erlangea* Schultz-Bip. (1853). The type, *E. plumosa* Schultz-Bip., of Gabon, is known to the author only from its description. *Erlangea* is technically distinguished from *Vernonia* s.l. and that part recognized here as *Cyanthillium* by the five, deciduous pappus segments that have been referred to as plumose. The type of *Erlangea* is described with sessile amplexicaule leaves, a feature that would be unusual in the usually narrowly petiolate *Cyanthillium.* As described, the type of *Erlangea* has a habit similar to *Vicoa* (*Inula*) *auriculata* Cass. and it may be close to *Erlangea schinzii* O. Hoffm. of northernmost Namibia, which also has sessile leaves. Examination of material matching the description of the type, and further evaluation of the pappus distinction, may show that the genus falls fully into the synonymy of *Cyanthillium.*

The genus *Cyanthillium* owes its early recognition to the presence of a deciduous pappus in the species group that includes the lectotype species. The broad achene and short deciduous pappus of *C. patula* places this species outside of typical *Vernonia.* Other pappus variations occur in *Cyanthillium* and have been the basis of further generic distinctions. The type species of *Triplotaxis* has a very distinctive, collar-like outer pappus that persists after the inner pappus has completely fallen. Other species from Africa that are described as having a pappal ring don't have the highly distinctive structure seen in *Triplotaxis* but have only a moderately expanded upper callus on the achene of a form seen in many Asteraceae. The latter species are not closely related to *Cyanthillium.* Other members of *Cyanthillium,* such as *C. cinereum,* have achene and pappus structures like those of typical *Vernonia,* without unusual rings or fragility. Because of the differences in pappus structure listed above, the species now placed in *Cyanthillium* were not suspected of forming a related group separate from *Vernonia* until the pollen study by Kingham (1976) and the recent study by Jeffrey (1988). Nevertheless, the species seem to share a generally herbaceous habit, herbaceous and usually narrowly petiolate leaves, and broadly to narrowly ovate, slightly acuminate involucral bracts, often with greenish outer surfaces and purplish margins. Jeffrey (1988) mentions various forms of T-shaped hairs in members of the group.

The pollen type of *Cyanthillium* is one of the many paleotropical types in the Vernonieae in which the colpus is not evident. Studies by the author show that the polar areas of the grains have a polar areole surrounded by a tier of five to seven areoles that variously match or straddle or fall between the pores below them. The polar organization is basically different from forms in the tribe that have well developed colpi. In the present group there is not even a consistent single areole above or below the pores. The major organizational feature of the grain is centered on the poles rather than the pores. SEM studies show that members of *Cyanthillium* are distinctive within the non-colporate species of the Old World by the modification of the basal columellae of the exine to form bridges under the crests. Points of attachment of the exine to the footlayer seem to be restricted to positions under the intersections of the crests. The precise pollen form is not presently known outside the genus, although similar forms without modified basal columellae are known in species belonging to the group cited by Jeffrey (1988), for which the name *Crystallopollen* Steetz in Peters seems to have priority.

The few available chromosome numbers in *Cyanthillium* fall within the range noted for paleotropical members of the tribe. Jones (1979a) reported N = 20 for *C. stelluliferum* (as *Triplotaxis*). This seems to be based on *X* = 10. Jones reported N = 9, 18, and ca. 18 for the widespread adventive *C. cinereum.* Jones also reported N = 10 for two species of the closely related genus *Erlangea,* including *E. remifolia* Wild & Pope, which I suspect is a member of *Cyanthillium.*

Cyanthillium has problems not seen in *Baccharoides,* and a monograph will be more difficult. The distribution is throughout the paleotropical region, and there are many variations within the group in obvious characters such as the achene and pappus.

The three combinations needed at present are as follows:

CYANTHILLIUM CINEREUM (L.)
H. Robinson, comb. nov.

Conyza cinerea L., Sp. Pl. 862. 1753.
Vernonia cinerea (L.) Less., Linnaea 4:291. 1829.
Senecioniodes cinerea (L.) Post & O. Kuntze, Lex. Gen. Phan. 2:515. 1903.

The species is the most widely distributed member of the genus. It occurs throughout the paleotropical region and is widely adventive in the Neotropics.

CYANTHILLIUM PATULUM (Ait.)
H. Robinson, comb. nov.

Conyza patula Ait., Hortus Kew. 3:184. 1789.
Isonema ovata Cass., Bull. Soc. Philom. Paris 1817: 152. 1817.
Conyza chinensis Lam., Encycl. 2:83. 1786, hom. illeg., non L.
Cyanthillium villosum Blume, Bijdr. Fl. Ned. Ind. 889. 1826.
Cyanthillium pubescens Blume, Bijdr. Fl. Ned. Ind. 890. 1826.
Centratherum chinense [Lam.] Less., Linnaea 4:320. 1829.
Vernonia chinensis (Less.) Less., Linnaea 6: 105, 674. 1831.
Cyanopis madagascariensis DC., Prodr. 5: 69. 1836.
Vernonia pratensis Klatt, Ann. K. K. Naturhist. Hofmus. 7:99. 1892.
Cacalia patula (Less.) O. Kuntze, Rev. Gen. Pl. 324. 1894.
Cyanthillium chinense (Lam.) Gleason, Bull. Torrey Bot. Club 40:306. 1913.

The species is cited by Gleason (1922) as occurring in tropical Asia, the East Indies, and being introduced into Guadeloupe. The species is now also credited to Madagascar on the basis of the newly synonymized *Cyanopsis madagascariensis* and *Vernonia pratensis.*

CYANTHILLIUM STELLULIFERUM (Benth.)
H. Robinson, comb. nov.

Herderia stellulifera Benth. in Hook. f. & Benth., Niger Fl. 425. 1849.
Triplotaxis stellulifera (Benth.) Hutch., Bull. Misc. Inform. 1914:356. 1914.

The distribution given by Jeffrey (1988) is Uganda, west and central tropical Africa and Angola.

Literature Cited

Gleason, H. A. 1922. Tribe 1. Vernonieae.—North American Flora 33:47–110.

Jeffrey, C. 1988. The Vernonieae in East Tropical Africa.—Kew Bulletin 43:195–277.

Jones, S. B. 1977. Vernonieae—Systematic review. Pp. 503–521 *in* V. H. Heywood et al., eds., The biology and chemistry of the Compositae. Academic Press, London, New York, 1189 pp.

———. 1979a. Chromosome numbers of Vernonieae (Compositae).—Bulletin of the Torrey Botanical Club 106:79–84.

———. 1979b. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the New World.—Rhodora 81:425–447.

———. 1980. Tribe Vernonieae. *In* J. F. Macbride, ed., Flora of Peru.—Fieldiana, Botany n. s. 5: 22–69.

———. 1981. Synoptic classification and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the Old World.—Rhodora 83:59–75.

Kingham, D. L. 1976. A study of the pollen morphology of tropical African and certain other Vernonieae (Compositae).—Kew Bulletin 31:9–26.

Robinson, H. 1987a. Studies of the *Lepidaploa* complex (Vernonieae: Asteraceae). I. The genus *Stenocephalum* Sch.Bip.—Proceedings of the Biological Society of Washington 100:578–583.

———. 1987b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). II. A new genus, *Echinocoryne.*—Proceedings of the Biological Society of Washington 100:563–589.

———. 1987c. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). III. Two new genera, *Cyrtocymura* and *Eirmocephala.*—Proceedings of the Biological Society of Washington 100: 844–855.

———. 1988a. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). IV. A new genus, *Lessingianthus.*—Proceedings of the Biological Society of Washington 101:929–951.

———. 1988b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). V. A new genus, *Chrysolaena.*—Proceedings of the Biological Society of Washington 101:952–958.

———. 1988c. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). VI. A new genus, *Aynia.*—Proceedings of the Biological Society of Washington 101:959–965.

———, & V. A. Funk. 1987. A phylogenetic analysis of *Leiboldia, Lepidonia,* and a new genus *Stramentopappus* (Vernonieae: Asteraceae).—Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 108:213–228.

———, & B. Kahn. 1986. Trinervate leaves, yellow flowers, tailed anthers, and pollen variation in *Distephanus* Cassini (Vernonieae: Asteraceae).—Proceedings of the Biological Society of Washington 99:493–501.

———, F. Bohlmann, & R. M. King. 1980. Chemosystematic notes on the Asteraceae. III. Natural subdivisions of the Vernonieae.—Phytologia 46:421–436.

Schultz-Bip., C. H. 1853. Triga novorum Cassiniacearum generum.—Flora 36:33–38.

Smith, C. E. 1971. Observations on stengelioid species of *Vernonia.* Agriculture Handbook no. 396. U.S.D.A., Agricultural Research Service.

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, SW7 5BD

Applications Published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 29 September 1989 in Vol. 46, Part 1 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, ICZN, British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

Case No.

2652 CHORISTIDAE Verrill, 1882 (Mollusca, Gastropoda) and CHORISTIDAE Esben-Petersen, 1915 (Insecta, Mecoptera): a proposal to remove the homonymy.

2682 *Fryeria* Gray, 1853 and *F. rueppelii* Bergh, 1869 (Mollusca, Gastropoda): proposed conservation.

2662 *Aphonopelma* Pocock, 1902 (Arachnida, Araneae) proposed precedence over *Rhechostica* Simon, 1892.

2696 *Ixodes angustus* Neumann, 1899 and *I. woodi* Bishopp, 1911 (Arachnida, Acari): proposed conservation by the replacement of the holotype of *I. angustus* by a neotype.

2672 *Castiarina* Gory & Laporte, 1837 (Insecta, Coleoptera): proposed conservation.

2690 *Helophorus brevipalpis* Bedel, 1881 (Insecta, Coleoptera): proposed precedence over *Helophorus creticus* Kiesenwetter, 1858.

2689 *Helophorus obscurellus* Poppius, 1907 (Insecta, Coleoptera): proposed precedence over *Helophorus fausti* Kuwert, 1887.

2716 *Ceratopogon puncticoollis* Becker, 1903 (currently *Culicoides puncticollis*; Insecta, Diptera): proposed precedence over *Ceratopogon algecirensis* Strobl, 1900.

2673 *Micropterus patachonicus* King, 1831 and *Anas pteneres* Forster, 1844 (both currently in *Tachyeres* Owen, 1875; Aves, Anseriformes): proposed conservation of the specific names.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Opinions Published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 29 September 1989 in Vol. 46, Part 1 of the *Bulletin of Zoological Nomenclature.*

Opinion

1549 EUGLENIDAE Stein, 1878 (Protista, Flagellata) and EUGLENIDAE Seidlitz, 1875 (Insecta, Coleoptera): homonymy removed, and ADERIDAE Winkler, 1927 (Insecta, Coleoptera): given precedence over EUGLENESIDAE Seidlitz, 1875.

1550 *Dysidea* Johnston, 1842 (Porifera, Keratosa): conserved.

1551 *Hypsibius* Ehrenberg, 1848 (Tardigrada): *Macrobiotus dujardini* Doyère, 1840 designated as the type species.

1552 *Dioctophyme* Collet-Meygret, 1802 (Nematoda): spelling confirmed.

1553 ATYIDAE De Haan, [1849] (Crustacea, Decapoda) and ATYIDAE Thiele, 1925 (Mollusca, Gastropoda): homonymy removed.

1554 *Cryptocoeloma* Miers, 1884 (Crustacea, Decapoda): *Cryptocoeloma haswelli* Rathbun, 1923 designated as the type species.

1555 *Parasigara* Poisson, 1957 (Insecta, Heteroptera): *Corisa transversa* Fieber, 1848 confirmed as the type species.

1556 *Dytiscus ater* De Geer, 1774 (currently *Ilybius ater*) and *Dytiscus planus* Fabricius, 1781 (currently *Hydroporus planus*; Insecta, Coleoptera): specific names conserved.

1557 *Elachista* Treitschke, 1833 (Insecta, Lepidoptera): conserved, and *E. bifasciella* Treitschke, 1833 confirmed as the type species.

1558 *Dacus parallelus* Wiedemann, 1830 (currently *Anastrepha parallela*; Insecta, Diptera): lectotype replaced.

1559 *Ludita* Nagy, 1967 (Insecta, Hymenoptera): *Tiphia villosa* Fabricius, 1793 designated as the type species.

1560 *Asterias squamata* Delle Chiaje, 1828 (currently *Amphipholis squamata*; Echinodermata, Ophiuroidea): specific name conserved.

1561 *Climacograptus manitoulinensis* Caley, 1936 (currently *Paraclimacograptus manitoulinensis*; Graptolithina): specific name conserved.

1562 *Anabas oxyrhynchus* Boulenger, 1902 (currently *Ctenopoma oxyrhynchum*; Osteichthyes, Perciformes): specific name not conserved.

1563 *Heliases ternatensis* Bleeker, 1856 (currently *Chromis ternatensis*; Osteichthyes, Perciformes): specific name conserved, and *Chromis viridis* (Cuvier, 1830): name adopted for the fish formerly known as *C. caerulea* (Cuvier, 1830).

1564 *Neamia octospina* Smith & Radcliffe in Radcliffe, 1912 (Osteichthyes, Perciformes): specific name conserved.

1565 *Platanista* Wagler, 1830 (Mammalia, Cetacea): conserved.

1566 *Megaloceros* Brookes, 1828 (Mammalia, Artiodactyla): original spelling emended.

REVIEWERS

The following people reviewed manuscripts for the *Proceedings* in 1989. A. Alvariño; W. D. Anderson, Jr.; C. Baldwin; R. C. Banks; K. Banse; J. Barlow; A. Bauer; A. R. Beaumont; R. L. Bezy; R. Bleiweiss; W. Blow; J. Bouillon; T. E. Bowman; G. Boxshall; G.-O. Brandorff; R. O. Brinkhurst; B. Brown; W. C. Brown; N. L. Bruce; R. C. Brusca; J. S. Buckeridge; J. E. Cadle; S. D. Cairns; D. R. Calder; D. K. Camp; A. F. Campaner; E. Campos; D. Canatella; M. D. Carleton; J. Carlton; R. S. Carney; J. L. Carr; F. A. Chace, Jr.; B. Chernoff; E. Coan; S. L. Coats; J. S. H. Collins; B. C. Coull; J. Cracraft; R. F. Cressey; R. I. Crombie; A. Crosnier; G. M. Davis; H. J. Dumont; R. J. Emry; S. Farkus, K. Fauchald; D. L. Felder; R. M. Feldman; S. V. Fink; W. L. Fink; J. F. Fitzpatrick, Jr.; B. A. Foster; L. R. Franz; R. C. Froeschner; V. A. Funk; A. L. Gardner; J. Garth; R. D. Gordon; G. R. Graves; K. Green; H. Griffith; C. Hand; A. S. Harold; G. Hartmann; L. R. Heaney; R. Heard; J. W. Hedgpeth; G. F. Hevel; R. W. Heyer; R. P. Higgins; A. Hirayama; J. Ho; J. T. Høeg; R. S. Hoffmann; J. R. Holsinger; W. D. Hope; P. Hutchins; T. Itô; K. Izawa; N. K. Johnson; J. Just; Z. Kabata; S. J. Keeley; B. Kensley; P. Knight-Jones; K. F. Koopman; R. K. Kropp; J. D. Kudenov; D. B. Lellinger; R. B. Manning; J. C. Markham; J. W. Martin; W. N. Mathis; R. W. McDiarmid; P. A. McLaughlin; J. G. Mead; M. Milligan; C. Mitchell; T. Miura; R. F. Modlin; B. L. Monroe; H. Morino; K. M. Muzik; C. W. Myers; P. Myers; N. A. Neff; D. Nelson; W. A. Newman; S. L. Olson; J. M. Orensanz; K. C. Parks; D. C. Parris; E. C. Peters; R. H. Pine; D. Polhemus; C. W. Potter; H. D. Pratt; R. J. Raikow; S. Rainer; J. V. Remsen; K. Reutzler; J. W. Reynolds; K. Riemann-Zueneck; C. B. Robbins; C. E. da Rocha; G. Rodriguez; R. H. Rosenblatt; D. Russell; J. M. Savage; S. A. Schaefer; H.-K. Schminke; R. T. Schuh; M. Schwartz; N. J. Scott; M. E. Seidel; W. F. Smith-Vaniz; V. G. Springer; D. H. Staples; W. C. Starnes; G. C. Steyskal; J. H. Stock; R. E. Strauss; J.-O. Stromberg; M. Telford; A. Tsukagoshi; M. Türkay; J.-W. Wagele; T. R. Waller; L. Watling; M. J. Wetzel; A. B. Williams; G. Wilson; W. W. Wirth; T. Yamaguchi; H. C. Yeatman; G. R. Zug; V. A. Zullo; R. L. Zusi.

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 Stop 108, Smithsonian Institution, Washington, D.C. 20560.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed in order of receipt by a board of Associate Editors and appropriate referees.

Proofs.—First proofs are submitted to authors for correction and approval. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, changes at proof stages, and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

Presentation.—Manuscripts should be typed **double-spaced throughout** (including tables, legends, and footnotes) on one side of 8½ × 11 inch sheets, with at least one inch of margin all around. Submit three copies complete with tables, figure captions, and figures (plus originals of the illustrations), and retain an author's copy. Pages must be numbered consecutively. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s') Address(es), Appendix, Figure Legends, Figures (each numbered and identified), Tables (**double-spaced throughout,** each table numbered with an Arabic numeral and with heading provided).

Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is required for descriptions and diagnoses. Literature citations in the text should be in abbreviated style (author, date, page), except in botanical synonymies, with unabbreviated citations of journals and books in the Literature Cited sections. Direct quotations in the text must be accompanied by author, date, **and pagination.** The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate figure and table placement in pencil in the margin of the manuscript. Plan illustrations in proportions that will efficiently use space on the type bed of the Proceedings. **Original illustrations should not exceed 15 × 24 inches.** Figures requiring solid black backgrounds should be indicated as such when the manuscript is submitted, but should not be masked.

CONTENTS

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 103 NUMBER 2
28 JUNE 1990
ISSN 0006-324X

PROCEEDINGS

Editor: C. Brian Robbins

Associate Editors

Classical Languages: George C. Steyskal
Plants: David B. Lellinger
Insects: Wayne N. Mathis
Invertebrates: Stephen D. Cairns
Frank D. Ferrari
Rafael Lemaitre
Vertebrates: G. David Johnson

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

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

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

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

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 257–264

PORITES COLONENSIS, NEW SPECIES OF STONY CORAL (ANTHOZOA: SCLERACTINIA) OFF THE CARIBBEAN COAST OF PANAMA

Vassil N. Zlatarski

Abstract.—A new species of *Porites* (*P. colonensis*) from off the Caribbean coast of Panama is described. It is common and has very thin, undulated, foliaceous colonies; pali; and has dark brown or red tissues with white or green polyp centers.

New species of shallow water corals are unusual, particularly in an area frequently visited by reef investigators. The new scleractinian from Panama, described below, is common, and very easily distinguished underwater and in the laboratory by color, colony shape, and skeletal elements.

Order Scleractinia Bourne, 1900
Suborder Fungiida Duncan, 1884
Superfamily Poritioidea Gray, 1842
Family Poritidae Gray, 1842
Genus *Porites* Link, 1807

not *Porites* Cuvier, 1798:678–679 (=*Galaxea* Oken, 1815; *Dendrophyllia* Blainville, 1830; *Mussa* Oken, 1815 sensu Veron and Pichon, 1982:141). (A proposal to suppress *Porites* Cuvier, 1798 is necessary in order to validate the priority of Link's authorship.)
Porites Link, 1807:162.
Neoporites Duchassaing & Michelotti, 1866: 191.
Cosmoporites Duchassaing & Michelotti, 1866:193.

Type species.—*Porites polymorphus* Link, 1807 (by tautonomy) = *Madrepora porites* Pallas, 1766 (in part).

This genus is cosmopolitan. Eocene-Recent. Abundant reef coral since Miocene.

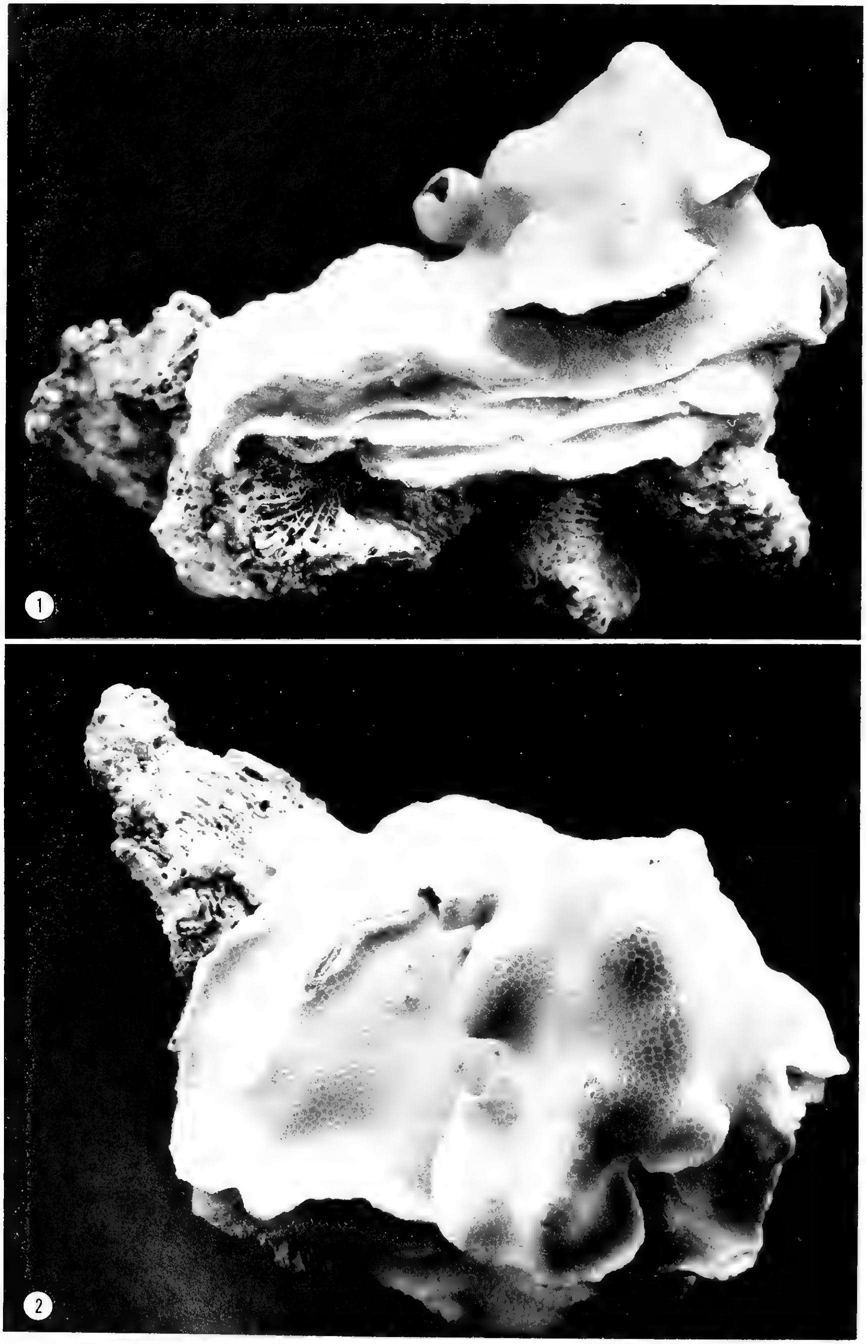
Porites colonensis, new species
Figs. 1–20

Etymology.—From the name of the town of Colon, Panama.

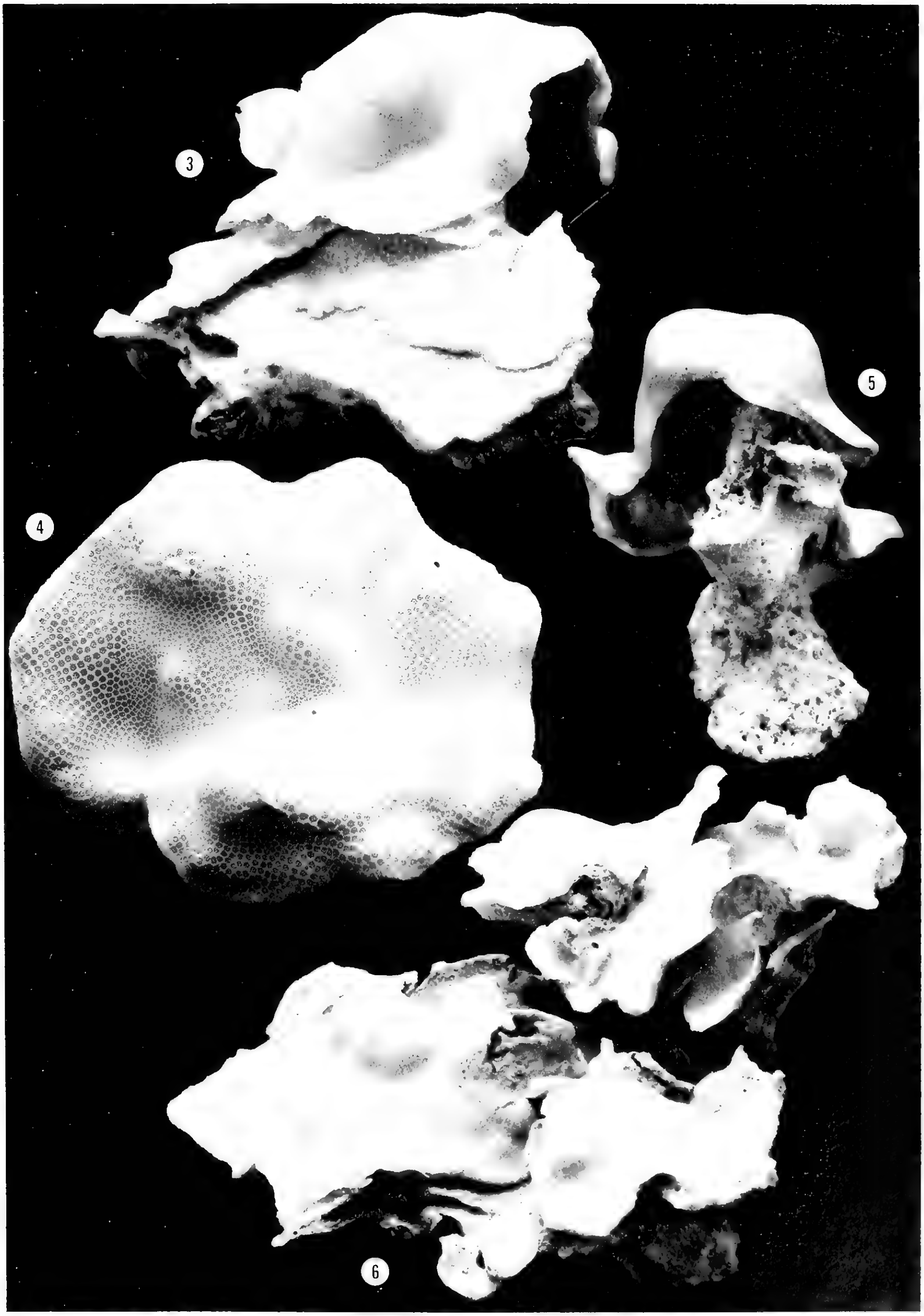
Diagnosis.—*Porites* with very thin, foliaceous, undulated colonies. Lower surface with concentric holotheca. Corallites distinct to poorly distinguishable. Axial structure absent (empty fossa) or present (from weak columella to massive columella with a central tubercle). Septal plan bisymmetrical, more or less clear; a dorsal directive septum, a ventral directive septum with two other septa fuse in triplet and four lateral pairs of septa arranged symmetrically in relation to the dorso-ventral axis. Five pali (one on the triplet, and one on each lateral pair), seldom six pali. Tissue color: ordinarily polyps are very dark brown with small bright white centers; polyps may be dark red with green centers. Distinguishing characters: foliaceous colony shape, presence of pali, and the dark (brown or red) color of the polyp with contrasting white or green centers.

Holotype.—USNM 82020 (Figs. 1, 2 and 7): Length 112 mm, width 93 mm, height 74 mm, thickness of the folia at peripheral edge 1–4 mm; collected 20 Aug 1987 by V. Zlatarski and H. Guzman.

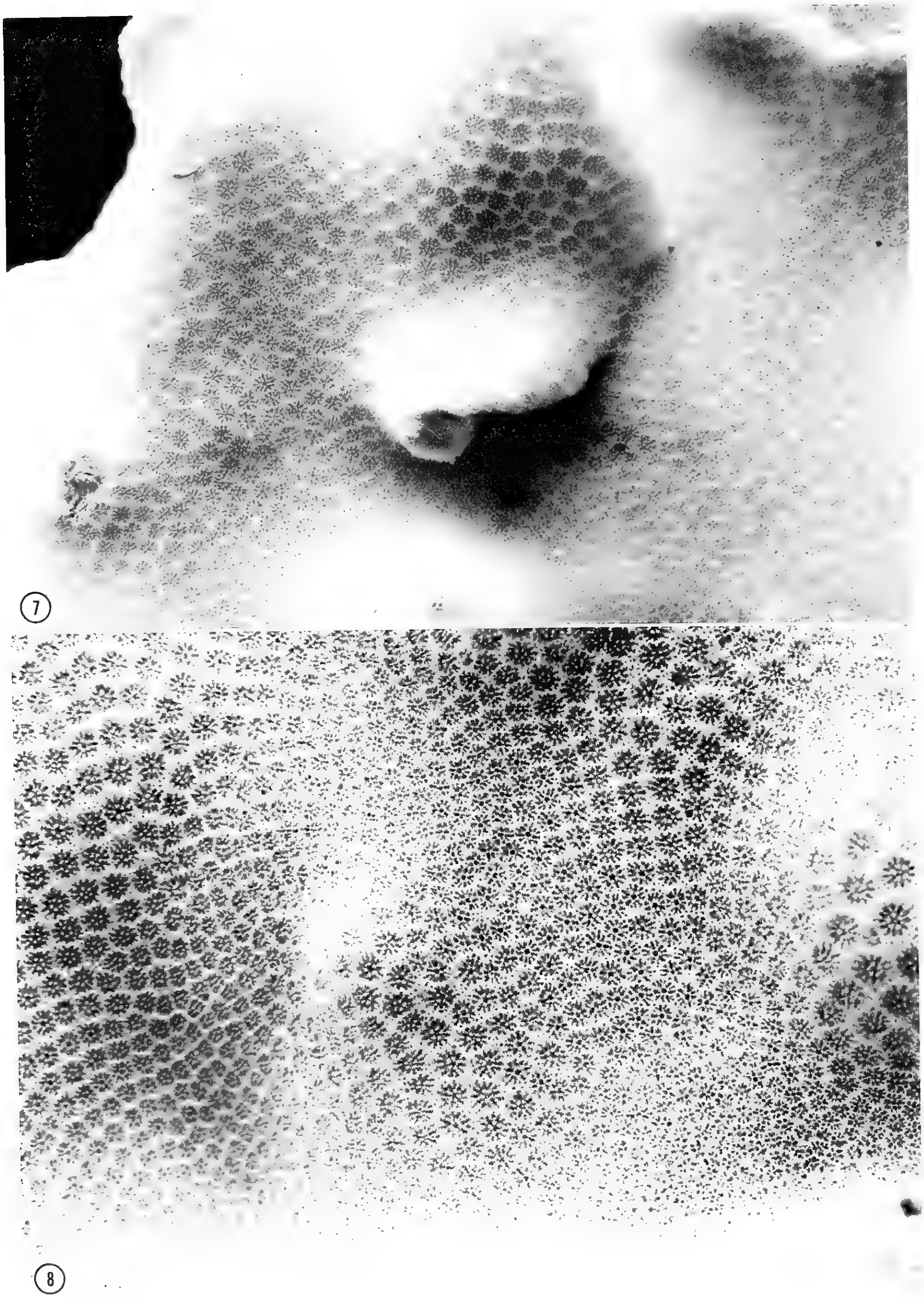
Paratypes.—USNM 82021–82054 (Figs.



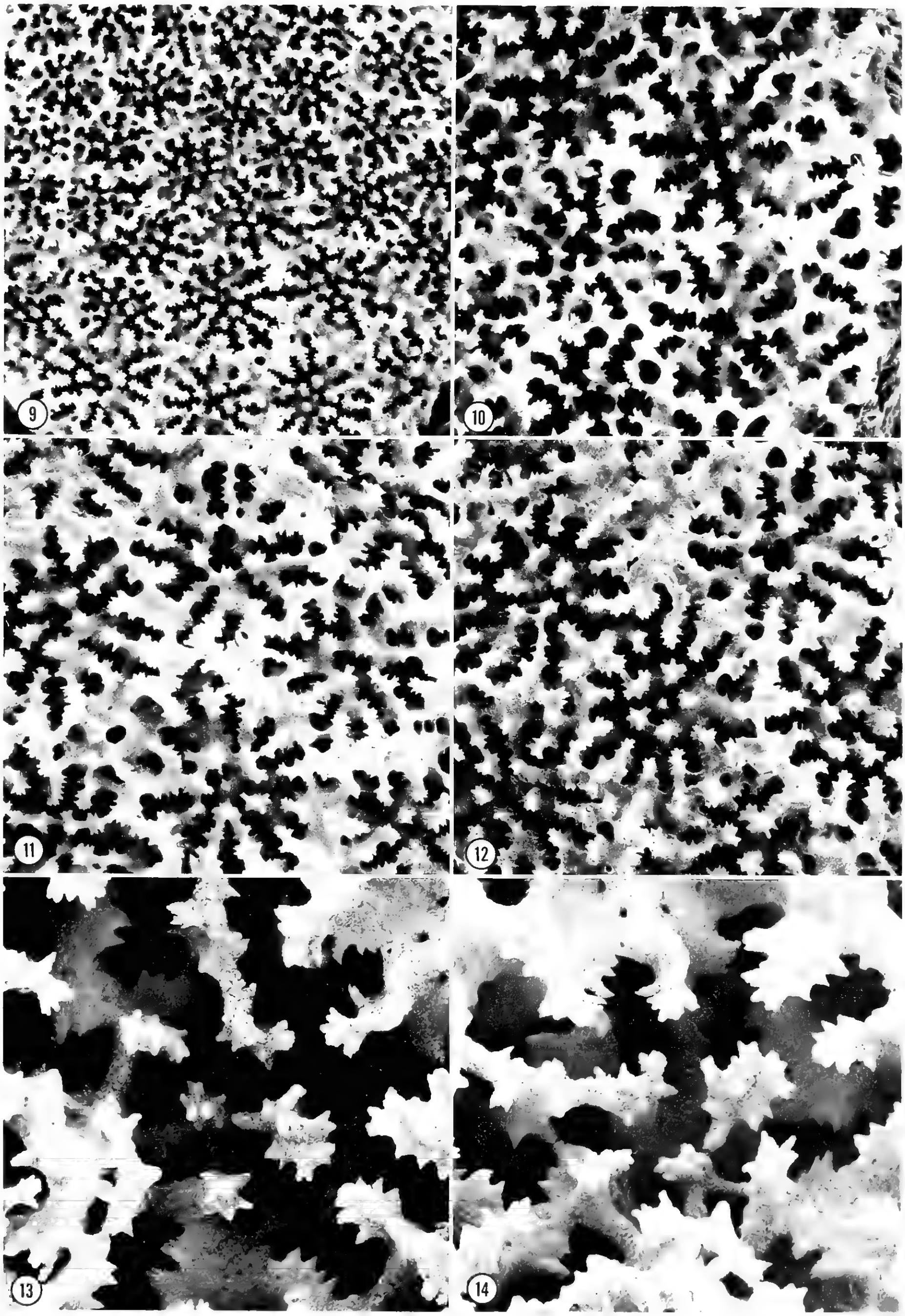
Figs. 1–2. *Porites colonensis,* holotype, USNM 82020: 1, Side view, colony growing on *Mussa angulossa* (Pallas, 1766) Oken, 1815; 2, Top view, both ×0.77.



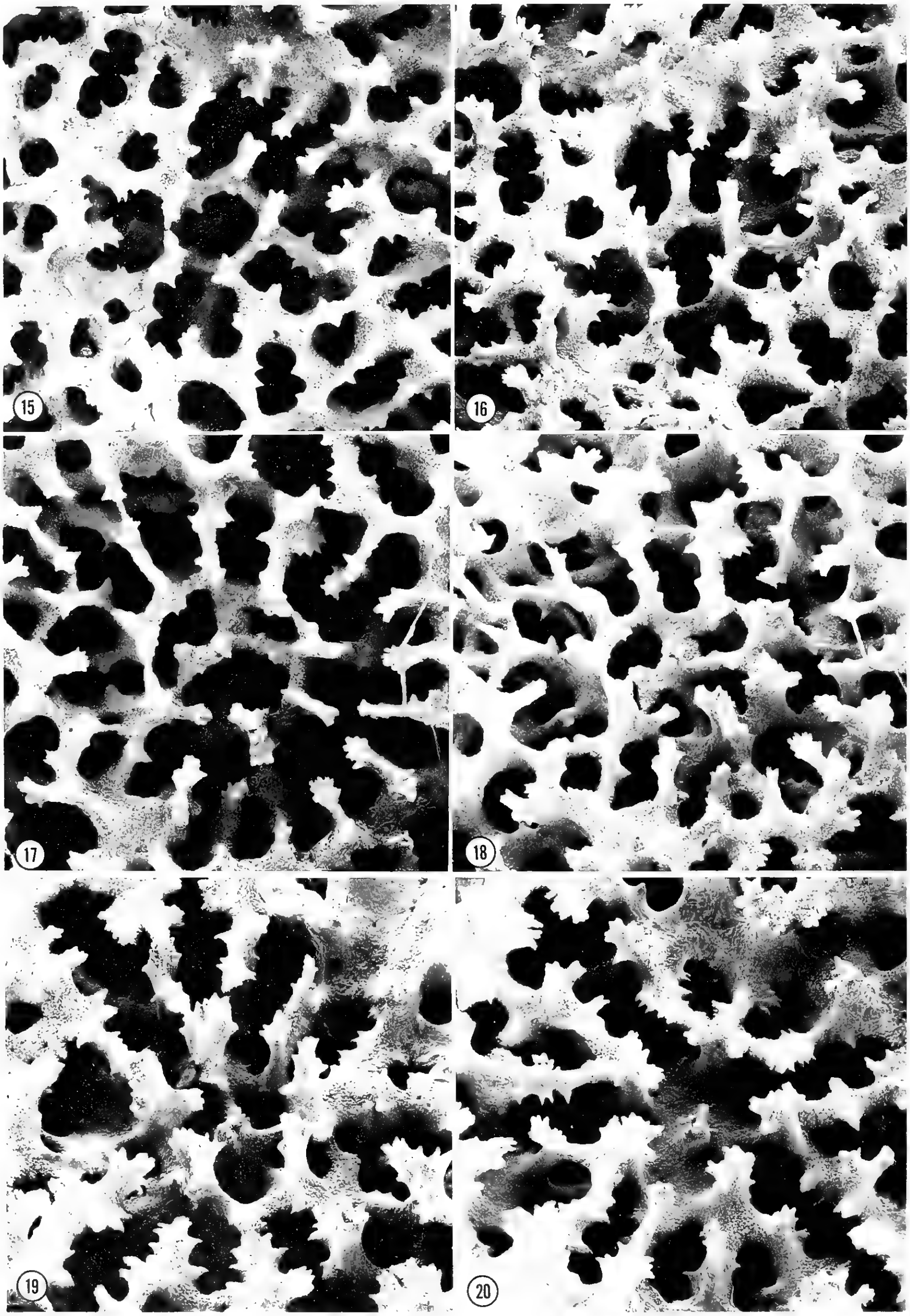
Figs. 3–6. *Porites colonensis,* paratypes, colony morphology: 3, USNM 82022; 4, Corallite size variation, USNM 82024; 5, USNM 82023; 6, USNM 82021, all figures ×0.77.



Figs. 7–8. *Porites colonensis,* pali, variation of skeletal structure and corallite diameter: 7, Holotype, USNM 82020, ×2.24; 8, Paratype, USNM 82024, ×3.2.



Figs. 9–14. *Porites colonensis,* paratype, USNM 82028, variability within one colony: 9, USNM 82028D, in the upper part of the photo—small corallites with thin septa, with axial fossa or with weak columella; in the lower part of the photo—much larger corallites with thicker septa and with weak or strong columella, ×11; 10, USNM 82028A, thin skeletal elements, not well distinguished corallites, presence of axial fossa or weak columella, ×19; 11, USNM 82028C, moderate thick skeletal elements, well distinguished corallites, presence of axial fossa or weak columella, ×19; 12, USNM 82028C, thick skeletal elements, well distinguished corallites, presence of axial fossa, weak or strong columella, ×19; 13–14, Vertical and oblique views of one columella, USNM 82028B, ×64.



Figs. 15–20. *Porites colonensis,* paratype, USNM 82027, variability within one colony—axial structure and ornamentation of septa and pali: 15–16, Vertical and oblique views of one axial fossa, USNM 82027B, ×38; 17–18, Vertical and oblique views of a weak columella, USNM 82027B, ×38; 19, Oblique view of weak columella, columella, USNM 82027A, ×45; 20, Massive columella with central tubercule, clear septal plan (down left—a dorsal directive septum, up right—a ventral directive septum) fused with two septa in a triplet, and four lateral pairs of septa arranged symmetrically in relation to the dorso-ventral axis, USNM 82027A, ×45.

3–6, 8–20), collected from 26 Jun 1987 to 23 Sep 1987, by V. Zlatarski and H. Guzman.

Type locality.—Off the southeast coast of the island of Largo Remo, east of Colon, Bahía Las Minas; depth 3 m.

Description.—Colony with irregular foliaceous form (Figs. 1–6), generally attached by a small central area to coralla of other Scleractinia (Fig. 1) or growing on sponges. Maximal colony diameter ranges from 4 to 13 cm. Peripheral edge of colony rounded, generally undulated. Folias of colony thin (generally 1–4 mm, seldom 6 mm). Colonies sometimes form foliaceous layers (Figs. 1, 3, 6) of which only the uppermost is alive. Lower surface of corallum covered by distinct rings of holotheca, concentric to the attachment of the colony. Calicular surface cerioid. Corallites vary from indistinguishable to quite discrete, their diameter measured from the middle of the wall varies from 0.6 to 1.3 mm. Skeletal elements not compact but porous, thus they do not have constant width and thickness, and therefore all measurements correspond only to the plane of the measurements. Corallites on concave areas of colony surface generally smaller than corallites on convex parts of the colony. In the first case calices not well distinguished, small (diameter 0.6–0.7 mm), and skeletal elements thin, but in the convex parts calices are well distinguished, well separated, larger (diameter 1.0–1.3) and wall and septa are thicker (Figs. 4, 8–12). Septal plan bisymmetrical, varying from unclear (Figs. 9, 10) to clear (Fig. 20). In clearly bisymmetrical plans dorsal directive septum is independent. Opposite to it is the ventral directive septum, which is fused with 2 other septa in triplet. Four lateral pairs of septa arranged symmetrically in relation to dorso-ventral axis. Septa ornamented by more or less inclined to vertical angular granules, varying in shape, size, number, distribution, and orientation (Figs. 9–20). Generally 5 pali surround corallite center (Figs. 7, 8), located on the top of triplet and on axial edge of each lateral pair. Sometimes there is a smaller 6th palus on axial edge of dorsal directive septum. The pali are vertical (Figs. 15–19) or inclined (Figs. 13, 14, 20); their granulation is variable in shape, number and distribution (Figs. 9–12). The axial structure (columella) is the most variable skeletal element, being present or absent in neighboring corallites (Figs. 10–12). When it is absent, the 5 (sometimes 6) pali are connected in a ring circumscribing the deep axial fossa (Figs. 8—center, 15, 16). When present, the columella may be parietal, formed by 4 or more continuations of the septa, not on the same level, toward the center of the calice (Figs. 17–19). Elsewhere, the columella may be considerable and even become massive, occupying all the space inside the pali, and furnished with a central tubercule (Fig. 20). The wall is a synapticulotheca.

The color of the living tissues is very dark brown with very bright white polyp centers or dark red with green centers.

Ecology.—Found on tilted reef slopes, at depths of 3 to 27 m; usually in small cavities (with approximately diameter 20 cm), fixed on dead parts of other Scleractinia or on Porifera.

Distribution.—Caribbean coast of Panama, from Colon to Isla Grande and in San Blas area. Localities of collected specimens: Largo Remo Island, depth 3 m, USNM 82020–82029, 82032, 82033, 82039–82054; Payardi (in front of the Refinery, depth 4.5 m, USNM 82030, 82031, 82034; Naranjo Abajo Island, depth 7 m, USNM 82038; Palina (El Mamey), USNM 82035, depth 8 m, USNM 82036, depth 2.8 m, USNM 82037, depth 3 m. Also observed at the last locality at 13 m and 17 m depths. Observed also near Portobelo, and in Holandes, San Blas area (depth 3–27 m).

Comparison and discussion.—*P. colonensis* differs from *P. astreoides* Lamarck, 1816 by a combination of three characters: the presence of pali, the foliaceous colony form, and the dark polyp color with white or green centers. It is distinguished from all branching *Porites* by its colony form and by the two colors of its living tissues. The poor knowledge of *P. branneri* Rathbun, 1888 in Caribbean waters makes it difficult to compare that species to other *Porites.* Nonetheless, the material described here is well distinguished by its colony shape, corallite and colony size, skeletal characters and tissue colors from the data existing on Brazilian *P. branneri* and the characters of its type specimens (USNM 10961, 10962).

In the area where *P. colonensis* was found, *P. astreoides* and the branching *Porites* were also observed, but colonies having intermediate characters between *P. colonensis* and the other *Porites* were not found. This observation and the presence of the character combination described previously are the reasons for describing it as a new species. Future studies will bring additional information about the polyps and the skeletal characteristics on different levels of biological organization, about the life history and the distribution of this new taxon, and will undoubtedly improve the taxonomy of the genus. It is clear that until now, no *Porites* has been described with these characters and that its representatives do not show intermediates with the representatives of the other living *Porites* species.

The only similar fossil species to *P. colonensis* is *P. trinitatis* Vaughan, 1926 (*in* Vaughan & Hoffmeister, 1926), from the Miocene of Trinidad. The types of *P. trinitatis* (holotype USNM M053674, and five paratypes USNM 68302) do not show sufficient details of the skeletal structures for a good comparison. Nevertheless, *P. colonensis* has thinner, undulated colony plates, and smaller corallites. (In *P. trinitatis* the diameter of the corallites is 1.25 mm–1.8 mm, in average 1.6 mm). Future studies should be done on more and better preserved fossil material.

Acknowledgments

This work was made possible by the support of the Smithsonian Institution. I would like to thank especially Chip Clark for the photography, and Hector Guzman and Ernesto Weil for the field assistance. The scanning electron photomicrographs were taken in S. E. M. laboratory of the National Museum of Natural History, Smithsonian Institution by Brian E. Kahn. I thank George C. Steyskal for advice on zoological nomenclature and K. R. Moore for technical assistance. I am grateful to Stephen D. Cairns, Stephen C. Jameson, Thomas E. Bowman and William J. Sando for reviewing the manuscript.

Literature Cited

Rathbun, R. 1888. Annotated catalogue of the species of *Porites* and *Synaraea* in the United States National Museum, with a description of a new species of *Porites.*—Proceedings of United States National Museum 10:354–366, pls. 15–19.

Vaughan, T. W., & J. E. Hoffmeister. 1926. Miocene corals from Trinidad.—Carnegie Institution of Washington, Publication No. 344, Papers of the Department of Marine Biology 23:107–134, pls. 1–7.

Veron, J. E. N., & M. Pichon. 1982. Scleractinia of Eastern Australia. Part IV. Family Poritidae.–AIMS Monograph Series 5:1–159.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 265–278

SOLENOTHECA, NEW HYOLITHA (MOLLUSCA) FROM THE ORDOVICIAN OF NORTH AMERICA

John M. Malinky

Abstract.—The first well-preserved hyoliths from the Ordovician of North America are here described as *Solenotheca bakerae* n. gen., n. sp., family Hyolithidae, order Hyolithida. This species seems to have been a rare component of soft-bottom, normal marine assemblages in Ordovician carbonate rocks, and thus far it appears to be endemic to North America. Poor preservation of the types of the North American Ordovician species *Hyolithes baconi* Whitfield, *H. multicinctus* Bradley, *H. pinniformis* Ruedemann, *H. pumilus* Ruedemann, *H. rhine* Ruedemann, and *H. versaillensis* Miller & Faber renders the generic identification of these species uncertain. *H. baconi* and *H. multicinctus* are included under *Solenotheca* with question; the other species cited above are retained tentatively in *Hyolithes.* Their names should only be used for the type specimens. The holotype of *H.? dubia* Miller & Faber is a triobite spine, and this species is here removed from the Hyolitha.

Hyolitha are locally abundant in Cambrian strata of marine origin, but are relatively rare in Ordovician and younger Paleozoic rocks. Cambrian hyoliths in the Soviet Union and China are currently the focus of considerable interest because of their utility in biostratigraphic subdivision of the Lower Cambrian (see Missarzhevsky 1969 and Qian et al. 1985 for detailed list of references). In contrast, except for several recent works (Marek 1967, 1983a, b; Malinky et al. 1987; Houbrick et al. 1988), post-Cambrian Paleozoic hyoliths have been little studied. This report constitutes the first study of North American Ordovician Hyolitha in which modern taxonomic methods are used.

The first hyolith described, *Hyolithes acutus* Eichwald (1840), was from the Ordovician of the eastern European Baltic region. Eichwald (1860) later described several other Ordovician species from that area. The earliest study of the Hyolitha to include detailed consideration of stratigraphic distribution in addition to taxonomy was that of Barrande (1867). Barrande's work was the first monograph ever devoted to hyoliths and other conical problematica, and he included Ordovician as well as younger hyolith species from central Europe. Other Ordovician species from central Europe and Scandinavia were described in later works by Novak (1891), Holm (1893), Reed (1909), and Zazvorka (1928). Thoral (1935) described a fauna of Tremadocian and Arenigian hyolith species from France (Marek 1983b), which included the first known orthothecid hyolith with preserved casts of the intestine and other internal structures (Houbrick et al. 1988). Thoral's specimens served in part as the basis for removing the Hyolitha from the Mollusca and assigning them to the extinct phylum Hyolitha by Runnegar et al. (1975). Marek & Yochelson (1976) continued to regard them as molluscs.

Until recently, species named by those early workers represented nearly one-third of all known Ordovician species. The other Ordovician species were discovered at widely scattered localities throughout the world, and were usually named incidentally in studies devoted to other organisms or to entire faunas. By the mid-20th century, a total of one hundred eleven Ordovician hyolith species had been named (Sinclair 1946).

Compared to Europe, hyoliths in the Ordovician of North America seem to be quite rare. In nearly a century of study, only nine North American species had been named (Sinclair 1946), and only one occurrence of a previously known European species had been reported (Matthew 1895). None of these species have ever been restudied, and with rare exceptions their names have not been used in the literature for any material except the types. Little is known of their stratigraphic or biogeographic distribution, and nothing of their phylogenetic relationships.

Marek (1963, 1966, 1967, 1983a, b) brought a new perspective to the study of the Hyolitha in general and to Ordovician hyoliths in particular. He reevaluated many of the European species named by Barrande and other early workers, and supplemented the original descriptions with new material from Europe and North Africa. The local abundance of hyoliths in Ordovician carbonate rocks of Baltoscandia was noted by Jaanusson (1984) and Jaanusson & Mutvei (1982) but they did not describe any taxa. With one recent exception (Malinky 1987), no attempt has been made to reevaluate any hyoliths from the Ordovician of North America until now.

Restudy of Ordovician hyoliths from North America indicates that specimens from the Middle Ordovician of the Upper Mississippi Valley region represent *Solenotheca bakerae* n. gen. n. sp., in the family Hyolithidae, order Hyolithida. Morphology of the types of the Ordovician species *Hyolithes baconi* Whitfield (1878) and *H. multicinctus* Bradley (1930) suggests affinity to *Solenotheca,* to which they are here reassigned with question. In contrast, poor preservation of the types of *H. pinniformis* Ruedemann (1912), *H. pumilus* Ruedemann (1926), *H. rhine* Ruedemann (1901), and *H. versaillensis* Miller & Faber (1894) renders the original descriptions of these species inadequate and their generic identifications uncertain; they are retained under *Hyolithes* with question.

The Ordovician hyolith species *Hyolithes vanuexmi* Walcott (1884) from the Eureka district in Nevada was reassigned to *Chelsonella* Malinky (1987), order Orthothecida, class Hyolitha. The type or types of the Ordovician species *H. crowelli* Roy (1941) and *H. parviusculus* (Hall 1862) cannot be located at present. These names should not be used for any other material until the types are located or until well preserved topotypes become available for study. Type specimens of *H.? dubius* Miller & Faber (1894) consist of trilobite spines, and that species is here reassigned to the Arthropoda. The holotype of *H. miseneri* (Foerste, 1917) is presently under study.

Distribution and Paleoecology

Marek's (1976) analyses of the geographic and stratigraphic distribution of fifteen Ordovician hyolith genera was the first and only study of its kind. He recognized two distinct hyolith assemblages in the Ordovician; one occurs in Baltoscandia whereas the other is common in central Europe and North Africa with rare representatives in Australia and South America. None of the genera in these assemblages have been identified unequivocally in North America. However, poor preservation complicates the recognition of any European hyolith taxa in North America. A specimen questionably assigned to the Ordovician genus *Elegantilites* Marek (1967) from Czechoslovakia was reported by Harrison & Harrison (1975) from the Silurian Brassfield Formation in Ohio. A species of the Ordovician genus *Joachimilites* Marek (1967), previously known only in Czechoslovakia has been identified tentatively from the Middle Cambrian Maryville Limestone in Alabama (Malinky 1988). Nonetheless, preliminary observations support the notion that North American hyoliths comprise a third distinct Ordovician assemblage characterized by *Solenotheca*. Published reports and illustrations of hyoliths from outside North America seem to indicate that *Solenotheca* is endemic to North America. This genus has not been identified yet in any of the well-preserved and relatively abundant Ordovician hyolith assemblages of central Europe or North Africa, or from older hyolith-bearing strata in the Soviet Union and China.

The stratigraphic distribution of *Solenotheca* is poorly known. The types of this genus were collected more than 75 years ago from the Upper Mississippi Valley region by an unknown worker, and geographic and stratigraphic details about those occurrences are not available. The age of *Solenotheca* cannot be determined more precisely than Middle Ordovician (Webers & Austin 1972) because specific localities and associated faunas are not known with certainty. Assignment of *Hyolithes baconi* Whitfield and *H. multicinctus* Bradley to *Solenotheca* does not extend the stratigraphic range of the genus because both of those species were also discovered in the Middle Ordovician. In addition, their inclusion under *Solenotheca* does not extend the geographic range significantly for they also were discovered in the Mississippi Valley region.

Solenotheca has only been reported thus far from carbonate rocks. Middle Ordovician carbonate strata of the Upper Mississippi Valley represent shallow, normal marine environments inhabited by soft-bottom benthic assemblages (Webers 1972). These assemblages are dominated by brachiopods, bryozoans and molluscs; hyoliths seem to have a sporadic distribution in these rocks and are rare at any given locality. Direct examination of type specimens and published accounts in the literature show that most other Ordovician hyoliths in North America occur in carbonates, although a few specimens are known from shale. This may be largely a bias of collection and preservation. Hyoliths in shale and other clastic rocks tend to preserve less well than limestone specimens and may have been overlooked or simply not collected because of preservation.

Fisher (1962) noted that hyoliths occur in a wide range of facies in the marine environment except for hypersaline and reef facies. His observations seem to be based primarily upon Cambrian occurrences. Material described herein and undescribed specimens in collections of the Smithsonian Institution suggest that Ordovician hyoliths were widely distributed geographically and in a variety of marine facies, but were rare overall within the marine environment. To date, assemblages of hundreds of individuals on bedding surfaces in sandstone or more rarely in limestone have not been observed in the Ordovician. Such occurrences are locally known in Cambrian sandstones of the Upper Mississippi Valley (Marek & Yochelson 1976) and in Cambrian limestones of west-central Montana. The relative scarcity of hyoliths in Ordovician and younger Paleozoic rocks may be related to their apparent mechanical inefficiency in comparison to gastropods or other more mobile benthos (Yochelson 1984).

Mode of life of the Hyolitha has been a matter of controversy until recently. Fisher (1962) suggested several possibilities, including benthic with venter down, benthic with the apex embedded in sediment, and nektic and planktic. Marek & Galle (1976) used the presence of an encrusting tabulate coral on the dorsum only of several Devonian hyoliths from central Europe to suggest that a benthic mode of life with venter resting upon the seafloor seemed most likely. Several Late Ordovician specimens from southwestern Ohio (USNM 50107A, USNM 50102A) lend support to their interpretation. These specimens are also encrusted by an epibiont which, in this instance is a bryozoan. Like the Devonian tabulate coral, the bryozoan also is confined

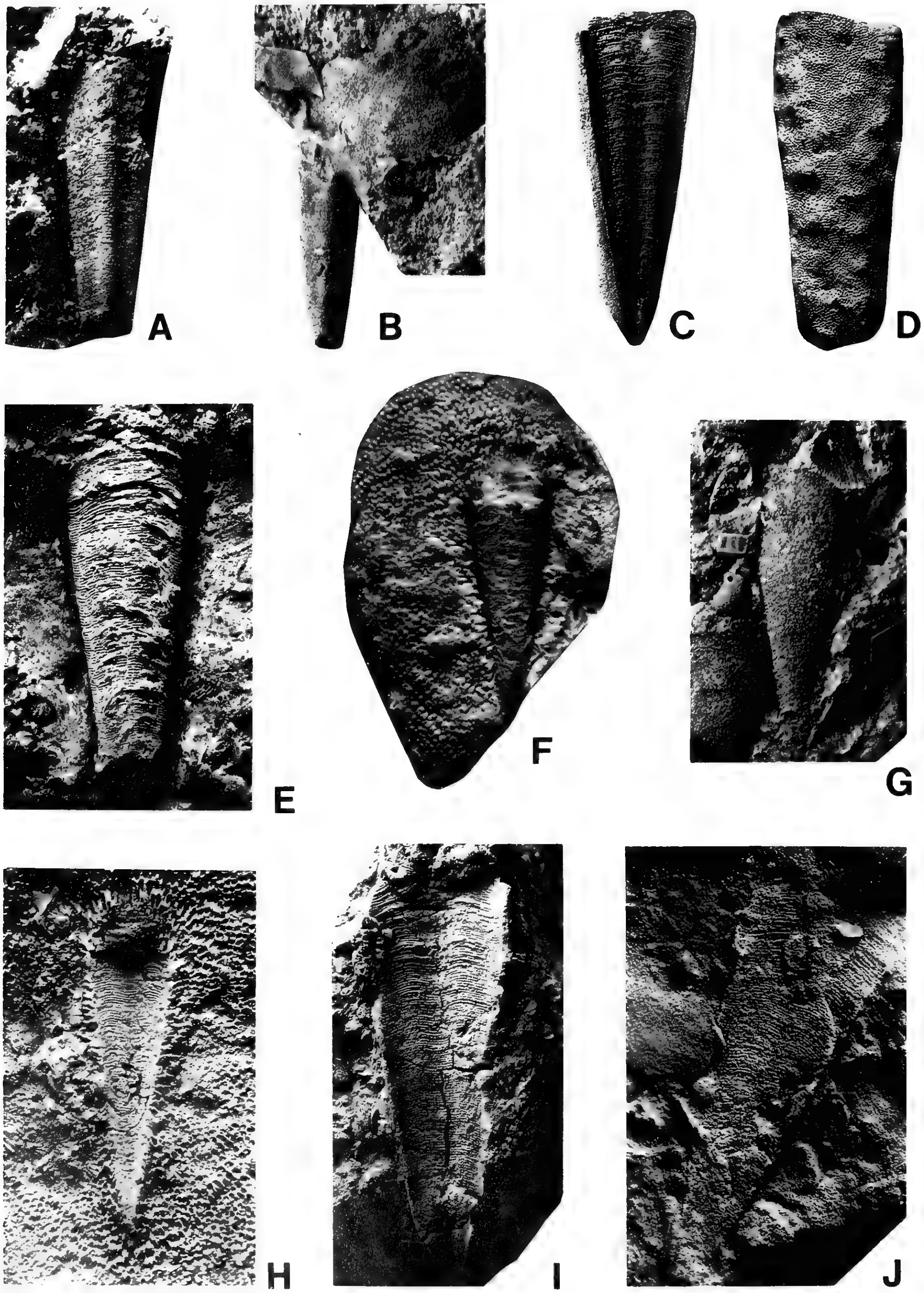


Fig. 1. A, E, *Hyolithes*? *multicinctus* Bradley: A, Paratype FMNH 5916B showing dorsum, ×3. E, Holotype FMNH 5916A showing dorsum, ×1.8, Missouri. B, G, *Solenotheca*? *baconi* (Whitfield): B, Paralectotype UCMP 34360A showing dorsum. G, Lectotype UCMP 35219 showing venter, Wisconsin. Both ×1.1. C, D, External

to the dorsum (Fig. 1C, D, F, H). Had the hyoliths lived with the dorsum down or with the apex imbedded in the sediment, both dorsum and venter would be covered with epibionts.

Repository designations used in this manuscript are: National Museum of Natural History, USNM; Field Museum of Natural History, FMNH; New York State Museum, NYSM; and Museum of Paleontology, University of California, Berkeley, UCMP.

Systematic Paleontology

Phylum Mollusca
Class Hyolitha Marek
Order Hyolithida Matthew
Family Hyolithidae Nicholson
Solenotheca, new genus

Type species.—*Solenotheca bakerae,* new species.

Included species.—Solenotheca bakerae. Hyolithes baconi Whitfield (1878), and *H. multicinctus* Bradley (1930) are possible representatives of this genus.

Diagnosis.—Hyolithid which has narrowly rounded dorsum with concavo-convex slopes; ligula short and aperture orthogonal (see Marek 1983a).

Remarks.—Knowledge of *Solenotheca* is derived from six well preserved specimens from the Upper Mississippi Valley region which formerly were listed as hypotypes of *Hyolithes baconi* Whitfield (1878) by an unknown worker. Thirty other specimens from widely scattered localities in the Mississippi Valley region are possible representatives of this genus, but incomplete preservation precludes confident identification of those specimens.

Solenotheca differs from all other genera currently included under the Hyolithidae (see Malinky 1988 for listing of genera in that family) by the presence of concavo-convex slopes on the dorsum. The only other hyoliths to possess a similar feature are members of the Family Similothecidae Malinky (1988) from the Lower Cambrian of Newfoundland. However, the dorsum on similothecid hyoliths terminates in a protruding keel on the longitudinal ridge. *Solenotheca* lacks a keel. Furthermore, *Solenotheca* has a cancellate pattern of ornament created by closely spaced transverse lirae and widely spaced longitudinal lirae; on the similothecid hyoliths the transverse ornament as well as longitudinal ornament is widely spaced. The features which characterize *Solenotheca* have not been reported on any Soviet or Chinese hyolith (Syssoiev 1962, 1968, 1974; Val'kov 1975; Qian 1977, 1978).

Stratigraphic range.—Middle Ordovician.

Etymology.—The name of the genus is derived from the Greek *solen,* meaning furrow, in reference to the concave slopes.

Solenotheca bakerae, new species
Fig. 2E–G

Diagnosis.—*Solenotheca* with widely spaced longitudinal lirae superimposed upon closely spaced transverse lirae and transverse threads which create a cancellate pattern on shell and internal mold.

Description.—Venter slightly inflated with narrowly rounded lateral margins. Dorsum low and narrowly rounded in middle. Adjacent slopes convex next to lateral margins, but are markedly concave elsewhere. Transverse outline of shell subtriangular; sides of triangle concave. Ventral ligula short and straight, broadly rounded anterior edge.

←
mold and dorsum of shell, respectively, of unidentifiable hyolith USNM 50107A showing bryozoan encrustation, ×2, Ohio. F, H, Latex cast and external mold, respectively, of unidentifiable hyolith USNM 50102A showing bryozoan encrustation; F, ×4, H, ×4.5, Ohio. I, External mold of unidentifiable hyolith USNM 50107B showing dorsum, ×2, Ohio. J, External mold of unidentifiable hyolith USNM 6833 showing venter(?), ×2, Ohio.

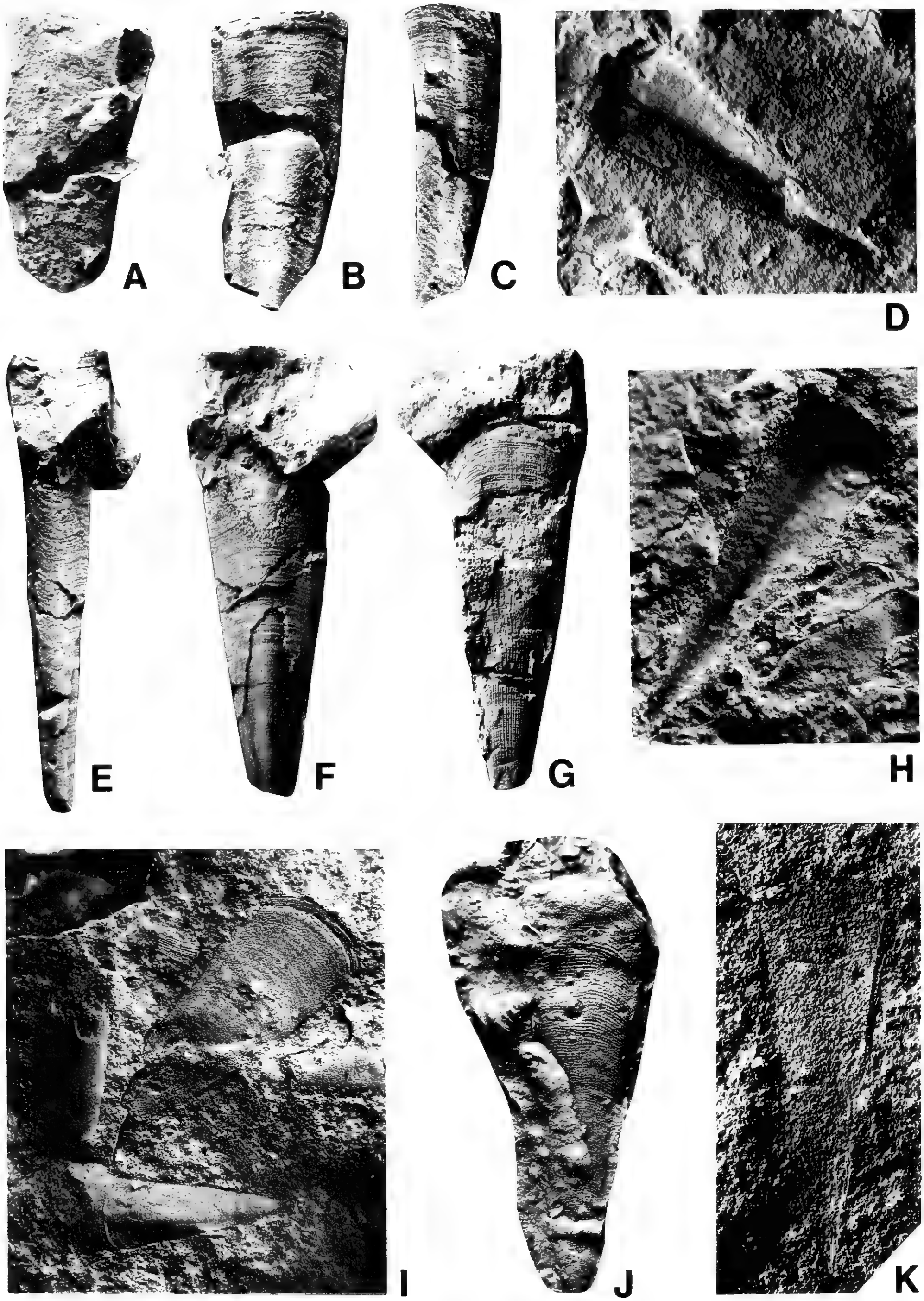


Fig. 2. A–C, *Hyolithes*? *rhine* Ruedemann: venter, dorsum and left lateral view, respectively, of holotype NYSM 3514, original shell, ×2, New York. D, H, *Hyolithes*? *pumilus* Ruedemann: D, paralectotype NYSM 9425B, dorsal(?) external mold, ×5.5, New York. H, lectotype NYSM 9425A, dorsal(?) external mold, ×1.6, New York. E–G, *Solenotheca bakerae* n. gen., n. sp: holotype USNM 50086A, right lateral, dorsal and ventral

Sides of ligula dip steeply away from anterior edge. Apertural rim orthogonal with shallow sinus along aperture on each lateral margin but not on dorsal margin. Apertural rim not flared. Apical end appears straight.

Shell covered with alternation of transverse threads and transverse lirae. Lirae parallel outline of aperture; on dorsum lirae transverse, and curve on lateral margins to follow apertural sinuses. On venter lirae follow edge of ligula. Fine, longitudinal lirae superimposed upon transverse ornament create cancellate pattern on shell. Internal mold also with cancellate pattern of ornament defined by transverse threads and lirae with longitudinal lirae superimposed upon them. Operculum unknown.

Remarks.—The holotype (Fig. 2E–G) is a steinkern covered with scattered fragments of shell; it measures 25.5 mm in length and has an apertural width and height of 9.5 mm and 5.0 mm respectively. Matrix adheres to the apertural end but enough detail is exposed so that the apertural rim can be seen. A small portion of the apical end is broken. Several other specimens are sufficiently well preserved to serve as paratypes. The types of this species were originally designated as hypotypes of *Hyolithes baconi* Whitfield (1878) by an unknown worker, probably because of a general resemblance in conch form between them. However, the types of *H. baconi* lack all details of the aperture and ligula, as well as ornament on the shell. No further comparison between the two species is possible.

Material.—All specimens reposited at USNM. Holotype 50086A and paratypes under 50086B, 50086C, 25269 and 2 paratypes under 25270. Specimens questionably referred to *Solenotheca* species indeterminate, are catalogued as follows: 11 under 15764A and 2 under 15764B; 11 under 50088; 1 under 25272, 4 under 50087A and 1 under 50087B.

Occurrence.—Geographic and stratigraphic information for all specimens is scant. Knowledge of occurrences is derived entirely from labels associated with the specimens. The holotype and paratypes 50086B and 50086C are from "Minneapolis, Minnesota." Paratype 25269 is from "5 m. n. Monroe, Green Co., Wis." This presumably means 5 miles north of Monroe. Paratypes 25270 are from "Black River (Platteville), Belleville, Wisconsin." The 11 specimens catalogued as 15764A, the 2 under 15764B and those under 50088 are all from "Beloit, Wis."; specimen 25272 is from "Platteville, Wisconsin"; specimens 50087A and 50087B are in a container labelled "Cannon Falls, Minnesota" but labels enclosed with the specimens say "chiefly from beneath sponge bed Platteville-Upper Dixon, Illinois." Labels with those specimens indicate that they were collected by E. O. Ulrich and R. S. Bassler in 1906, although there is no indication as to which locality is correct (Fig. 3).

Webers & Austin (1972) recognized five Middle Ordovician formations which encompass several hundred meters of carbonate rock in the Upper Mississippi valley region. The Platteville, Decorah and Galena formations contain layers of limestone or dolostone as well as other lithologies. In the absence of any detailed data on localities or associated faunas, confident assignment of any of the specimens cited above to formation is impossible at this time. The age of strata in these areas is Middle Ordovician (Webers & Austin 1972).

Stratigraphic range.—Middle Ordovician.

Etymology.—The species is named for Cathy Baker, Simpson College.

←

views, respectively, original shell, ×2.8, Minnesota. I, Slab under USNM 78431A showing venters of unidentifiable Ordovician hyoliths, ×2, Missouri. J, Unidentifiable Ordovician hyolith, USNM 50087B, venter, ×2, Ohio. K, *Hyolithes*? *pinniformis* Ruedemann. Holotype(?) NYSM 9423, venter(?), ×5.3, New York.

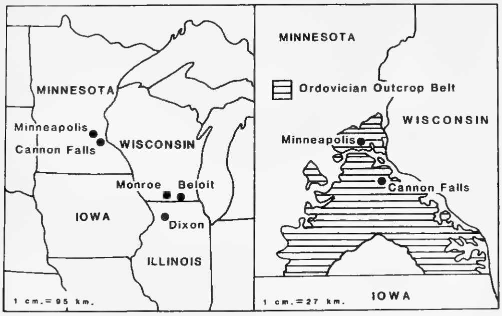


Fig. 3. Generalized locality map for holotype and paratypes of *Solenotheca bakerae* n. gen., n. sp.

Class Hyolitha incertae sedis

Solenotheca? *baconi* (Whitfield, 1878)

Fig. 1B, G

Hyolithes baconi Whitfield, 1878:77; 1882: 225, pl. 6, figs. 9–11.—Sinclair, 1946:74.

Description.—Venter flat toward middle but becomes slightly inflated toward narrowly rounded lateral margins. Dorsum low and narrowly rounded in center; adjacent slopes appear nearly flat to slightly concave. Ligula appears long and straight. Apical single small and apical end straight. Complete dorsum, aperture, shell and operculum unknown.

Remarks.—Type material of this species consists of dolomitized steinkerns from which all details except the proportions of the conch have been obscured by diagenesis. All specimens are embedded in matrix, from which extraction intact would probably be impossible. Specimen UCMP 32519 (Fig. 1G) is here designated the lectotype; it measures 34.0 mm in length and is 11.0 mm wide near the apertural end. The paralectotypes (Fig. 1B) are comparable to the lectotype in size.

This species was named and described but not illustrated by Whitfield (1878). His initial description was repeated nearly verbatim slightly later (Whitfield 1882) and was accompanied by drawings (pl. 6, figs. 9–11). The drawings show this species to have two longitudinal sulci on the dorsum and transverse lirae on both dorsum and venter. The drawings also depict a short ligula with a broad anterior edge, and a low dorsum. No specimens in the type lot match these illustrations; there is no evidence for the sulci or lirae shown. The drawings are apparently reconstructions of how Whitfield thought complete, well preserved specimens of this species should appear. The gently concave dorsal slopes suggest affinity to *Solenotheca,* to which this species is referred with question.

Material.—Lectotype UCMP 32519 with paralectotypes on specimens under UCMP 34360-A and UCMP 34360-B.

Occurrence.—According to Whitfield (1878:77), these specimens were discovered "in the hard bluish layers of the Trenton group, below Carpenter's quarry, near Beloit, Wisconsin." Beloit is located in southern Rock County near the border of Illinois and Wisconsin. The age of the species is Middle Ordovician.

Solenotheca? *multicincta* (Bradley, 1930)

Fig. 1A, E

Hyolithes multicinctus Bradley, 1930:240, pl. 25, fig. 13.—Sinclair, 1946:78.

Description.—Conch with small apical angle and apical end appears straight. Dorsum low and narrowly rounded; slopes on dorsum appear slightly concave. Lateral margins narrowly rounded and dorsal apertural rim appears orthogonal. Shell covered with closely spaced transverse lirae; lirae curve slightly in middle of dorsum to create shallow sinus but are transverse elsewhere. Dorsum covered with fine, closely spaced longitudinal lirae; on lateral margins lirae also curved to create shallow sinus. Venter, complete apertural end and operculum unknown.

Remarks.—Knowledge of this species is derived from the holotype (Fig. 1E) and a specimen included in this species as a paratype (Fig. 1A). The holotype measures 26.0 mm in length, and has an apertural width of 9.6 mm; the paratype is comparable in size. Both specimens retain the original shell, but each is embedded partly in matrix so that only the dorsum is exposed. Any attempt to extract these specimens from the matrix would probably destroy them.

Bradley (1930) noted comparison between this species and *H. baconi* Whitfield (1878), but he seems to have compared his specimens to Whitfield's illustrations rather than to Whitfield's specimens. No comparison between the types of these species is possible because of preservation. Bradley (1930) also reported minor differences of ornament between *H. multicinctus* and *H. miseneri* (Foerste, 1917) as a basis for separating these species. Foerste (1917) stated that *H. miseneri* has a cancellate pattern on the dorsum formed by the intersection of transverse and longitudinal lirae, whereas Bradley (1930) stated that all lirae on *H. multicinctus* are transverse. Bradley (1930) was mistaken on that point, for a reexamination of the types of *H. multicinctus* demonstrates that fine longitudinal lirae occur on the dorsum of those specimens, suggesting that both forms may belong to the same species. Concave slopes on the dorsum of *H. multicinctus* suggest placement under *Solenotheca,* to which this species is now assigned with question. Assignment to genus for *H. miseneri* (Foerste, 1917) awaits further study of that specimen.

Material.—Holotype FMNH 5916A and paratype FMNH 5916B.

Occurrence.—Bradley (1930:241) cited the occurrence as "Kimmswick limestone near Glen Park, Missouri." The age of the species is Middle Ordovician.

Hyolithes? *pinniformis* Ruedemann, 1912
Fig. 2K

Hyolithes pinniformis Ruedemann, 1912: 111, pl. 7, figs. 12, 13.—Sinclair, 1946: 79.

Description.—Conch with subtriangular outline; apical angle appears small and apical end appears straight. The shell, and all other details of conch, and operculum, unknown.

Remarks.—The holotype (Fig. 2K) is the only known specimen of this species. It consists of a subtriangular impression on a bedding surface in black shale. That specimen measures 11.3 mm in length, and has a maximum width near the apertural end of 3.2 mm. Preservation of this specimen is extremely poor; even the most elementary morphologic features, such as the ligula or any distinguishing features of dorsum and venter are lacking. Ruedemann's (1912) drawings of this species (pl. 7, figs. 11, 12) depict a shell with a complete aperture and lirae on the exterior. They bear no resemblance to the specimen described and illustrated herein. Perhaps the drawings are reconstructions of how Ruedemann thought complete specimens of this species should appear, or perhaps the illustrated specimen is lost. This species cannot be properly diagnosed using only the specimen described herein.

Material.—Holotype(?) NYSM 9423.

Occurrence.—Ruedemann (1912:111) cited the occurrence as: "Canajaharie shale at Canajaharie, N. Y." Canajaharie is located in Montgomery County in central New York. The age of the species is Middle Ordovician.

Hyolithes? *pumilus* Ruedemann, 1926
Fig. 2D, H

Hyolithes pumilus Ruedemann, 1926:77, pl. 10, figs. 5, 6.—Sinclair, 1946:79.

Description.—Dorsum inflated and narrowly rounded in center; lateral margins narrowly rounded. Apical angle small and apical end appears straight. Complete apertural end, shell, venter and operculum unknown.

Remarks.—This species is represented by two poorly preserved external molds on a slab of dark gray shale that also contains ostracods and a "syntype" of *Rafinesquina* *alternata centristriata* Ruedemann. Specimen NYSM 9425A (Fig. 2H) is here designated the lectotype; it measures 9.3 mm in length and has an apertural width of 4.0 mm. The paralectotype (NYSM 9425B) (Fig. 2D) is similar in size and preservation to the lectotype. Both specimens are smooth and featureless, and neither retains a shell or an operculum.

Ruedemann (1926, pl. 77, figs. 5, 6) illustrated specimens of this species that he refers to as the holotype (fig. 5) and paratype (fig. 6). In one drawing, the holotype possesses a short ligula which is broadly rounded at the anterior edge, and it appears to have a longitudinal sulcus near the middle of the dorsum. Another drawing depicts a paratype that is less well preserved and lacks the ligula and sulcus. None of the existing specimens match Ruedemann's illustrations. Either his drawings are reconstructions of how he thought well preserved specimens of this species should appear, or the illustrated specimens are lost.

Material.—Lectotype NYSM 9425A and paralectotype NYSM 9425B.

Occurrence.—Ruedemann (1926:78) reported that the slab of shale containing both specimens was discovered in "zone I of the lower Lorraine (Whetstone Gulf) shale, in the Whetstone and Lorraine gulfs." The age of the species is Late Ordovician.

Hyolithes rhine Ruedemann, 1901
Fig. 2A–C

Hyolithes rhine Ruedemann, 1901:36, pl. 2, figs. 12–15.—Sinclair, 1946:79.

Description.—Venter slightly inflated with narrowly rounded lateral margins. Dorsum inflated and narrowly rounded in center; slopes on dorsum slightly inflated. Apical end appears straight, and apical angle small. Faint longitudinal sulcus near each edge of the dorsum; sulcus extends along entire length of dorsum but becomes shallow near apical end. Shell covered with faint transverse lirae on dorsum. Lirae curve slightly in middle of dorsum to form shallow sinus; apertural rim may be orthogonal. Internal mold of venter smooth. Complete apertural end and operculum unknown.

Remarks.—The holotype (Fig. 2A–C) is the only known specimen of this species. It measures 21.0 mm in length, and has an apertural width and height of 10.2 mm and 6.2 mm respectively. The shell is preserved locally on the dorsum, but is absent on the venter. The holotype was broken out of limestone, and an impression of the outer surface of the shell remains in the matrix as a counterpart of the holotype. The counterpart is an impression of the dorsum rather than the venter as Ruedemann (1901) believed.

The dorsal lirae of *H. rhine* resemble those of *H. multicinctus* Bradley (1930), but the lirae on *H. rhine* are less conspicuous. Ruedemann (1901) compared this species to drawings of *H. baconi* Whitfield and *H. multicinctus* Bradley, but detailed comparison between these species is precluded by the absence of important taxonomic features on each.

Hyolithes rhine possesses longitudinal sulci on the dorsum, a feature shared with only three other hyolith species: *Hyolithes acutus* Eichwald (1840), the type species of that genus, from the Ordovician of Estonia, *H. crebescens* Resser & Endo (1937) from the Middle Cambrian of China, and *Hallotheca aclis* (Hall, 1876) from the Devonian of New York. Nonetheless, various other features of the conch of each form suggest that each form probably represents a different species.

Material.—Holotype NYSM 3514.

Occurrence.—Ruedemann (1901) did not cite a specific occurrence for this species, but he named it in a study of the fauna of the Trenton conglomerate at Rysedorph Hill, Rensselaer County, New York. The introduction of the work includes generalized information about a number of localities on Rysedorph Hill, and several outcrops are marked with arrows in a photograph of the hill. The specific outcrop which yielded the type of this species is not

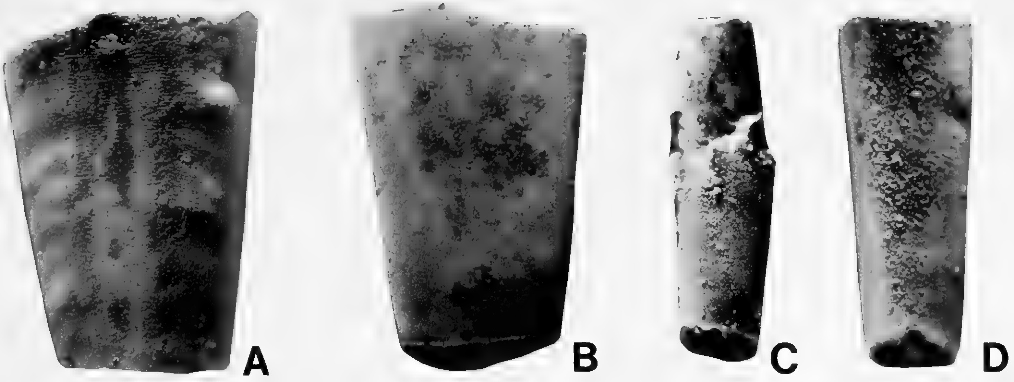


Fig. 4. A, B, D, *Hyolithes*? *versaillensis* Miller & Faber: dorsal, ventral and right lateral views, respectively, of lectotype FMNH 8876A, ×17, Indiana. C, specimen FMNH 8881 formerly assigned to *Hyolithes*? *dubia* Miller & Faber, lateral view, ×12, Indiana.

indicated. The age of the species is Middle Ordovician.

Hyolithes? *versaillensis* Miller & Faber, 1894
Fig. 4A, B, D

Hyolithes versaillensis Miller & Faber, 1894: 15; pl. 8, figs. 20–22.—Cummings, 1908: 965, pl. 42, figs. 4, 4a.—Sinclair, 1946: 81.

Description.—Venter flat to slightly inflated, with narrowly rounded lateral margins. Dorsum inflated and broadly rounded, and transverse shape subtriangular. Apical end appears straight, and apical angle small. Several widely spaced ribs on internal mold of dorsum; internal mold of venter smooth. Complete aperture, shell, and operculum unknown.

Remarks.—Type material of this species consists of eight specimens; specimen FMNH 8876-A (Fig. 4A, B, D) is here designated the lectotype. That specimen measures 2.9 mm in length, and has an apertural width and height of 2.2 mm and 1.3 mm respectively. All paralectotypes are comparable to the lectotype in size. Every specimen of this species is a partially weathered limonitized steinkern. No specimen is complete and none is operculate.

Miller & Faber (1894) thought that these specimens were casts rather than internal molds, and based their species diagnosis on the supposed "smoothness" of the shell. They also noted that "there are not many characters to ascribe to this species" (p. 155) and as a result, their description is generalized and lacks detail. The diagnosis of this species and the illustrations (pl. 8, figs. 20–22) are inadequate to characterize this species because few features are preserved.

Material.—Lectotype FMNH 8876A and seven paralectotypes under 8876B.

Occurrence.—Miller & Faber (1894:155) reported that this species "is quite common in the upper part of the Hudson River Group, at Versailles, Indiana, associated with *Palaeoconcha faberi, Cyclora pulcella* and other small fossils." Versailles is located in Ripley County in southeastern Indiana. The age of the Hudson River group is Late Ordovician.

Class Trilobita incerate sedis
Genus and species indeterminate
Fig. 4C

Hyolithes? *dubius* Miller & Faber, 1894:155, pl. 8, fig. 23.—Cummings, 1908:964, pl. 42, fig. 3.—Sinclair, 1946:75.

Description.—"Conch" tubular and apical angle small. Taper of conch so slight that both ends appear of equal diameter. Shell and internal mold smooth; both ends unknown.

Remarks.—The holotype (Fig. 4C) and only specimen of this species measures 4.2 mm in length with a diameter of 1.0 mm. The original skeletal material is largely intact, although at the narrower end a small section of the internal mold is exposed. The specimen is broken at both ends, and no other features than those cited above are preserved.

Miller & Faber (1894) did not recognize that the original skeletal material is preserved on this specimen, for they cited the specimen as being a "cast." They were apparently uncertain about the affinity of this species, and assigned it to *Hyolithes* with question. They suspected affinity to calymenid trilobites which occur in the same strata as this species. However, because all the trilobite fossils of which they were aware were intact, they ruled out the possibility that the type of *H.*? *dubius* might be a fragment of a trilobite spine. They noted that this species is "like *Hyolithes versaillensis,* with which it is associated, and it would seem, therefore, impossible that it (*H.*? *dubius*) should represent the broken spines of trilobites" (p. 156). The two species are quite dissimilar in terms of both morphology and preservation. *H.*? *dubius* lacks any evidence for hyolith affinity such as a shell with transverse growth lirae or an operculum. It is without question the spine of a trilobite.

Material.—Holotype FMNH 8881.

Occurrence.—Miller & Faber (1894:156) cited the occurrence as "the upper part of the Hudson River Group, at Versailles, Indiana, associated with *Palaeoconcha faberi, Cyclora pulcella, Hyolithes versaillensis,* and other small fossils." The age is Late Ordovician.

Acknowledgments

I wish to thank the National Museum of Natural History for support of this project in the form of a Postdoctoral Fellowship. I wish to thank R. E. Grant, J. Pojeta, E. L. Yochelson, R. H. Mapes and an anonymous reviewer for their helpful comments on this manuscript at various stages of completion. I am grateful to J. Thompson for her assistance in arranging loans of specimens for this study. I would also like to thank the curatorial staffs at the Field Museum of Natural History, Museum of Paleontology, University of California, Berkeley, and the New York State Museum for their generous loan of specimens.

Literature Cited

Barrande, J. 1867. System silurien du centre de la Boheme. Ordres des Pteropodes, 3. Published by the author, Prague and Paris, 179 pp.

Bradley, J. H. 1930. Faunas of the Kimmswick Limestone of Illinois and Missouri.—Walker Museum Contributions 2:465–479.

Cummings, E. R. 1908. The stratigraphy and paleontology of the Cincinnati series of Indiana.—Indiana Geological Survey Annual Report 32: 605–1189.

Eichwald, E. 1840. Ueber das silurische Schichtensystem in Estland. Zeitschrift für Natür- und Heilkunde, 1 and 2, St. Petersburg, 210 pp.

———. 1860. Lethaea rossica ou paleontologie de la Russie. E. Schweizerbart, Stuttgart, 1657 pp.

Fisher, D. W. 1962. Small conoidal shells of uncertain affinities. Pp. W98–W143 *in* R. C. Moore, ed., Treatise on invertebrate paleontology. Part W. Miscellanea. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.

Foerste, A. G. 1917. Notes on the Richmond and related fossils.—Journal of the Cincinnati Society of Natural History 22:42–55.

Hall, J. 1862. Contributions to paleontology; comprising descriptions of new species of fossils, from the Upper Helderburg, Hamilton and Chemung Groups.—New York State Cabinet of Natural History 15:29–198.

———. 1876. Illustrations of Devonian fossils: Gasteropoda, Pteropoda and Cephalopoda (plates only).—New York State Geological Survey, 74 pl.

Harrison, W. B., & L. K. Harrison. 1975. A Maquoketa-like molluscan community in the Brassfield Formation (Early Silurian) of Adams County, Ohio.—Bulletins of American Paleontology 67: 193–234.

Holm, G. 1893. Sveriges kambrisk-siluriska Hyolithidae och Conulariidae. Sveriges Geologiska Undersorning, C, 112, Stockholm, 172 pp.

Houbrick, R. S., W. Sturmer, & E. L. Yochelson. 1988. Rare Mollusca from the lower Devonian Hunsruck Slate of southern Germany.—Lethaia 21: 395–402.

Jaanusson, V. 1984. Ordovician benthic macrofaunal associations. Pp. 127–139 *in* D. L. Bruton, ed., Aspects of the Ordovician System.

———, & H. Mutvei. 1982. Ordovician of Oland. IV International Symposium, Ordovician System. Guide to Excursions, 3. Section of Palaeozoology. Swedish Museum of Natural History, 23 pp.

Malinky, J. 1987. Taxonomic revision of lower and middle Paleozoic Orthothecida (Hyolitha) from North America and China.—Journal of Paleontology 61:942–959.

———. 1988. Early Paleozoic Hyolitha from North America: Reexamination of Walcott's and Resser's type specimens.—Journal of Paleontology 62:218–233.

———, R. M. Linsley, & E. L. Yochelson. 1987. Taxonomic revision of Hyolitha from the Middle Paleozoic of North America.—Journal of Paleontology 61:1173–1186.

Marek, L. 1963. New knowledge on the morphology of *Hyolithes.*—Sbornik Geologickych Ved Paleontology 1:53–72.

———. 1966. New hyolithid genera from the Ordovician of Bohemia.—Casopis Narodniho Musea 135:89–92.

———. 1967. The class Hyolitha in the Caradoc of Bohemia.—Sbornik Geologickych Ved Palaeontology 9:51–113.

———. 1976. The distribution of the Mediterranean Ordovician Hyolitha. Pp. 491–499 *in* M. G. Bassett, ed., The Ordovician system: Proceedings of a Palaeontological Society symposium. University of Wales Press and National Museum of Wales, Cardiff.

———. 1983a. The Ordovician hyoliths from Anti-Atlas (Morocco).—Sbornik Naradniho Muzea v Praze, Acta Musei Nationalis 39, 35 pp.

———. 1983b. The hyoliths in the Arenigian of Montagne Noire. Pp. 57–62 *in* R. Courtessole, L. Marek, J. Pillet, G. Ubaghs, & D. Vizcaino, eds., Calymenina, Echinodermata et Hyolitha de l'Ordovicien inferieur de la Montagne Noire (France Meridionale).—Memoire de la Societe Scientifiques de l'Aude.

———, & A. Galle. 1976. The tabulate coral *Hyostragulum,* an epizoan with bearing on hyolithid ecology and systematics.—Lethaia 9:51–64.

———, & E. L. Yochelson. 1976. Aspects of the biology of Hyolitha.—Lethaia 9:65–82.

Matthew, G. F. 1895. Traces of the Ordovician system on the Atlantic Coast.—Transactions of the Royal Society of Canada 1 (2nd series):253–271.

Miller, S. A., & C. L. Faber. 1894. Description of some Cincinnati fossils.—Journal of the Cincinnati Society of Natural History 17:137–158.

Missarzhevsky, V. V. 1969. Paleontologic part. Pp. 112–320 *in* M. E. Raaben, ed., The Tommotian Stage and the Lower Cambrian boundary problem. Nauka Publishers, Moscow.

Novak, O. 1891. Zur Kenntniss der Fauna der Etage F-fl, in der palaeozischen Schichtengruppen Böhmens. Abhandlungen der königlische Gesellschaft der Wissenschaften 7, 48 pp.

Qian, Y. 1977. Hyolitha and some problematica from the Lower Cambrian Meishucun Stage in central and S.W. China.—Acta Palaeontologica Sinica 16:255–275.

———. 1978. The Early Cambrian hyolithids in central and southwest China and their stratigraphical significance.—Memoirs of the Nanjing Institute of Geology and Palaeontology, Academia Sinica 11:1–38.

———, Wen Yu, Diyong Liu, & Zongzhe Wang. 1985. Restudy of the Precambrian–Cambrian boundary section at Meishucun of Jinning, Yunnan.—Kexue Tongbao 30:1086–1090.

Reed, F. R. C. 1909. Lower Palaeozoic Hyolithidae from Girvan.—Transactions of the Royal Society of Edinburgh 47:203–222.

Resser, C. E., & R. Endo. 1937. Descriptions of the fossils. Pp. 103–301 *in* R. Endo & C. E. Resser, The Sinian and Cambrian formations and fossils from southern Manchukuo.—Manchurian Science Museum Bulletin 1.

Roy, S. K. 1941. Contributions to paleontology.—Field Museum of Natural History, Geology series 4:203–220.

Ruedemann, R. 1901. Trenton conglomerate of Rysedorph Hill, Rensselaer County, New York, and its fauna.—New York State Museum Bulletin 49:3–114.

———. 1912. The Lower Siluric shales of the Mohawk Valley.—New York State Museum Bulletin 162, 151 pp.

———. 1926. The Utica and Lorraine formations of New York.—New York State Museum Bulletin 272, 227 pp.

Runnegar, B., J. Pojeta, J. Neal, J. D. Taylor, M. E. Taylor, & G. McClung. 1975. Biology of the Hyolitha.—Lethaia 13:21–25.

Sinclair, G. W. 1946. Notes on the nomenclature of *Hyolithes.*—Journal of Paleontology 20:72–85.

Syssoiev, V. A. 1962. Cambrian hyolithids from the lower slope of the Aldan Shield. Akademiya Nauk S.S.S.R., 63 pp.

———. 1968. Stratigraphy and hyolithids of the oldest Cambrian beds of the Siberian Platform. Nauka Publishers, Yakutsk, 67 pp.

———. 1974. Biostratigraphy and paleontology of the lower Cambrian of Europe and western Asia. Akademiya Nauk S.S.S.R., 248 pp.

Thoral, M. 1935. Contribution a l'etude paleontologique de l'Ordovicien inferieur de la Montagne et revision sommaire de la faune cambrienne de la Montagne Noire. Montpellier, 362 pp.

Val'kov, A. K. 1975. Biostratigraphy and hyolithids of the lower Cambrian of the northeast of the Siberian Platform. Akademiya Nauk S.S.S.R., 188 pp.

Walcott, C. D. 1884. Paleontology of the Eureka District, Nevada.—U.S. Geological Survey Monograph 8, 298 pp.

Webers, G. F. 1972. Paleoecology of the Cambrian and Ordovician strata of Minnesota. Pp. 474–484 *in* P. K. Sims & G. B. Morey, eds., Geology of Minnesota: A centennial volume. Minnesota Geological Survey, Minneapolis.

———, & G. S. Austin. 1972. Field trip guidebook for Paleozoic and Mesozoic rocks of southern Minnesota. Minnesota Geological Survey Guidebook Series No. 4.

Whitfield, R. P. 1878. Preliminary descriptions of new species of fossils from the lower geological formations of Wisconsin.—Wisconsin Geological Survey Annual Report for 1877, 50–89.

———. 1882. Paleontology. Geology of Wisconsin.—Wisconsin Geological Survey, 163–363.

Yochelson, E. L. 1984. Speculative functional morphology and morphology that could not function: The example of *Hyolithes* and *Biconulites.*—Malacology 25:255–264.

Zazvorka, V. 1928. Revision of the Hyolithi from dγ.—Palaeontographica Bohemiae 13:1–22.

University of Maryland, European Division, APO New York, 09102.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 279–299

A NEW *PYRGULOPSIS* (GASTROPODA: HYDROBIIDAE) FROM SOUTHEASTERN CALIFORNIA, WITH A MODEL FOR HISTORICAL DEVELOPMENT OF THE DEATH VALLEY HYDROGRAPHIC SYSTEM

Robert Hershler and William L. Pratt

Abstract.—*Pyrgulopsis giulianii,* new species, from a few, mid-elevation streams in southern Sierra Nevada (Indian Wells and Kern River Valleys), is described and new records for three other local congeners also are given. Details of shell form and penial morphology distinguish the new snail from related forms found in Owens Valley. Zoogeographic patterns of Death Valley System *Pyrgulopsis* support the hypothesis that a highly integrated pluvial drainage was present in the region, and also suggest that the system had various historic connections (possibly non-contemporaneous with the above) to adjacent areas. A model of drainage evolution of the Death Valley System is presented, based on distributional data of hydrobiids and other organisms of perennial waters.

This is the third and final paper in a series on systematics of springsnails (Gastropoda: Hydrobiidae) from Death Valley System, southeastern California and southwestern Nevada. Earlier contributions dealt with fauna from the Ash Meadows spring oasis in Amargosa Desert (Hershler & Sada 1987), and Owens and Amargosa Basins (exclusive of above, Hershler 1989). Results of survey of remaining portions of the system and adjacent areas are summarized herein, including description of a new *Pyrgulopsis* and new records for three other congeners. A model for historical development of drainage in the Death Valley System is presented, largely based on zoogeography of resident *Pyrgulopsis.*

Materials and Methods

Localities visited during this portion of the survey are listed in Appendix 1, and consisted of low- to mid-elevation springs and perennial streams. Fuller treatments of taxa (other than the new species) are in Hershler (1989) and Hershler & Sada (1987). Shell morphometric methodology is that of Hershler (1989). Dots on distribution maps represent one or several closely spaced localities. Repositories of material examined are indicated in the text as follows: LACM—Los Angeles County Museum of Natural History; SBMNH—Santa Barbara Museum of Natural History; UNLVM—University of Nevada at Las Vegas Museum of Natural History; USNM—National Museum of Natural History; WBM—Walter Miller personal collection.

Systematics

Family Hydrobiidae Troschel, 1857
Genus *Pyrgulopsis* Call & Pilsbry, 1886
Pyrgulopsis giulianii, new species
Southern Sierra Nevada springsnail
Figs. 1–4

Pyrgulopsis cf. *stearnsiana.*—Hershler, 1989:194 (Sage, Sand Canyons; figs. 37–40).

Material examined.—California. Kern County: Stream in Sage Canyon, USNM 853520, 857975; Stream in Sand Canyon, USNM 860444 (holotype), 853519 (para-

Table 1. Shell parameters for *Pyrgulopsis giulianii.* UNSM catalog number and number of specimens (in parentheses) are given beneath locality name. WH = number of whorls, SH = shell height, SW = shell width, LBW = length of body whorl, WBW = width of body whorl, AL = aperture length, AW = aperture width, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, SA = aperture shape.

		Locality			
Parameter		Sand Canyon 853519 (10)	Sage Canyon 853520 (15)	Ninemile Canyon 860446 (6)	Cow Canyon 860448 (8)
WH	mean	4.13	4.15	4.25	4.44
	SD	0.13	0.16	0.27	0.18
	range	4.00–4.25	4.00–4.50	4.00–4.50	4.00–4.50
SH		2.43 (mm)	2.58	3.33	3.16
		0.19	0.14	0.41	0.15
		2.06–2.74	2.39–2.87	2.82–3.99	3.01–3.48
SW		1.68	1.67	2.26	2.17
		0.11	0.13	0.25	0.12
		1.45–1.81	1.52–2.04	2.26–2.60	1.98–2.37
LBW		1.90	1.99	2.55	2.38
		0.16	0.11	0.23	0.10
		1.61–2.13	1.83–2.22	2.27–2.78	2.24–2.49
WBW		1.43	1.48	1.82	1.77
		0.08	0.08	0.18	0.08
		1.27–1.53	1.37–1.61	1.56–2.08	1.65–1.89
AL		1.21	1.18	1.59	1.55
		0.11	0.08	0.13	0.07
		1.03–1.36	1.06–1.39	1.41–1.76	1.35–1.55
AW		0.97	0.96	1.31	1.21
		0.07	0.05	0.13	0.06
		0.88–1.06	0.88–1.13	1.16–1.49	1.08–1.26
W		1.95	1.99	1.88	1.65
		0.15	0.24	0.18	0.19
		1.69–2.23	1.59–1.89	1.61–2.14	1.45–2.03
D		0.60	0.62	0.58	0.56
		0.04	0.06	0.04	0.03
		0.54–0.68	0.51–0.74	0.50–0.62	0.51–0.61
T		4.90	6.29	4.84	4.65
		0.47	0.47	0.91	0.51
		4.27–5.65	4.32–8.61	3.84–5.96	4.04–5.31
SA		1.25	1.23	1.22	1.21
		0.06	0.06	0.04	0.06
		1.14–1.36	1.13–1.34	1.19–1.29	1.15–1.30

types), 857974, SBMNH 35140 (paratypes); Stream in Sand Canyon, 3.7 km up canyon from US 6, WBM 4230, 4387; Small streamlet, S Fork Short Canyon, USNM 860445; Stream in Ninemile Canyon, USNM 860446; Stream in Grapevine Canyon, USNM 860447; Stream in Grapevine Canyon, 7.2 km up canyon from US 6, WBM 4229, 4360; Stream in Cow Canyon, USNM 860448.

Diagnosis.—A small- to moderate-sized species with ovate conic shell. Penis small relative to head/foot; penial lobe reduced, filament elongate relative to remaining penis. Penial glandular ridges 1–4; ventral ridge sometimes borne on low swelling.

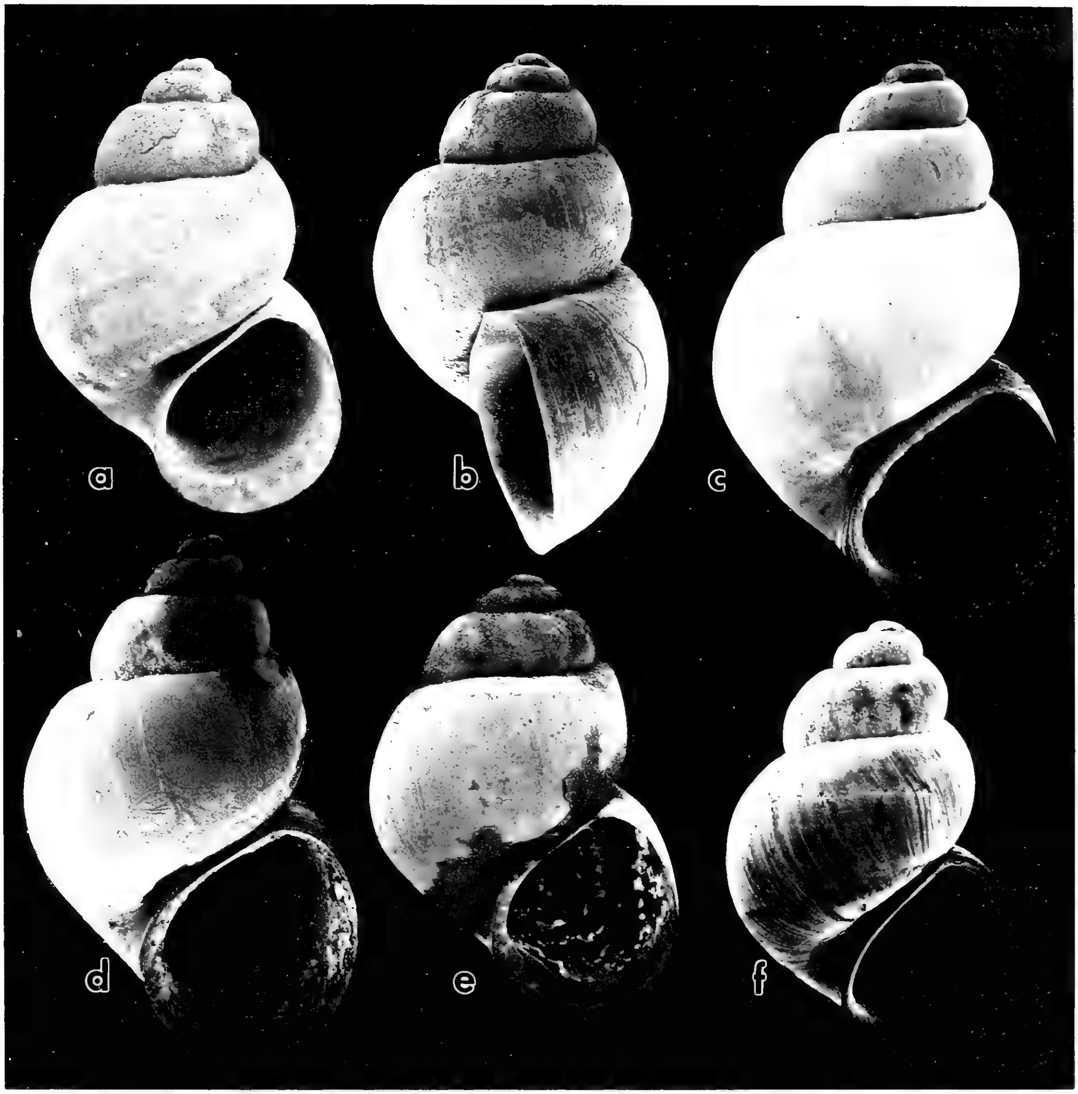


Fig. 1. Scanning electron micrographs of shells of *Pyrgulopsis giulianii,* new species: a, b, USNM 860444, holotype (standard and side views); c, USNM 860447; d, USNM 860446; e, USNM 860448; f, USNM 860445. The holotype is 2.75 mm tall (other micrographs are printed at the same scale).

Description.—Shell morphometric data are in Table 1. Shell (Fig. 1) 2.0–4.0 mm high, height/width, 130–170%. Apex protruding (Fig. 2e). Whorls, 4.0–4.5, slightly to moderately convex, with indented sutures and slight sub-sutural shoulders. Aperture ovate, angled above, about half as tall as body whorl. Inner lip straighter than outer, slightly to moderately thickened and reflected, adnate to small portion of or slightly separated from body whorl. Outer lip thin; apertural plane slightly tilted relative to coiling axis. Umbilicus slit-like to moderately open. Shell surface usually encrusted with brown-black deposits.

Operculum (Fig. 2f) paucispiral, with eccentric nucleus; whorls, 3–4. Opercular surface attached to foot bearing elongate (ca.

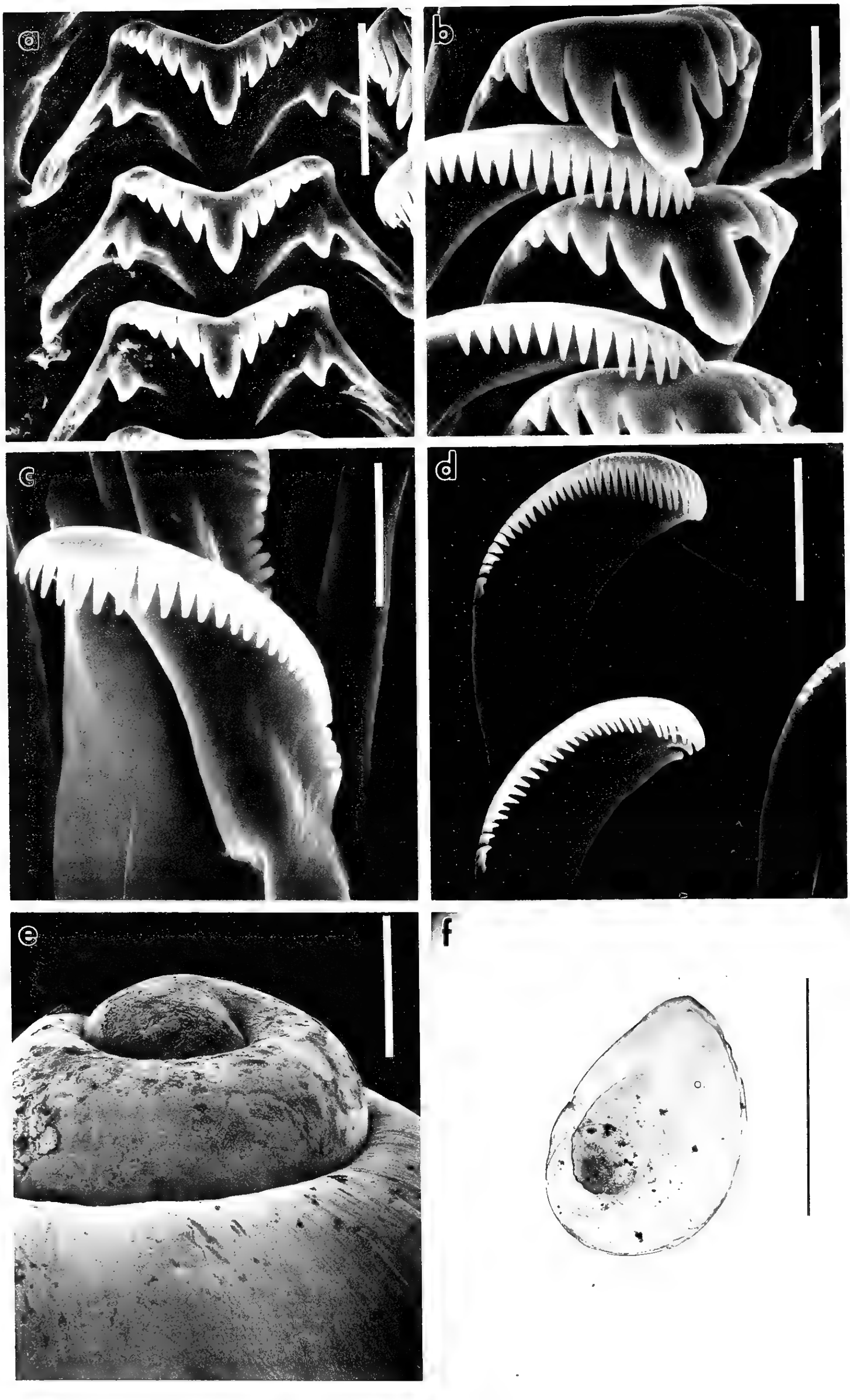


Fig. 2. *Pyrgulopsis giulianii*: a–d, Radula, USNM 860448 (a, Centrals, bar = 12.0 μm; b, Laterals and inner marginals, bar = 8.6 μm; c, Inner marginal, bar = 7.5 μm; d, Outer marginals, bar = 8.6 μm); e, Shell apex (bar = 136 μm), USNM 860447; f, Dorsal view of operculum showing thickened callus (bar = 1.0 mm), USNM 853519.

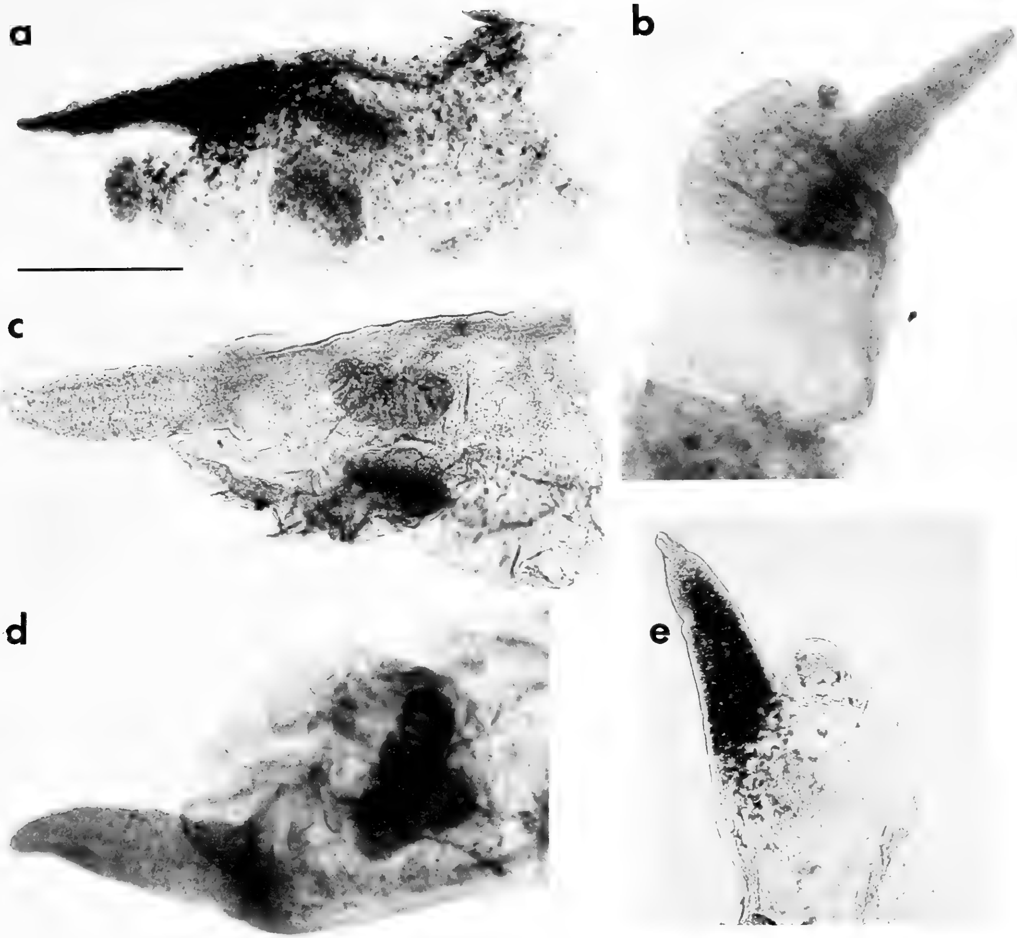


Fig. 3. Penes (whole mounts) of *P. giulianii*: a–c, Dorsal aspects; d, e, Ventral (a, e, USNM 857974, bar = 0.25 mm [others to scale]; b–d, WBM 4229). Note stained glandular ridges (both dorsal and ventral examples visible) and black subepithelial pigment (mostly in penial filaments).

50% of operculum length), gently curved, thickened, non-calcareous, amber callus (similar to those described for congeners by Taylor 1987). Dark, grey-black epithelial pigment on most of snout (except distal tip), proximal portion of cephalic tentacles, along anterior and posterior edges of sides of head/foot, and part or all of operculigerous lobe. Pigment on central portions of sides of neck absent to dark (dense subepithelial pigment cluster present in area).

Ctenidial filaments, ca. 20. Osphradium ca. 25% of ctenidium length. Style sac and remaining stomach ca. equal in length. Small caecal chamber present. Radular (Fig. 2a–d) formula: 5(6)-1-5(6), 2(3,4)-1-3(4,5), 23-29, 23-35 (from two populations). Central tooth broadly trapezoidal; basal cusps short, triangular; basal process moderately excavated. Penis (Fig. 3) rarely protruding beyond edge of mantle collar, usually of stunted appearance, relatively flat (apart from ventral swelling), longer than wide. Filament slender, sub-equal to remaining penis length. Reduced lobe short relative to filament length. Tip of lobe usually ornamented with small glandular ridge; somewhat larger, single ridges on dorsal penial surface

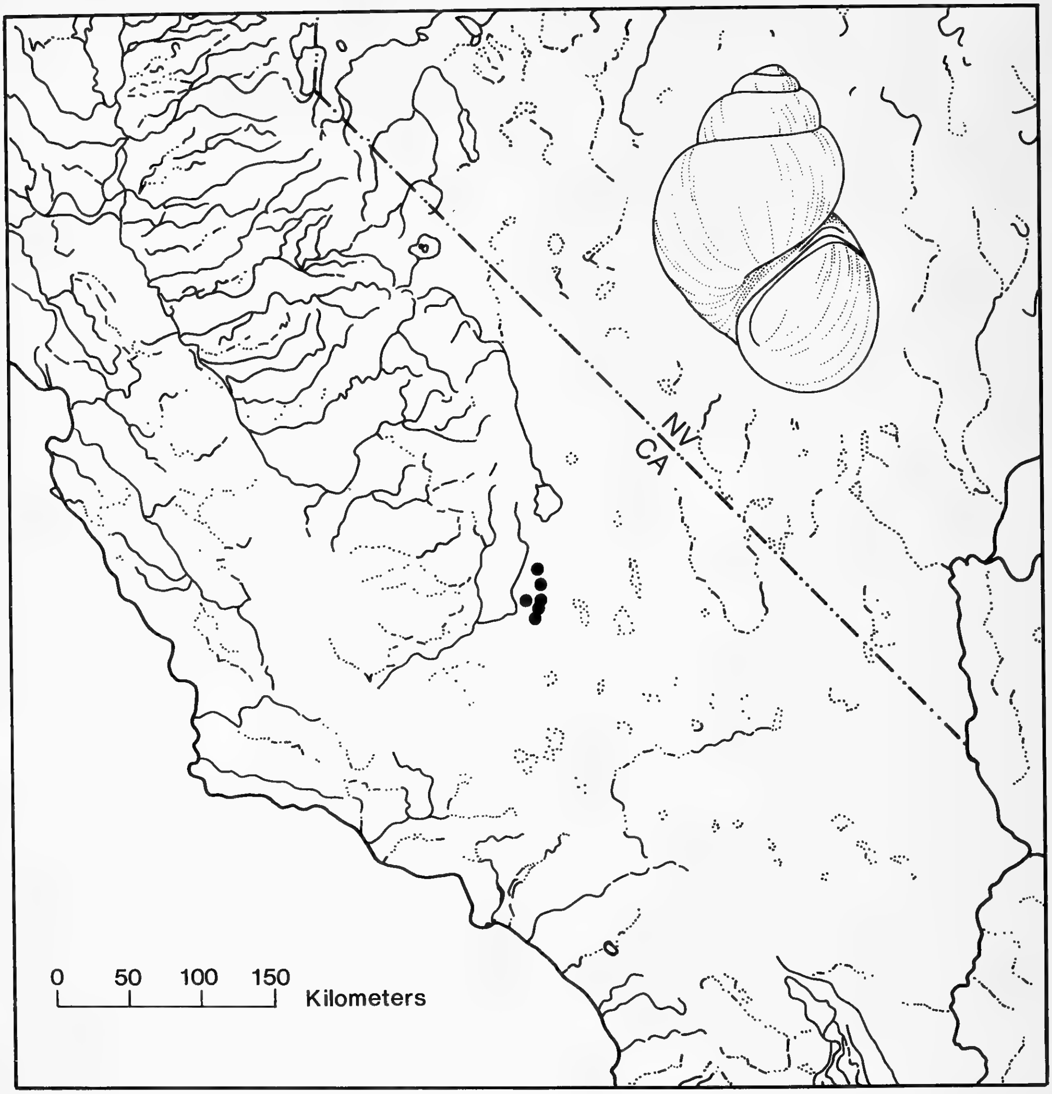


Fig. 4. Distribution of *P. giulianii.*

at central position ca. halfway between base of penis and base of filament, on ventral surface near (sometimes on) inner edge. A single specimen (from Cow Canyon) had a small fourth ridge located on dorsal surface between ridge on lobe and central dorsal ridge. Filament with dark sub-epithelial pigment streak; pigment granules also scattered throughout small area surrounding base of filament. Albumen gland sub-equal to capsule gland. Seminal receptacle small, positioned anterior to bursa copulatrix. Bursa copulatrix small relative to capsule gland, positioned partly posterior to gland.

Type locality.—A moderate-sized stream in floor of Sand Canyon, Kern County (center of section 7, T 25S, R 38E; ca. 1068 m elevation) (Hershler 1989:fig. 8d). Snails common in shallow water (<0.5 m), on watercress.

Distribution and habitat.—Known from six small- to moderate-sized streams in southern Sierra Nevada, of which five are in western Indian Wells Valley and one is in adjacent Kern River Valley (Fig. 4).

Etymology.—Named after Derham Giuliani, an avid student and indefatiguable collector of Great Basin biota, who discovered a number of new localities of *Pyrgulopsis* in Owens Valley area.

Remarks.—Hershler (1989) tentatively assigned this snail to *P. stearnsiana* (Pilsbry) based on similarity of shell, but later comparison with near-topotypical, preserved material of the latter revealed striking differences in their penes and indicated separate species status for the populations in southern Sierra Nevada. *Pyrgulopsis giulianii* is distinguished from close allies found in Owens Valley (to the north) by its combination of large size, moderately elongate shell, and small penis with small lobe and very reduced ventral swelling.

Pyrgulopsis micrococcus (Pilsbry, 1893)
Fig. 5

Amnicola micrococcus Pilsbry *in* Stearns, 1893:277 (Small spring in Oasis Valley, Nevada; fig. 1).

Pyrgulopsis micrococcus.—Hershler & Sada, 1987:788 (numerous localities, mostly in Ash Meadows; figs. 8a, 9–16).

Pyrgulopsis micrococcus.—Hershler, 1989: 182 (numerous localities; figs. 17c, d, 20–25).

Paludestrina stearnsiana.—Berry, 1909:78 (Rill near mouth of Mill Creek Canyon).

Amnicola stearnsiana.—Berry, 1948:59 (Mill Creek Canyon).

Paludestrina longinqua.—Hannibal, 1912: 34 (Spring branch, mouth of Mill Canon, fide Berry 1909).

Hydrobia sp.—Taylor, 1954:69 (Old Woman Springs, Inyo Co.).

Material examined.—California. San Bernardino County: Mohave River at Barstow, USNM 713484; Old Woman Springs, 20.8 km SE of Lucerne Valley, LACM 106639, 107741; USNM 526395; Cushenbury Springs, 16 km SE of Lucerne Valley, LACM 106640, 106660, 106661, WBM 4270, USNM 860449; Box S Spring, 2.6 km SE of Lucerne Valley, LACM 106641; Box Spring (probably same as above), WBM 4266; Broadbent Spring, 10.2 km ESE of Lucerne Valley, LACM 106639, WBM 4264; Bear Lake, USNM 175096; Roadside spring between N shore highway and Big Bear Lake at point 1.2 km E of road which crosses lake, WBM 4274; Spring-fed pond between N shore road and Big Bear Lake, at point 1.6 km W of road which crosses lake, WBM 4276; Spring zone SW of Big Bear Ranger Station, USNM 860450; Spring, S side of CA Highway 18, N side Big Bear Lake, LACM 106644; Rill near mouth of Mill Creek Canyon, LACM 106646, 106647; Small stream, Mill Creek Canyon, SE of CA Highway 38, 0.34 km NE of Power House Canyon Bridge, LACM 106645; Mill Creek at Thurman Flats Picnic Area, USNM 860451; Spring 4.5 km up Mill Creek Rd. from junction with Yucaipa Rd., WBM 4263. Nevada. Clark County: Cold Creek, UNLVM 3212; Willow Creek, UNLVM 3451.

Diagnosis.—A small-sized species, with globose to ovate-conic shell. Penis with moderate-sized lobe; distal edge of lobe usually ornamented with small glandular ridge.

Remarks.—This snail is very similar, even in general form of penis and disposition of glandular ridge, to *P. stearnsiana* (Pilsbry), which occurs in Central California, "from Sonoma County to Monterey County along the coast and inland in the foothills of the Sierra Nevada" (Taylor 1981:152). The sole reliable distinguishing feature appears to be the larger and longer penial lobe of *P. micrococcus*, but study of additional material of *P. stearnsiana* will be necessary to determine generality of this difference.

Populations in San Bernardino Mountains are separated from remaining range of *P. micrococcus* to the north by poorly watered (and apparently snailless) Mohave Desert (but note that an old collection was taken from an intermediate locale at Barstow). Populations in the headwaters of the Willow Creek drainage (which enters Indian Springs Valley) on the northeast slope of Spring Range are apparently relicts from pre-Wisconsin time, since the snail is absent from well-studied (26 samples) late Wisconsin sediments from the valley floor at the mouth of Willow Creek (Quade & Pratt 1989).

Pyrgulopsis owensensis Hershler, 1989
Fig. 6

"Undescribed form of *Fontelicella*"(?).—Taylor 1985:318 (Owens Valley, E Fork Walker River; unfigd.).

Pyrgulopsis owensensis Hershler, 1989:187 (numerous localities in eastern Owens Valley; figs. 26a–d, 27–32).

Material examined.—California. Mono County: Spring, W side East Fork Walker River, USNM 860452.—Nevada. Lyon County: Spring at Wiley Ranch, USNM 860453.

Diagnosis.—A small- to moderate-sized species with globose to ovate-conic shell. Penis large relative to head/foot; lobe enlarged, filament short. Penial glandular ridges, 2–6; ventral ridge borne on pronounced swelling.

Remarks.—Populations in Walker Basin represent significant range extension of species (previously known only from Owens Valley) into pluvial Lahontan System.

Pyrgulopsis wongi Hershler, 1989
Fig. 7

Pyrgulopsis wongi Hershler, 1989:196 (numerous localities in Owens Valley area; figs. 41–47).

Material examined.—California. Mono County: Springs SW of Conway Summit, USNM 860454; Spring, Pizona, USNM 869034; Upper Pizona Spring, USNM 869035; Spring in West Queen Canyon, USNM 860511; Truman Spring, USNM 860512. Inyo County: Spring NW corner of Round Valley, USNM 860455; Spring, SW corner of Round Valley, USNM 860456; "Smoke Spring," USNM 853926; Springs, Marble Canyon, USNM 860457 (upper spring), 860458 (lower); Spring, 1.2 km NW of Big Pine Spring, USNM 860459; Spring at McMurry Meadows, USNM 860513; Spring on N side of Red Mountain, USNM 860514; Spring in canyon N of McGann Springs, USNM 860515; McGann Springs, USNM 869036; Tub Springs, USNM 869037; Spring, 0.1 km N of Independence Creek, USNM 860460; Springs SW of Lone Pine, USNM 869038 (North), USNM 869039 (South); Spring at Lower Diaz Creek, USNM 869040; Springs at Upper Diaz Creek, USNM 869041 (North), USNM 869042 (South); Spring S of Carrol Creek, USNM 869043; Stream, Talus Canyon, USNM 860461; Canyon N of Johnson Canyon, USNM 853925; Johnson Canyon, USNM 853928; Stream, Tunawee Canyon, USNM 860462; Canyon S of Tunawee Canyon, USNM 853927; Stream, Sacatar Canyon, USNM 860463 (N Fork), USNM 860464 (S Fork). Nevada. Esmeralda County: Springs at Dyer Ranch, USNM 860465. Mineral County: Huntoon Spring, USNM 869033.

Diagnosis.—A small- to moderate-sized species with globose to low conical shell. Penis elongate and broad relative to head/foot; filament large and lobe moderate-sized. Glandular ridges, 7–12, of which two are borne on prominent ventral swellings located near distal edge of lobe.

Remarks.—The Inyo County populations fall into previously known range of species. Localities in Fish Lake Valley and Mono Valley represent significant range extensions. The latter area, with a recent history of significant volcanic activity (Gilbert et al. 1968, Kilbourne et al. 1980), previously had been considered devoid of perennial water mollusks (Taylor 1985:318).

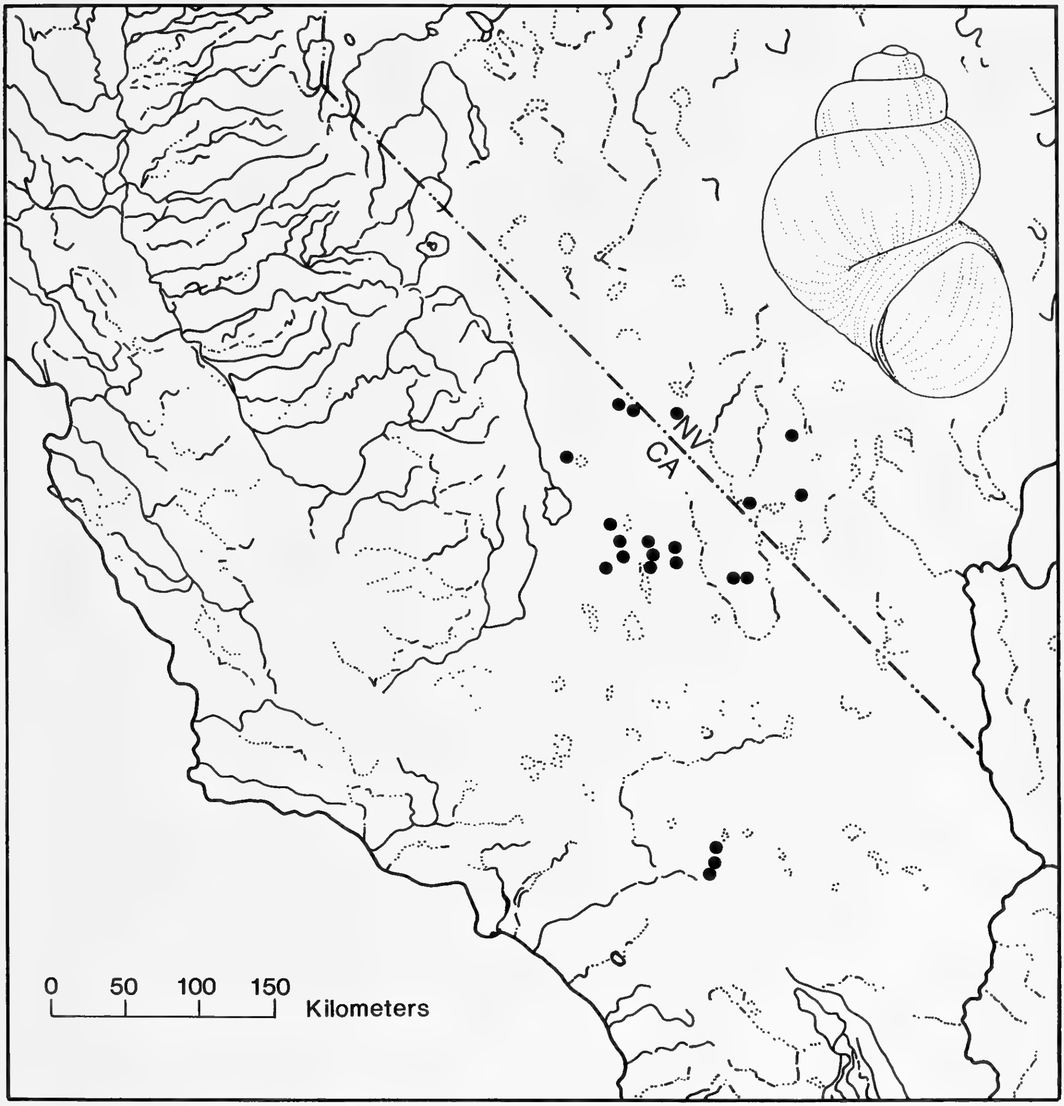


Fig. 5. Distribution of *P. micrococcus* (Pilsbry).

Discussion

In an earlier paper, Hershler (1989) concluded that springsnail zoogeography (in part) supports the frequently advocated hypothesis that a highly integrated pluvial drainage was present in Death Valley System (Fig. 8) during late Quaternary, pluvial period (10,000–100,000 B.P.). These data also provide evidence of historic connections between the system and adjacent regions, some of which were probably pre-Quaternary. Results of this study support this conclusion insofar as additional examples of both of the above features have been discovered, which are synthesized with the earlier data below.

Pyrgulopsis is the most diverse (13 spp.) and among the most widespread genera of

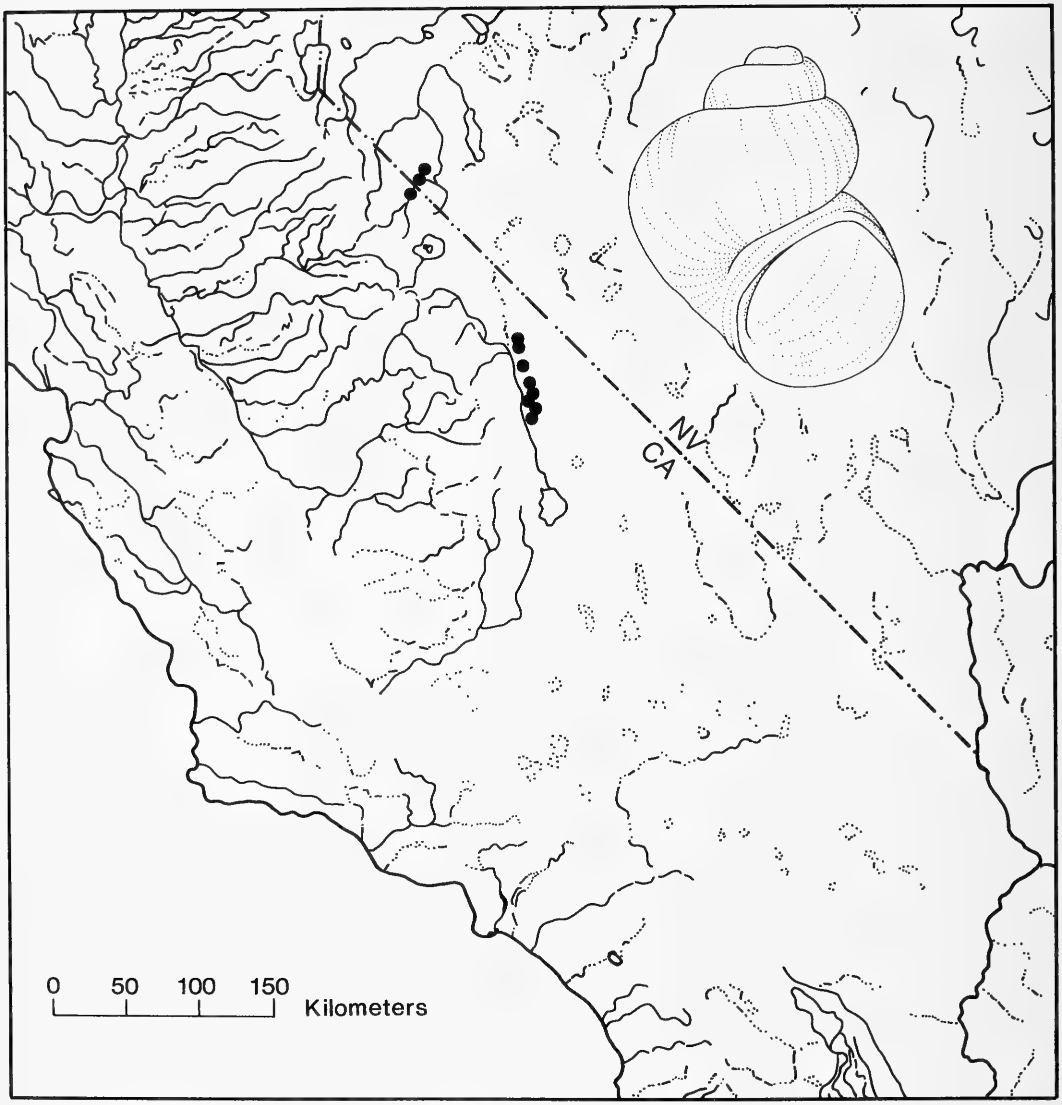


Fig. 6. Distribution of *P. owensensis* Hershler.

freshwater mollusks in the Death Valley System, and therefore is a highly suitable subject for zoogeographic inquiry. Other prosobranchs associated with perennial waters, *Tryonia* Stimpson, 1865 (Hydrobiidae), and *Assiminea* Fleming, 1828 (Assimineidae), are less diverse and considerably more localized in the system (Taylor 1985, Hershler 1987, Hershler & Sada 1987, Hershler 1989), and largely are excluded from further discussion.

Distributions of Death Valley System *Pyrgulopsis* are summarized in Table 2. For purposes of discussion, it is assumed that non-aquatic dispersal of these snails is insignificant, on a large scale, and that distribution of a species reflects past or present continuity or near-continuity of aquatic habitat.

Evidence for pluvial integration of Death

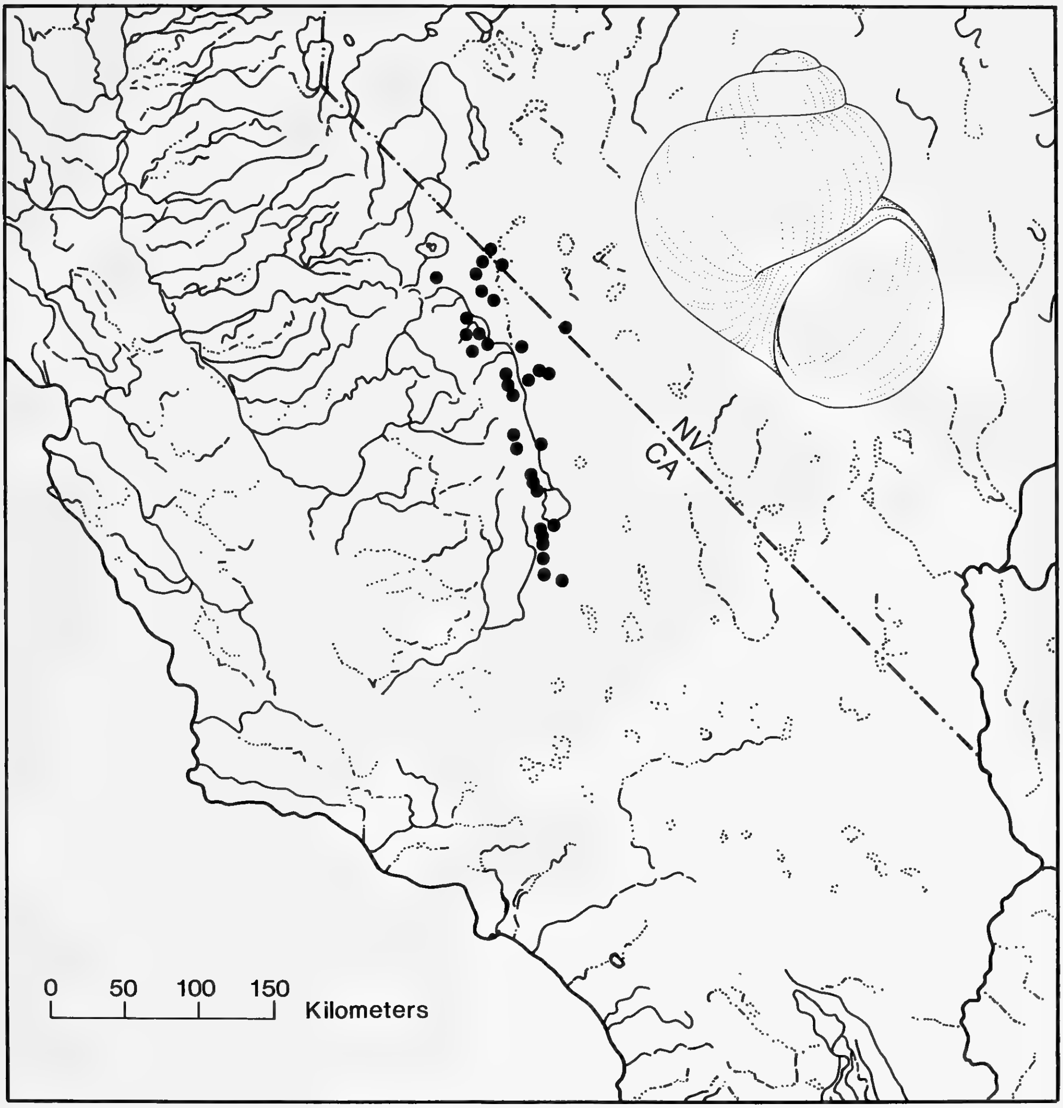


Fig. 7. Distribution of *P. wongi* Hershler.

Valley System is provided by distributions of two of the more widespread forms. The range of *Pyrgulopsis wongi* (Fig. 7) closely approximates pluvial Owens River drainage, as this snail extends from Mono Valley through both Adobe and Long Valleys into Owens Valley. This supports inclusion of the former valley (currently without surficial water connection to Owens Basin and considered of uncertain historic relationships by Hubbs & Miller 1948:79) in pluvial Owens River drainage. Distribution of *P. micrococcus* (Fig. 5) similarly supports integration of now-isolated sub-units of pluvial Amargosa River drainage (i.e., sites along modern course of river, Ash Meadows, northern Death Valley). This species also has been found (Quade & Pratt, pers. comm.) in Wisconsin pluvial sediments of Chicago Valley, a now dry tributary of the

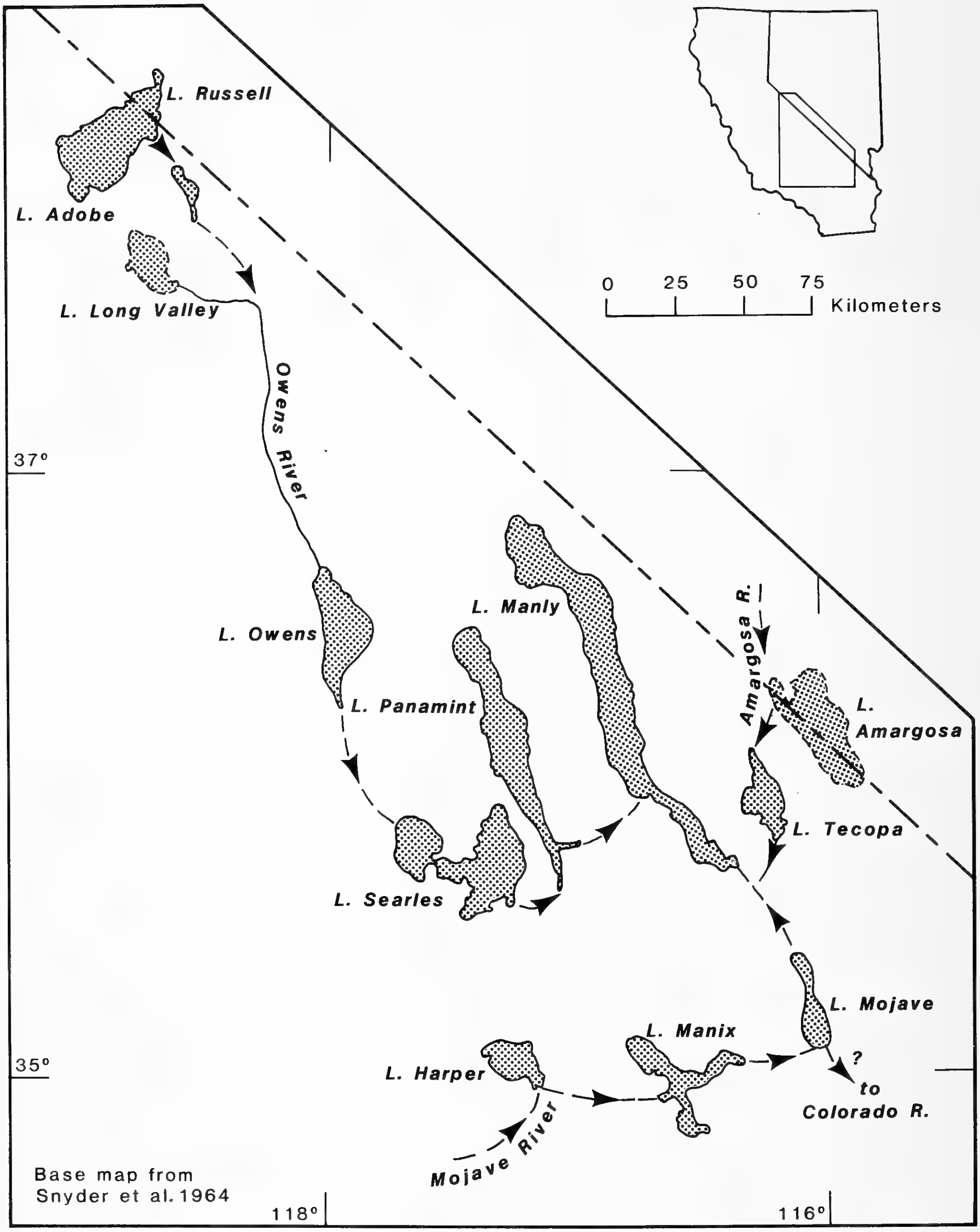


Fig. 8. Pleistocene Death Valley System showing drainage relations (not necessarily contemporaneous). Stippled areas encircled by dashed lines may not have contained lakes for significant portions of the pluvial period.

Amargosa Basin, together with two other snails from Amargosa drainage, *Tryonia variegata* Hershler and Sada and an undescribed *Assiminea* species now living at Ash Meadows and elsewhere in the drainage. In addition, presence of *P. micrococcus* in Panamint Valley and San Bernardino Mountains more generally supports pluvial integration of the three rivers comprising Death Valley System (Owens, Amargosa, Mohave).

Snail distributions also imply the following historic drainage connections: a) between Owens Basin and both Lahontan System, and Deep Springs and Fish Lake Valleys; b) between lower Owens Basin and adjacent Kern River Valley; c) between Mohave and Los Angeles Basins; d) between Amargosa Basin and both Frenchman Flat and Indian Springs Valley; and e) between the system and Saline Valley.

Implied connections between Amargosa Basin and both Frenchman Flat and Indian Springs Valley (which do not currently drain into the system) are intriguing because these areas are currently separated by low, presumably labile divides of alluvial material and could have drained to the Amargosa possibly during the Quaternary ("alluvial cone [drainage] connection" of Hubbs & Miller 1948:147). However, other examples are clearly untenable within the framework of modern regional topography and probably reflect Neogene conditions. For instance, distribution of *P. wongi* implies former aquatic connections between Owens Basin and Deep Springs and Fish Lake Valleys to the east. These areas are profoundly separated by White Mountains, and surficial water connections between them during pluvial period is extremely unlikely. (The latter two valleys drained [if at all] into Lahontan System [Miller 1928, Hubbs & Miller 1948].) Note, however, that inception of Basin and Range was a relatively recent event (ca. 2–6 million years B.P.) in Owens Valley area (Bachman 1979, Giovannetti 1979, St. Amand-Roquemore 1979) and distribution of *P. wongi* could reflect prior drainage relationships. A second example involves *P. micrococcus,* whose distribution suggests a former aquatic connection between Saline Valley and pluvial Owens drainage. Saline Valley is a small, but deeply downthrown basin that probably was closed to external drainage during pluvial times (Hubbs & Miller 1948). The valley is separated from Panamint Valley (which was part of the pluvial Owens System) by the Nelson Range, which connects the Inyo and Cottonwood Ranges. However, Grapevine Canyon, at the eastern end of the Nelson

Table 2. Distributions of *Pyrgulopsis* spp. Basins or valleys considered part of the Death Valley System by Hubbs & Miller (1948:table 1) are indicated by asterisks.

Species	Distribution
P. aardahli	Northern Owens Valley*
P. amargosae	Lower Amargosa Basin*
P. crystalis	Ash Meadows (Amargosa Basin)*
P. erythropoma	Ash Meadows (Amargosa Basin)*
P. fairbanksensis	Ash Meadows (Amargosa Basin)*
P. giulianii	Indian Wells Valley,* Kern River Valley
P. isolatus	Ash Meadows (Amargosa Basin)*
P. micrococcus	Frenchman Flat, Indian Springs Valley, Amargosa Basin,* Northern Death Valley,* Panamint Valley,* Saline Valley, San Bernardino Mtns. (Mohave,* Los Angeles Basins)
P. nana	Ash Meadows (Amargosa Basin)*
P. owensensis	Owens Valley,* E Fork Walker Basin
P. perturbata	Northern Owens Valley*
P. pisteri	Ash Meadows (Amargosa Basin)*
P. wongi	Mono Valley,* Long Valley,* Adobe Valley,* Owens Valley,* Huntoon Valley, Deep Springs Valley, Fish Lake Valley

Range, is the trace of a predominantly slip-strike fault (Cemen et al. 1985:fig. 1), and restoring 10 km of movement along this fault would open Saline Valley to Panamint Valley drainage.

Taxonomic affinities of Death Valley System *Pyrgulopsis* can only be addressed in a general sense owing to relative paucity of data on adjacent extra-limital faunas, but are consistent with the above in that they point toward a diverse origin of resident forms. *Pyrgulopsis wongi* from western portion of system (and Lahontan System) is not closely related to other local forms, but is very similar to *P. californiensis* (Gregg & Taylor), from west and south of the system (Taylor 1981:152). Also present in Owens Basin is an apparent species flock, comprising *P. owensensis* and three local endemics, without obvious affinities to other snails found in the system. The presence of *P. owensensis* in Lahontan System suggests possible derivation of the Owens Basin group from the north via Neogene Owens River. Note that *P. nevadensis* (Stearns), from Lahontan System, has a pattern of penial glandular ridges (discerned in rehydrated material; Hershler & Thompson 1987) suggesting a close relationship with this group. *Pyrgulopsis micrococcus* has affinities with *P. amargosae* Hershler from lower Amargosa Basin, but is much more similar to *P. stearnsiana* from west of the system. Ash Meadows endemics include (at least) two species flocks composed of pairs of very similar forms: a) *P. erythropoma* (Pilsbry) and *P. crystalis* Hershler & Sada, having trochoid shells and unlobed penes bearing single, central ventral glandular ridge; and b) *P. nanus* Hershler & Sada and *P. isolatus* Hershler & Sada, having globose-conic shells and large-lobed penes bearing single glandular ridge at terminus of lobe. Inclusion of *P. pisteri* in the former group and *P. fairbanksensis* Hershler & Sada in the latter is conjectured on basis of general penial similarity, but these display other significant morphological differences from respective group members and may represent additional lineages. Ash Meadows snails are dissimilar to an undescribed form of the nearby Las Vegas and Pahrump Valleys, which is closely related to *P. deserta* (Pilsbry) from Virgin Basin; and preliminary observations suggest that the fauna, except *P. micrococcus,* instead was derived from that of White River drainage. For example, *P. fairbanksensis* is similar to undescribed taxa from Pahranagat, White River, and Railroad Valleys in southeastern Nevada, whereas both *P. nana* and *P. isolatus* closely resemble *P. avernalis* (Pilsbry) of Moapa warm springs complex (also in southeast Nevada).

A hypothetical model of the history of Death Valley System and adjacent drainages is described below, based on both geological evidence and distributions of springsnails and other fauna of perennial waters. The model, which partly conforms to interpretations advanced by Hubbs & Miller (1948), Taylor (1985), and Minckley et al. (1986), is heuristic in intention, and presented as a framework for testing hypotheses generated from study of zoogeography of regional aquatic organisms.

In early Miocene time (Fig. 9), the Mohave River region probably drained to the Pacific, in the Los Angeles Basin area, as did most of the region immediately east of the present Sierra Nevada.[1] Fauna in these drainages included progenitors of the present Pacific coastal *Pyrgulopsis* and snails in Mohave System which gave rise to *P. micrococcus*. The White–Virgin River region,

---

[1] Occurrence of *P. micrococcus* in San Bernardino Mountains, Los Angeles Basin, suggests former drainage of the Mohave through this area. Three other freshwater mollusks (*Anodonta californiensis* Lea, *Pisidium compressum* Prime, *Valvata humeralis* Say) also occur (or occurred until recently) in both Los Angeles Basin and Death Valley System and not in coastal California immediately to the north (Taylor 1981, 1985). Additionally, one of the three primary freshwater fishes of Los Angeles Basin, *Pantosteus santaanae* (Snyder), may have originated within the ancestral Colorado River drainage (Smith 1966, Minckley et al. 1986).

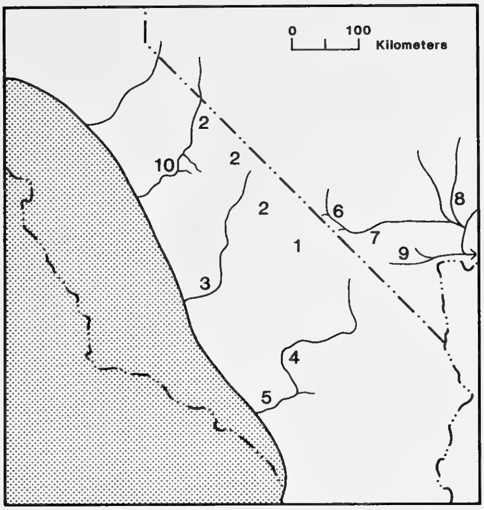


Fig. 9. Death Valley System and adjacent drainages during early Miocene, >16 Ma, before the development of basin and range structure. Screened areas are Pacific Ocean. Drainage lines are diagrammatic. It is doubtful whether any drainage, possibly excepting the San Joaquin on west slope of Sierra Nevada (Huber 1981) even approximately followed its modern course at this time. 1 = Future area of Death Valley; 2 = Future area of Owens drainage; 3 = Discharge of Owens–Kern drainage to Pacific; 4 = Ancestral Mohave River; 5 = Los Angeles Basin area; 6 = Amargosa River (included for convenience, existence in early Miocene uncertain); 7 = Ash Meadows; 8 = White–Virgin River system; 9 = Pahrump Valley (present location, which dates from late Miocene); 10 = Ancestral San Joaquin River.

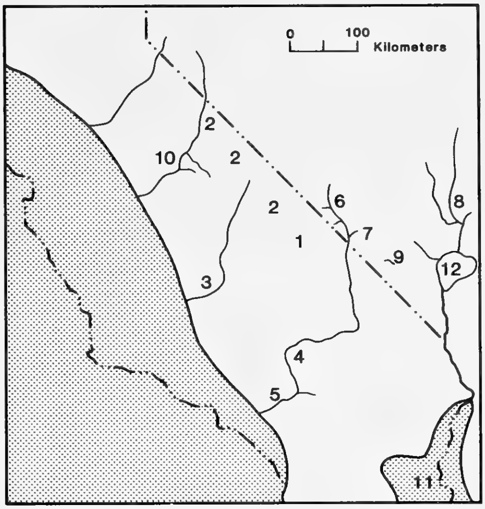


Fig. 10. Death Valley System and adjacent drainages during later Miocene, <15 Ma, after development of basin and range structure in southern Nevada. 1 = Death Valley region; 2 = Owens drainage region; 3 = Discharge of Owens–Kern drainage to Pacific; 4 = Ancestral Mohave River; 5 = Los Angeles Basin area; 6 = Amargosa River (see note in Fig. 9); 7 = Ash Meadows; 8 = White–Virgin River system; 9 = Pahrump Valley (see note in Fig. 9); 10 = Ancestral San Joaquin River; 11 = Bouse Embayment; 12 = "Lake Hualapai."

including the ancestral Amargosa and Colorado Rivers, drained eastward across northern Arizona and southeastern Utah to the Gulf of Mexico (Nilsen & McKee 1979), and was then inhabited by progenitors of the present Moapa River and Ash Meadows species complexes.

Shift to an extensional tectonic regime and uplift of the basin ranges in the late Miocene (Dickinson 1979) produced major alterations in drainage relations (Fig. 10). Uplift of the Spring, Sheep, Las Vegas, Pahranagat, and associated minor ranges, severed the Amargosa Basin; transferring its drainage to the Death Valley System and introducing progenitors of the Ash Meadows *Pyrgulopsis* to the system.[2] *Pyrgulopsis micrococcus* penetrated upstream into the Amargosa drainage and presumably gave rise to the local *P. amargosae.* Direction of flow of Colorado River was reversed, with the river coursing westward in approximately its modern path. Ponding in the present Lake Mead–Lake Mohave area produced the Hualapai limestones. These have been interpreted as marine (Blair & Armstrong 1979), but Taylor (1983) showed that the late Miocene molluscan fauna, as far downstream as Parker Dam, consisted of typically freshwater species (and not the marine taxa characteristic of the Bouse Embayment). Accordingly, we map the area of the Hualapai

---

[2] Progenitors of the endemic goodeid fish *Empetrichthys* (sister group to *Crenichthys* of White River drainage; Parenti 1981) also may have been introduced by this event.

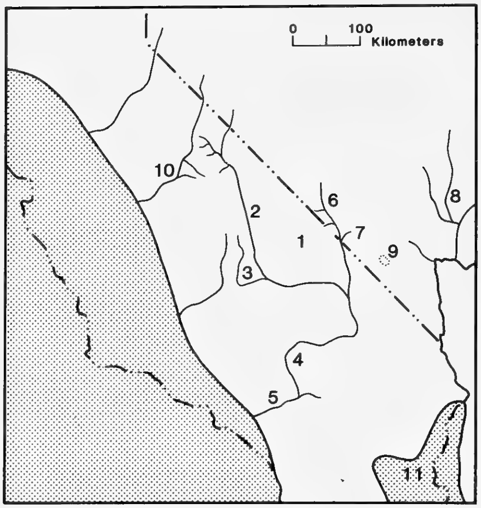


Fig. 11. Death Valley System and adjacent drainages during middle Pliocene, ca. 5 Ma, after initiation of major tilting of Sierra Nevada block fault. 1 = Death Valley region; 2 = Owens River; 3 = South Fork Kern River; 4 = Ancestral Mohave River; 5 = Los Angeles Basin area; 6 = Amargosa River; 7 = Ash Meadows; 8 = White–Virgin River system; 9 = Pahrump Valley; 10 = Ancestral San Joaquin River; 11 = Bouse Embayment.

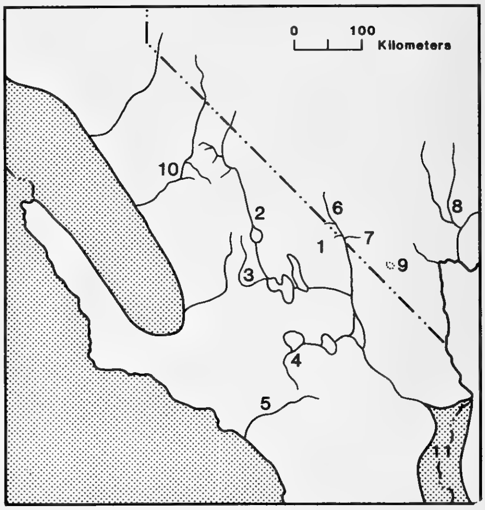


Fig. 12. Death Valley System and adjacent drainages during late Pliocene, ca. 4 Ma, after uplift of Transverse Ranges and before formation of Death Valley graben. 1 = Death Valley region; 2 = Owens River; 3 = South Fork Kern River; 4 = Mohave River; 5 = Los Angeles Basin; 6 = Amargosa River; 7 = Ash Meadows; 8 = White–Virgin River system; 9 = Pahrump Valley; 10 = Ancestral San Joaquin River; 11 = Bouse Embayment.

member as a lake, informally termed "Lake Hualapai." Note that Taylor (1983:294) recorded *P. avernalis,* presently surviving in the Moapa River drainage, in the Hualapai sediments.

During Pliocene time, tilting of the Sierra Nevada fault block beheaded trans-montane drainage, which was diverted southwards and formed the Owens River, which drained to the Pacific via Mohave River. Uplift began at the south, moving northwards (Huber 1981). Various evidence indicates that Owens Valley was forming by 6 Ma (see above), and the present Owens drainage probably was formed by not long after that time (Fig. 11). Coastal *Pyrgulopsis* of the *P. californiensis* group were transferred with the beheaded source areas, and gave rise to *P. wongi.* Severence of the trans-montane headwaters of the San Joaquin River is dated at 3.2 Ma; thereafter drainage was to the Mono Basin, and over the southern sill to the Owens River (Huber 1981). This drainage change may have allowed progenitors of the *Pyrgulopsis owensensis* group to invade the system from the north.[3] The South Fork Kern River was tributary to the Owens Basin.[4] Walker Pass, inter-

---

[3] In addition to *P. owensensis* and *P. wongi,* two other freshwater mollusks (*Helisoma newberryi* [Lea], *Vorticifex effusus* [Lea]) occurred in Lahontan and Death Valley Systems during historic times (Taylor 1981). These and another three Lahontan species (*Pisidium ultramontanum* Prime, *Valvata utahensis* Call, *Stagnicola kingi* [Meek]) were widespread within the latter during the Quaternary (Taylor 1985). The Tui Chub, *Gila bicolor* (Girard), also occurs in both areas (although differentiated in Owens and Mohave drainages; Miller 1973), and several other fishes of Death Valley System are closely related to Lahontan fauna (Minckley et al. 1986).

[4] As evidenced by distribution of *P. giulianii.* Schreck and Behnke (1971) suggested a similar drainage connection based on relationships of endemic Upper Kern River Valley golden trout, *Salmo aguabonita* Jordan.

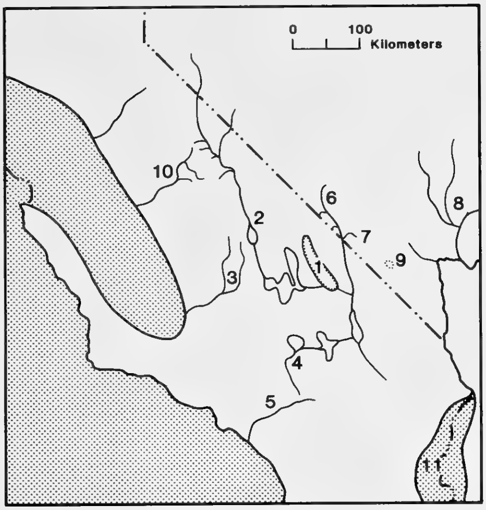


Fig. 13. Death Valley System and adjacent drainages during late Pliocene, <3 Ma, after formation of Death Valley graben and beheadal of ancestral San Joaquin drainage. 1 = Death Valley region; 2 = Owens River; 3 = South Fork Kern River; 4 = Mohave River; 5 = Los Angeles Basin; 6 = Amargosa River; 7 = Ash Meadows; 8 = White–Virgin River system; 9 = Pahrump Valley; 10 = San Joaquin River; 11 = Bouse Embayment.

preted as a wind gap in this model, is approximately 700 m above the margin of Indian Wells Valley, suggesting that drainage severence occurred no earlier than 2.5 Ma (based on uplift rates in the Deadman's Pass area; Huber 1981), and possibly more recently as uplift rates increased southwards. During the late Pliocene (Fig. 12), uplift of the Transverse Ranges, which enclose the present internal drainage of the Mohave Desert, resulted from compression accompanying the northward movement of the crustal block west of the San Andreas Rift zone (Woodburne 1975). Drainage direction of the Mohave River was reversed, probably with considerable dislocation, rerouting, and ponding. Drainage of the Death Valley System was shifted from the Los Angeles Basin to the Bouse Embayment. Deposition in basins east of the San Bernardino Mountains apparently shifted from eastern-derived to western-derived sediments around the Hemphillian-Blancan transition (Woodburne 1975). Late Pliocene tilting of the Sierra Nevada block (Cole & Armentrout 1979) transferred South Fork Kern River from the Owens to the Kern system. Development of internal drainage in the Death Valley rift occurred in early Pleistocene, establishing a new base level and transferring the drainage sump of the Death Valley System from the Bouse Embayment to Death Valley (Fig. 13), thereby completing development of the present system.[5]

Acknowledgments

Fieldwork was supported (in part) by California Fish and Game (Contract FG7342). Bureau of Land Management (Ridgecrest Resource Area) and California Fish and Game (Bishop Office) loaned vehicles and provided other logistic support. Collecting permits were provided by State of California and Joshua Tree National Monument. Assistance in the field was provided by J. Aardahl, M. Blymyer, J. Farrell (BLM); D. Wong (California Fish and Game); W. Cassidy (Fort Irwin); R. Moon and associates (Joshua Tree National Monument); D. Giuliani, S. Denton-Pratt, and D. Sada. Material was loaned by Dr. J. McLean and C. Coney (LACM), and Drs. W. B. Miller and E. Hochberg (personal collection of former, loaned through SBMNH). The assistance of the Scanning Electron Microscopy Laboratory (NMNH) is greatly appreciated. M.

---

[5] Although extensional tectonics of the Death Valley region have been extensively studied (e.g., Wernicke et al. 1988 and references cited therein), little has been published regarding drainage. Cemen et al. (1985) recorded a late Pliocene (to 4 Ma) basin oriented roughly from north of the Black Mountains to Salt Creek, at approximately a 45° angle to the present valley. Hunt and Mabey (1966) made a convincing case for deposition of the "no. 2 gravel" alluvial fans, estimated at 0.5 Ma, under an external drainage regime. They considered major movement of the normal fault along which the valley has been downthrown to be late Quaternary in age.

Ryan and P. Greenhall (both NMNH, Invertebrate Zoology) drafted maps, and prepared and digitized camera lucida drawings of shells, respectively. The section on history of the Mohave–Death Valley region benefited from comments by D. L. Weide.

Literature Cited

Bachman, S. B. 1979. Pliocene–Pleistocene break-up of the Sierra Nevada–White–Inyo Mountains block and formation of Owens Valley.—Geology 6:461–463.

Berry, E. G. 1948. Snails collected for the schistosomiasis investigations.—United States National Institute of Health Bulletin 189:55–69.

Berry, S. S. 1909. The known Mollusca from San Bernardino County, California.—Nautilus 23: 73–79.

Blair, W. N., & A. K. Armstrong. 1979. Hualapai Limestone member of the Muddy Creek Formation: The youngest deposit predating the Grand Canyon, southeastern Nevada and northwestern Arizona.—United States Geological Survey Professional Paper 1111:1–14.

Cemen, I., L. A. Wright, & K. L. Verosub. 1985. Cenozoic sedimentation and sequence of deformational events at the southeastern end of Furnace Creek strike-slip fault zone, Death Valley region, California. Pp. 127–141 *in* K. T. Biddle & N. Christie-Beck, eds., Strike-slip deformation, basin formation and sedimentation.—Society of Economic Palaeontologists and Mineralogists Special Publication 37.

Cole, M. R., & J. M. Armentrout. 1979. Neogene paleogeography of the western United States. Pp. 297–323 *in* J. M. Armentrout, M. R. Cole, & H. TerBest, eds., Cenozoic paleogeography of the western United States.—Society of Economic Paleontologists and Mineralogists, Pacific Section, Pacific Coast Paleogeography Symposium 3.

Dickinson, W. R. 1979. Cenozoic plate tectonics setting of the Cordilleran region in the United States. Pp. 1–13 *in* J. M. Armentrout, M. R. Cole, & H. TerBest, eds., Cenozoic paleogeography of the western United States.—Society of Economic Paleontologists and Mineralogists, Pacific Section, Pacific Coast Paleogeography Symposium 3.

Gilbert, C. M., M. N. Christensen, Y. Al-Rawi, & K. R. Lajoie. 1968. Structural and volcanic history of Mono Basin, California–Nevada.—Geological Society of America Memoir 116:275–329.

Giovannetti, D. 1979. Volcanism and sedimentation associated with the formation of southern Owens Valley.—Geological Society of America Annual Meeting Abstracts 11:79.

Hannibal, H. 1912. The aquatic molluscs of southern California and adjacent regions, a transition fauna.—Bulletin of the Southern California Academy of Sciences 11:18–46.

Hershler, R. 1987. Redescription of *Assiminea infima* Berry 1947 from Death Valley, California.—Veliger 29:274–288.

———. 1989. Springsnails (Gastropoda: Hydrobiidae) of Owens and Amargosa (exclusive of Ash Meadows) River drainages, Death Valley System, California–Nevada.—Proceedings of the Biological Society of Washington 102:176–248.

———, & D. W. Sada. 1987. Springsnails (Gastropoda: Hydrobiidae) of Ash Meadows, Amargosa Basin, California–Nevada.—Proceedings of the Biological Society of Washington 100: 776–843.

———, & F. G. Thompson. 1987. North American Hydrobiidae (Gastropoda: Rissoacea): Redescription and systematic relationships of *Tryonia* Stimpson, 1865 and *Pyrgulopsis* Call and Pilsbry, 1886.—Nautilus 101:25–32.

Hubbs, C. L., & R. R. Miller. 1948. Correlation between fish distribution and hydrographic history in the desert basins of western United States. Pp. 17–166 *in* The Great Basin, with emphasis on Glacial and Postglacial times.—Bulletin of the University of Utah 38, Biological Series 10.

Huber, N. K. 1981. Amount and timing of uplift and tilt of the central Sierra Nevada—Evidence from the upper San Joaquin Basin.—United States Geological Survey Professional Paper 1197:1–28.

Hunt, C. B., & D. R. Mabey. 1966. Stratigraphy and structure, Death Valley, California.—United States Geological Survey Professional Paper 494A:1–162.

Kilbourne, R. T., C. W. Chesterman, & S. H. Hood. 1980. Recent volcanism in the Mono Basin–Long Valley region of Mono County, California.—California Division of Mines and Geology, Special Report 150:7–22.

Miller, R. R. 1973. Two new fishes, *Gila bicolor snyderi* and *Catastomus fumeiventris,* from the Owens River basin, California.—Occasional Papers of the Museum of Zoology, University of Michigan 667:1–19.

Miller, W. J. 1928. Geology of Deep Spring Valley, California.—Journal of Geology 36:510–525.

Minckley, W. L., D. A. Hendrickson, & C. E. Bond. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. Pp. 519–613 (+ bibliography) *in* C. H. Hocutt & E. O. Wiley, eds., The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Nilsen, T. H., & E. H. McKee. 1979. Paleogene paleogeography of the western United States. Pp. 257–276 *in* J. M. Armentrout, M. R. Cole, & H. TerBest, eds., Cenozoic paleogeography of the western United States.—Society of Economic Paleontologists and Mineralogists, Pacific Section, Pacific Coast Paleogeography Symposium 3.

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha).—Bulletin of the American Museum of Natural History 168:335–557.

Quade, J., & W. L. Pratt. 1989. Late Wisconsin groundwater discharge environments of the southwestern Indian Springs Valley, southern Nevada.—Quaternary Research 31:351–370.

St. Amand, P., & G. R. Roquemore. 1979. Tertiary and Holocene development of the southern Sierra Nevada and Coso Range, California.—Tectonophysics 52:409–410 (abstract).

Schreck, C. B., & R. J. Behnke. 1971. Trouts of the upper Kern River Basin, California, with reference to systematics and evolution of western North American *Salmo*.—Journal of the Fisheries Research Board of Canada 28:987–998.

Smith, G. R. 1966. Distribution and evolution of the North American catostomid fishes of the genus *Pantosteus* subgenus *Catostomus*.—Miscellaneous Publications of the Museum of Zoology, University of Michigan 129:1–132.

Stearns, R. E. C. 1893. Report on land and freshwater shells collected in California and Nevada by the Death Valley Expedition, including a few additional species obtained by Dr. C. Hart Merriam and assistants in parts of the southwestern United States.—North American Fauna 7:269–283.

Taylor, D. W. 1954. Nonmarine mollusks from the upper Miocene Barstow Formation, California.—United States Geological Survey Professional Paper 254C:67–80.

———. 1981. Freshwater mollusks of California: A distributional checklist.—California Fish and Game 67:140–163.

———. 1983. Late Tertiary mollusks from the lower Colorado River Valley.—University of Michigan, Museum of Paleontology Contribution 26: 289–298.

———. 1985. Evolution of freshwater drainages and molluscs in western North America. Pp. 265–321 *in* C. J. Hocutt & A. B. Leviton, eds., Late Cenozoic history of the Pacific Northwest.—American Association for the Advancement of Science, San Francisco, California.

———. 1987. Fresh-water molluscs from New Mexico and vicinity.—New Mexico Bureau of Mines & Mineral Resources Bulletin 116:1–50.

Wernicke, B., G. J. Axen, & J. K. Snow. 1988. Basin and range extensional tectonics at the latitude of Las Vegas, Nevada.—Geological Society of America Bulletin 100:1738–1757.

Woodburne, M. O. 1975. Cenozoic stratigraphy of the Transverse Ranges and adjacent areas, southern California.—Geological Society of America Special Paper 162:1–91.

(RH) NHB STOP 118, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (WLP) Museum of Natural History, University of Nevada, Las Vegas, 4505 Maryland Parkway S, Las Vegas, Nevada 89154.

Appendix

Localities visited. Data are name of site, county, state, township and range coordinates, elevation of site, and date of visitation.

I. Walker Basin and environs. Cedar Creek (unnamed on topo sheet), Slinkard Valley, Mono Co., CA; T 8N, R 22E, NE ¼ sec. 9, 2025 m, 7-12-88.—"Tin Cup" Spring, Mono Co., CA; T 9N, R 22E, NW ¼ sec. 20, 1928 m, 7-12-88.—Spring in unnamed canyon, Slinkard Valley, Mono Co., CA; T 9N, R 22E, SE ¼ sec. 19, 2050 m, 7-12-88.—Springs by cabin, Slinkard Valley, Mono Co., CA; T 8N, R 22E, NE ¼ sec. 9, 1983 m, 7-12-88.—Springs in SE corner of Slinkard Valley, Mono Co., CA; T 8N, R 22E, SW ¼ sec. 15, 2135 m, 7-12-88.—Springs in SE corner of Slinkard Valley (ca. 75 m SE of above), Mono Co., CA; T 8N, R 22E, SW ¼ sec. 15, 2135 m, 7-12-88.—Springs entering small creek in northern Little Antelope Valley, Mono Co., CA; T 8N, R 22E, SE ¼ sec. 13, 1684 m, 7-12-88.—Springs in meadow in northern Little Antelope Valley, Mono Co., CA; T 8N, R 23E, NW ¼ sec. 19, 1684 m, 7-12-88.—Spring N of Camp Antelope, Mono Co., CA; T 8N, R 23E, NE ¼ sec. 16, 1708 m, 7-14-88.—Leakage from holding tank (of spring), Spring Creek Canyon, Mono Co., CA; T 8N, R 23E, SW ¼ sec. 23, 1952 m, 7-13-88.—Spring zone along E side of West Walker River in canyon, Mono Co., CA; T 6N, R 23E, NE ¼ sec. 9, 2013 m, 7-13-88.—Spring zone along W side of Little Walker River upstream from above, Mono Co., CA; T 6N, R 23E, SW ¼ sec. 15, 2050 m, 7-12-88.—Brownie Creek, Mono Co., CA; T 6N, R 22E, SW ¼ sec. 27, 2184 m, 7-13-88.—Spring by Cloudburst Creek, Mono Co., CA; T 6N, R 22E, NE ¼ sec. 27, 2159 m, 7-13-88.—Spring at Marine Corps Center, Mono Co., CA; T 6N, R 22E, NW ¼ sec. 24, 2080 m, 7-13-88.—Seeps along Junction Creek, Mono Co., CA; T 6N, R 23E, NE ¼ sec. 20, 2098 m, 7-12-88.—Spring along E side of Little Walker River, Mono Co., CA; T 5N, R 23E, NE ¼ sec. 4, 2263 m, 7-14-88.—Burcham Creek, Mono Co., CA; T 6N, R 23E, NW ¼ sec. 11, 2257 m, 7-12-88.—Stream along Burcham Flat Road, Mono Co., CA; T 6N, R 23E, SW ¼ sec. 14, 2211 m, 7-12-88.—Fales Hot Springs, Mono Co., CA; T 6N, R 23E, SE ¼ sec. 24, 2227 m, 7-12-88.—Stream, Yaney Canyon, Mono Co., CA; T 5N, R 24E, SE ¼ sec. 15, 2098 m, 7-12-88.—Spring W of Bridgeport Ranger Station, Mono Co., CA; T 5N, R 24E, NW ¼ sec. 23, 2098 m, 7-12-88.—Spring just S of above, Mono Co., CA; T 5N, R 24E, NW ¼ sec. 23, 2074 m, 7-13-88.—Buckeye Hot Spring (seepage), Mono Co., CA; T 4N, R 24E, NE ¼ sec. 4, 2166 m, 7-13-88.—Seepage along Buckeye Creek, Mono Co., CA; T 4N, R 24E, NW ¼ sec. 4, 2166 m, 7-13-88.—Spring N of Twin Lakes, Mono Co., CA; Matterhorn Peak, CA (15), T 4N, R 24E, NW ¼ sec. 28, 2318 m, 7-13-88.—Summers Creek and springs in Summers Meadows, Mono Co., CA; T 3N, R 25E, NW ¼ sec. 6, 2172 m, 7-13-88.—Stream from Cameron Canyon, Mono Co., CA; T 3N, R 25E, NE ¼ sec. 6, 2135 m, 7-13-88.—Spring SW of Little Bodie Mine, Mono Co., CA; T 3N, R 25E, SW ¼ sec. 1, 2306 m, 7-11-88.—Spring ca. 0.4 km NE of above, Mono Co., CA; T 3N, R 25E, SW ¼ sec. 1, 2306 m, 7-11-88.—Warm Springs, Mono Co., CA; T 4N, R 26E, SW ¼ sec. 16, 2342 m, 7-11-88.—The Hot Springs, Mono Co., CA; T 4N, R 25E, NW ¼ sec. 9, 2013 m, 7-11-88.—Travertine Springs, Mono Co., CA; T 5N, R 25E, SW ¼ sec. 34, 2050 m, 7-11-88.—Small springs along East Walker River NW of Bridgeport, Mono Co., CA, between 1952–2013 m: seep with pool, E side of river, T 6N, R 25E, NW ¼ sec. 26; piped spring on W side of river, T 6N, R 25E, NW ¼ sec. 23, 7-11-88; seep on E side of river, T 6N, R 25E, SE ¼ sec. 14, 7-13-88; spring W of river and just N of Murphy Creek, T 6N, R 25E, NE ¼ sec. 14, 7-14-88; seeps (2) on steep hill along E side of river, T 6N, R 25E, SW ¼ sec. 12, 7-13 and 14-88; small seeps on W side of river, T 6N, R 25E, SW ¼ sec. 12.—Spring at Wiley Ranch, Lyon Co., NV; T 8N, R 25E, NW ¼ sec. 5, 1922 m, 7-11-88.

II. Mono Basin. Springs SW of Conway Summit, Mono Co., CA; T 2N, R 25E, NE ¼ sec. 2, 2318 m, 11-8-88.

III. Adobe Valley and environs. Spring, Pizona, Adobe Valley, Mono Co., CA; T 1N, R 31E, SE ¼ sec. 4, 2135 m, 5-27-89.—Upper Pizona Spring, Adobe Valley, CA; T 1N, R 31E, SW ¼ sec. 11, 2227 m, 5-27-89.—Huntoon Spring, Huntoon Valley, NV; Huntoon Valley, NV–CA (15) (sections unplated), 11.4 km NW from SE corner of quadrangle, 1891 m, 5-28-89.

IV. Fish Lake Valley. Springs ca. 2.4 km SW of The Crossing, Esmeralda Co., NV; T 1S, R 36E, SW ¼ sec. 16, 1449 m, 7-16-88.—Spring just NE of The Crossing, Esmeralda Co., NV; T 1S, R 36E, NE ¼ sec. 10, 1449 m, 7-16-88.—Springs at Dyer Ranch, Esmeralda Co., NV; T 2S, R 35E, SE ¼ sec. 13, 1440 m, 7-16-88.—Spring W of cemetery, Esmeralda Co., NV; T 2S, R 35E, SW ¼ sec. 24, 1458 m, 7-16-88.—Seep in canyon WSW of Dyer School, Esmeralda Co., NV; Mt. Barcroft, CA–NV (15), 12.5 km SE of NW corner of quadrangle, 1684 m, 7-16-88.—Cottonwood Creek, Inyo Co., CA; T 6S, R 37E, NW ¼ sec. 5, 1708 m, 7-16-88.

V. Owens Basin. Spring in West Queen Canyon, Mineral Co., NV; T 1N, R 32E, SW ¼ sec. 16, 2013 m.—Truman Spring, Mineral Co., NV; T 1N, R 32E, SW ¼ sec. 7, 2166 m.—Spring NW corner of Round Valley, Inyo Co., CA; T 5S, R 31E, NW ¼ sec. 25, 1800 m.—Spring, SW corner of Round Valley, Inyo Co., CA; T 6S, R 31E, SE ¼ sec. 31, 1586 m, 8-12-88.—Springs, Marble Canyon, Inyo Co., CA; T 7S, R 35E, SE ¼ sec. 35, SW ¼ sec. 36, 1891–2074 m.—Spring, 1.2 km NW of Big Pine Spring, Inyo Co., CA; T 9S, R 33E, NW ¼ sec. 16, 2074 m, 5-14-88.—Spring at McMurry Meadows, Inyo Co., CA; T 10S, R 33E, NW ¼ sec. 22, 2044 m.—Spring on N side of Red Mountain, T 11S, R 34E, SE ¼ sec. 31, 1403 m.—Spring in canyon north of McGann Springs, Inyo Co., CA; Mt. Pinchot, CA (15), 13.6 km NW of SE corner of quadrangle.—McGann Springs, Inyo Co., CA; T 13S, R 34E, NW ¼ sec. 4, 1708 m, 5-21-89.—Tub Springs, Inyo Co., CA; T 13S, R 34E, SE ¼ sec. 17, 1952 m, 4-30-89.—Spring, 0.1 km N of Independence Creek, Inyo Co., CA; T 13S, R 34E, SW ¼ sec. 21, 1830 m, 6-21-88.—Springs SW of Lone Pine, Inyo Co., CA; T 16S, R 36E, SE ¼ sec. 2, 1952 m, 4-29-89.—Spring at Lower Diaz Creek, Inyo Co., CA; T 16S, R 36E, SE ¼ sec. 5, 1312 m, 4-29-89.—Springs at Upper Diaz Creek, Inyo Co., CA; Lone Pine, CA (15), 10.3 km NE from SW corner of quadrangle, 1830 m, 5-27-89.—Spring in canyon 1.6 km S of Carrol Creek, Inyo Co., CA; Lone Pine, CA (15), 7.5 km SW from NE corner of quadrangle, 1617 m, 5-9-89.—Stream, Talus Canyon, Inyo Co., CA; Monache Mtn., CA (15), 10 km NNW from SE corner of quadrangle, 1830 m, 10-2-88.—Stream, Tunawee Canyon, Inyo Co., CA; Monache Mtn., CA (15), 7.5 km NNW from SE corner of quadrangle, 1769 m, 3-28-88.—Stream, Sacatar Canyon, Inyo Co., CA; T 23S, R 37E, secs. 3–4, 1769–1830 m, 5-18-88.

VI. Indian Wells Valley. Stream, Ninemile Canyon, Inyo Co., CA; Lamont Peak, CA (7.5), 2.1 km SSW from NE corner of quadrangle, 1769 m, 7-18-88.—Stream, Grapevine Canyon, Inyo Co., CA; T 25S, R 37E, NE ¼ sec. 23, 1281 m, 4-14-88.—Stream, Short Canyon, Inyo Co., CA; T 25S, R 38E, SW ¼ sec. 31.

VII. Mohave Basin and envions. Spring, Cow Canyon, Kern River Valley, Kern Co., CA; Walker Pass, CA (7.5), 5.0 km WSW from NE corner of quadrangle, 1330 m, 11-4-88.—Canebrake Creek, Kern River Valley, Kern Co., CA; T 25S, R 36E, SW ¼ sec. 14, 1086 m, 11-4-88.—Spring, Spring Canyon, Kern River Valley, Kern Co., CA; T 25S, R 36E, SE ¼ sec. 34, 1171 m, 11-4-88.—Brown Spring, Kern Co., CA; T 27S, R 35E, NW ¼ sec. 5, 946 m, 11-4-88.—Kelso Creek, SW of Rocky Point, Kern Co., CA; T 27S, R 35E, NW ¼ sec. 20, 988 m, 11-4-88.—Horse Canyon Spring (and spring just to E), Kern Co., CA; Horse Canyon, CA (7.5), 7.6 km SSW of NW corner of quadrangle, 1464 m, 7-18-88.—Bird Spring (dry), Kern Co., CA; Horse Canyon, CA (7.5), 4.1 km ENE of SW corner of quadrangle, 1208 m, 7-18-88.—Frog Spring, Kern Co., CA; T 28S, R 35E, NE ¼ sec. 10, 1196 m, 11-4-88.—Shoemaker Spring, Kern Co., CA; T 28S, R 35E, center of section 12, 1452 m, 11-4-88.—Butterbredt Spring, Kern Co., CA; T 29S, R 36E, SE ¼ sec. 28, 1281 m, 11-3-88.—Spring, Poleline Canyon, Kern Co., CA; T 30S, R 37E, NE ¼ sec. 8, 854 m, 11-3-88.—Alphie Spring, Kern Co., CA; T 29S, R 36E, SE ¼ sec. 35, 964 m, 11-3-88.—Spring, Hoffman Canyon, Kern Co., CA; T 30S, R 36E, SW ¼ sec. 3, 1098 m, 11-3-88.—Sweetwater Spring, Kern Co., CA; T 32S, R 34E, SE ¼ sec. 14, 1388 m, 7-20-88.—Springs S of Proctor Lake, Kern Co., CA; T 32S, R 34E, S ½ sec. 32, 1257 m, 7-20-88.—Spring, Bean Canyon, Kern Co., CA; T 10N, R 14W, SW ¼ sec. 4, 1238 m, 11-3-88.—Indian Spring, Los Angeles Co., CA; T 7N, R 14W, SE ¼ sec. 18, 891 m, 7-21-88.—Little Rock Creek, ca. 8 km upstream from dam, Los Angeles Co., CA; Juniper Hills, CA (7.5), 5.7 km NNE from SW corner of quadrangle, 1159 m, 11-5-88.—Pallet Creek, Big Rock Creek, Los Angeles Co., CA; T 4N, R 9W, SW ¼ sec. 6, 1086 m, 7-21-88.—Icy Springs, Los Angeles Co., CA; T 3N, R 9W, NE ¼ sec. 1, 1757 m, 11-5-88.—Spring, Sawmill Canyon, Los Angeles Co., CA; T 3N, R 8W, NE ¼ sec. 11, 2074 m, 11-12-88.—Spring, Grapevine Canyon, San Bernardino Co., CA; T 4N, R 2W, NW ¼ sec. 26, 1147 m, 11-6-88.—Rabbit Springs, San Bernardino Co., CA; T 4N, R 1W, NW ¼ sec. 11, 885 m, 7-21-88.—Broadbent Spring (unnamed on topo sheet), San Bernardino Co., CA; T 3N, R 1E, NW ¼ sec. 3, 1144 m, 7-21-88.—Cushenbury Springs, San Bernardino Co., CA; T 3N, R 1E, NE ¼ sec. 10, 1251 m, 7-21-88.—Cottonwood Spring (dry), San Bernardino Co., CA; T 4N, R 2E, SE ¼ sec. 25, 970 m, 7-21-88.—Spring NW of Old Woman Springs (dry), San Bernardino Co., CA; T 4N, R 3E, NE ¼ sec. 31, 976 m, 7-22-88.—Old Woman Springs, San Bernardino Co., CA; T 4N, R 3E, NE ¼ sec. 31, 985 m, 7-22-88.—Two Hole Spring, San Bernardino Co., CA; Old Woman Springs, CA (15), 11.1 km NE of SW corner of quadrangle, 1165 m, 7-22-88.—Spring zone SW of Big Bear Ranger Station, San Bernardino Co., CA; T 2N, R 1E, NW ¼ sec. 17, 2074 m, 7-21-88.—Springs SW of Fawnskin, San Bernardino Co., CA; T 2N, R 1W, SW ¼ sec. 14, 2089 m, 7-21-88.—Mill Creek at Thurman Flats Picnic Area, San Bernardino Co., CA; T 1S, R 1W, NE ¼ sec. 8, 1074 m, 7-27-88.—Little Morongo Creek, below Morongo Lakes, CA; T 1S, R 4E, SE ¼ sec. 24, 756 m, 11-11-88.—Spring, Big Morongo Canyon (upper portion), San Bernardino Co., CA; T 1S, R 4E, SE ¼ sec. 18, 1110 m, 11-6-88.—Springs, Big Morongo Canyon (lower portion), San Bernardino Co., CA; T 1S, R 4E, SE ¼ sec. 28, 744 m, 11-10-88.—Spring, Smith Water Canyon, Riverside Co., CA; T 2S, R 7E, NW ¼ sec. 5, 1293 m, 11-10-88.—Fortynine Palms Oasis, San Bernardino Co., CA; Queen Mtn., CA (7.5), 3.1 km SE of NW corner of quadrangle, 854 m, 11-10-88.—Garlic Spring, San Bernardino Co., CA; T 13N, R 3E, SW ¼ sec. 11, 708 m, 4-9-86.—Mohave River, Afton Canyon, San Bernardino Co., CA; T 11N, R 5E, SW ¼ sec. 13, 428 m, 4-10-86.—Seepage, W side of Soda Lake, San Bernardino Co., CA; T 12N, R 8E, NW ¼ sec. 2, 290 m, 7-22-88.—Old Mormon Spring (dry), San Bernardino Co., CA; Avawatz Pass, CA (15), 1.8 km NNW of SE corner of quadrangle, 634 m, 11-9-88.—Snake Spring, Granite Mtns., San Bernardino Co., CA; T 8N, R 13E, SE ¼ sec. 5, 1220 m, 11-7-88.—Cottonwood Spring, Granite Mtns., San Bernardino Co., CA; T 8N, R 13E, NW ¼ sec. 7, 1366 m, 11-7-88.—Arrowhead Spring, Providence Mtns., San Bernardino Co., CA; T 9N, R 13E, SE ¼ sec. 22, 1208 m, 11-7-88.—Van Winkle Spring, San Bernardino Co., CA; T 8N, R 13E, NW ¼ sec. 23, 1098 m, 11-8-88.—Goldstone Spring, Mid Hills, San Bernardino Co., CA; T 10N, R 14E, SW ¼ sec. 31, 1415 m, 11-8-88.—Live Oak Spring, Mid Hills, San Bernardino Co., CA; T 13N, R 13E, NW ¼ sec. 19, 1568 m, 11-7-88.—Keystone Spring, Mid Hills, San Bernardino Co., CA; T 14N, R 16E, NW ¼ sec. 29, 1781 m, 7-23-88.—Dove Spring (dry), New York Mtns., San Bernardino Co., CA; T 15N, R 17E, SW ¼ sec. 19, 1452 m, 7-23-88.—Pachalka Spring, Clark Mtn., San Bernardino Co., CA; T 17N, R 12.5E, NE ¼ sec. 36, 1488 m, 7-23-88.—Ivanpah Springs, Clark Mtn., San Bernardino Co., CA; T 17N, R 13E, SE ¼ sec. 24, 1269 m, 7-23-88.—Bonanza Spring, Clipper Mtns., San Bernardino Co., CA; T 7N, R 15E, NW ¼ sec. 22, 634 m, 11-14-88.—Piute Spring, San Bernardino Co., CA; T 12N, R 18E, NW ¼ sec. 24, 915 m, 7-25-88.

VIII. Amargosa Basin and environs. Choppo Spring, Inyo Co., CA; T 21N, R 7E, SE ¼ sec. 2, 610 m, 7-25-88.—Tule Spring (dry), California Valley, San Bernardino Co., CA; Tecopa, CA (15), 8.8 km NNW of SE corner of quadrangle, 720 m, 7-25-88.—Beck Spring, Kingston Range, San Bernardino Co., CA; T 20N, R 10E, NE ¼ sec. 31, 1354 m, 7-25-88.—Cold Creek, Clark Co., NV; T 18S, R 55E, NE ¼ sec. 1, 1867 m, 9-5-77.—Willow Creek, Clark Co., NV; T 18S, R 55E, NE ¼ sec. 2, 1830 m, 7-31-77.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 300–303

SOME TARDIGRADES FROM COLORADO, WITH A DESCRIPTION OF A NEW SPECIES OF *MACROBIOTUS* (MACROBIOTIDAE: EUTARDIGRADA)

R. Deedee Kathman

Abstract.—Fourteen species of tardigrades were found above 3200 m on Mt. Evans and an additional species was found at 3963 m at Guenella Pass, Colorado. One of the species from Mt. Evans, *Macrobiotus caelicola,* is new to science. It differs from other *Macrobiotus* species by having a combination of the following characters: the presence of ventral and dorsal pores covering its body, the large size and shape of the claws and dentate lunules, two macroplacoids and no microplacoid, and the shape and size of the eggs.

Thirty-one species of tardigrades have been reported from Colorado (Higgins 1959, Baumann 1960, Landreth & Thomas 1970, Anderson et al. 1984, Beasley 1989). The most recent of these publications (Beasley 1989) increased the number from 17 species to the present 31. During the present study, 15 species were collected: five are new to Colorado and one is new to science.

Materials and Methods

Five samples of moss were collected on Mt. Evans between 3262 m and the summit at 4348 m, and one sample each was collected at 3659 m and 3963 m at Guenella Pass, both in Clear Creek County, Colorado, U.S.A. All seven samples were collected on 11–12 Aug 1986.

Each sample of moss was placed in a paper bag and air-dried for several months, then removed from the bag, placed in a stoppered funnel and allowed to soak in water for eight hours, after which the moss was removed and shaken in a separate container of water several times. The water and its contents were poured through a 45 μm sieve to retain the tardigrades, which were placed in a gridded petri dish and extracted under a stereomicroscope. Each tardigrade was placed directly into Hoyer's mounting medium on a microscope slide and overlain with a cover slip. After complete drying of the mountant, the cover slip was ringed with nail polish to prevent further air penetration.

Identifications were made using a phase-contrast compound microscope with oil immersion. All measurements were made using a calibrated eyepiece micrometer. All drawings were done with a drawing tube attached to the compound microscope.

Results

All seven samples contained tardigrades, with a total of 263 individuals belonging to 8 genera and 15 species, distributed among the sites as shown in Table 1. One of these species, *Isohypsibius pappi,* is new to North America, and three of the species, *Hebesuncus conjungens, Diphascon nodulosum* and *D. pingue,* are reported from Colorado for the first time. The new species, *Macrobiotus caelicola,* is described below.

Taxonomic Account

Eutardigrada Marcus, 1927
Macrobiotidae Thulin, 1928
Macrobiotus Schultze, 1834
Macrobiotus caelicola, new species
Fig. 1

Description.—Holotype. Total length 620 μm; colorless; eyes present (Fig. 1A). Entire ventral and dorsal surfaces covered with ir-

Table 1. Numbers of individuals in each species found at two locations in Clear Creek County, Colorado. General distributions and descriptions for each species are given in Ramazzotti and Maucci (1983).

	Guenella Pass		Mt. Evans			
	3659 m	3963 m	3262 m	3811 m	4299 m	4348 m
Echiniscus blumi Richters, 1903		19				
Echiniscus wendti Richters, 1903		1			1	
Milnesium tardigradum Doyère, 1840	1	91			15	
Hypsibius convergens (Urbanowicz, 1925)	1		2			1
Ramazzottius oberhaeuseri (Doyère, 1840)			4		1	
Isohypsibius pappi (Iharos, 1966)			1			
Isohypsibius landalti (Iharos, 1966)			1			
Hebesuncus conjungens (Thulin, 1911)				2		
Diphascon nodulosum (Ramazzotti, 1957)			8			
Diphascon pingue (Marcus, 1936)			1			11
Diphascon recamieri Richters, 1911				1		
Macrobiotus caelicola new species					46	
Macrobiotus harmsworthi Murray, 1907			16	2		1
Macrobiotus hufelandi Schultze, 1834			3	9		10
Minibiotus intermedius (Plate, 1888)		2		1		

regularly-shaped, equal-sized pores (example of pores in posterior end shown in Fig. 1A). Buccal lamellae present. Buccal ring with distinct dentation. Buccal tube with ventral tube support; buccopharyngeal tube 66 μm long, 5 μm wide. Pharyngeal bulb large, wider than long; apophyses large; 2 macroplacoids, the first 8 μm long, the second 6 μm long; no microplacoid (Fig. 1B). Furcae as shown in Fig. 1C. Doubleclaws large, Y-shaped; 2 large accessory points on each primary branch; primary branch long and thin, 17.5 μm in leg II, 32.5 μm in leg IV; secondary branch short and close to base, 12.5 μm in leg II, 20 μm in leg IV; lunules large and dentate (Fig. 1D, E). Sclerotized bar below the claws on the first 3 pairs of legs (Fig. 2D). USNM 235439.

Paratypes.—Total length up to 668 μm. Buccopharyngeal tube length 66–70 μm, width 5–6 μm, distance between stylet support insertion and end of tube (= pharyngeal tube length) 13–15 μm. First macroplacoid length 8–10 μm, second macroplacoid length 6–8 μm, with the first always longer than the second. Sclerotized bar below the claws in all specimens. 45 specimens: USNM 235440–235442; 2 specimens in Dastych collection (Hamburg, West Germany); 2 specimens in Kristensen collection (University of Copenhagen, Denmark); remaining specimens in Kathman collection (Sidney, British Columbia).

Eggs.—Eggs round, up to 124 μm in diameter; covered with projections up to 34 μm long (Fig. 1F); projections thin, with dark patches on exterior, apices divided into multi-tipped points, some with tiny setae projecting from them (Fig. 1G); egg surface smooth between projections. USNM 2354431–235444.

Type locality.—All specimens were collected on 11 Aug 1986 at 4299 m, Mt. Evans, Clear Creek County, Colorado, U.S.A.

Etymology.—*Caelicola* is a masculine Latin word meaning dweller in heaven; this species is thus named because it was found at such a high altitude as well as pertaining to the surname of the person in charge of the Mt. Evans Research Station, Dr. Robert Angell.

Discussion

This is the first report of a *Macrobiotus* species with a sclerotized bar below the claws. It is generally thicker and larger than

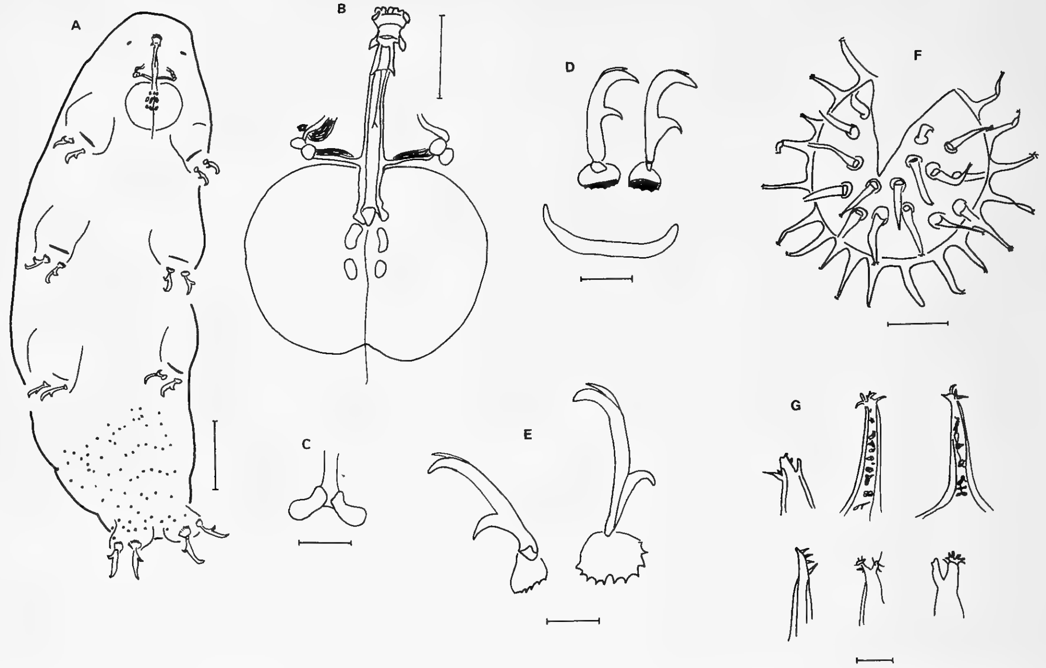


Fig. 1. *Macrobiotus caelicola.* A, Entire animal, ventral view, pores cover entire ventral and dorsal surfaces; B, Buccopharyngeal apparatus; C, Furca; D, Claws of 2nd leg; E, Claws of 4th leg; F, Egg (split); G, Projections on egg. Scale bars in μm as follows: A, 80; B, 24; C, D, 10; E, 12; F, 40; G, 12.

those bars found in species of *Diphascon* or *Isohypsibius,* at least superficially more closely resembling the leg plate of some echiniscids. The lower portion of the bar appears to have two distinct elliptical areas with fine spine-like granulation, but these could not be clearly discerned using light microscopy, even at 2000× magnification and using phase contrast lenses.

This species is most similar to *Macrobiotus islandicus* Richters, 1904 but differs in the following characters. *Macrobiotus islandicus* has small pores arranged in transverse rows on the dorsal and lateral surfaces, while *M. caelicola* has irregularly-spaced pores not in transverse bands covering both the dorsal and ventral surfaces. The width of the buccal tube for *M. islandicus* is much larger than for *M. caelicola,* with the width to length ratio being approximately 14% for *M. islandicus* and 7.5–8.5% for *M. caelicola.* There is a curve in the rostral part of the buccal tube for *M. islandicus,* while the buccal tube for *M. caelicola* is straight. Both macroplacoids are longer in *M. islandicus* than in *M. caelicola,* and their profiles are smooth in *M. islandicus* but rough-edged in *M. caelicola.* In *M. islandicus* the secondary branch of each doubleclaw is inserted halfway or slightly more than halfway up the primary branch, while in *M. caelicola* the secondary branch is inserted approximately one-third of the distance from the base of the primary branch; both branches are longer and thinner in *M. caelicola.* The lunules are always obvious and dentate in *M. caelicola.* The eggs of *M. caelicola* are larger (mean diameter of 120 μm) than for *M. islandicus* (90–100 μm diameter). The projections on the eggs of *M. islandicus* are 11–12 μm maximum length, while those of *M. caelicola* are much longer (mean length = 20 μm for 9 eggs), reaching 34 μm in some eggs. No other *Macrobiotus* species have eggs with the characters of *M. caelicola.* If eggs are not used for differentiation from other species, there are only two other moss-dwelling *Macrobiotus* species with the combined characters of cuticular pores, two macroplacoids, and no microplacoid. They are *M. islandicus* and *Macrobiotus annae* Richters, 1908. *M. caelicola* differs from *M. islandicus* as discussed above, and from *M. annae* in that *M. annae* is a small tardigrade (length to 370 μm) and has a narrow buccal tube (3 μm), a small oval pharynx, small claws, and small smooth lunules.

The 15 species of tardigrades collected during this study increase the number known from Colorado from 31 to 37. Although all 15 species were collected at high altitudes, none of them appear to be restricted to these altitudes, since all of them (except the newly reported species) have been reported elsewhere at much lower altitudes.

Acknowledgments

I wish to thank R. M. Kristensen and H. Dastych for examining several of the species and identifying *M. caelicola* as a new species. Thanks are also due R. O. Brinkhurst for collecting the moss while teaching at the Mt. Evans Research Station of the University of Denver.

Literature Cited

Anderson, R. V., R. E. Ingham, J. A. Trofymow, & D. C. Coleman. 1984. Soil mesofaunal distribution in relation to habitat types in a shortgrass prairie.—Pedobiologia 26:257–261.

Baumann, H. 1960. Beitrag zur Kenntnis der Tardigraden in Nord-Amerika.—Zoologischer Anzeiger 165:123–128.

Beasley, C. W. 1989. Taradigrada from Gunnison County, Colorado, with the description of a new species, *Diphascon craigi.*—The Southwestern Naturalist. (In Press)

Higgins, R. P. 1959. Life history of *Macrobiotus islandicus* Richters with notes on other tardigrades from Colorado.—Transactions of the American Microscopical Society 78:137–154.

Landreth, K., Jr., & B. O. Thomas. 1970. Studies of the egg laying process in Tardigrada [*Hypsibius (Isohypsibius) augusti*] in Weld County.—Journal of the Colorado–Wyoming Academy of Science 7:9.

Ramazzotti, G., & W. Maucci. 1983. Il phylum Tardigrada.—Memorie dell'Istituto Italiano di Idrobiologia 41:1–1012.

Department of Biology, P.O. Box 1700, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2; (Present address) 10651 Blue Heron Road, Sidney, British Columbia, Canada V8L 3X9.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 304–310

PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS, VII. ON SOME RARE SPECIES FROM THE FLORES SEA, INDONESIA

K. Nakamura and C. Allan Child

Abstract.—During a fisheries research cruise by the Japanese fisheries research vessel *Hakuho Maru,* in the Flores Sea, Indonesia, a joint cruise with LON-LIPI, Indonesia, WESTPAC, IOC-UNESCO, and the Ocean Research Institute of the University of Tokyo, two trawling stations resulted in the capture of several rare species of pycnogonids. Two of these species were taken only for the second time since their original descriptions in 1908; *Bathyzetes setiger* (Loman), and *Ascorhynchus levissimus* Loman. They are refigured and discussed in light of current morphological knowledge. Three other species rare in literature were taken and are discussed; *Hemichela micrasterias* Stock, *Pallenopsis tydemani tydemani* Loman, and *Colossendeis leptorhynchus* Hoek, while the cosmopolitan species *C. macerrima* Wilson was also taken. *Pigrogromitus timsanus* Calman, collected at a shore station near the Celebes, has also been included.

During the course of joint research cruise KH-85-1 in the Flores Sea, Indonesia, involving LON-LIPI, Indonesia, and WESTPAC, IOC-UNESCO with the vessel *Hakuho Maru,* Ocean Research Institute of the University of Tokyo, two trawl stations were made in about 600 meters which resulted in the capture of five rare or little known pycnogonids. Two of these species, *Ascorhynchus levissimus* Loman and *Bathyzetes setiger* (Loman), were taken only for the second time since their description in 1908. Three other species, *Hemichela micrasterias* Stock, *Pallenopsis tydemani tydemani* Loman, and *Colossendeis leptorhynchus* Hoek, have few specimens recorded in literature and are thus relatively rare. The very common *Colossendeis macerrima* Wilson was also captured at one of the stations. This frequency of capture suggests a rich faunal assemblage, particularly from so few stations. This richness is in keeping with the literature of Indonesian pycnogonids which has, since the first large monograph by Loman in 1908, consistently proved that there are great numbers of pycnogonid species and specimens to be found in this huge archipelago.

Stock (1953) recorded additional pycnogonid fauna in his Indonesia–Philippine report and there have been other Indonesian faunal listings in subsequent reports on that region (Stock 1954, 1968, 1983, 1985). The rarity of the many species known to inhabit Indonesia may be in part due to the past minimal collecting frequency for the whole archipelago, particularly in the deeper slope and basin areas of its various seas.

The distribution pattern of the two rarest species, known from their two captures only, is, of course, central Indonesia. That of *Hemichela micrasterias* is along a corridor from Indonesia to central Japan, including the Philippines. The distribution of *Pallenopsis t. tydemani* is only known from Indonesia and Japan, from 100 to 800 meters. Members of the genus *Colossendeis* have usually been found to be cosmopolitan in deep waters. This may hold true for *C. leptorhynchus* which is known from the Atlantic and Pacific Oceans and is certainly true for *C. macerrima*. Another cosmopolitan or at least pantropical species, *Pigrogromitus timsanus* Calman, was taken incidentally at a shore station just prior to the Flores Sea stations.

Systematics

Family Ammotheidae

Genus *Ascorhynchus* Sars

Ascorhynchus levissimus Loman

Fig. 1A–D

Ascorhynchus levissimus Loman, 1908:33–34, pl. IV, figs. 46–51.—Stock, 1953:304 [key]; 1975:130 [text].

Material examined.—Flores Sea: 05°56.0′S, 119°29.0′E, 630–657 m, sta. KH85-1, B-1, 12 Feb 1985 (1 ♀).

Distribution.—This is the second specimen of this species known since Loman described the first, also from the Flores Sea (07°24′S, 118°15.2′E). His specimen was from slightly deeper water, 794 m. It is thus confined, to our knowledge, to the Flores Sea, but since the entire archipelago is so rarely collected, particularly its deeper slopes and basins, the species may have a wider distribution when other collections from adjacent slopes and basins become known.

Remarks.—From examination of the above specimen, Loman's type specimen also appears to be a female, judging from the oviger sixth segment which lacks the usual tuft of setae common to males of the larger species of *Ascorhynchus*. The ocular tubercle is less a broadly rounded hump than in Loman's type figures. In the *Hakuho Maru* specimen, it is more abbreviated with its anterior surface joined to the neck at a sharper angle and it has unpigmented eyes which are readily discernible, at least in their upper halves.

The only other major difference between the two specimens is that the anterior pair of propodal claws in this specimen are tiny triangular points not as long as the propodal diameter. In Loman's figure of the entire specimen (pl. IV, fig. 48), the propodal claws are indistinctly illustrated as approximately equal in size. The remaining six claws of the specimen in hand are about 0.3 the propodal length and the tarsus and propodus of each are almost equal in length. A set of figures are provided herein as the type figures are somewhat diagrammatic and do not provide details of currently recognized critical characters.

This giant species was inadvertently omitted from a recent key (Child 1987:906–907) to the very large species of this genus. It can be followed to couplet three, second part, where it would be listed as having a tarsus equal to or slightly longer than the propodus, a very shortened propodal claw on the first pair of legs, and a second scape segment longer than the first, both of which form the chelifore, along with a tiny chela of very reduced size.

Genus *Bathyzetes* Stock, 1955

Bathyzetes setiger (Loman, 1908)

Fig. 1E–G

Eurycyde setigera Loman, 1908:29–30, pl. V, figs. 52–58.

Bathyzetes setiger.—Stock, 1955:261, 262 [key], fig. 24.

Material examined.—Flores Sea: 05°54.9′S, 119°29.5′E, 558–593 m, sta. KH85-1, B-2, 12 Feb 1985 (1 ♀).

Distribution.—This record, like the last one, marks only the second time this species has been collected, but like other species in this report, it is possibly not as rare as the frequency of collections from deeper Indonesian seas. Loman's four type specimens came from further north, in the Molucca Sea, off northeastern Sulawesi (Celebes) Island, in 1165–1264 meters. This second capture extends its distribution south into the Flores Sea, and into shallower waters at a minimum depth of 558 meters.

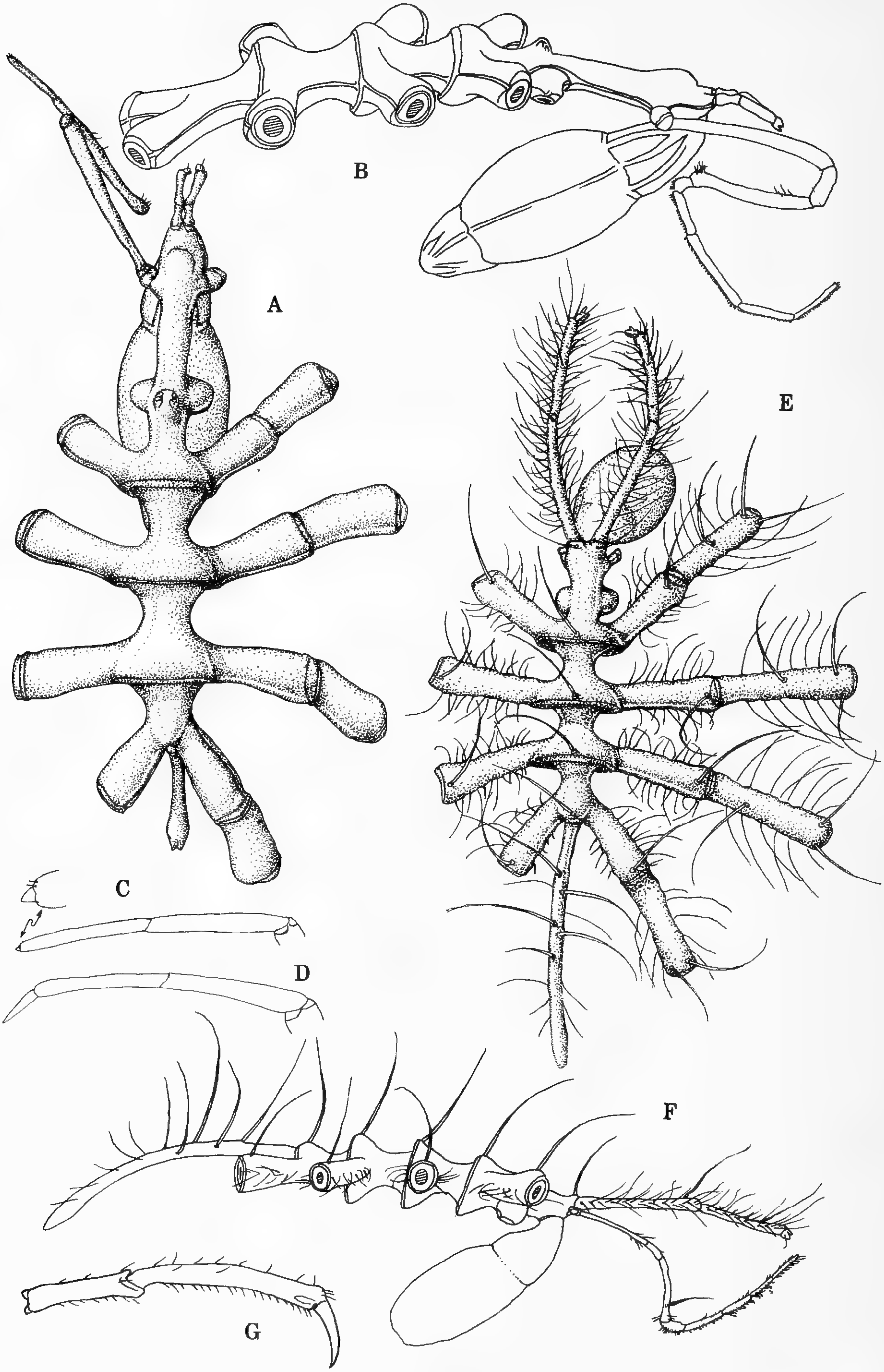


Fig. 1 *Ascorhynchus levissimum* Loman, female: A, Trunk, dorsal view; B, Trunk, lateral view; C, Terminal segments of first leg, with terminal claw enlarged; D, Terminal segments of fourth leg. *Bathyzetes setiger* (Loman), female: E, Trunk, dorsal view; F, Trunk, lateral view; G, Terminal segments of third leg.

Remarks.—Thanks to J. H. Stock, Institute for Taxonomic Zoology, University of Amsterdam, we were permitted to examine Loman's syntypes of this species and of *B. virago* (Loman). The two species are very closely related and could be synonymized except for the differences in size, setae size and arrangement, palp segment length ratios, and differences in the strigilis segments of the oviger. Loman's *B. setiger* is twice the size of *B. virago,* a difference which is not a valid species diagnostic character in itself (e.g., the great size differences in specimens of *Anoplodactylus lentus* Wilson). *Bathyzetes setiger* has a seventh palp segment longer than the eighth while this segment is shorter than the eighth in *B. virago.*

As Stock (1955:262, fig. 24) illustrated the terminal oviger segments differ in the two species. *B. setiger* has a longer terminal claw extending well beyond the enlarged distal denticulate spine, while the claw of *B. virago* is hardly longer than the denticulate spine with which it is paired. In the two specimens we examined from the type series, *B. virago* appears notably more setose with many more long slender setae on the chelifores and legs than in *B. setiger.* The above female agrees in most all characters with *B. setiger* except that it appears to have even fewer setae than the syntype. The very long dorsodistal setae of the trunk and lateral processes are even more prominent with fewer short setae around each. It would be difficult to confuse either of these setose species with a species of another genus, particularly with the absence of any form of ocular tubercle on either of the *Bathyzetes* species.

Genus *Hemichela* Stock, 1954

Hemichela micrasterias Stock

Hemichela micrasterias Stock, 1954:90–94, figs. 42–43; 1985:153–155, figs. 1–11.—Staples, 1982:464–465 [text].—Child, 1988a:10.—Nakamura & Child (1990).

Material examined.—Flores Sea: 05°56.0′S, 119°29.0′E, 630–657 m, sta. KH85-1, B-1, 12 Feb 1985 (1 subadult); 05°54.9′S, 119°29.5′E, 558–593 m, sta. KH85-1, B-2, 12 Feb 1985 (1 ovig ♀ 1, juv).

Distribution.—This species was originally described from one Indonesian specimen and has recently been recorded from the Philippines (Child 1988a:10) and Japan (Nakamura & Child 1990). This distribution more or less follows a corridor theory (Child 1983:699, 713, 1988b:55) proposed as relating western Pacific species distributions to a pathway extending from at least as far south as New Zealand to as far north as the Japanese Islands. The known distribution of several genera (*Austrodecus, Hemichela, Cheilopallene,* and others) and a number of species (this species being one example) appear to follow the western Pacific island archipelagoes north and south, presumably in accordance with north–south current trends among these islands. The previously known depths at which this species was taken were 20–84 meters, but the above specimens are the first from much greater depths; 558–657 meters.

Remarks.—This genus is closely related to *Paranymphon* in most characters except for the loss in adults of the immovable chelae fingers and a few other differences in less conspicuous characters. The lateral process tubercles, for instance, are very similar in the two genera but the tubercles, for *Hemichela,* are much larger in these specimens from the Flores Sea than those illustrated by Stock (1954:91, fig. 42a) for the type. They are at least equal in length to or even larger than the tubercles of *P. spinosum* Caullery, and much taller than those of *P. magnidigitatum* Hong & Kim (1987). Both genera have lateral dendritic spines or tubercles on the anterior and posterior of their lateral processes, at least in the male, and have very tall ocular tubercles and abdomina.

The above specimens have no suggestion of eyes, in keeping with their deeper water habitats, and their ocular tubercles are much more slender distally, with prominent lateral sensory papillae. The ocular tubercle of Stock's type specimen is distally broader and has darker areas suggesting eyes.

The chelae develop their single finger aspect very late in the subadult stage. The juvenile has two well-developed chela fingers on each chelifore with teeth equal to those of the type specimen. The subadult from station B-1 has fully formed ovigers but an immovable finger is still present on both chelae, but it is reduced in size relative to the movable finger. Only in adults with fully developed sexual characters is the immovable finger missing or fully atrophied.

Family Callipallenidae Hilton
Genus *Pigrogromitus* Calman, 1927
Pigrogromitus timsanus Calman

Pigrogromitus timsanus Calman, 1927:408–410, fig. 104a–f.—Child, 1988a:21 [literature].

Material examined.—Sulawesi (Celebes) Island: Samalona Island, just off Ujung Pandang (Makassar), coll. Dr. T. Miura, 2 m, 8 Feb 1985 (1 ♂).

Distribution.—This species is pantropical and in the Indo-Pacific, follows a north–south distribution from Australia through the island archipelagoes to at least as far north as the Ryukyu Islands. It has only been taken in shallow localities.

Genus *Pallenopsis* Wilson, 1881
Subgenus *(Bathypallenopsis)* Stock, 1975
Pallenopsis (Bathypallenopsis) tydemani tydemani Loman

Pallenopsis tydemani Loman, 1908:65–66, pl. 10, figs. 139–145.—Hedgpeth, 1949: 277, fig. 36i, j.—Utinomi, 1951:160; 1971:323.

Pallenopsis (Bathypallenopsis) tydemani tydemani.—Stock, 1975:1032 [text], fig. 31c, 1035–1036 [text].

Material examined.—Flores Sea: 05°54.9′S, 119°29.5′E, 558–593 m, sta. KH85-1, B-2, 12 Feb 1985 (1 ♀).

Distribution.—This is another species represented in Loman's pioneering monograph on the Indonesian fauna. He originally described it from specimens taken in the Flores Sea in 694 and 794 m, and it has since been collected off Kyushu and Honshu Islands in Japan in about 800 and 100–200 m respectively. This female was collected just northeast of the syntypes.

Remarks.—The specimen has only one leg which survived the rigors of the trawl, but the ovigers are much like those figured by Stock (1975:1033, fig. 31c) of the syntype.

There are apparently only six specimens of this species recorded in the literature, making it another rarity, but it is adequately figured by Hedgpeth, Loman, and Stock.

Family Colossendeidae Hoek
Genus *Colossendeis* Jarzynsky
Colossendeis leptorhynchus Hoek, 1881

Colossendeis leptorhynchus Hoek, 1881:64–65, pl. VIII, figs. 3–7.—Stock, 1978:402, 406–408, fig. 21; 1981:454–455; 1983: 299–300; 1986:417.

Colossendeis pennata Pushkin, 1970:1490–1492, fig. 2.

Material examined.—Flores Sea: 05°56.0′S, 119°29.0′E, 630–657 m, sta. KH85-1, B-1, 12 Feb 1985 (1 ♀); 05°54.9′S, 119°29.5′E, 558–593 m, sta. KH85-1, B-2, 12 Feb 1985 (1 ♀).

Distribution.—This species is found in predominantly Southern Hemisphere deep-water localities and could be cosmopolitan in distribution if enough specimens were known from a few other collecting sites. It has not been taken yet in the Indian Ocean, for instance. Hoek's types were taken from off Valpariso, Chile, and the species has been taken in the Walvis Basin off southern Africa, in Indonesia, the Philippines, and the Caribbean Basin in depths of 531–3675 m.

Remarks.—The tarsus of the species and these specimens is almost twice the propodal length and the sixth palp segment is very slightly shorter than the slender seventh. The seventh segment is slightly longer than the combined length of the terminal three segments. The tarsus is notably long in this species, longer than that of its nearest relation, *C. macerrima* Wilson, but the terminal claw is longer than described for the syntype by Stock (1978:402). The claws of the above specimens are less than four times shorter than the propodus while those described by Stock are slightly more than six times shorter. All of these characters, except for claw length, conform to Stock's description of Hoek's syntypes and tend to reinforce the separation of this species from others with which it has been synonymized in the past.

Colossendeis macerrima Wilson, 1881

Colossendeis macerrima Wilson, 1881:246–247, pl. I, figs. 9–12, pl. V, fig. 32.—Fry & Hedgpeth, 1969:53, figs. 7, 8 [literature].—Stock, 1978:400–401, fig. 2M.

Colossendeis villegentei A. Milne-Edwards, 1881:933.

Colossendeis leptorhynchus var. *septentrionalis* Caullery, 1896:362–363.

Material examined.—Flores Sea: 05°54.9'S, 119°29.5'E, 558–593 m, sta. KH85-1, B-2, 12 Feb 1985 (1 ♀).

Distribution.—This is a cosmopolitan deep-water species found from about 400 to almost 4000 m.

Remarks.—This is another species with a very long slender proboscis which is usually slightly upturned distally. The third segment of the palp, as emphasized by Stock (1978:400–401), is notably shorter than the fifth segment, shorter in this ratio than with any other related species. Palp segments 6 and 7 are not as long as in *C. leptorhynchus*, and are approximately equal in length while lacking the slender proportions of Hoek's species. The two species are otherwise difficult to separate as they tend to be of similar sizes along with having slender proboscides, the most immediately obvious character of the species. The comparative figures given by Stock (1978:fig. 2) are excellent for separating these two species along with *C. cucurbita* Cole.

Acknowledgments

We wish to thank Dr. Masumi Horikoshi, chief scientist of this cruise and Dr. Suguru Ohta of the Ocean Research Institute, the University of Tokyo, for their generosity and kindnesses to one of us (KN). We also thank Dr. Shigeo Gamo, Yokohama National University, for the loan of a net and Dr. Tomoyuki Miura, Kagoshima University, for his collaboration in shore collecting. We acknowledge with thanks the help of Dr. J. H. Stock, Institute of Taxonomic Zoology, University of Amsterdam, for loaning syntype specimens of Loman's *Bathyzetes*.

Literature Cited

Calman, W. T. 1927. 28. Report on the Pycnogonida. Zoological Results of the Cambridge Expedition to the Suez Canal, 1924.—Transactions of the Zoological Society of London 22(3):403–410, 3 figs.

Caullery, M. 1896. Pycnogonides. Resultats scientifiques de la campagne du *Caudan* dans le golfe de Gascogne, aout–sept. 1895.—Annales de l'Universite de Lyon 26:361–364, pl. XII.

Child, C. A. 1983. Pycnogonida of the Western Pacific Islands, II: Guam and the Palau Islands.—Proceedings of the Biological Society of Washington 96(4):698–714, 5 figs.

———. 1987. New and little known Pycnogonida from Antarctic and Subantarctic waters.—Proceedings of the Biological Society of Washington 100(4):902–916, 6 figs.

———. 1988a. Pycnogonida of the Western Pacific Islands, III: Recent Smithsonian–Philippine expeditions.—Smithsonian Contributions to Zoology 468:i-iv, 1-32, 12 figs.

———. 1988b. Pycnogonida from Aldabra Atoll.—Bulletin of the Biological Society of Washington 8:45–78, 9 figs.

Fry, W. G., & J. W. Hedgpeth. 1969. Pycnogonida. 1. Colossendeidae, Pycnogonidae, Endeidae, Ammotheidae.—Fauna of the Ross Sea, 7. Memoirs of the New Zealand Oceanographic Institute 49:1–139, 1 pl., 209 figs., 16 tabs.

Hedgpeth, J. W. 1949. Report on the Pycnogonida collected by the *Albatross* in Japanese waters in 1900 and 1906.—Proceedings of the United States National Museum 98(3231):233–321, figs. 18–51.

Hoek, P. P. C. 1881. Report on the Pycnogonida dredged by *HMS Challenger* 1873–76.—Reports of the Scientific Results of the Exploring Voyage of *HMS Challenger* 3(10):1–167, 21 pls., 2 figs.

Hong, J.-S., & I. H. Kim. 1987. Korean pycnogonids chiefly based on the collections of the Korea Ocean Research and Development Institute.—Korean Journal of Systematic Zoology 3(2);137–164, 17 figs., 1 tab.

Loman, J. C. C. 1908. Die Pantopoden der Siboga-Expedition.—Siboga Expeditie Monographie 40: 1–88, I-XV, 4 figs.

Milne-Edwards, A. 1881. Compte rendu sommaire d'une exploration zoologique faite dans l'Atlantique, a bord du navire le *Travailleur.*—Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, Paris 93:931–936.

Nakamura, K., & C. A. Child. 1990. Pycnogonida from waters adjacent to Japan.—Smithsonian Contributions to Zoology (in press).

Pushkin, A. F. 1970. [New species of the genus *Colossendeis* (Pantopoda).]—Zoologicheskii Zhurnal 49(10):1488–1496, 4 figs. [In Russian with English summary.]

Staples, D. A. 1982. Pycnogonida of the Calliope River and Auckland Creek, Queensland.—Memoirs of the Queensland Museum 20(3):455–471, 5 figs., 1 pl.

Stock, J. H. 1953. Contributions to the knowledge of the pycnogonid fauna of the East Indian Archipelago. Biological Results of the Snellius Expedition, XVII.—Temminckia 9:276–313, 18 figs.

———. 1954. Pycnogonida from Indo-West Pacific, Australian and New Zealand waters. Papers from Dr Th. Mortensen's Pacific Expedition 1914–1916.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn 116:1–168, 81 figs.

———. 1955. Pycnogonida from the West Indies, Central America and the Pacific Coast of North America. Papers from Dr Th. Mortensen's Pacific Expedition 1914–1916.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn, 117:209–266, 26 figs.

———. 1975. Pycnogonida from the continental shelf, slope, and deep sea of the tropical Atlantic and East Pacific. Biological results of the University of Miami deep-sea expeditions, 108.—Bulletin of Marine Science 24(4):957–1092, 59 figs.

———. 1978. Abyssal Pycnogonida from the Northeastern Atlantic Basin, Part II.—Cahiers de Biologie marine 19:397–413, 3 figs.

———. 1981. Abyssal Pycnogonida from the Walvis Basin, Southern Atlantic.—Cahiers de Biologie marine 22:453–471, 8 figs.

———. 1983. Pycnogonides des campagnes CORINDON et MUSORSTOM II (detroit de Makassar et Philippines), avec description de *Pallenopsis dentifera* sp. nov.—Bulletin du Museum National d'Histoire Naturelle, Paris (4)5, sec. A(1):299–305, 10 figs.

———. 1985. Deux Pycnogonides rares, recoltes pendant la campagne CORINDON II dans le detroit de makassar, Indonesie.—Bulletin Zoologisch Museum, Universiteit van Amsterdam 10(18):153–158, 22 figs.

———. 1986. Pycnogonida from the Caribbean and the Straits of Florida. Biological results of the University of Miami deep-sea expeditions.—Bulletin of Marine Science 38(3):399–441, 15 figs.

Utinomi, H. 1951. On some pycnogonids from the sea around Kii Peninsula.—Publications of the Seto Marine Biological Laboratory 1(4):159–168, 2 figs.

———. 1971. Records of Pycnogonida from shallow waters of Japan.—Publications of the Seto Marine Biological Laboratory 18(5):317–347.

Wilson, E. B. 1881. Report on the Pycnogonida. Reports on the results of dredging . . . *Blake.*—Bulletin of the Museum of Comparative Zoology, Harvard 8(12):239–256, pls. I–V.

(KN) Faculty of Education, Yokohama National University, 156 Tokiwadai, Hodogaya-ku, Yokohama 240, Kanagawa Prefecture, Japan; (CAC) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 311–335

PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS, VIII. RECENT COLLECTIONS FROM ISLANDS OF THE GREAT BARRIER REEF, AUSTRALIA

C. Allan Child

Abstract.—Eleven pycnogonid species were known from the Great Barrier Reef of Australia, from Torres Strait to the vicinity of Gladstone. Fifteen species are added to the known number with nine species previously known from other localities and six species new to science. These were taken from islands in the northern section (Lizard Island) and the southern section (Heron Island) of the Barrier Reef. The six new species are *Ammothella prolixa, Tanystylum haswelli, Seguapallene crassa, Nymphon draconis, Anoplodactylus brucei,* and *Rhynchothorax vallatus.* The new species are described and figured, the distribution of all species is included without conclusions concerning distribution patterns due to the paucity of this material and other records of Barrier Reef species, and remarks on species affinities are included.

This report treats two small collections of about 100 specimens comprising fifteen named species plus two unnamed for lack of suitable material in eleven genera representing six families of the Pycnogonida. The collections were taken from two small island groups; Lizard Island (14°38′S) in the northern section of the Barrier Reef, and Heron Island (23°27′S) at the southern end of the Reef, plus one species taken at Orpheus Island approximately in the middle of the Reef archipelago. Collecting on Lizard and Heron Islands was greatly facilitated by the presence of marine laboratories on both islands, while a resort on Orpheus Island made collecting there much easier.

Among the fifteen named species reported herein from these islands are six new species; *Ammothella prolixa, Tanystylum haswelli, Seguapallene crassa, Anoplodactylus brucei, Nymphon draconis,* and *Rhynchothorax vallatus.* This high incidence of new species (40%) reflects the sparse amount of collecting done in these islands for such microorganisms.

This is not the first report on pycnogonids from the Great Barrier Reef, although it is the first to treat Reef species exclusively. Haswell (1885) was the first to report on a species (*Nymphopsis armatus*) from the Queensland coast, although it was not strictly from a Barrier Reef locality. Carpenter (1892, 1893) was the next specialist to report on Reef species with four taken off Murray Island in Torres Strait. His species were; *Parapallene australiensis* (Hoek), *P. haddoni* Carpenter, *Rhopalorhynchus clavipes* Carpenter, and *Ascorhynchus tenuirostre* Carpenter.

His work was followed by that of Flynn (1918, 1919a, b, 1929) who redescribed the types of Haswell and described five other species from Australia, only four of which were taken in the Barrier Reef area. The new species described by Flynn (1929) from near the Barrier Reef are: *Ascorhynchus melwardi* Flynn (near Cape York, northernmost Queensland), *Nymphopsis armatus* Haswell (Lindeman Island, Whitsunday Passage), *Pallenopsis hoeki* (Miers) (near Cape York), and *Parapallene famelica* Flynn (Lindeman Island).

Other Australian species have been described and the distribution of known species extended, but since Flynn's 1929 paper, no other Barrier Reef species were described until Stock (1954) listed *Anoplodactylus longiceps* Stock from Lindeman Island. Clark (1963) described *Pycnogonum torresi* Clark from Torres Strait on the northernmost Barrier Reef and listed *Ascorhynchus minutum* Hoek from a coral reef off Port Curtis at Gladstone.

Staples (1982) described several species from the Calliope River at Gladstone, but there have been no reports of pycnogonids from the Barrier Reef itself since Clark's paper reporting on the total Australian pycnogonid fauna known at that time. Staples also noted that there were at the time twenty-eight species known from Queensland, but only eleven of these were taken on or in close proximity to the Great Barrier Reef.

This report adds fifteen species to the eleven species known for a total of twenty-six now known from the Reef. Only one of the previously known species from the Reef was taken in the collections represented in this report while nine species are known from the Australian mainland or from more distant localities and six are reported as new species. The most probable reason for this lack of similarity in collections is undoubtedly due to differences in collecting methods. While many specimens were previously taken over the years fortuitously by trawl or other macrocollecting devices, the Lizard and Heron Island collections were made for their microorganism contents, thereby greatly enriching our knowledge of these tiny organisms of the Great Barrier Reef.

The previously known species comprising most of this report have a tendency to be distributed in a northern array above the equator, suggesting only that there has been more collecting to the north than in most Australian and New Zealand waters. One species is known to be pantropical–temperate while two have a broad Indo-west Pacific distribution. Another has only been taken before in New Zealand, while two are known from either one or both sides of Australia to Indonesia or the Philippines, and three are known only from the Philippines or from there plus other western Pacific localities. One species has been taken previously only in Japan and Korea, providing a very disjunct picture of its distribution. All are shallow water inhabitants.

Very little can be inferred from these distributional bits and pieces and no clear pictures of distribution can be taken from such small groups of species. The only clear picture we get from the data in this report is that the Great Barrier Reef is apparently rich in species judging by this small sampling from two of the hundreds of islands. The presence of six previously undescribed species out of the fifteen in these collections suggests that very little collecting of minute forms has been done in these localities, and that intensive collecting over most of the length of the Barrier Reef might increase the number of new and known species by tenfold.

Systematics

Family Ammotheidae Dohrn

Genus *Achelia* Hodge

Achelia assimilis (Haswell)

Ammothea assimilis Haswell, 1884:1026–1027, pl. LIV, figs. 5–9.

Achelia (*Ignavogriphus*) *assimilis*.—Fry & Hedgpeth, 1969:106, figs. 152, 153, 156, tab. 13, 14 [literature].

Achelia assimilis.—Child, 1988b:2

Material examined.—Heron Island: southern reef flat, on alcyonarian, coll. A. J. Bruce, 16 Jan 1977 (1 juv); rubble on SW reef crest, coll. N. Bruce, 2 Jun 1978 (1 juv); rubble on reef flat, coll. N. Bruce, 6 Jun 1978 (2 m).

Lizard Island: off Casuarina Beach, coral with *Halimeda* and red algae clumps, 2 m, coll. B. Kensley, sta. K-L1, 27 May 1980 (2 juv); southern tip, coral rubble on patch reef, 1 m, sta. JDT/LIZ-3, 23 Jan 1989 (1 ♂, 1 juv); S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 189 (6 ♂, ♀); Lizard Head, rubble bank in 2 m, sta. JDT/LIZ-15, 31 Jan 1989 (10 ♂, ♀, juv); Lizard Head, small rubble in sand, 2 m, sta. JDT/LIZ-19, 2 Feb 1989 (4 ♂, ♀).

Distribution.—Haswell's long-known species has been taken in many southern hemisphere localities along with records from Indonesia and the Philippines. It has a mainly littoral to shallow depth range.

Remarks.—There may possibly be more than one species hiding under the umbrella of this name. It is an extremely variable species with figures in the literature having almost no tubercles to specimens figured with extreme tuberculation.

Genus *Ammothella* Verrill
Ammothella prolixa, new species
Fig. 1

Material examined.—Lizard Island: Watson's Bay, SW border, reef and sand flat rubble in 1–7 m, sta. JDT/LIZ-7, 25 Jan 1989 (1 ♂, holotype, 1 ♀, 2 juv, paratypes).

Other material.—Orpheus Island, just off Townsville: cove S of resort, rubble in 1–2 m, sta. JDT/OPH-1, 12 Feb 1989 (2 ♀).

Lizard Island: North Point, rubble at bottom of cliff, 12 m, sta. JDT/LIZ-13, 28 Jan 1989 (1 ♀); S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♀, 1 juv); off Casuarina Beach, coral with *Halimeda* clumps and red algae, 2 m, sta. K-L1, 27 May 1980 (1 juv).

Description.—Size very small, leg span 8 mm. Trunk and lateral processes slender, elongate, fully segmented, glabrous except for tiny paired or single dorsodistal tubercles on lateral processes. Lateral processes 2 to 2.5 times longer than their maximum diameters, constricted proximally, swollen distally, separated by slightly more than twice their diameters distally. Neck moderately narrow, expanded distally, without setae or tubercles. Ocular tubercle very slender proximally, expanded to club-shape distally, slightly more than 4 times longer than maximum diameter, eyes fully distal, large, well pigmented. Abdomen very long, slender, longer than proboscis, erect, curving toward posterior, armed with median and distal fields of tubular and pointed spines. Median field with 6 tubular spines, 2 dorsal are longer than those lateral and ventral, and 2 shorter lateral pointed spines. Distal field with 2 long tubular spines and 2 shorter pointed spines, with 2 very short setae lateral to anus.

Proboscis with extreme basal and distal constrictions and very swollen median section, originating from extended proximoventral pedestal on trunk anterior.

Chelifores slender, slightly longer than proboscis, lightly spinose. First scape segment only half length of second segment, first armed with single lateral seta distally, second with short proximal tubular spine, 2 median tubular spines and 1 long pointed spine, one distal tubular spine with 4 long pointed spines on inflated terminus of scape. Chela with atrophied movable finger on bulbous palm lacking immovable finger but with single long lateral seta.

Palp very long, slender, segments only moderately armed with ventral setae. First segment not longer than wide, armed with single lateral seta longer than segment diameter. Second segment almost as long as fourth, the longest segment, second armed with 2 moderately long lateral setae. Fourth with 3 long lateral and distal setae, several shorter endal setae, and a lateral elevated pore at median length. Fifth and sixth segments subequal, half length of fourth, armed moderately with short setae, some slightly longer than segment diameter. Seventh and eighth increasingly shorter, with few ventral setae, ninth longer, almost as long as fifth and sixth segments, armed with moderate number of short ventral and distal setae. Entire palp about 1.5 times longer than proboscis.

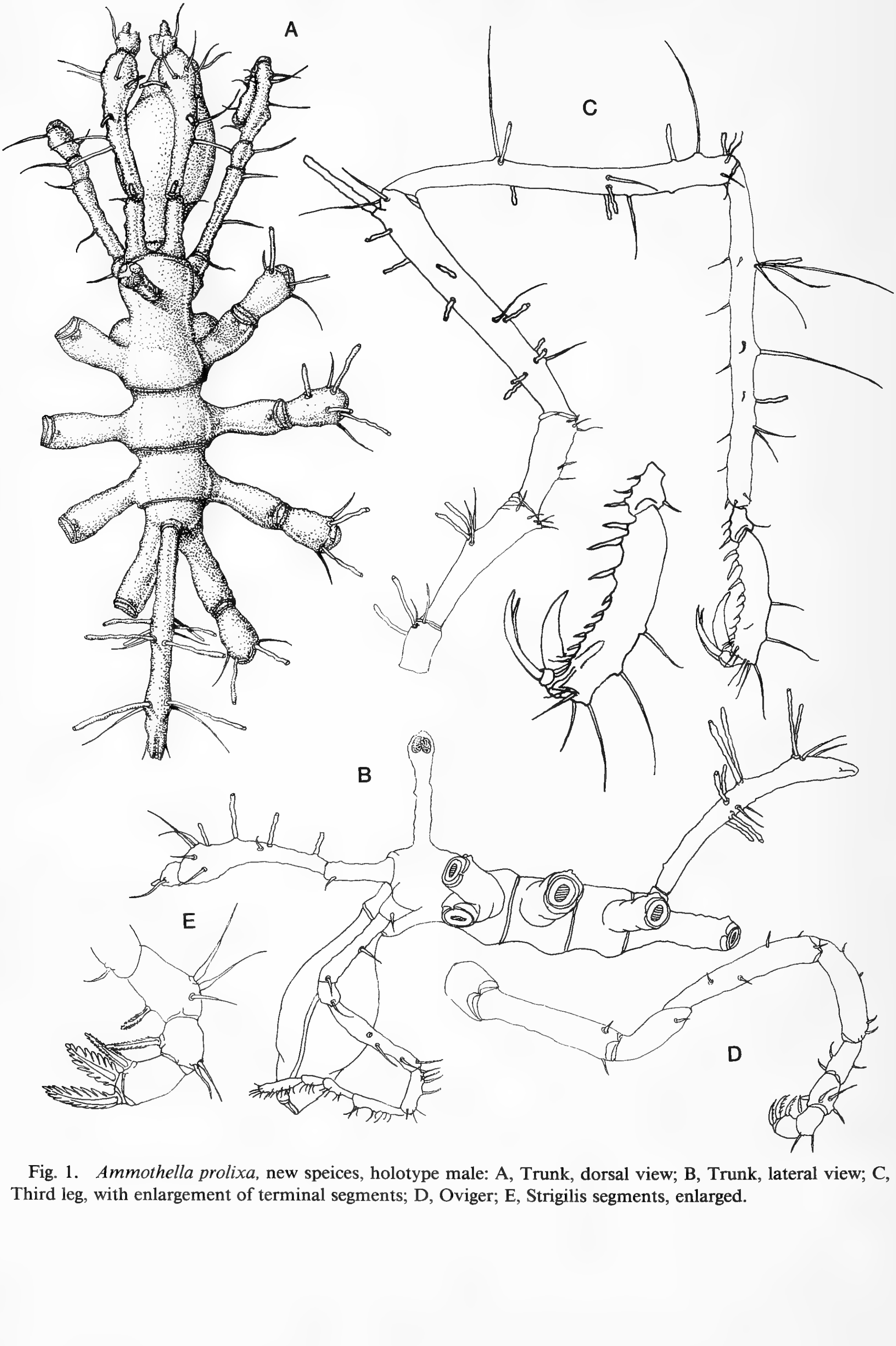


Fig. 1. *Ammothella prolixa,* new speices, holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg, with enlargement of terminal segments; D, Oviger; E, Strigilis segments, enlarged.

Oviger typical of genus, longest segments with 1 to several short lateral setae. Second and fourth segments longest, second almost as long as fourth. Strigilis weak, seventh segment armed with 3 long ectal setae and 1 endal denticulate spine smaller than those of more distal segments. Eighth with 2 ectal setae and 1 endal denticulate spine, ninth without ectal setae but 1 endal denticulate spine. Tenth segment a tiny knob with 2 very broad denticulate spines having at least 8 serrations per side.

Legs slender, well armed with tubular and pointed spines. First and second coxae with paired dorsolateral tubular spines, paired lateral long pointed spines, and fringe of short setae laterally and ventrally on second coxae. Third coxae without long spines but with several short ventral setae. First tibiae the longest segment, longer than second tibiae which are longer than femorae. All major segments with 3–9 tubular spines randomly placed and 4–8 long pointed spines, those on dorsal tibiae up to 6 times longer than diameter of segment. Femoral cement gland tube placed dorsodistally, a robust cylinder almost twice femoral diameter. Tarsus very short, subtriangular, with 2 setae and 1 spine ventrally. Propodus moderately short, slightly curved, with 3 well separated heel spines, 6 small sole spines, and few dorsal and distal setae longer than segment diameter. Claw relatively short, only little over half propodal length, auxiliary claws almost as long as main claw.

Female: very similar to male but of slightly larger size. Oviger second and fourth segments notably shorter than those of male. Sexual pores on all second coxae ventrodistally.

Measurements (holotype, in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 0.85; trunk width (across 2nd lateral processes), 0.59; proboscis length, 0.53; abdomen length, 0.62; third leg, coxa 1, 0.12; coxa 2, 0.35; coxa 3, 0.31; femur, 0.74; tibia 1, 0.85; tibia 2, 0.8; tarsus, 0.09; propodus, 0.31; claw, 0.14.

Distribution.—The species is known from the type locality, Lizard Island, in the northern sector of the Barrier Reef, and from Orpheus Island, in the middle section of the Reef, all in shallow depths to 12 m.

Etymology.—This species is named (Latin: stretched out, long) for its elongate slender trunk and appendages.

Remarks.—This species was at first glance reminiscent of *Ammothella elegantula* Stock, another slender attenuated species. Further examination brought many small differences to light, such as the very slender proboscis of *A. elegantula,* its abdomen without large spines, the lack of any tubular spines on Stock's species, the long lateral spines of the lateral processes and the similar spines of the first two coxae, the broad neck, and the very short terminal palp segments, all characters quite different from this new species.

This species is another addition to the *appendiculata–rugulosa* group of species in this genus, species having tubular and pointed spines, long ocular tubercles, long curved abdomina with spine fields, and legs with similar segment length ratios and spination. This species group is larger, with 18 species, than the group of 15 species without these spines. Of the 18 species having tubular spines, this species is closest to the known Pacific species; *A. indica* Stock, *A. alcalai* Child, and possibly *A. pacifica* Hilton. It can be compared least with *A. pacifica* of the three because Hilton's species is much more compact with lateral process setae, shorter ocular tubercle and abdomen, and many more tubular spines on each major leg segment.

The new species is very similar to the more slender *A. indica,* particularly in a comparison of the legs, ovigers, and palps of both species. The differences are found in the more widely separated lateral processes of the new species along with its shorter oviger segments, fewer tubular leg spines, lack of a tubular spine on the first scape segments, rounded ocular tubercle apex, a shorter propodus, and fewer denticulate spines on the female oviger, while having a denticulate spine on the eighth male oviger segment which is lacking on that of *A. indica.*

This new species appears to be closest to *A. alcalai,* recently described from the Philippines (Child 1988a:2–4, fig. 1). The lateral processes of the new species are placed farther apart than in *A. alcalai* (and are farther apart than those of all other species discussed herein), but both species have small lateral process dorsodistal tubercles. The tubular and pointed spines of *A. alcalai* are predominantly much shorter than those placed in corresponding positions on *A. prolixa,* and the distal palp segments are notably shorter than those of the new species.

The one character which separates this new species from almost all others of the *appendiculata–rugulosa* group is that of the anteroventral extension of the trunk which acts as a pedestal for the proboscis base. In most species, the proboscis originates directly from the flat trunk anterior between and ventral to the palp and chelifore insertions, and there is no anterior trunk extension or pedestal present.

Ammothella stauromata Child

Ammothella stauromata Child, 1982:271–273, fig. 1; 1988a;5, 7; 1988c:809–810.

Material examined.—Lizard Island: S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂, 2 ♀).

Distribution.—This species is known from Enewetak Atoll, Marshall Islands, the northern and southern Philippines, and American Samoa, in depths of 0–3 m.

This additional record further extends the broadening distribution known for this species to a more southern locality. Few specimens have been taken in any known locality, but *A. stauromata* appears to have a particularly wide western Pacific islands distribution. It has not yet been taken in the Indian Ocean.

Remarks.—The only other species of *Ammothella* with large mediandorsal trunk tubercles found in Australia is *A. thetidis* Clark, a species with many striking differences from *A. stauromata.* Clark's species lacks the mediandorsal tubercle on the posterior rim of the first trunk segment, a tubercle which is present on this species. Clark's species is apparently blind while this species has prominent eyes, the proboscis of Clark's species is bulbous and without constrictions while that of this species has a modified tripartite shape similar to proboscides of many species of *Ascorhynchus.* This species has elongate palp segments in comparison with those of Clark's, and there are large paired first coxae tubercles on this species while Clark's is without these tubercles. There are a number of other small differences between the two species.

There are few other *Ammothella* species known with large dorsal tubercles, and this species shares even fewer characters with these other species than with *A. thetidis.*

Genus *Eurycyde* Schioedte

Eurycyde setosa Child

Eurycyde setosa Child, 1988a:8–10, fig. 3.

Material examined.—Lizard Island: S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂, 1 ♀).

Distribution.—This species was recently described from a male collected in the northern Philippines at Batan Island, in 0–4 m. This second and third specimen greatly extend its known distribution southerly to the northern Great Barrier Reef, but within the known depth range of the type.

This is perhaps another of the growing list of species with known distribution along a corridor extending from Australia and New Zealand north to at least the Philippines and sometimes to Japan. There are undoubtedly many more species sharing this extremely rich corridor and their capture must await extended and close collecting on the Barrier Reef, New Guinea, and particularly in Indonesia and the Philippines where the benthic microfauna remains little known.

Remarks.—These two specimens have only slight differences from the type specimen, a male. The major difference is in the first coxae tubercles which in this male are slightly shorter and bear only very few tiny setae instead of the longer and heavily setose tubercles of the type. It should be noted that the coxae tubercles of the female are only slightly smaller than those of the male, although the female is a good bit larger in most measurements than the male.

The abdomen of the type is missing, but can be described from the two specimens in hand. It is only slightly longer than the ocular tubercle, is swollen distally, and armed with six long distal feathered spines, each longer than the abdomen itself, and placed in a dorsolateral fan arrangement with one slightly shorter feathered spine placed ventrally and more proximal than the dorsolateral fan. There are also two short lateral setae adjacent to the anus. The remaining characters agree very well with the type male.

Genus *Tanystylum* Miers
Tanystylum haswelli, new species
Fig. 2

Material examined.—Lizard Island: Lizard Head, rubble bank in 2 m, sta. JDT/LIZ-15, 31 Jan 1989 (1 ♂, holotype).

Description.—Size very tiny, leg span 6 mm. Trunk subcircular in dorsal outline, slightly wider than long, unsegmented. Lateral processes contiguous, even squeezed together. Ocular segment anterior rim extending only slightly beyond lateral process rims, armed with single lateral setae, ocular tubercle slightly posterior to anterior rim of segment, little wider than tall, with small slender apical tubercle anteriorly and two low bumps posterolaterally. Eyes large, darkly pigmented.

Proboscis widest at base, moderately inflated, tapering gradually to cylindrical tip circling flat lips. Abdomen short, carried almost horizontally, extending only slightly beyond tips of fourth lateral processes, originating from a low bulge between bases of third lateral processes, armed with distal fringe of six short setae.

Chelifores single-segmented, tubercle-like, blunt, curved inward, carried at very elevated angle, each armed with 4–5 short distal setae.

Palp four-segmented, little longer than proboscis, originating with broad basal segment only as long as its proximal diameter. Second segment consisting of coalesced second and third segments, the juncture evident beneath integument, armed with 4–5 ectal setae and 2–3 ventrodistal setae, none as long as segment diameter. Third segment only little longer than its diameter, armed with 2–3 short ventrodistal setae. Fourth segment a curved cylinder about 3.5 times longer than its diameter, armed with many ventral and distal setae mostly longer than its diameter.

Oviger fourth and fifth segments subequal in length, armed with few short recurved spines laterally. Second segment very slightly shorter, armed with 1–2 short lateral spines. Sixth and seventh segments short, their combined length not as long as fifth segment, armed with several stout recurved spines, in greater numbers on sixth segment, and 1–2 short distal setae on seventh segment. Seventh lacks spinose distal apophysis. Terminal three segments each shorter than last, eighth rounded, armed with 3 distal setae longer than segment diameter, without spines. Ninth a short curved cylinder without spines, with single distal seta longer than segment diameter. Tenth segment a tiny bud, broader than long, armed with 2 stout straight spines lacking any form of denticulation.

Legs very stout, the major segments armed with dorsal bulges bearing several setae each. First coxae not as long as their diameters, armed with low laterodistal tubercle on anterior surface bearing 2 short setae. Posterior surface armed with 1–4 short latero-

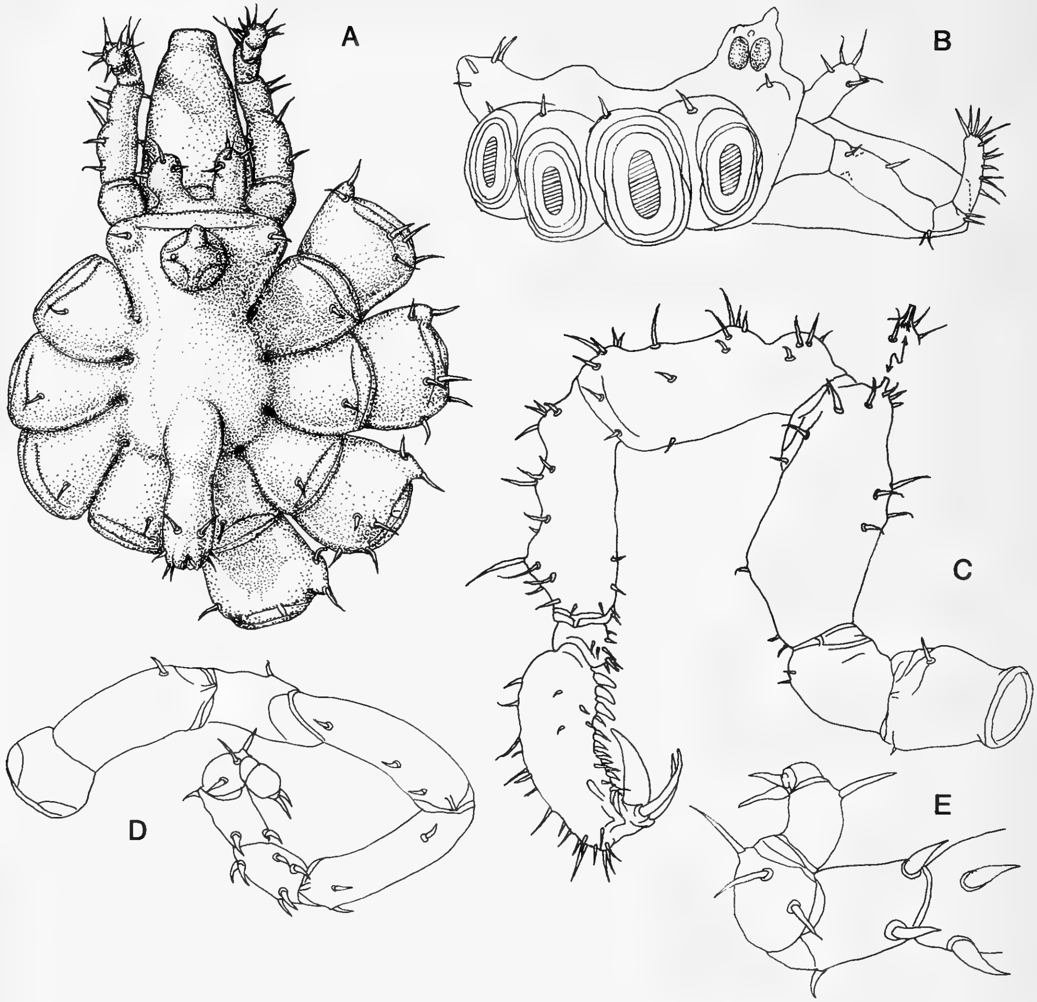


Fig. 2. *Tanystylum haswelli,* new species, holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg, with enlargement of cement gland tube; D, Oviger; E, Strigilis segments, enlarged.

distal setae. Second coxae with 2 laterodistal setae, third with few ventrodistal setae. Femur with large ventromedian bulge bearing 1–2 short setae, a large dorsomedian bulge with 4–5 longer setae, and a fringe of 7–8 distal setae. Cement gland orifice a short tiny tube tapering to constricted tip. Femur slightly longer than tibiae which are equal in length. Tibiae armed with many short setae mostly on dorsal bulges. Tarsus very short, heavily setose ventrally. Propodus stout, only slightly curved, armed with 3 stout heel spines, about 5 shorter sole spines, many short flanking setae, and few short dorsal and distal setae. Claw broad, short, less than half propodal length, auxiliary claws more slender, almost as long as main claw.

Female of the species unknown.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 0.6; trunk width (across 2nd lateral processes), 0.66; proboscis length, 0.35; abdomen length (from bulge anterior), 0.28;

third leg, coxa 1, 0.19; coxa 2, 0.26; coxa 3, 0.22; femur, 0.5; tibia 1, 0.44; tibia 2, 0.44; tarsus, 0.06; propodus, 0.39; claw, 0.16.

Distribution.—The species is known only from its type locality, Lizard Island on the northern Great Barrier Reef, in 2 m.

Etymology.—The new species is named for Dr. William A. Haswell who, following Hoek's offshore records of Australian species taken by the *Challenger,* provided the first substantial knowledge of Australian pycnogonids.

Remarks.—This specimen appeared to be *T. orbiculare* Wilson at first examination. Specimens identified as Wilson's species have been found along the littoral of eastern Australia, although there is some question as to whether or not they are indeed this far flung species (Clark 1977:332). The unique type of Wilson's *T. orbiculare* (unfortunately a female without ovigers—the male ovigers bear the diagnostic characters) was examined for purposes of comparison. A set of figures of the type is presented herein (Fig. 3), along with a male oviger from a specimen taken near the type locality by Wilson himself. The type specimen of this species has not been figured adequately for many years.

The new species differs from *T. orbiculare* mainly in the palps and abdomen. The abdomen of Wilson's species is notably longer and extends almost the length of the first coxae of the fourth leg pair, it has no basal bulge and is swollen in dorsal view rather than having a median constriction as in the new species. The lateral processes are larger in girth in relation to the trunk size in the new species, and the terminal palp segment is notably longer than that of Wilson's species. The palp of *T. orbiculare* has a variable number of segments, ranging sometimes from four to as many as seven in some specimens. The large ventral bulge on each femur of the new species is not present on the femorae of *T. orbiculare,* but most of the remaining characters of these two species are very similar. Both species have male ovigers without the characteristic seventh segment apophysis.

This new species has some similarities to *T. hooperi* Clark (1977:325–327, figs. 20–30), another species found on the New South Wales coast of Australia. The major difference between these two species is that *T. hooperi* has the male oviger bearing a seventh segment apophysis. The two species have very similar abdomina, proboscides, and legs, but the palps are quite different.

Perhaps a species with greater similarities to the new species than *T. hooperi* is *T. bredini* Child (1970:296–299, fig. 3) in which males of both species have ovigers without a seventh segment apophysis. There are a number of other similarities between these species including the proboscis, four-segmented palps, ovigers, legs, and ocular tubercle and abdomen. The differences lie in *T. bredini* having anterior and posterior lateral process tubercles, larger first coxae tubercles, a slightly more tapering proboscis, shorter auxiliary claws, and a much shorter terminal palp segment. It is possible that these differences might be reduced or eliminated by examination of a large suite of specimens, but with only one male available of the new species, I will keep the Australian specimen separate from the Society Islands species until more Lizard Island specimens can be collected for examination.

Family Callipallenidae Hilton
Genus *Callipallene* Flynn
Callipallene species indeterminate

?*Callipallene emaciata* subsp. Stock, 1954: 46–48, figs. 19h, i, 20c–e.

Material examined.—Heron Island: SW reef crest, rubble in 0–1 m, coll. N. Bruce, 2 Jun 1978 (1 ♂).

Lizard Island: S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♀); Lizard Head, rubble bank in 2 m, sta. JDT/LIZ-15, 31 Jan 1989 (1 ♀); SW of Lizard Head, rubble zone in 1.5 m, sta. JDT/LIZ-17, 1 Feb 1989 (1 ♀); Lizard

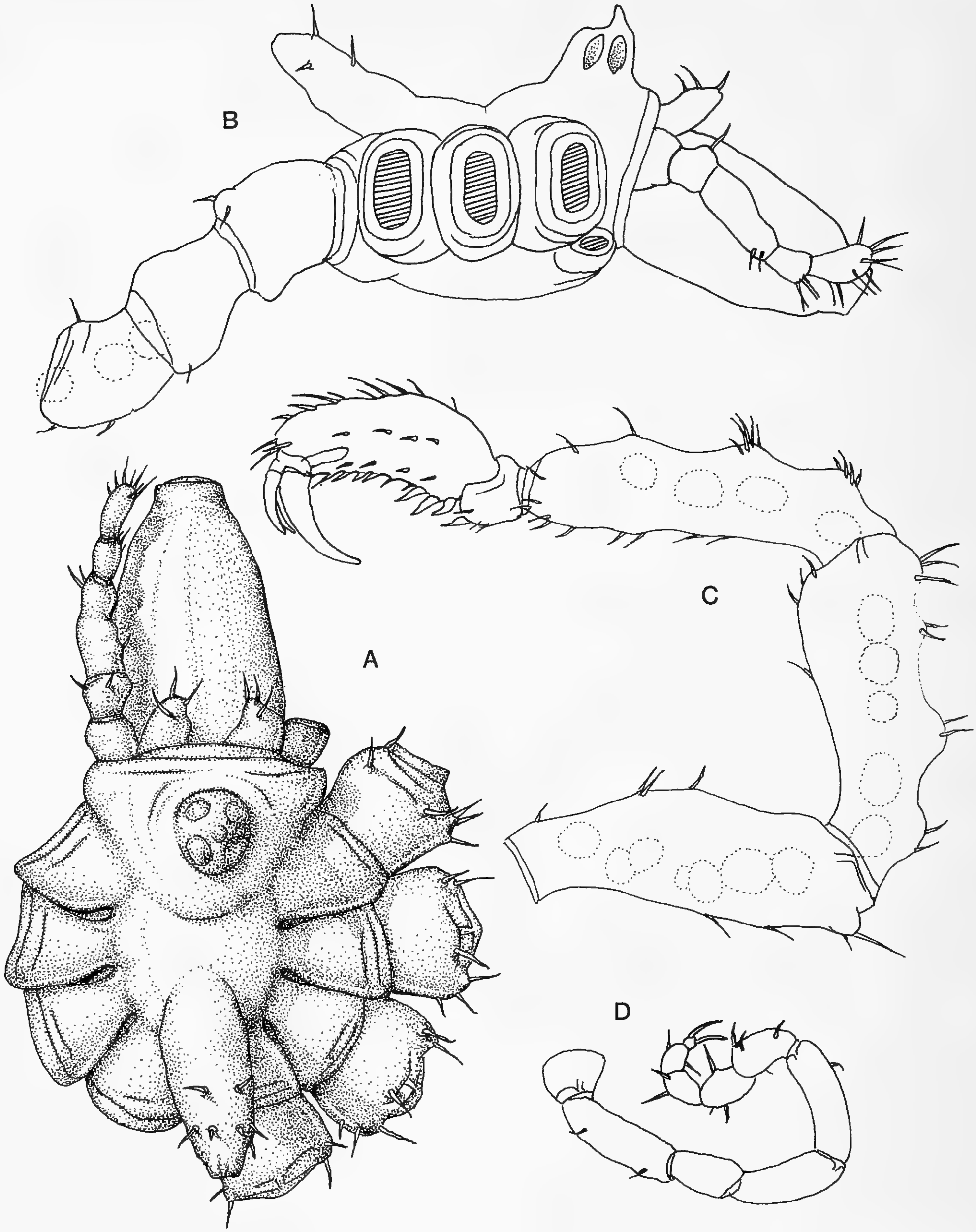


Fig. 3. *Tanystylum orbiculare* Wilson, holotype female: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg, with ova indicated within. Nontype male: D, Oviger.

Head, small rubble in sand, 2 m, sta. JDT/LIZ-19, 2 Feb 1989 (2 ♀).

Distribution.—In spite of the very shallow water in which these specimens were taken, they agree in almost all respects with Stock's figures for his unnamed subspecies. His material came from 65 fathoms (119 m) off Three Kings Island, New Zealand.

Remarks.—The figures given by Stock emphasize the statement he made (1954:46) that "the specimens have almost no striking features." The above specimens also agree with this comment and I must therefore refrain from naming them. Having only one male among five females does not constitute an adequate number of specimens to justify adding another new species in this highly variable genus.

These specimens agree in the neck and trunk habitus figured by Stock (1954:47, fig. 20d), but have a few more long setae on the chelae and laterally on the legs. The propodus is almost exactly as that figured (fig. 19i), and the ocular tubercle has the same small conical apex. The legs of the above specimens bear the low swellings of the femorae and first tibiae as in Stock's fig. 20e. There is nothing unique about any of these characters among the many species in this genus to warrant erecting another species from this scant material.

Genus *Cheilopallene* Stock

Cheilopallene nodulosa Hong & Kim

Cheilopallene nodulosa Hong & Kim, 1987: 153–155, fig. 12.—Nakamura & Child (1990).

Material examined.—Lizard Island: North Point, rubble at bottom of cliff, 12 m, sta. JDT/LIZ-13, 28 Jan 1989 (2 ♀).

Distribution.—Hong & Kim recently described this species from a female and a juvenile found on the west coast of Korea in floating *Sargassum* weed. Nakamura & Child (1990) list it among the fauna of the Japanese Islands, and it appears herein on the Great Barrier Reef as a third recorded locality. The above record at 12 m is the deepest recorded capture. This new record extends the distribution for this species greatly to the south and into the southern hemisphere, suggesting that it is another of the growing list of species inhabiting a north–south corridor of related localities from Australia through the western Pacific Islands and to Japan and Korea.

Remarks.—The female figured by Hong & Kim (1987:fig. 12) is apparently a subadult with incompletely developed ovigers. The above females appear to be fully adult and agree in almost all respects with the characters of the type except for the ovigers and the placement of several small tubercles. The ovigers of the females above have segment lengths in agreement with those of the type, but each segment from the fourth onward has a stout lateral spine on the dorsodistal surface. The strigilis has fully denticulate spines in the formula 3:3:3:4, with several tiny teeth on both the ectal and endal surfaces of the terminal claw imparting a frayed or worn appearance. The denticulate spines each bear 3–4 lateral serrations per side and are broad and short.

The peculiar lateral bulges or "baloons" at the proximal margins of each scape are present on both these specimens, suggesting that they are a normal character of the anatomy rather than an artifact. Hong & Kim did not figure the tiny setose tubercles over the insertion of each scape nor the similar tubercles of the first lateral processes (single) and the first coxae (double). These tubercles are relatively inconspicuous and could easily be overlooked.

Genus *Seguapallene* Pushkin

Seguapallene crassa, new species

Fig. 4

Material examined.—Lizard Island: Lizard Head, rubble bank in 2 m, sta. JDT/LIZ-15, 31 Jan 1989 (1 ♂, holotype, 1 ♂, 2 ♀, paratypes).

Other material.—Lizard Island: S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂ with eggs, 1 ♂, 2 ♀); Lizard Head, small rubble in sand, 2 m, sta. JDT/LIZ-19, 2 Feb 1989 (1 ♂ with eggs, 1 ♀); Palfrey Island, near SW point, rubble in 1 m, sta. JDT/LIZ-21, 6 Feb 1989 (1 juv); Lizard Island, off Casuarina Beach, coral with *Halimeda* clumps and red algae in 2 m, sta. K-L1, 27 May 1980 (1 ♂ with eggs, 1 ♀).

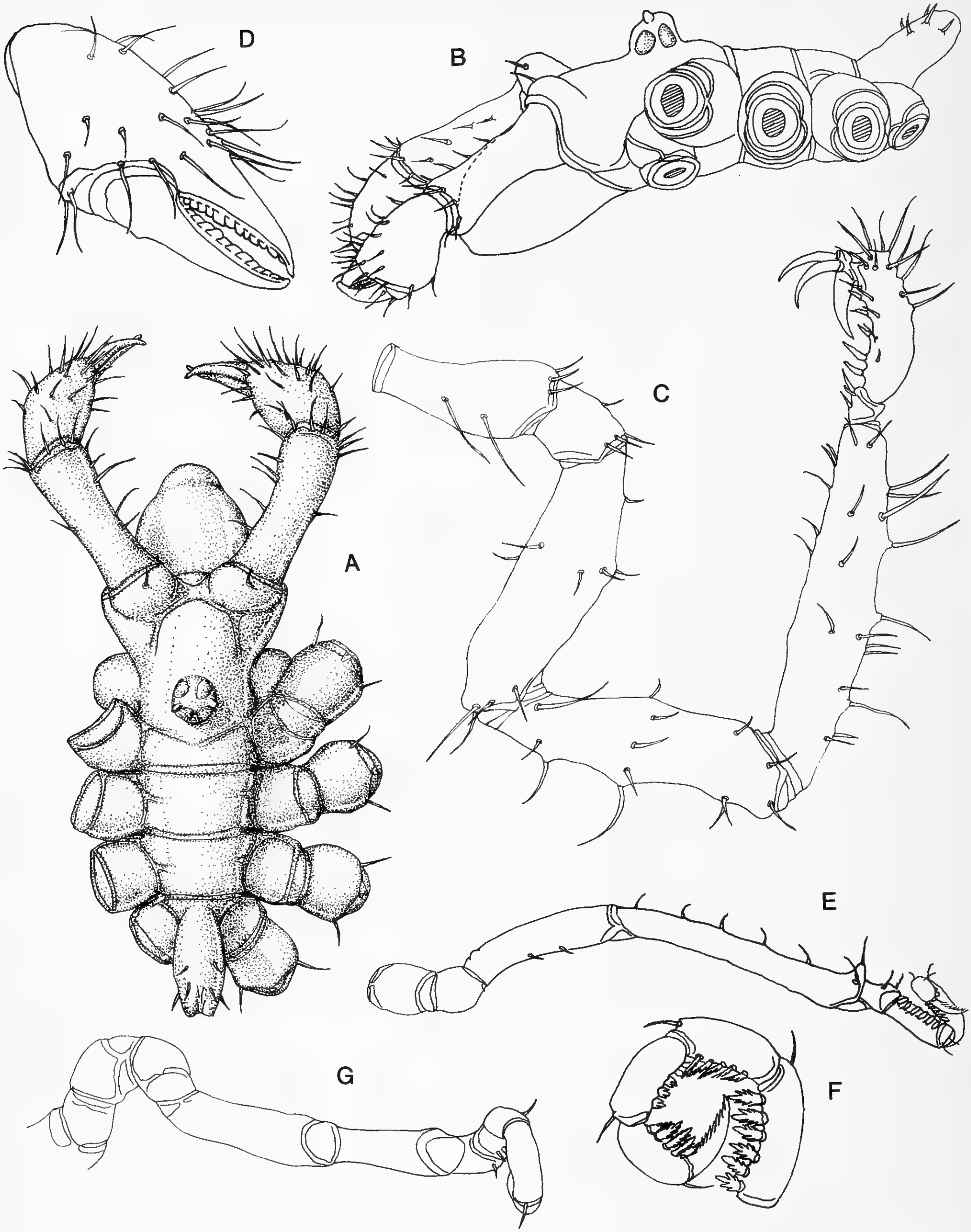


Fig. 4. *Seguapallene crassa,* new species, holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg; D, Chela; E, Oviger; F, Strigilis segments, enlarged. Paratype female: G, Oviger.

Description.—Size very small, leg span about 6 mm. Trunk fully segmented, stout, lateral processes crowded, touching to slightly separated, each only as long as its diameter or slightly shorter, glabrous, suture line at base of each lateral process and neck prominent. Neck moderately short, flanked by extremely large oviger bases and extending to broad expansion at chelfore insertions. Ocular tubercle at neck midpoint over oviger bases, about as tall as wide, eyes prominent, well pigmented, with large sensory papillae on horn-like tubercles at apex. Abdomen moderately short, carried at low oblique angle, inflated in dorsal view, armed with 6 short distal setae.

Proboscis short, rotund, a broad cylinder proximally, tapering abruptly distally to very small oral surface. Lips flat, without setae or other adornment.

Chelifores 2-segmented, inserting into raised crests or cowls on neck anterior. Scape robust, moderately setose with several endal and dorsodistal setae shorter than segment diameter. Chela palm triangular, armed with distal fringe of setae with greater numbers at junction of palm and immovable finger. Fingers moderately slender, curved only at tips, glabrous, with 12 block-shaped teeth on each finger.

Oviger fourth segment slightly curved, armed with 2–3 short endal setae, segment about 0.6 as long as fifth. Fifth segment with 6–7 ectal setae and small distal apophysis with apical seta. Sixth segment very short, shorter than any strigilis segment, armed with 2 lateral setae. Strigilis segments each shorter than last, armed with dorsodistal seta each and endal denticulate spines in the formula 6:5:5:5, with a terminal claw having 7–8 endal serrations. Denticulate spines with 2–5 serrations per side.

Legs stout, moderately setose, second tibiae the longest segment, femorae longer than first tibiae, terminal leg segments small in relation to proximal leg segments. First coxae with 2 short laterodistal setae, second coxae with 2 long lateral setae per side and fringe of shorter ventrodistal setae, third coxae with few ventral and ventrodistal setae. Femorae with fringe of short setae around the median length, several distal setae with single longer dorsodistal seta, cement gland pores not evident. First tibiae with 2 long proximolateral setae, a fringe of short median and distal setae, with long proximal, median, and distal setae on dorsal surface. Second tibiae with several dorsal and dorsolateral setae, those along median line longest, several short lateral setae, and few ventrodistal setae. Tarsus very short, semitriangular, with 3–4 ventral setae and 1 spine. Propodus very small, slightly curved, with 2 heel spines, 4–5 slender sole spines, and many distal and dorsodistal setae longer than segment diameter. Claw robust, short, less than half propodal length, slightly curved, auxiliaries more slender, almost as long as main claw.

Female slightly larger in most measurements, oviger segments four and five much shorter than those of male, fifth shorter than fourth and without distal apophysis. Oviger strigilis spine formula: 6:5:4:5, with 9 terminal claw serrations. Major oviger segments without setae or recurved spines. Neck equal in length to that of male.

Measurements of holotype (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 0.7; trunk width (across 1st lateral processes), 0.46; proboscis length, 0.26; abdomen length, 0.16; third leg, coxa 1, 0.18; coxa 2, 0.32; coxa 3, 0.15; femur, 0.54; tibia 1, 0.5; tibia 2, 0.64; tarsus, 0.07; propodus, 0.27; claw, 0.12.

Distribution.—This species is known from its type locality, Lizard Island, from a rubble bank at Lizard Head, in 2 m, and from other Lizard Island localities.

Etymology.—The specific name (Latin: thick, stout) refers to the stout trunk with its closely crowded lateral processes.

Remarks.—There were only two species known in this genus, one of the many genera in this cumbersome family. These are *S. insignatus* Pushkin, the type of the genus, and *S. micronesica* Child. The distribution of these species is extremely disjunct with Pushkin's species found in the subantarctic Crozet Islands, and *S. micronesica* found in the tropical Palau Islands. This third species is another from the tropics and is closest to *S. micronesica.*

Pushkin's species has lateral process tubercles and an oviger with shorter fourth and fifth segments, the latter lacking a distal apophysis, both characters which are different in the two tropical species.

The new species differs from *S. micronesica* in having much more compacted lateral processes which are more robust, shorter leg segments which are also rather robust, a smaller propodus with a more typical claw rather than the short one of *S. micronesica,* and a chela with block-like closely set teeth rather than well separated triangular teeth. The new species is about 0.3 smaller than the Palauan species, but both have very similar ocular tubercles, abdomina, proboscides, chelifores, and sometimes prominent suture lines on the trunk.

Family Nymphonidae Wilson
Genus *Nymphon* Fabricius
Nymphon draconis, new species
Fig. 5

Material examined.—Lizard Island: S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂, holotype, 3 ♂ with eggs, 1 juv, 1 larva, paratypes).

Other material.—Lizard Island: Lizard Head, rubble bank in 2 m, sta. JDT/LIZ-15, 31 Jan 1989 (1 ♀); SW of Lizard Head, rubble zone in 1.5 m, sta. JDT/LIZ-17, 1 Feb 1989 (1 ♀); Lizard Head, small rubble in sand, 2 m, sta. JDT/LIZ-19, 2 Feb 1989 (1 ♂, 2 ♀, 3 juv); off Casuarina Beach, rubble with encrusting and red algal turf in 2 m, sta. K-L2, 27 May 1980 (1 juv).

Description.—Size moderately small, leg span 11.4 mm. Trunk fully segmented, segments fairly short, bulbous, not longer than wide, lateral processes short, slightly longer than wide, separated by more than their diameters in anterior pairs, less than their diameters in posterior pairs, glabrous. Neck short, without parallel sides, oviger implantation bulges just anterior to first lateral processes, occupying half neck length, neck armed with short seta over insertion of each chelifore. Ocular tubercle low, only slightly taller than basal width, eyes large, anterior pair larger than posterior pair, ocular tubercle capped with pair of short lateral sensory tubercles. Abdomen very short, semierect, a tapering truncate cone armed with pair of short lateral setae.

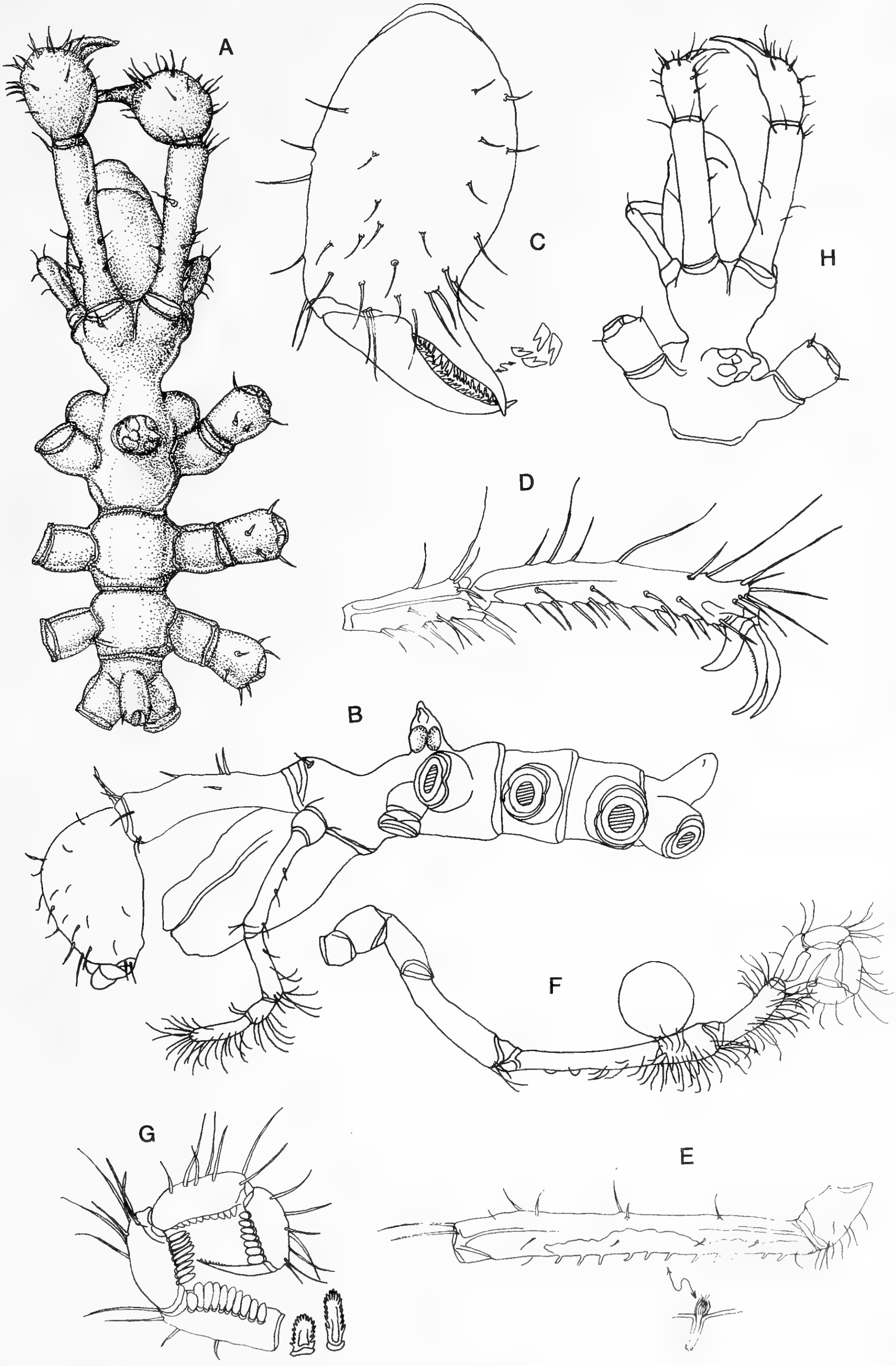
Proboscis barrel-shaped, widest swelling at midpoint, tapering distally to cylinder, lips almost flat.

Chelifores very large, chelae massive, globular, moderately setose. Scape as long as proboscis, slightly swollen distally, armed with few short dorsal and lateral setae. Chela very swollen, palm ovoid, much larger than short fingers. Fingers armed with closely crowded unevenly bifurcate teeth, 11 on each finger, fingers carried at sharp lateral angle to palm.

Palp segments relatively short, second segment longest, third and fifth subequal in length, first and fourth little longer than their diameters. Second segment with few short lateral and distal setae, third with many ventral setae longer than segment diameter, fourth and fifth with many long ventral and lateral setae, some about 3 segment diam-

→

Fig. 5. *Nymphon draconis,* new species, holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Chela, with enlargement of four teeth; D, Terminal leg segments, enlarged; E, Femur, showing cement gland and tubes; F, Oviger with egg attached; G, Strigilis segments, enlarged, with proximal and distal denticulate spines further enlarged. Paratype female: H, Trunk anterior, dorsal view.


A
C
H
D
B
F
G
E

eters in length. Terminal segment slightly curved.

Oviger fifth segment longest, swollen distally, without apophysis, fourth segment about 0.6 length of fifth. Fourth armed with few distal setae, 2 longer than segment diameter. Fifth armed with many setae increasing in numbers and length distally. Sixth segment with many long setae mostly endal, with greater numbers distally. Strigilis segments increasingly shorter with terminal segment shortest, armed with 2 to many long ectal setae, some twice as long as segment diameter, and endal denticulate spines in the formula 10:10:10:7, with terminal claw only slightly shorter than tenth segment. Claw with few tiny distal setules, without teeth. Denticulate spines with pair of wider lateral serrations proximally and many smaller distal serrations, distal spines of each segment longer than proximal spines.

Legs moderately slender, with few dorsal setae, more ventral setae, second tibiae 0.3 longer than first tibiae, femorae slightly shorter than first tibiae. Femorae with 10–11 conspicuous ventral cement gland tubes, each slender, less than half femoral diameter in length, placed in row along 0.7 of femoral length. Each major segment with 3 long distal setae. Tarsus cylindrical, distally inflated, about half propodal length, armed with 4–5 long ectal setae and many endal setae along with 2 slender spines. Propodus slender, very slightly curved, armed with 7–8 slender sole spines alternating with 2–3 sole setae between spines, without heel or heel spines, but with row of short lateral setae and several long dorsal and distal setae, the longest about 3 times segment diameter. Claw very reduced, broad, very curved, without endal setules. Auxiliaries about 0.3 longer than main claw, well curved distally, armed with few tiny endal setules proximally.

Female slightly larger in most measurements than male, neck equal in length to male's. Chelae not inflated, palm a curved cylinder, fingers slightly longer than those of male and armed with 12–13 unevenly bifurcate teeth. Oviger fourth and fifth segments shorter, fifth not clubbed distally, none of the segments with the long setae of the male oviger, but rather few short setae.

Measurements of holotype (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 1.23; trunk width (across 2nd lateral processes), 0.55; proboscis length, 0.56; abdomen length, 0.15; third leg, coxa 1, 0.17; coxa 2, 0.49; coxa 3, 0.22; femur, 1.04; tibia 1, 1.4; tibia 2, 1.66; tarsus, 0.21; propodus, 0.4; claw, 0.07; auxiliaries, 0.11.

Distribution.—This species is known from its type locality, south of Lizard Head Peninsula on Lizard Island in 2 m, and from other Lizard Island localities in 1.5–2 m.

Etymology.—The species name (Latin: *draconis,* a dragon-like lizard) is a play on the name Lizard Island, its type locality.

Remarks.—This new species is the eleventh reported of the *N. aequidigitatus* group discussed recently by Child (1988b:67–68). It fits well in the key of the ten known species at couplet 8 with *N. megacheles* Child, and couplet 9 with *N. biformidens* Stock and *N. aequidigitatus* Haswell, the three species with which it is most closely allied. Members of the *aequidigitatus* group have, besides the diagnostic characters of the genus, another set of characters more or less in common which involve chelae teeth usually being bifurcate, a longer than usual terminal palp segment, often very inflated chelae in the males, an oviger claw lacking the usual endal teeth, and auxiliary claws often longer than the short main claw with any or all of these claws bearing endal setules or rugosities. Some members of the group may be without one or more of these characters.

This new species differs from *N. megacheles* in having a slightly longer trunk with the lateral processes wider apart as a consequence, somewhat shorter legs with more setae, and a much longer tarsus in relation to propodal length and a much shorter main claw. The tarsus of *N. megacheles* is extremely short and both it and the propodus have robust heel spines. The type of *N. megacheles* is listed as a female, but the large inflated chelae and long setose fifth oviger segment suggest that it is actually a male. As far as is known, only males have the very inflated chelae in this group while those of the female are the more typical semicylindrical shape. The strigilis terminal claw differs between these two species in that the new species claw has few endal setules while that of *N. megacheles* has an endal lamina. None of the species of this group have the conspicuous cement gland tubes of the new species.

There are many similarities between this new species and *N. biformidens,* including those of neck and trunk habitus, leg segment length ratios, tarsus and propodus relative lengths, main and auxiliary claw lengths, and palp and chelifore similarities. The differences are in a shorter ocular tubercle lacking the lateral "horns" of *N. draconis,* the slender strigilis claw and shorter strigilis segments (those of a female specimen were compared with Stock's species figures which are also of a female), the very different chelae teeth which are all bifurcate in the new species while not all are bifurcate in *N. biformidens,* and the very different oviger denticulate spines which, in the new species, are more like those of the genus *Callipallene* in having many tiny distal serrations. The denticulate spines of Stock's species have 7–8 larger lateral serrations per side.

The new species has fewer characters in common with Haswell's *N. aequidigitatus.* It has longer chelae fingers in relation to palm length and the fingers bear many more teeth. It also has slightly longer leg segments with far fewer setae, particularly the longer setae, a third palp segment longer than the terminal segment, again also lacking the long setae of the new species, and a very different oviger which lacks most of the long setae present on the oviger of the new species.

Males of several of the *aequidigitatus* group are unknown, but where they are known, none display the conspicuous femoral cement gland tubes of this new species.

Family Phoxichilidiidae Sars
Genus *Anoplodactylus* Wilson
Anoplodatylus batangensis (Helfer)

Pycnosoma batangense Helfer, 1938:174–176, fig. 6a–c.

Anoplodactylus batangensis.—Stock, 1968: 54 [early literature].—Child, 1988a:14 [later literature].

Material examined.—Lizard Island: between Palfrey and South Islands, dead coral rubble with algal turf in 3 m, sta. K-L11, 30 May 1980 (1 ♂ with eggs, 1 ♀); S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (3 ♂, 1 ♀); SW of Lizard Head, rubble zone in 1.5 m, sta. JDT/LIZ-17, 1 Feb 1989 (1 ♀).

Distribution.—This species has a pantropical distribution in littoral and shallow depths. The above records mark the first time it has been taken in Australian waters.

Anoplodacatylus brucei, new species
Fig. 6

Material examined.—Heron Island: rubble from 6.2 m, sta. HI/26/5 coll. A. J. Bruce, 28 Apr 1978 (1 ♂, holotype).

Description.—Size moderately small, leg span 14.6 mm. Trunk lightly segmented, first segmentation line fully encircling trunk, second lighter, difficult to discern laterally, third only a hint, not encircling trunk. Anterior pair of lateral processes longest, each succeeding posterior pair shorter to last pair which are wider than long. Lateral processes separated by their maximum diameters or slightly less, armed with short dorso- and laterodistal setae numbering 4 on anterior pair, 3 on middle pairs, and 1 on posterior pair. Neck fairly short, flanked by lateral expansions or "wings" bearing rudimentary

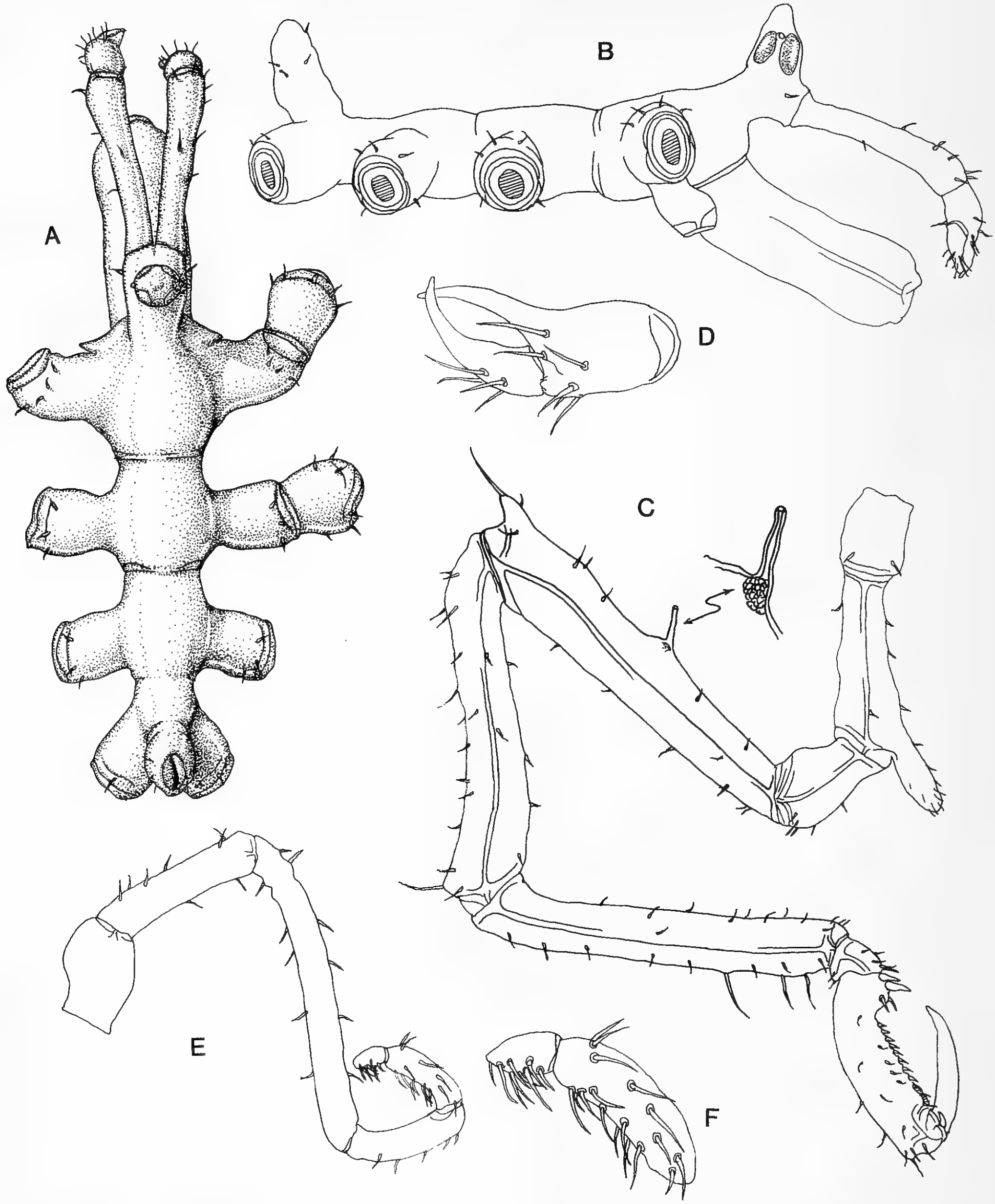


Fig. 6. *Anoplodactylus brucei,* new species, holotype male: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg, with cement gland and tube, enlarged; D, Chela; E, Oviger; F, Terminal two strigilis segments, enlarged.

palp buds which point laterally rather than anteriorly. Neck armed with single seta per side. Ocular tubercle moderately large with broad base occupying most of neck dorsally, little taller than wide, with broad rounded apical cone. Eyes large, anterior pair slightly larger than posterior pair, darkly pigmented, occupying most of ocular tubercle at its midpoint. Abdomen rather short, erect, swollen from constricted base, tip tapering, armed with 6–7 short lateral and dorsal setae.

Proboscis a cylinder curving anteriorly, slightly swollen distally, lips rounded.

Chelifores moderately short, scape not as long as proboscis, with slight distal inflation, armed with few dorsodistal and lateral setae. Chelae long, slender, palm a cylinder twice as long as its diameter, armed with few setae encircling finger bases. Movable finger longer than immovable finger, well curved, overlapping immovable finger at tip, armed with 4 ectal setae longer than finger diameter. Immovable finger not as curved, about equal in length to palm. Fingers without teeth.

Ovigers moderately slender, rather setose. Third segment longest, almost twice length of second segment, with proximal constriction, both armed with few short lateral setae. Fourth segment with several short ectal setae, fifth and sixth equal in combined length to fourth, fifth with many recurved setae, sixth with pad of 8–9 similar setae on one side only, segment about 0.3 as long as fifth segment.

Legs lightly setose, moderately long. Second coxae of third and fourth pair with long ventrodistal sexual tubercle equal in length to segment diameter, armed with many short setae. Femur the longest segment, with short dorsodistal tubercle half as long as segment diameter, armed with seta as long as segment diameter. Cement gland a long tube slightly over half femoral diameter, arising from low bulge at midpoint of segment. Tibiae subequal in length, with short dorsal, lateral, and ventral setae and single longer dorsodistal seta. Tarsus very short, subtriangular, with several short ventral setae. Propodus robust, moderately long, with well marked heel bearing 2 broad spines, the distal one larger than proximal spine, 3 distal stout setae, and 9–10 short sole spines with very short lamina at claw base. Claw stout, curved at tip, 0.6 as long as propodus, with tiny curved auxiliaries at base.

Female of the species unknown.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 1.87; trunk width (across 1st lateral processes), 1.06; proboscis length, 0.89; abdomen length, 0.35; third leg, coxa 1, 0.29; coxa 2, 0.83; coxa 3, 0.4; femur, 1.39; tibia 1, 1.3; tibia 2, 1.31; tarsus, 0.16; propodus, 0.66; claw, 0.46.

Distribution.—The new species is known only from Heron Island, its type locality, in 6.2 m.

Etymology.—I take pleasure in naming this species for Alexander J. (Sandy) Bruce, sometime collecting partner, expedition cabin mate, collector of this specimen, prolific author and systematist of pontoniid shrimp of the world, and Director of the Natural Sciences section of the Northern Territories Museum of Arts and Sciences, Darwin, Australia.

Remarks.—This new species has little to differentiate it from many others in this genus and there are several species quite similar to this one among the *Anoplodactylus* legions. Similar species are *A. digitatus* (Böhm) and its cousin *A. paradigitatus* Child, *A. erectus* Cole, *A. californicus* Hall, and *A. allotrius* Child. All have some characters agreeing with those of the new species. Most of the similarities are found in the legs as all share a long sexual tubercle on the second coxae of the posterior legs, a single cement gland tube, sometimes a dorsodistal tubercle on the femorae, and other similarities of the propodus.

The legs of *A. erectus* are almost exactly like those of the new species except that Cole's species does not have the small dorsodistal tubercle on the femur. One of Cole's paratype specimens was examined for comparison and this specimen has small slender dorsodistal lateral process tubercles which are lacking in the new species. Many specimens of *A. erectus* from Panama do not have these tubercles or else have low bumps in their place, so this character is inconsistent and not a good diagnostic feature. The lateral processes of *A. erectus* are notably longer than those of the new species, as is the third oviger segment and the ocular tubercle. The laterally projecting palp buds of the new species are apparently unique as other species with this character have the buds pointing toward the anterior of the specimen.

Both *A. digitatus* and *A. paradigitatus* have legs with very similar characters to those of *A. brucei,* except that the second coxae sexual tubercles are not as long as those of the new species, the lateral processes are longer in the two species, and the proboscis is of a very different shape with females of the two species. Females of these species have small alar processes on the proximoventral surfaces of their proboscides. Unfortunately, a female of the new species is not available for comparison. Neither of the other species have palp buds suggesting any similarity to those of *A. brucei.*

Hall's species (with the recently synonymized *A. portus* Calman) also has very similar legs, trunk habitus, chelae, and ocular tubercle, but the chelifore scapes are much shorter, the lateral processes are much closer together, the oviger terminal segment is much shorter and has quite different setation, and the femoral cement gland tube is a truncate cone rather than a slender tube as in *A. brucei.*

The new species has even less similarity to *A. allotrius,* but has legs which agree in most characters. The sexual tubercle is much shorter than in the new species and the lateral processes are closer together, the chelae have longer fingers with several teeth on the movable finger, the scapes are shorter, there are low lateral process tubercles, and the oviger terminal segments (fifth and sixth) are shorter and with fewer setae than the same segments of the new species.

Although *A. brucei* has no outstanding character to set it off from all others, I believe that the shades of difference in the several characters discussed are sufficient to separate this species from all others known in the genus.

Anoplodactylus chamorrus Child

Anoplodacatylus chamorrus Child, 1983: 705–707, fig. 3; 1988a:16.

Material examined.—Lizard Island: between Palfrey and South Islands, dead coral rubble with algal turf in 3 m, sta. K-L11, 30 May 1980 (1 ♂ with eggs, 1 ♂, 2 ♀); same locality, coral rubble with algal turf on reef crest in 0.3 m, sta. K-L12, 31 May 1980 (1 ♂ with eggs, 3 ♀); S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂).

Distribution.—This species was recently described from specimens taken in Guam, and it has more recently been taken in several localities in the southern Philippines. These records greatly extend its range to the south but add nothing to the known depth range.

Remarks.—The lateral processes are closely crowded in this small compact species and there are few other such compact species known in the Pacific. Such compact species of this genus were previously grouped under the genus *Halosoma,* now synonymized under *Anoplodactylus.* The only Australian species known with this compact character is *A. haswelli* (Flynn). The Guamian species differs from Flynn's by having broad lateral "wings" between the neck and first lateral processes, small lateral process dorsodistal tubercles, a conspicuous cement gland tube on the femorae, and several other smaller differences.

The species differs from other more northerly distributed compact species such as *A. crassus* Nakamura & Child, *A. viridintestinalis* (Cole), and perhaps *A. monotrema* Stock, in having the lateral neck wings mentioned above. Some compact species have conspicuous oviger bulges of the male in this location, but few have these broad anterior wings with tiny palp vestiges along their first lateral process margins.

Anoplodactylus glandulifer Stock

Anoplodactylus glandulifer Stock, 1954:80–84, fig. 36.—Child, 1982:273–274 [literature]; 1988b:58–59; 1988c:813.

Material examined.—Lizard Island: North Point, rubble at bottom of cliff, 12 m, sta. JDT/LIZ-13, 28 Jan 1989 (1 ♀); Lizard Head, small rubble in sand, 2 m, sta. JDT/LIZ-19, 2 Feb 1989 (1 ♂, 1 questionable larva).

Distribution.—This species has been taken in many localities from the Red Sea and Indian Ocean to as far east as the Samoa Islands. These records mark its first capture on the Great Barrier Reef. It is known from 0–12 m.

Remarks.—The conspicuous cement gland cups number from 2 to 4 per femur, and serve as a good recognition character in males in a genus where the cement gland is much more often served by a single orifice per femur. Females, of course, are difficult to distinguish as a particular species from other similar species without accompanying males, but both sexes in this species have very long propodal lamina which sets them off from those many species with shorter lamina. The female from station 13 is only provisionally placed in this species due to lack of an accompanying male. This female propodus agrees well with *A. glandulifer* as does the ocular tubercle and lateral process placement, and is little different from other females examined of this species.

Anoplodactylus longiceps Stock

Anoplodactylus longicollis Williams, 1941: 36–38, figs. 2–5 (preoccupied).

Anoplodactylus longiceps Stock, 1951:16 [footnote]; 1954:83 [text]; 1956:97–98, fig. 14c, d.—Clark, 1963:56 [key].—Child, 1975:20, fig. 9f.

Material examined.—Lizard Island: North Point, rubble at bottom of cliff in 12 m, sta. JDT/LIZ-13, 28 Jan 1989 (1 damaged ♀); S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂).

Distribution.—This species is known from the east and west coasts of Australia in tropical to temperate waters, and from the Kei Islands in eastern Indonesia in depths of 28–134 m. These records establish the species at Lizard Island on the Barrier Reef and in much shallower water at 2 and 12 m.

Remarks.—This very long slender species is easily recognized with its very widely separated lateral processes, tall ocular tubercle with a long slender apical cone, slim legs with a long femoral dorsodistal tubercle and two low cement gland cups, and its moderately short proboscis.

This species is reminiscent of another very elongate species, *A. attenuatus* Child, from the Philippines. The Philippine species has lateral processes spaced even wider than in this species and also lacks the femoral dorsodistal tubercle, has a shorter oviger, has a crenulate major heel spine on the propodus, lacks the usual tiny auxiliary claws, and has a very different ocular tubercle which is shorter than its width. Both species, though, have a widely spaced pair of cement gland cups on each femur. They are probably quite closely related, having possibly originated from a single parent stock.

Anoplodactylus species indeterminate

Material examined.—Lizard Island: off Casuarina Beach, coral with *Halimeda* clumps and red algae in 2 m, sta. K-L1, 27 May 1980 (1 larva); between Palfrey and South Islands, dead coral rubble with algal turf in 3 m, sta. K-L11, 30 May 1980 (1 larva); point between Anchor Bay and Watson's Bay, coral rubble in 2 m, sta. JDT/LIZ-5, 24 Jan 1989 (1 ♀); Lizard Head, small rubble in sand, 2 m, sta. JDT/LIZ-19, 2 Feb 1989 (1 juv).

Remarks.—The juvenile and larvae are too immature for determination and the female is unlike other species in these collec-

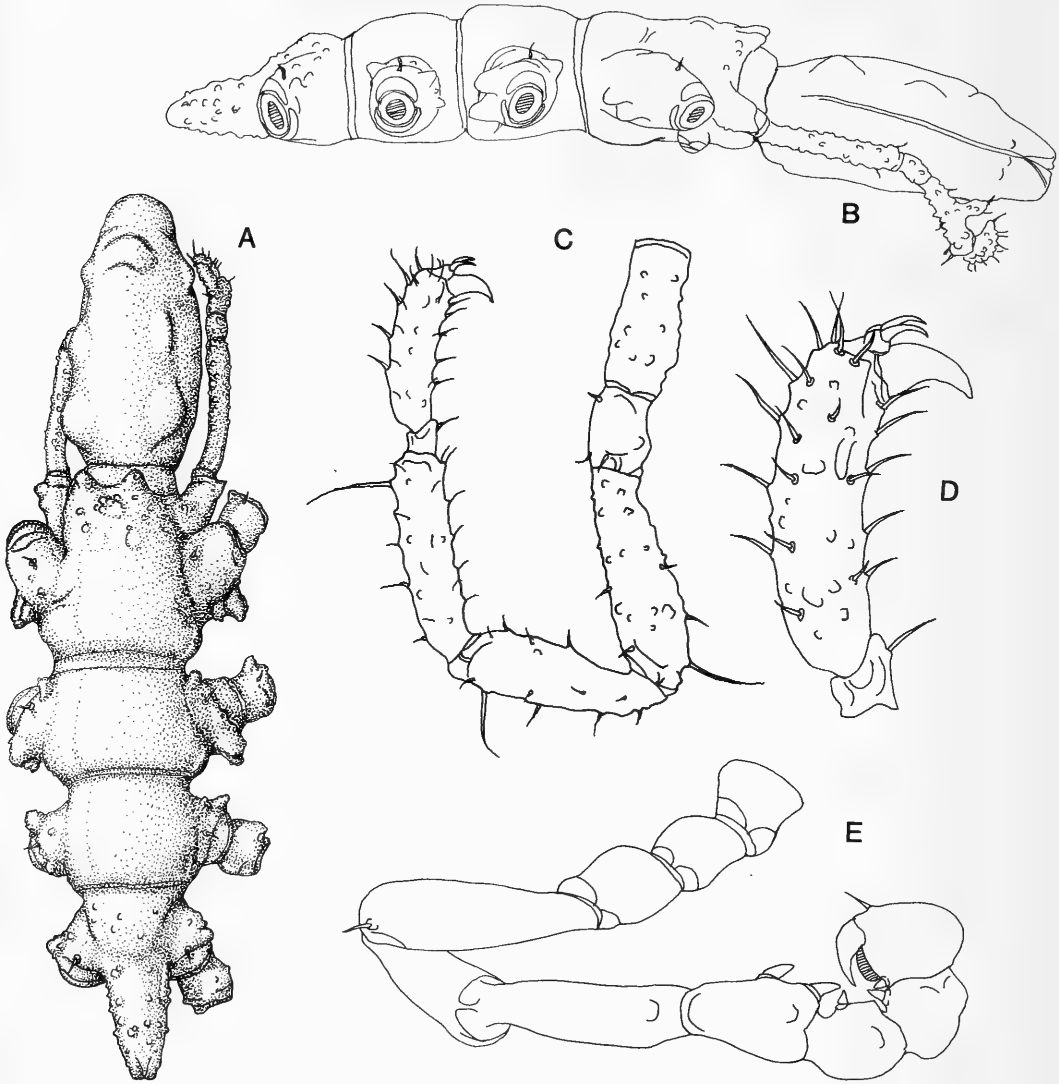


Fig. 7. *Rhynchothorax vallatus,* new species, holotype female: A, Trunk, dorsal view; B, Trunk, lateral view; C, First leg; D, First leg terminal segments, enlarged; E, Oviger, greatly enlarged.

tions and shows little similarity to published figures of other species from Australia.

Genus *Endeis* Philippi, 1843
Endeis biserata Stock

Endeis biserata Stock, 1968:57–60, fig. 21; 1970:1; 1974:17; 1979:28–30, fig. 9.—Child, 1988a:20.

Phoxichilus meridionalis Loman (non Böhm, 1879), 1908:78–79.

Material examined.—Lizard Island: Watson's Bay, SW border, reef and sand flat rubble in 1–7 m, sta. JDT/LIZ-7, 25 Jan 1989 (1 ♀, 1 juv); S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♂).

Distribution.—This is a wide-ranging species having been taken from Brazil, the Red Sea, Indian Ocean, Indonesia, Hawaii, and the Philippines in 0–37 m. These records place it to the south of its nearest known capture in Indonesia, on the northern Great Barrier Reef and well within its known depth range.

Remarks.—The male from station 14 lacks the long dorsodistal tubercles of the femorae, but has a moderately long and very robust spine in its place. This femoral spine is flanked by two shorter broad spines. Most of the small spines of the trunk and legs are short but very broad, a character not found or at least not remarked on by Stock in his description. The male is otherwise very like the type and other specimens figured in Stock's fig. 21 (1968:57). The leg length ratios, the propodal configuration, trunk habitus, oviger, and the leg lateral spines are all very like those shown in the figures. The female has the dorsodistal femoral tubercles, but those of the above specimen are slightly longer than that shown in Stock's fig. 21e.

Family Rhynchothoracidae Thompson
Genus *Rhynchothorax* Costa
Rhynchothorax vallatus, new species
Fig. 7

Material examined.—Lizard Island: S of Lizard Head Peninsula, rubble in 2 m, sta. JDT/LIZ-14, 29 Jan 1989 (1 ♀, holotype).

Description.—Size very tiny, leg span only 3.2 mm across second lateral processes. Trunk fully segmented, covered with tiny granular papillae as are appendages, with greater numbers of papillae on extremities. Trunk moderately slender, without other adornment. Lateral processes very short, not as long as their diameters, widely separated, tubercular, armed with short dorsomedian seta each. First lateral processes with pair of posterior tubercles as broad as their length, second processes with similar pair of posterior tubercles and smaller anterior tubercle at lateral process bases. Third lateral processes with small anterior tubercle and smaller posterior tubercle, fourth with only small anterior tubercle. Ocular tubercle and eyes lacking, with pair of broad, low, anterior-pointing tubercles in their place. Neck moderately narrow, flanked by short cylindrical tubercles as bases for palps, each bearing low ectal tubercle. Abdomen short, with broad base, tapering to small rounded anus, extending to less than half second coxal lengths on fourth legs.

Proboscis typical for genus, with 2 paired dorsolateral swellings, constricted at base and distally at lips, carried horizontally, without labial fringe or lamina on antimeres.

Palps 4-segmented, with prominent papillae. First segment cylindrical, as long as combined length of terminal 3 segments, armed with few distal setae. Second segment short, cylindrical, not as long as twice its diameter. Third segment slightly more than half length of first, armed with few short setae and dorsal tubercle slightly longer than segment diameter, placed slightly distal to dorsal midpoint of segment. Fourth segment short, little longer than second, recurved dorsally to height of third segment tubercle, armed with few short ectal setae.

Oviger also typical, tiny, fourth and sixth segments subequal. Seventh segment swollen distally, armed with 2 short broad endal spines, eighth and ninth segments shorter, subequal in length, armed with single small endal spine each. Tenth segment broader than long, armed with ectal seta, tiny endal basal spine, curved endal lamina, and broad curved claw which closes onto lamina.

Legs of approximately equal size except for second coxae on fourth leg pair which are 0.3 shorter than coxae 2 of other legs. Second coxae of anterior 3 pairs twice length of first coxae, femorae the longest segments with first tibiae longer than second. Three major segments armed with dorsodistal setae longer than segment diameters and several short setae increasing in numbers on distal leg segments. Tarsus very short, with single sole seta. Propodus short, inflated, slightly curved, armed with 4–5 sole setae, several short lateral setae, and several dorsal setae almost as long as propodal diameter. Claw short, broad, well curved, auxiliaries present, short, slender, less than half main claw length.

Male of species unknown.

Measurements (in mm).—Trunk length (proboscis insertion to tip 4th lateral processes), 0.91; trunk width (across 1st lateral processes), 0.44; proboscis length, 0.57; abdomen length, 0.19; first leg, coxa 1, 0.1; coxa 2, 0.16; coxa 3, 0.09; femur, 0.26; tibia 1, 0.25; tibia 2, 0.23; tarsus, 0.04; propodus, 0.18; claw, 0.05.

Distribution.—This species is known from its type locality only, south of Lizard Head Peninsula, Lizard Island, in 2 m.

Etymology.—The name proposed for this species is a play on the Great Barrier Reef (Latin: surrounded by a wall or rampart) which surrounds Lizard Island with a rampart of coral.

Remarks.—This new species has a few characters close to the juvenile type of *R. malaccensis* Stock (1968:20–22, fig. 6), a species known from the Straits of Malacca, Indonesia. The similarities are mostly found in the proboscis and trunk. The lateral processes are similar, but in Stock's species they are placed much closer together. The proboscides have the dorsolateral bulges in both species and are of similar lengths.

The new species is closest to *R. philopsammum* Hedgpeth (1951:111–115, fig. 3) from the west coast of North America. Here again, the lateral processes of Hedgpeth's species are similar to the new species, including the tubercles size and placement, but the lateral processes themselves are placed very close together rather than well separated as in the new species. There are similarities in the appendages of both species, but the third palp segment is shorter in the new species than in Hedgpeth's species. Also in the palp, the first and third segments (second and fourth segments according to his text, mistaking the palp bases as segments instead of lateral extensions of the trunk anterior) are subequal in Hedgpeth's species while this does not hold true for *R. vallatus*. The tubercle of the third palp segment is much more distally placed in *R. philopsammum* than in the new species.

The main and auxiliary claws differ in lengths between the two species, being much shorter in *R. vallatus,* and the femur is longer than the tibiae in the new species, but femur and first tibia are equal in length in Hedgpeth's species. Finally, the first coxae of *R. philopsammum* have several small dorsodistal tubercles, particularly on the second and third pairs, while the first coxae of this new species have a single low tubercle only on the anterior surface of the first three leg pairs.

The fact that these two species are separated in their distribution by the breadth of the Pacific Ocean is not in itself a valid reason to separate these species, but this fact combined with the various subtle differences discussed above should serve to maintain the two as separate species.

Acknowledgments

I wish to thank the collectors; J. D. Thomas, B. F. Kensley, and J. Clark for their specimens from Lizard and Orpheus Islands, and A. J. (Sandy) Bruce and Niel Bruce, his son, for the Heron Island collections. Holotype specimens are deposited in the Australian Museum, Sydney, while other specimens are deposited in the National Museum of Natural History, Smithsonian Institution, under catalog numbers of the old U.S. National Museum.

Literature Cited

For the literature published prior to 1978, see the complete bibliography published by Fry & Stock 1978. A Pycnogonid Bibliography, *in* Sea Spiders (Pycnogonida).—Zoological Journal of the Linnean Society of London, 63(1+2):197–238.

Child, C. A. 1982. Pycnogonida of the Western Pacific Islands, I. The Marshall Islands.—Proceedings of the Biological Society of Washington 95:270–281, figs. 1–3.

———. 1983. Pycnogonida of the Western Pacific

Islands, II. Guam and the Palau Islands.—Proceedings of the Biological Society of Washington 96:698–714, figs. 1–5.

———. 1988a. Pycnogonida of the Western Pacific Islands, III. Recent Smithsonian–Philippine expeditions.—Smithsonian Contributions to Zoology 468:1–32, figs. 1–12.

———. 1988b. Pycnogonida from Aldabra Atoll.—Bulletin of the Biological Society of Washington 8:45–78, figs. 1–9.

———. 1988c. Pycnogonida of the Western Pacific Islands, V. A Collection by the *Kakuyo Maru* from Samoa.—Proceedings of the Biological Society of Washington 101:809–816, figs. 1–2.

Clark, W. C. 1977. The genus *Tanystylum* Miers, 1879 (Pycnogonida) in the southern oceans.—Journal of the Royal Society of New Zealand 7(3):313–338, figs. 1–67.

Hong, J.-S., I.-H. Kim. 1987. Korean pycnogonids chiefly based on the collections of the Korea Ocean Research and Development Institute.—The Korean Journal of Systematic Zoology 3(2): 137–164, figs. 1–17.

Nakamura, K., & C. A. Child. 1990. Pycnogonida of waters adjacent to Japan.—Smithsonian Contributions to Zoology (in press).

Stock, J. H. 1979. Pycnogonida from the mediolittoral and infralittoral zones in the tropical western Atlantic.—Studies on the Fauna of Curaçao and other Caribbean Islands 59(184):1–32, figs. 1–9.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 336–340

CANTHOCAMPTUS (*ELAPHOIDELLA*) *STRIBLINGI*, NEW SPECIES (COPEPODA: HARPACTICOIDA) FROM COSTA RICA

Janet W. Reid

Abstract.—The male of *Canthocamptus* s. l. (*Elaphoidella*) *striblingi*, a new species of harpacticoid copepod from the Monteverde Cloud Forest Preserve, Costa Rica, is distinguished within its subgenus by the biarticulate endopods of legs 1 and 4; the exopod of leg 5 and the endopod of leg 2 each having 4 setae; and the unmodified spines of the exopod of leg 4. The female is unknown.

In a collection of aquatic invertebrates from bromeliads in Costa Rica made by Dr. James B. Stribling, there occurred a single male specimen of a previously undescribed species of harpacticoid copepod belonging to the large cosmopolitan genus *Canthocamptus* Westwood, 1836, subgenus *Elaphoidella* Chappuis, 1928.

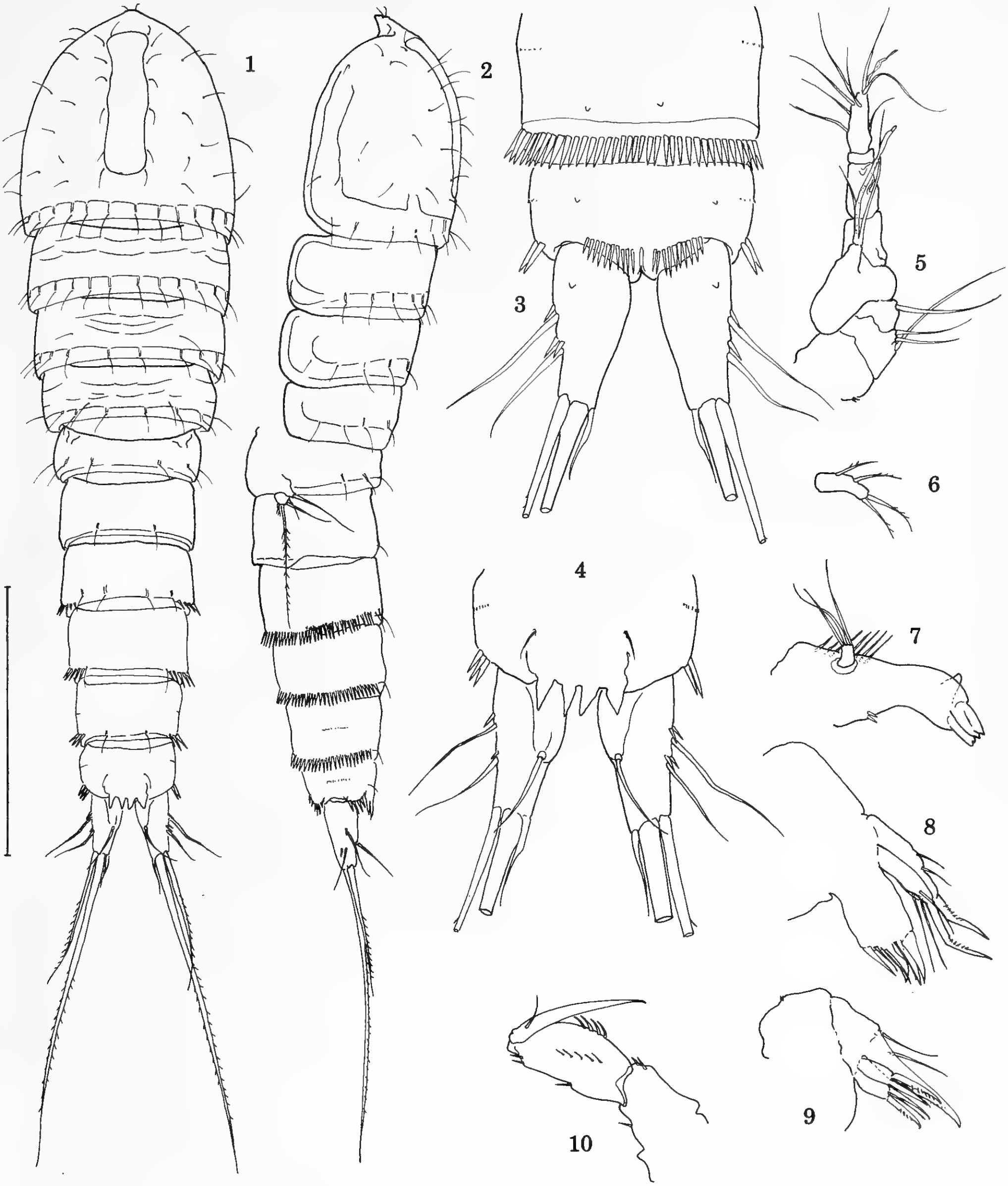
Order Harpacticoida Sars, 1903
Family Canthocamptidae Sars, 1906
Genus *Canthocamptus* Westwood, 1836
Subgenus *Elaphoidella* Chappuis, 1928
Canthocamptus (*Elaphoidella*) *striblingi*,
new species
Figs. 1–15

Type material.—1 ♂, from water contained in narrow-leaved epiphytic bromeliad in Monteverde Cloud Forest Preserve, Costa Rica, altitude about 750 m, 27 Aug 1988, dissected on one slide (USNM 243304), deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Male.—Body (Figs. 1–4) cylindrical; length, excluding caudal setae, in lactic acid 0.64 mm. Cephalosome with oblong nuchal organ. Posterior hyaline frills of all somites smooth; urosomites 3–5 each with single row of uniform, slender spinules on lateral and ventral posterior margins, each spinule row continuous ventrally. Anal somite with row of 4 spinules on each side and ventral row of 10 spinules above each caudal ramus; anal operculum with 4 large, somewhat irregular teeth. Caudal ramus 2 times longer than broad, with little-developed dorsal ridge ending in dorsal seta inserted just anterior to insertion of posterior lateral seta; anterior lateral seta slightly longer than posterior lateral seta. Small innermost terminal seta of ramus about half length of ramus. Inner margin of ramus without ornament.

Rostrum (Fig. 2) projecting in lateral view, with rounded apex bearing 2 subapical rostral filaments. Antennule (Fig. 5) about half length of cephalosome, geniculate, with esthetascs on articles 4 and 8. Antenna (broken in dissection) with allobasis; uniarticulate exopod (Fig. 6) bearing 4 setae. Mandible (Fig. 7) with uniarticulate palp bearing 3 terminal setae. Maxillule (Fig. 8) with precoxal arthrite having 4 teeth and 3 setae; coxa with 1 stout seta bent at midlength and 1 slender seta; basis with 1 stout seta bent at midlength and 4 slender setae. Maxilla (Fig. 9) with 2 endites each with 3 terminal setae; basis with claw and 2 setae. Maxilliped (Fig. 10) prehensile; basis without seta; endopod with comb of 4 or 5 spinules on anterior and posterior surface, plus few spinules on dorsal surface.

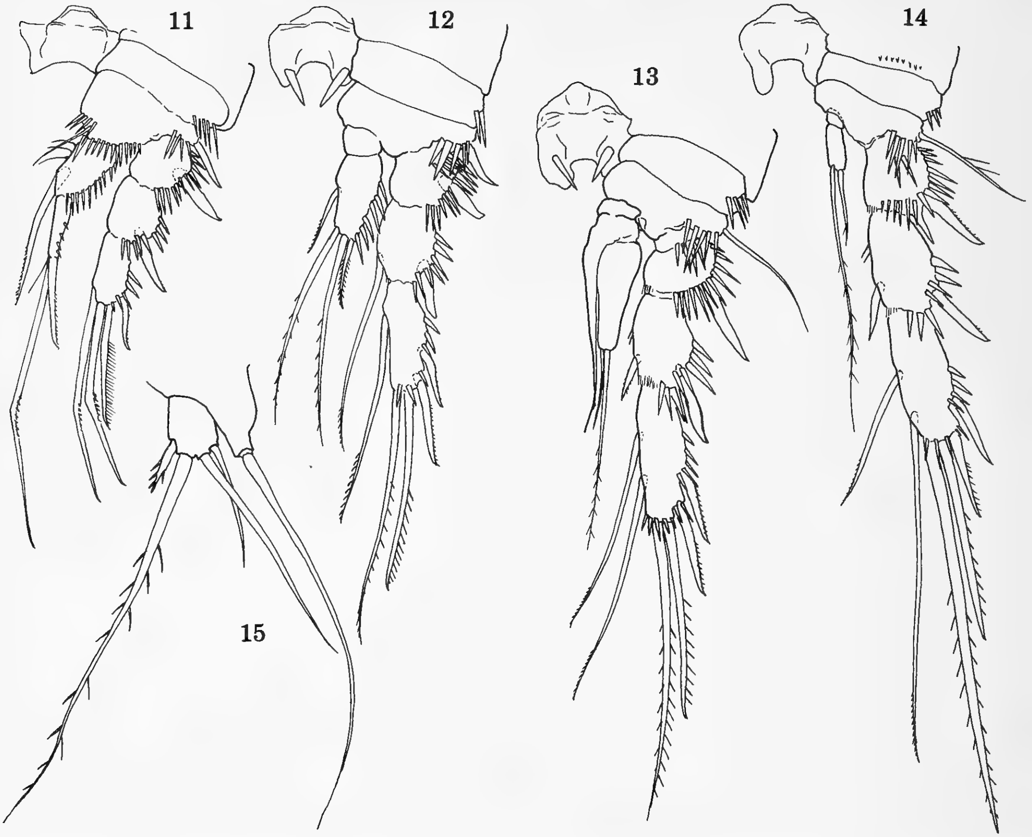
Swimming legs 1–4 (Figs. 11–14) each with exopod of 3 articles and endopod of 2 articles, except endopod of leg 3 consisting



Figs. 1–10. *Canthocamptus* (*Elaphoidella*) *striblingi*, new species, male: 1, Habitus, dorsal; 2, Habitus, lateral; 3, Posterior urosomites and caudal rami, ventral; 4, Anal somite and caudal rami, dorsal; 5, Antennule, some setae not drawn; 6, Exopod of antenna; 7, Mandible; 8, Maxillule; 9, Maxilla; 10, Maxilliped. Scale for Figs. 1 and 2, 200 μm; remaining figures not to same scale.

of 3 articles of which article 2 bears apophysis. Setation formula for major armament as follows:

Leg 1	basis 1-1	exopod 0-1; 0-1; 0,2,2 endopod 1-0; 1,2,0
Leg 2	basis 0-1	exopod 0-1; 1-1; 1,2,2 endopod 0-0; 2,2,0
Leg 3	basis 0-1	exopod 0-1; 1-1; 2,2,2 endopod 0-0; 1-0; 0,2,0
Leg 4	basis 0-1	exopod 0-1; 1-1; 2,2,2 endopod 0-0; 0,2,0



Figs. 11–15. *Canthocamptus* (*Elaphoidella*) *striblingi,* new species, male: 11, Leg 1; 12, Leg 2; 13, Leg 3; 14, Leg 4; 15, Leg 5. (Not to same scale.)

Leg 5 (Figs. 2, 15) with exopod bearing 4 setae; 2 innermost setae coarsely plumed, 2 outermost setae naked. Basipods of both fifth legs fused, lacking armament. Leg 6 (Fig. 2) represented only by simple, slightly elevated plate.

Female.—Unknown.

Etymology.—The new species is named in honor of its collector, Dr. James B. Stribling.

Remarks.—Hamond (1987 [1988]) returned 18 superspecific taxa within the family Canthocamptidae, including *Elaphoidella* Chappuis, to the status of subgenera of the genus *Canthocamptus* Westwood, pending eventual revision of the family. Approximately 140 species are presently assigned to the genus (now subgenus) *Elaphoidella* Chappuis, which was recently revised and split into four genera by Apostolov (1985). Two of Apostolov's proposed new genera correspond to Lang's (1948) *Elaphoidella* Group X, which included species having biarticulate endopods of leg 1; Apostolov's proposed *Elaphoidellopsis* is further distinguished primarily by having biarticulate endopods of leg 4. There are 18 previously known species and subspecies in this group; Apostolov's inclusion of *Elaphoidella sewelli* Chappuis, 1928 and its subspecies in *Elaphoidellopsis* is inexplicable, since these have leg 1 endopods of 3 articles and therefore fall in Apostolov's *Elaphoidella.*

The new Costa Rican species falls within *Elaphoidellopsis* Apostolov. However, Hamond (1987 [1988]) argued convincingly for retention of most canthocamptids within the broad category *Canthocamptus* until the morphology of most species, particularly type-species of the various superspecific taxa, can be described by contemporary standards. Apostolov (1985) partly redescribed *Canthocamptus elaphoides* Chappuis, 1923, type species of *Elaphoidella* Chappuis; unfortunately, *C. elaphoides,* according to Apostolov, is extremely polymorphic and the taxon may even represent a collective species! Apostolov resolved the problem of great variability in setation of swimming legs, and in other characters, of many species of *Elaphoidella* by proposing a simple scheme relying primarily on the number of articles of the swimming legs. However, he failed to present any argument as to why this arrangement might represent a more natural grouping than, for example, Lang's (1948) ten-group division. Apostolov's brief diagnoses of his proposed new genera contain mutual inconsistencies, omissions, and errors, and are seriously incomplete; for instance, his entire diagnosis of the male of *Elaphoidellopsis* consists of pointing out the "marked sexual dimorphism" in legs 3–5. It remains to be seen whether these proposed subgroups will be sustained after examination of the subgenus *Elaphoidella* by modern systematic methods. On the other hand, Apostolov has furnished a valuable service in providing a list of species of this very large group. His keys contain a number of errors, such as the placement of *E. sewelli,* mentioned above; and some apparent typographical mistakes. However, the keys are more or less mechanically useful in species discrimination, as I have employed one in the following discussion, without wishing to imply acceptance of these proposed groupings in a systematic sense.

In Apostolov's key to *Elaphoidellopsis, Canthocamptus striblingi* keys to *E.* (now *Canthocamptus*) *siolii* (Kiefer, 1967); but *C. striblingi* is easily distinguished by having a longer caudal ramus without spinules on the inner margin; the ramus of *C. siolii* is only slightly longer than broad and has a group of spinules on the distal part of the inner margin. Kiefer also reported only 3 setae on leg 2 endopod 2, but his figure (Kiefer 1967: fig. 25) seems to show a socket on the outer distal corner of that article. The 3 large opercular teeth of *C. siolii* also may not be a reliable distinguishing character, since the number of opercular teeth may vary within a species, and Kiefer described *C. siolii* from only two male specimens. Males of the three other neotropical species in this group all have 2 modified spines on leg 4 exopod 3, only 3 setae on leg 5 exopod, and differ otherwise in setation of swimming legs. These are *C. crenobia* (Petkovski, 1973), *C. einslei* (Petkovski, 1973), and *C. subcrenobia* (Petkovski, 1980), all from Cuba. *C. siolii* is known only from the upper Rio Negro, an affluent of the Amazon River, Brazil.

Acknowledgments

The University of Wisconsin (Madison) is thanked for funding Dr. J. B. Stribling's field work in Costa Rica. A Smithsonian Senior Postdoctoral Fellowship supported the preparation of this article. Several anonymous reviewers made valuable suggestions for improvement of the manuscript.

Literature Cited

Apostolov, A. 1985. Étude sur quelques copépodes harpacticoides du genre *Elaphoidella* Chappuis, 1929 de Bulgarie avec une révision du genre.—Acta Musei Macedonici Scientiarum Naturalium 17(7/145):133–167.

Chappuis, P. A. 1928. Zur Kenntnis der Mikrofauna von Britisch Indien. III. Copepoda Harpacticoida.—Records of the Indian Museum 30(4): 375–385.

Hamond, R. 1987(1988). Non-marine harpacticoid copepods of Australia. I. Canthocamptidae of the genus *Canthocamptus* Westwood s. lat. and *Fibulacamptus,* gen. nov., and including the description of a related new species of *Cantho-*

camptus from New Caledonia.—Invertebrate Taxonomy 1(8):1023–1247.

Kiefer, F. 1967. Neue Copepoda Harpacticoida aus dem Amazonasgebiet.—Crustaceana 13(1):114–122.

Lang, K. 1948. Monographie der Harpacticiden. Nordiska Bokhandeln, Stockholm, 1682 pp.

Petkovski, T. K. 1973. Subterrane Süsswasser-Harpacticoida von Kuba (Vorläufige Mitteilung).—Résultats des Expéditions Biospéologiques Cubano-Roumaines à Cuba 1:125–141.

———. 1980. Fünf neue *Elaphoidella*-Arten (Copepoda, Harpacticoida) aus den subterranen Gewässern von Kuba.—Acta Musei Macedonici Scientiarum Naturalium 16(2/135):33–70.

Department of Invertebrate Zoology, NHB-163, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 341–349

TACHIDIUS INCISIPES KLIE AND OTHER HARPACTICOIDS FROM NORTHWESTERN CANADA (CRUSTACEA: COPEPODA)

Edward B. Reed

Abstract.—Twelve species of harpacticoid copepods are reported from the shores of fresh and brackish lakes and ponds in northern Northwest Territories and Yukon Territory. *Attheyella ussuriensis* Rylov is a new record for North America and *Tachidius incisipes* Klie a new record for Canada.

The Southern Party of the Canadian Arctic Expedition 1913–1918 collected marine and freshwater Copepoda from localities between Vancouver Island, B.C. and Coronation Gulf, N.W.T. (Johansen 1922). Marsh (1920) and Johansen (1922) commented on the importance of Canadian Arctic Expedition collections as the first from a region that was little known in regard to micro-crustacean fauna. In their reports neither Johansen nor Marsh mentioned harpacticoid copepods, although both discussed species of calanoid and cyclopoid copepods. Willey (1920) recorded eight known species of harpacticoids and described an additional three as new to science; most were marine species but at least one was found in fresh-to-brackish water. Records for harpacticoids have lagged behind those for calanoids and cyclopoids although several investigations have added to the knowledge of freshwater copepods in the northern reaches of Yukon and Northwest Territories since the Canadian Arctic Expedition. The purpose of this paper is to furnish specific site records for several species of harpacticoids; two of which may be the first for Canadian waters.

Participation in an excursion to Yellowknife and Inuvik, N.W.T. following the XIXth Congress of the International Association of Limnology (SIL) in 1974, afforded me the opportunity to collect along margins of lakes and ponds.

Specimens were examined and dissected in glycerin or lactic acid (Humes & Gooding 1964). Insofar as possible, examination and drawings were made without cover slips.

Species were determined primarily by the key of Wilson & Yeatman (1959). Preliminary identifications were confirmed by comparing specimens with the descriptions found in Gurney (1932), Lang (1948), Borutzky (1952), and Dussart (1967).

Waters Sampled

Because the harpacticoid collections were opportunistic grab samples, there are few data on the waters sampled. Frame and Grace Lakes (Table 1) occupy rock basins with emergent vegetation in protected areas. Grace Lake is about 63 ha in surface and 9 m in mean depth (Brunskill, pers. comm. 1974). The Fort Franklin sample came from a pond about 0.1 ha in area and 20 cm deep in a muskeg at the edge of the village. This pond and the roadside ditch on the Hay River road at Yellowknife contained brown water and much vegetation.

The Tuktoyaktuk ponds are beach ponds in the sense of Johansen (1922), that is, they are only a little above sea level and situated quite close to the seashore but are not directly connected to the sea. These ponds undoubtedly receive Arctic Ocean water during onshore storm surge, as indicated by the presence of stranded driftwood. Meijer-

Table 1. Species of harpacticoid copepods collected from Northwest and Yukon Territories, 1974.

Locality	Coordinates	*Tachidius incisipes* Klie, 1913	*T. discipes* Giesbrecht, 1882	*Nitocra spinipes* Boeck, 1864	*Mesochra rapiens* (Schmeil, 1894)	*Attheyella nordenskioldii* (Lilljeborg, 1902)	*A. ussuriensis* Rylov, 1932	*Moraria duthiei* T. & A. Scott, 1896	*M. mrazeki* T. Scott, 1902	*Bryocamptus hutchinsoni* Kiefer, 1929	*B. vejdovskyi* (Mrazeki, 1893)	*Onychocamptus mohammed* (Blanchard & Richard, 1891)	*Halectinosoma* sp., *Pseudobradya* sp.?
Yellowknife, N.W.T.	62°30′N, 115°17′W												
Frame Lake				X					X				
Grace Lake						X							
Roadside ditch on Hay River road ca. 17 km northwest of Yellowknife										X			
Fort Franklin, N.W.T.	65°12′N, 123°25′W												
Small pond near village						X					X		
Inuvik, N.W.T.	68°21′N, 133°44′W												
Small pond near Campbell Creek on Dempster Highway							X						
Tuktoyaktuk	69°27′N, 133°2′W												
a. Beach pond		X	X		X							X	X
b. Beach pond				X								X	
c. Beach pond				X								X	
Shingle Point, Y.T.	68°56′N, 137°15′W												
Pond								X			X		

Table 2. Comparison of three species of *Tachidius.*

	T. discipes	*T. incisipes*	*T. spitzbergensis*
♀♀	antennule 7 articles	9 articles	7 articles
	antenna exp 2 setae	at least 5 setae	3 setae
	seg. 3, P1-4 5,6,6,5 spines & setae	5,6,5,5	5,6,5,5
	seg. 3 enp P-4 5,5,5,5	6,6,6,6	5,5,5,5
	P5 9 setae and spines	9	8
	anal operculum 12 or more spinules	several small spinules	smooth
		genital field with prominent U-shaped canal	
♂♂		spinules lacking	spinules present
	spinules on chitinous ridge on antennule article 1	at least 5 setae	3 ?
	antenna exp 2 setae	P2 not modified	P2 modified
	P2 enp article 2 modified; article 3 with apical setae	less than 9, usually 7	6
	P5 5 to 8 usually 7 setae and spines	spinules	spinules
	anal operculum with spinules		

ing (1975) found electrical conductivity of 4776 and 2370 μSiemens in water from two Tuktoyaktuk ponds. Meijering and I likely sampled different ponds, although both sampled the same day.

Shingle Point is also on the coast of the Arctic Ocean; however, the pond sampled here lies on top of a low bluff above the beach and probably does not receive storm surge seawater.

Species Identified

Nine of 16 samples contained 12 species of harpacticoid copepods (Table 1). In the following accounts, N.W.T. and Y.T. forms that fell within descriptions provided by the above manuals are listed without comment.

Tachidiidae

Several males and females plainly referable to the genus *Tachidius* were collected from Tuktoyaktuk beach ponds (Table 1). The females were clearly *T. incisipes* on the basis of antennule of 9 articles, setae and spine formula of P1–P4 and U-shaped canal in the genital segment (Table 2).

The presence of a modified P2 indicated that the males were not *incisipes.* The close similarities of males of *discipes* and *spitzbergensis* are evident from Table 2. Olofsson (1917) noted the morphological closeness of male *discipes* and *spitzbergensis* and distinguished between them on the number of setae and spines on P5. Given the variability in the armament of P5 in *discipes* (Lang 1948, Dussart 1967) this does not seem a reliable characteristic. Lang (1948) synonomized *spitzbergensis* with *discipes*; however Wilson and Yeatman (1959) retained *spitzbergensis* in their key, using setation of P5 to separate the males and absence of spinules on the anal operculum of *spitzbergensis* to separate females. On the basis of setation of P5, the Tuktoyaktuk males were assigned to *T. discipes.*

Tachidius incisipes Klie, 1913

Seven females ranged in length from 0.75 to 0.82 mm. Metasome slightly flattened, widest at second thoracic segment. Rostrum small, pointed. Nuchal organ and lateral discs oval and discs present on all thoracic segments (Fig. 1). Genital field with U-shaped canal leading from genital pore to seminal receptacle (Fig. 2). Anal operculum with many spinules on free margin, row of fine spinules extending from operculum base down each side. Caudal rami longer than broad (Fig. 3). Oblique row of spinules on dorsal and mesial surfaces, two dorsal setae set close together, outer caudal seta spine-like and about twice length of inner seta. Both medial setae jointed and having straight-sided basal sections which constrict abruptly, longer about 2.5 times the length of the shorter. Antennule of 9 segments (Fig. 4). Antenna of 4 segments, exopodite 2-segmented with a total of 5 setae (Fig. 5). Mandible with biramus palp, blade with one large blunt tooth and smaller teeth (Fig. 6). Outer surface with a process which Gurney (1932, fig. 403) depicted as a bump is clearly hook-like when seen in side view. Maxillule of two segments (Fig. 7) and maxilla of 3 endites, coxa-basis and an exopod, although segmentation not always distinct (Fig. 8). Maxilliped 3-segmented (Fig. 9), with a terminal claw.

Both rami of legs 1–4 of three articles, basopodites with prominent mounds densely fringed with long hairs, outer mound appearing to project between rami when legs are viewed anteriorly. P1 basipod spines large, article 3 of exopod with three spines and three setae, spines of exopod smooth (Fig. 10). P2 lateral spines of exopod articles 1 and 2, smooth; article 3, one marginal spine smooth and one toothed (Fig. 11), anterior face of endopod article 3 with two rows of spinules. P3 with prominent blade-like spinules on outer margin of exopodite segments and and article 2 of endopod, endopod article 3 with a total of six spines and setae (Fig. 12). P4 with rows of spinules on anterior face of all exopodite articles, endopod article 3 with a total of five spines and setae (Fig. 13). The numbers and arrangement of spines and setae agree with those given by Lang (1948:282). P5 a single plate with a total of eight spines and setae (Fig. 2).

Tachidius discipes Giesbrecht, 1882

The Tuktoyaktuk males were compatible with the specific characters as given by Oloffson (1917), Gurney (1932), Lang (1948), and Wilson & Yeatman (1959) in three regards: modified endopodite P2, antennule, and P5. The second segment of P2 endopodite of Tuktoyaktuk animals has a stout projection which overlaps a notch on segment three and bears two setae that are set close together at its inner distal angle (Fig. 14).

The first article of the antennule enlarged and bearing a rounded prominence, armed with small marginal spinules (Fig. 15). The inner lobe of P5 with 3 spines and the outer, 2 spines and 2 setae (Fig. 16).

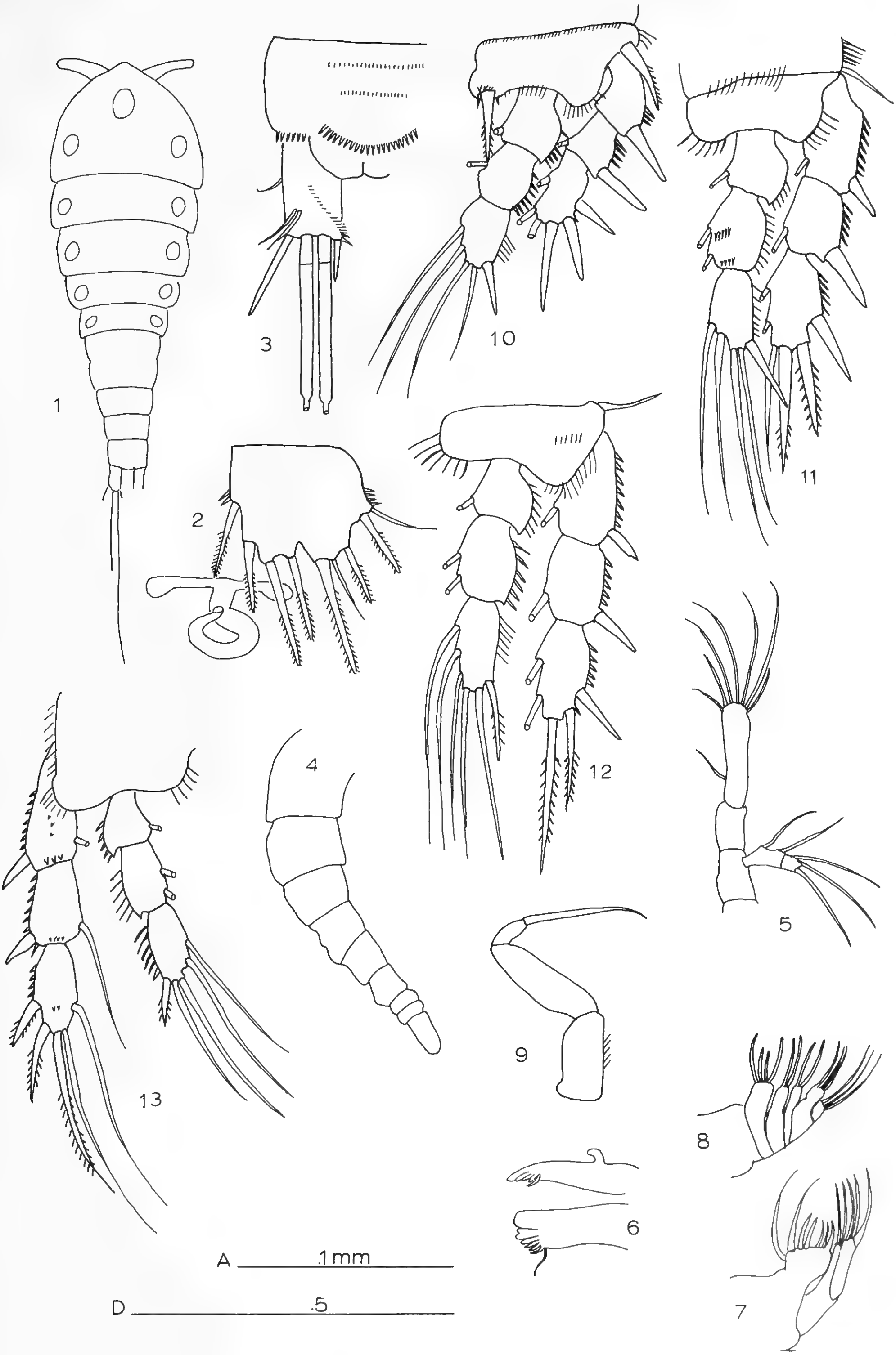
The occurrence of a sample with two species of *Tachidius* each represented by one sex only may not be as strange as it appears at first view. Olofsson (1918) reported *T. longicornis* (= *T. incisipes*) and *T. spitzbergensis* occurring together in several samples from four lakes on Spitsbergen. Moreover, the numbers of each sex were often quite unequal. Seventeen individuals, all female, of *T. brevicornis* (= *T. discipes*) were found in one sample from a creek mouth at Bernard Harbour, N.W.T. (Willey 1920).

Atteyella (*Mrazekiella*) *ussuriensis*
Rylov, 1932

Rylov (1932) described *Attheyella ussuriensis* from females collected in small puddle-like ponds on the shore of the Ussuri River near Khabarovsk (135°5′E, 48°30′N). Rylov did not find males and the species seems not to have been reported since the

→

Figs. 1–15. Female *Tachidius incisipes*: 1, Habitus. 2, Genital field and P5. 3, Caudal ramus and anal operculum. 4, Antennule, setation omitted. 5, Antenna. 6, Mandible blade. 7, Maxillule. 8, Maxilla. 9, Maxilliped. 10, Pl. Feathering on setae omitted. 11, P2. 12, P3. 13, P4. Scale D: Fig. 1. Scale A: Figs. 2–13.


1
2
3
10
11
12
5
4
9
13
8
6
7
A .1mm
D .5

original description, since both Lang (1948) and Borutzky (1952) used Rylov's figures.

One female was found in a collection from a pond at Campbell Creek near Inuvik. This female was readily identified in the keys of Lang and Borutzky and agreed with Rylov's description in regard to rami, enlarged base of caudal seta 2 (Fig. 17), form, size and number of teeth on the anal operculum (Fig. 17) and spines on P5 (Fig. 18). Rylov figured the spines of the basal article of P5 without sockets. This was also the case with the Campbell Creek female. Borutzky noted that the characteristic structure of P5 differentiates *ussuriensis* from all other species of *Attheyella.*

Moraria duthiei T. & A. Scott, 1896

One female was taken from a pond at Shingle Point (Table 1). Ramus with a dorsal chitinous ridge which terminated posteriorly in a sharp point (Fig. 19); anal operculum roughly triangular with a blunt point and eroded margin (Fig. 19); P5 exopodite jointed, feathering on setae sparse, some smooth (Fig. 20). This individual had a peculiar knob on the outer of the middle caudal setae (Fig. 19).

Bryocamptus (*Bryocamptus*) *hutchinsoni* Kiefer, 1929

A few specimens were collected from a roadside ditch near Yellowknife. These animals were like the typical form in possessing non-bifid spinules on the anal operculum and in characteristics of the ramus as given by Kiefer (1929) and Wilson & Yeatman (1959). A form in which the spinules are bifid occurs widely in Alaska, western Canada and western United States (Wilson & Yeatman 1959).

Bryocamputus (*Bryocamptus*) *vejdovskyi* (Mrazek, 1893)

Five males were collected at Fort Franklin and one male at Shingle Point (Table 1).

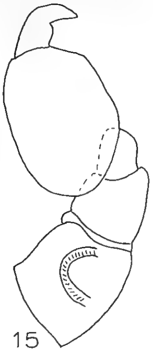
B. vejdovskyi is a member of the morphologically variable *minutus* group (Wilson 1956). In addition to sexual dimorphism there is geographical variation. Typical females possess only one well developed caudal seta, non-bifid anal operculum spines, the ramus terminates in a spinous process on its outer distal corner; males possess 3 well developed caudal seta, lack spinous process, and endopod P4 article 2 with 4 setae (Wilson & Yeatman 1959). Willey (1925) described as *Canthocamptus minusculus* a form in which the female lacked the spinous process on the outer, distal margin of the ramus. Willey had only four females, some of which had bifid operculum spines and some, simple spines. Willey believed *minusculus* to be the North American form of *Canthocamptus vejdovskyi* Mrazek (Willey 1925:157). Kiefer (1934) gave the name *Bryocamptus vejdovskyi* forma *minutiformis* to specimens with bifid anal operculum spinules, but which were otherwise typical *B. vejdovskyi* (Wilson & Yeatman 1959).

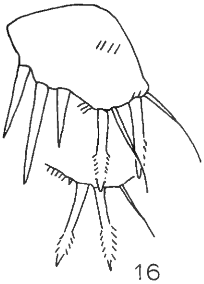
The Shingle Point male appeared to be typical *B. vejdovskyi* and had simple operculum spines (Fig. 21). This male possessed large teeth-like spines on the ventral surface of the last abdominal segment at the base of the caudal ramus; these spines were not mentioned by Lang (1948) or Wilson &

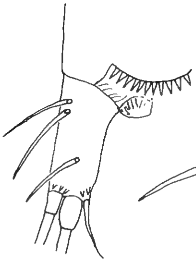
→

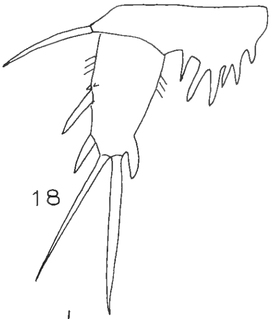
Figs. 16–27. Male *Tachidius discipes*: 14, Endopod P2. 15, Antennule. 16, P5 and P6. Female *Attheyella ussuriensis*: 17, Caudal ramus and anal operculum. 18, P5. Female *Moraria duthiei*: 19, Caudal ramus and operculum. 20, P5. Male *Bryocamptus vejdovskyi*: 21, Caudal ramus and anal operculum. 22, P2. 23, P3. 24, P4. 25, Female *Halectinosoma, Pseudobradya* sp.? 26, Mandible blade. 27, P5. Scale A: Figs. 14–18. Scale B: Figs 19 and 20. Scale C: Figs. 26 and 17.

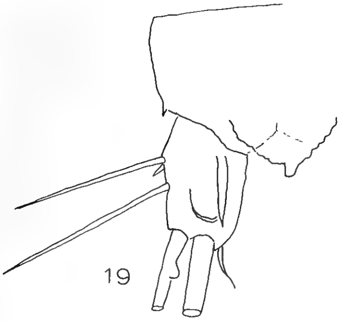

14

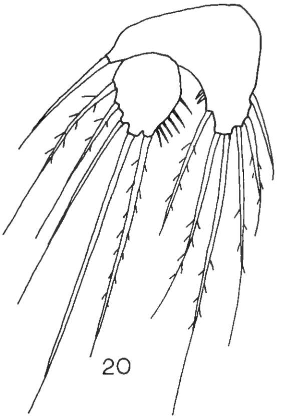

15

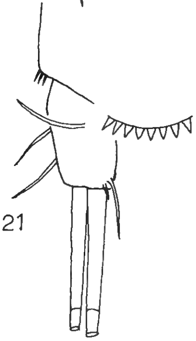

16

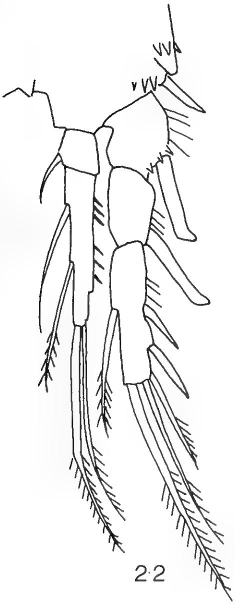

17

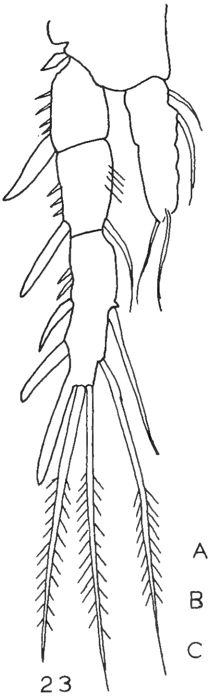

18

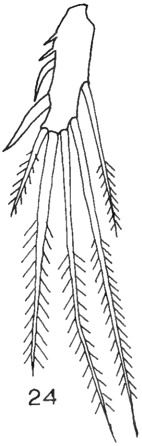

19

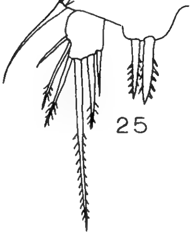

20

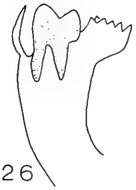

21


22


23


24

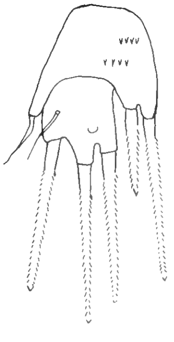

25


26

A .1mm

B .05

C .04


27

Yeatman (1959). The Fort Franklin males differed from the Shingle Point male only in having bifid operculum spinules, resembling *B. v.* forma *minutiformis* in this character.

The large spines on the outer margins of exopodites of P2 (Fig. 22), P3 (Fig. 23) and the terminal article of P4 (Fig. 24) were completely smooth in the Shingle Point male. The terminal article of P2 endopodite (Fig. 22) and P5 of the Shingle Point male were similar to figures of these appendages in Lang (1948) except that the two spines on the inner lobe of P5 appeared relatively shorter and stouter (Fig. 25).

Laophontidae

Onchyocamptus mohammed
(Blanchard & Richard, 1891)

Several males and females were collected from ponds a, b, and c, Tuktoyaktuk. Willey (1923) described as a new species, *Laophonte calamorum* from Lake St. John, Quebec. Lang (1948) regarded *L. calamorum* as a synonym of *O. mohammed.*

Ectinosomatidae

Halectinosoma?

The Tuktoyaktuk pond sample contained two female harpacticoids, 0.59 and 0.66 mm in length, that were clearly referable to Ectinosomatidae.

In addition to familial and generic features, the Shingle Point animals possessed these features: markedly conical caudal rami, length 1.5 and 1.8 times the width at base; abdominal segment of larger female densely covered both dorsally and ventrally with very tiny spinules; abdominal segment of smaller appeared covered with tiny pits. Hyaline lappets which project from the rear margin of the last abdominal segment over the bases of the caudal setae in many ectinosomatids could not be seen on either female. Both possessed a hyaline pseudo-operculum with smooth margin. The larger female had an egg sac containing 6–8 fairly large ova.

Lang (1965) stated that the mandibles reveal useful specific characters in the genera *Ectinosoma* and *Halectinosoma.* The cutting edge of the mandibles of the Tuktoyaktuk females had a heavily sclerotized bidentate pars incisiva and six-dentate lacina (Fig. 26). All marginal setae of P5 stout and spine-like, the longest reaching to posterior margin of genital segment; surface setae inconspicuous; two rows of small spinules on anterior surface of basopodite (Fig. 27).

The maxillae were destroyed during dissection; the structure of this appendage would have permitted distinctions between *Halectinosoma* and *Pseudobradya.*

At least four species of Ectinosomatidae have been reported from coastal waters of N.W.T. and northern Alaska. The Canadian Arctic Expedition collected *Pseudobradya minor* (T. & A. Scott, 1896) and *Ectinosoma neglectum* Sars, 1904 at Bernard Harbour on Dolphin and Union Straits, N.W.T., and *E. finmarchicum* from Camden Bay, Collinson Point, Alaska (Willey 1920). Wilson (1973) identified *Pseudobradya major* (Olofsson, 1917) from Nuwuk Lake, a landlocked brackish water pond, Point Barrow, Alaska.

On the basis of characters of P5, caudal rami, antenna and other features, the Tuktoyaktuk females did not seem to conform to descriptions of ectinosomatids reported from northwestern coastal waters. Too little is known about these ectinosomatids to decide if they represent undescribed species; this must await more specimens.

Discussion

These records of *Bryocamptus vejdovskyi* extend the ranges of forms with bifid and simple opercular spines but do not clarify their relationship.

The harpacticoids taken at Tuktoyaktuk are members of genera with well-recognized euryhaline distributions (Lang 1948, Wilson & Yeatman 1959). *Bryocamptus hutchinsoni* appears to be known from North America only; otherwise, with the possible exception of *Attheyella ussuriensis,* the harpacticoids found in N.W.T. and Y.T. samples are species of wide geographical distribution particularly in the Palearctic and Nearctic Regions. Some species such as *Tachidius incisipes* and *Moraria duthiei* seem mostly northern in occurrence; others such as *Onychocamptus mohammed* and *Nitocra spinipes* extend into Africa and Asia Minor.

Ackowledgments

I extend special thanks to Dr. Janet W. Reid, National Museum of Natural History, Smithsonian Institution, for advice, useful comments on a draft manuscript and for providing pieces of literature from the C. B. Wilson copepod library. Drs. C. J. Brunskill and M. C. Healey organized and ably lead the post-congress excursion. Two anonymous reviewers provided helpful comments.

Literature Cited

Borutzky, E. V. 1952. Fauna of U.S.S.R. Crustacea. Vol. 3. no. 4. Freshwater Harpacticoida. Zoological Institute, Academy of Sciences, Moscow, Israel Program of Scientific Translation, 1964.

Dussart, Bernard. 1967. Les Copepodes Des Eaux Continentales D'Europe Occidentale. Tome I: Calanoides et Harpacticoides. N. Boubee et Cie, Paris.

Gurney, Robert. 1932. British fresh-water Copepoda. Vol. 2. Ray Society, London, 336 pp.

Humes, A. G., & R. U. Gooding. 1964. A method for studying the external anatomy of copepods.—Crustaceana 6:238–240.

Johansen, Frits. 1922. The crustacean life of some arctic lagoons, lakes and ponds. Report of the Canadian Arctic Expedition 1913–18. Vol. VII. Part N. F. A. Acland, Ottawa, 25 pp.

Kiefer, Friedrich. 1929. Zur Kenntnis der freilebenden Copepoden Nordamerikas.—Zoologischer Anzeiger 86:97–100.

———. 1934. Neue Ruderfusskrebse aus Nordamerika.—Zoologischer Anzeiger 108:206–297.

Lang, Karl. 1948. Monographie der Harpacticiden. Hakan Ohlsson, Lund, 1682 pp.

———. 1965. Copepoda Harpacticoida from the California Pacific coast.—Kungliga Svenaka, Vetenskoppsahademiens Handlingar Series 4, 10(2): 1–560 + 6 pls.

Marsh, C. D. 1920. Freshwater Copepoda. Report of the Canadian Arctic Expedition 1913–18. Vol. VIII. Part J. J de Labroquerie Tache, Ottawa, 25 pp.

Meijering, M. P. D. 1975. Notes on the systematics and ecology of *Daphnia pulex* Leydig in northern Canada.—Internationale Revue der Gesamten Hydrobiologie und Hydrographie 60: 691–703.

Olofsson, Ossian. 1917. Beitrag zur Kenntnis der Harpacticiden—Familien Ectinosomidae, Canthocamptidae (Gen. *Maraenobiotus*) und Tachidiidae nebst Beschreibungen einiger neuen und wenig bekannten, arktischen Brackwasser-und Susswasser-Arten.—Zoologiska Bidrag fran Uppsala 6:1–39 + 7 pls.

———. 1918. Studien über die Susswasserfauna Spitzbergens.—Zoologiska Bidrag fran Uppsala 6:183–648.

Rylov, V. M. 1932. Resultats scientifigues de l'Expedition hydrofaunistique du Musee zoologique dans Siberia orientale en 1927. IV. Les Eucopepodes d'eau douce de la region de l'Oussauri (Crustacea). Travaux de L'Institute Zoologique, Leningrad, 1:248–280 + 6 pls.

Willey, A. A. 1920. Marine Copepoda. Report of the Canadian Arctic Expedition 1913–18. Vol. VIII. Part K. Thomas Mulvey, Ottawa, 47 pp.

———. 1923. Notes on the distribution of free-living Copepoda in Canadian waters.—Contributions to Canadian Biology and Fisheries. New Series I:303–334.

———. 1925. Northern Cyclopidae and Canthocamptidae.—Transactions of the Royal Society of Canada, 3rd Series, 19:137–158 + 3 pls.

Wilson, M. S. 1956. North American harpacticoid copepods. 1. Comments of the known freshwater species of the Canthocamptidae. 2. *Canthocamptus oregonensis* n. sp. from Oregon and California.—Transactions of the American Microscopical Society 75:290–307.

———. 1973. North American harpacticoid copepods 10. *Pseudobradya major* (Olofsson, 1917) n. comb. from Nuwuk Lake, Alaska, with a checklist of copepod associates.—Transactions American Microscopical Society 92:657–662.

———, & H. C. Yeatman. 1959. Harpacticoida. Pp. 815–861 *in* W. T. Edmondson, ed., Fresh-water biology. John Wiley & Sons, Inc., New York.

Department of Biology, Colorado State University, Fort Collins, Colorado 80521; (Postal address) 1901 Stover Street, Fort Collins, Colorado 80525.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 350–352

THE OCCURRENCE OF *SPHAEROMA SERRATUM* (FABRICIUS, 1787) IN THE WESTERN SOUTH ATLANTIC (CRUSTACEA: ISOPODA)

Ana Marta Roux and Ricardo Bastida

Abstract.—The European species *Sphaeroma serratum* is extending its range on the Argentine coast. It was probably introduced by ships in the harbor of Mar del Plata (Argentina) and subsequently spread to adjacent rocky intertidal communities and other harbors of the Buenos Aires Province. A key is given for identification of known southwestern Atlantic species of *Sphaeroma.*

Sphaeroma serratum was first recorded from the Atlantic coast of Europe, later from the Mediterranean and Atlantic coasts of northern Africa and more recently from the Black Sea, southern Africa and western Australia (Kensley 1978, Jacobs 1987). *Sphaeroma serratum* has been known from Buenos Aires Province since 1964, where it was known only from Mar del Plata harbor (38°08′S, 57°31′W) having been found in samples taken during fouling studies (Bastida 1968, 1971; Bastida et al. 1980). It has since been found as part of fouling communities in other harbors in Argentina, e.g., Puerto Quequén (38°36′S, 58°40′W), Ingeniero White (38°47′S, 62°14′W) and Puerto Belgrano (38°54′S, 62°06′W) (Bastida 1972, Bastida & Torti 1973, Bastida & Brankevich 1982, Martínez et al. 1984). Having colonized these harbor areas, in recent years *Sphaeroma serratum* has spread to natural rocky areas around Mar del Plata and has become a member of the local intertidal community (Bastida & L'Hoste 1976).

Sphaeroma serratum has not yet been found on the Patagonian coasts, but its chances of colonization are thought to be high. The wide sandy beaches of Buenos Aires probably acted as a natural barrier to the spread of the species southward (Escofet et al. 1979). *Sphaeroma serratum* has not been recorded from the coast of Uruguay and Brazil, althought the genus is represented in Brazil by three other species, *Sphaeroma terebrans* Bate, 1866, *S. anandalei* Stebbing, 1911, and *S. walkeri* Stebbing, 1905 (Loyola e Silva 1960, Pires 1982). The distribution of *Sphaeroma serratum* north of Argentina may be limited by the estuary of the Río de la Plata due to its great extension and the influence of its waters on Argentine and Uruguayan coasts. The method of introduction of *Sphaeroma serratum* was probably as part of the fouling community on the hull of ships arriving in Argentina. This transportation was observed for *Sphaeroma walkeri* in Victoria Harbor (Hong Kong) and its dispersal to areas around Hong Kong (Mak et al. 1985). Other methods of transportation could have been by ballast water (Carlton & Iverson 1981) and less probably by pieces of wood floating adrift. Burrowed pieces of wood found in coastal areas are frequently inhabited by specimens of *Sphaeroma serratum,* which obtain protection in the teredine galleries and holes (Bastida & Torti 1972).

Key to the Southwestern Atlantic Species of *Sphaeroma*

1. Pleotelson triangular, apex pointed. Pereon with tubercles. Mandible without lacinia mobilis . . . *S. terebrans*

– Pleotelson spoon-shaped, apex markedly rounded. Body with or without tubercles. Mandible with or without lacinia mobilis 2

2. Pereon and pleon without tubercles. Left mandible with lacinia mobilis .... *S. serratum*

– Body with tubercles. Left mandible with or without lacinia mobilis ... 3

3. Pereon with numerous round tubercles. Pleotelson with 2 submedian rows of tubercles, diverging from the base and almost reaching the apex. Left mandible with true lacinia mobilis .... *S. walkeri*

– Pereon with transversally elongate tubercles. Pleotelson with 2 pair of tubercles situated on either side of the midline, followed by a single median tubercle. Mandible without true lacinia mobilis ..... *S. anandalei*

Material

One hundred fifty specimens of *Sphaeroma serratum* from different localities of the Buenos Aires Province were analyzed. The studied material is deposited in the collection of the Laboratory of Benthic and Fouling communities of the INIDEP (Mar del Plata, Argentina) and 12 specimens from the port of Mar del Plata are deposited in the National Museum of Natural History, Washington, D.C., USNM 139316.

Acknowledgments

The authors wish to express their gratitude to Dr. Brian Kensley and Dr. Thomas Bowman for their kind suggestions. This is contribution No. 611 of INIDEP.

Literature Cited

Bastida, R. 1968. Preliminary notes of the marine fouling at the Port of Mar del Plata, Argentina.—Proceedings of the 2nd International Congress on Marine Corrosion and Fouling. Compte-Rendu, Athens, Greece, pp. 557–562.

———. 1971. Las incrustaciones biológicas en el Puerto de Mar del Plata. Período 1966/67.—Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Hidrobiología 3(2):203–285.

———. 1972. Studies of fouling communities along Argentine Coasts.—Proceedings of the 3rd International Congress on Marine Corrosion and Fouling, Gaithersburg, Maryland, U.S.A., pp. 847–864.

———. 1973. Estudio preliminar sobre las incrustaciones biológicas de Puerto Belgrano (Argentina).—Corosión y Protección 5:3–11.

———, & G. Brankevich. 1982. Estudios ecológicos sobre las comunidades incrustantes de Puerto Quequén (Argentina). II. Características del Macrofouling.—Cidepint Anales 1982:156–193.

———, & S. L'Hoste. 1976. Relaciones tróficas de las comunidades incrustantes ("Fouling") del Puerto de Mar del Plata.—LEMIT Anales 3-1976, Serie II 329:159–203.

———, & M. R. Torti. 1972. Organismos perforantes de las costas argentinas. I. La presencia de *Lyrodus pedicellatus* (Quatrefages, 1849) (Mollusca, Pelecypoda) en el Puerto de Mar del Plata. Clave para el reconocimiento de los Teredinidae Sudamericanos.—Physis 31(82):39–50.

———, M. Trivi de Mandri, V. Lichtschein de Bastida, & M. Stupak. 1980. Ecological aspects of marine fouling at the Port of Mar del Plata (Argentina).—V Congreso Internacional de Corrosión Marina e Incrustaciones. Sección Biología Marina, Barcelona, España, pp. 229–320.

Carlton, J. T., & E. W. Iverson. 1981. Biogeography and natural history of *Sphaeroma walkeri* Stebbing (Crustacea: Isopoda) and its introduction to San Diego Bay, California.—Journal of Natural History, London 15:31–48.

Escofet, A., N. Gianuca, S. Maytía, & V. Scarabino. 1979. Playas arenosas del Atlántico Sudoccidental entre los 29° y 43°LS. Consideraciones generales y esquema biocenológico.—Memorias del Seminario sobre Ecología Bentónica y Sedimentación de la Plataforma Continental del Atlántico Sur, Montevideo, Uruguay, UNESCO:245–258.

Jacobs, B. J. M. 1987. A taxonomic revision of the European, Mediterranean and NW African species generally placed in *Sphaeroma* Bosc, 1802 (Isopoda: Flabellifera: Sphaeromatidae).—Zoologische Verhandelingen 238:1–71.

Kensley, B. 1978. Guide to the marine isopods of southern Africa.—South African Museum, Cape Town, 173 pp.

Loyola e Silva, J. 1960. Sphaeromatidae do litoral Brasileiro (Isopoda—Crustacea).—Boletim da Universidade do Paraná Zoología 4:1–182.

Mak, P. M. S., Z. G. Huang, & B. S. Morton. 1985. *Sphaeroma walkeri* Stebbing (Isopoda, Sphaeromatidae) introduced into and established in Hong Kong.—Crustaceana 49(1):75–82.

Martínez, D., R. Bastida, & G. Brankevich. 1984. Ecological aspects of marine fouling at the Port of Ingeniero White (Argentina).—Proceedings of the VI International Congress on Marine Corrosion and Fouling, Marine Biology, Athens, Greece, pp. 521–537.

Pires, A. M. S. 1982. Sphaeromatidae (Isopoda Flabellifera) da zona entre marés e fundos rasos dos Estados de São Paulo e Rio de Janeiro.—Boletim do Instituto Oceanográfico, São Paulo 31(2):43–55.

Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), C.C. 175 Playa Grande, 7600 Mar del Plata, Argentina.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 353–357

THE STATUS OF THE CARIDEAN SHRIMP *PANDALINA MODESTA* (BATE, 1888) (CRUSTACEA: DECAPODA: PANDALIDAE) WITH REDESCRIPTION OF THE SPECIES

E. Macpherson

Abstract.—The identity of *Pandalus modestus* Bate, 1888 from South Africa is studied. The species belongs to the genus *Pandalina* Calman, 1899. Comparison with the other species of the genus revealed that Bate's species is closely related to *Pandalina profunda* Holthuis, 1946 from European and west African waters. However, both species are easily distinguished by the length of the pereopods, clearly longer in *P. modesta.*

Bate (1888) described a new species of pandalid shrimps under the name *Pandalus modestus* from South Africa (Agulhas Bank, 274 m [= 150 fms] depth). The species was later cited in the same area, under the same name, by Stebbing (1914) and by Barnard (1950), who questionably synonymized the species with *Pandalina brevirostris* (Rathke, 1843), a common species in the European coasts. The same author suggested that the species should be synonymous with *Pandalina profunda* Holthuis, 1946, from European and west African waters.

The differences between *Pandalina brevirostris* and *Pandalina profunda* were definitely established by Greve (1967). This author indicated that there is really only one reliable difference separating the two species: the spinose extent on the ambulatory dactyls. However, the identity of the specimens from southern Africa remained unresolved (Crosnier & Forest 1973).

Unfortunately, Bate's type is in a poor condition; the rostrum is broken and the pereopods are lost (Crosnier & Forest 1973). Therefore, in this study specimens collected around the type locality (Cape area) have been used for a comparison with the two species of *Pandalina.*

This comparison revealed that the specimens from southern Africa actually represent a different species of the genus *Pandalina* Calman, 1899; therefore, Bate's species should be validated. Because of the problems of identity and distribution that have existed with *Pandalus modestus,* the species is here redescribed.

Specimens used for this study came from the collections of the South African Museum, Cape Town (SAM), Muséum national d'Histoire naturelle, Paris (MNHN) and Instituto de Ciencias del Mar, Barcelona (ICM). The abbreviation CL indicates carapace length excluding rostrum.

Pandalina modesta (Bate, 1888)
Figs. 1, 2

Pandalus modestus Bate, 1888:670, pl. 114, fig. 4.—Stebbing, 1910:392.—Stebbing, 1914:36.

Pandalina brevirostris.—Barnard, 1947: 384.—Barnard, 1950:676, fig. 126a–e.—Kensley, 1981:28 (not *Pandalina brevirostris* Rathke, 1843).

Pandalina profunda.—Macpherson, 1983: 64 (not *Pandalina profunda* Holthuis, 1946).

Material examined.—Off Cape area and East London: 12 ♀ (CL = 5.0–6.8 mm), 2 ovig. ♀ (CL = 5.4–5.5 mm), 4 ♂ (CL = 5.7–6.5 mm), R/V *Pieter Faure,* 268–360 m (several samples together), SAM A8396–8398.—1 ♀ (CL = 4.5 mm), SAM A13280.—1 ♀ (CL = 6.1 mm), SAM A13642.—1 ♀ (CL = 5.7 mm), SAM A1280.—South of Namibia: 1 ♀ (CL = 7.1 mm), 26°42′S, 14°06′E, 395 m, ICM D1047.

Description.—Rostrum horizontal, not nearly reaching level of end of penultimate antennular segment, around 0.5 times length of carapace; dorsal margin armed with 8 to 10 teeth, 5 proximals being movable; lower margin bearing 2 to 4 teeth. Antennal spine stronger than pterygostomian spine.

Abdomen with 3rd somite rounded posteriorly, unarmed, slightly overhanging 4th segment. Pleura of 3 anterior somites broadly rounded, of 4th and 5th bearing sharp tooth. Sixth somite slightly less than 2 times as long as 5th somite (length measured on dorsal margin) and less than 2.5 times maximum height. Telson as long as 6th somite, with 7 or 8 pairs of dorso-lateral spines and 2 longer pairs on apex.

Eyes broadly subpyriform, maximum diameter about 0.2 times carapace length; ocellus present, slightly constricted at juncture with cornea.

Antennular peduncle with small tooth on inner margin of basal segment. Ultimate and penultimate segment of similar length.

Antennal scale with lateral margin nearly straight, about 0.7 to 0.8 times as long as carapace, 5.0 times as long as wide, distolateral tooth not overreaching blade.

Mouth parts as illustrated. Third maxilliped with epipod; endopod slightly overreaching antennal scale, armed terminally with long, slender apical and few subapical spines; penultimate segment about 0.5 times as long as terminal segment. Exopod absent.

Pereopods with well-developed epipods on 4 anterior pairs. First pereopod slender, overreaching antennular peduncle by length of propodus. Second left pereopod longer than right. Right overreaching antennular peduncle by somewhat less than length of chela; merus occurring at level of anterior border of basicerite; carpus with 4 to 6 segments and about 1.8 times long as chela. Left overreaching antennular peduncle by somewhat less than half carpus length; carpus composed of 16 to 21 articles and somewhat less than 5 times chela length. Third pereopod with carpus clearly overreaching antennular peduncle; ischium with 1 or 2 posterior spines; merus occurring pterygostomian angle by 0.4 of merus; merus about 2 times as long as carpus, armed with 11 to 14 posterior and outer spines; carpus bearing 6 to 9 posterior and outer spines; propodus almost two times length of carpus and 3.0 to 3.8 times length of dactylus, having 10 to 18 posterior spines; dactylus armed with 3 or 4 spines on proximal half of posterior margin. Fourth pereopod with carpus clearly occurring penultimate segment of antennular peduncle. Ischium with 2 or 3 posterior spines; merus about 2 times length of carpus, armed with 14 to 18 posterior and outer spines; merus occurring pterygostomian angle by 0.2 of merus length; carpus having 5 to 7 posterior and outer spines; propodus 1.7 to 2.0 times length of carpus and about 4.5 times length of dactylus, bearing 12 to 14 posterior spines; dactylus armed with 3 or 4 spines on the proximal half of posterior margin. Fifth pereopod with merus clearly not reaching pterygostomian angle; ischium with 1 or 2 small posterior spines; merus about 1.7 times length of carpus, having 10 to 13 posterior and outer spines; carpus armed with 4 outer spines; propodus almost two times carpus length and 4.3 to 5.0 times as long as dactylus and bearing 9 or 10 posterior spines; dactylus with 3 spines on proximal 2/3 of posterior margin.

Uropods overreaching end of telson; exopodite longer than endopodite and bearing movable spine.

Remarks.—*Pandalina brevirostris* is closely related to *P. profunda* but it is readily differentiated by the length of the dactylus of 3rd–5th pereopod and the part of the dactylus bearing posterior spines. In *P. profunda* the dactylus is long and slender with the posterior margin carrying spines only in the proximal half. In *P. brevirostris* the dac-

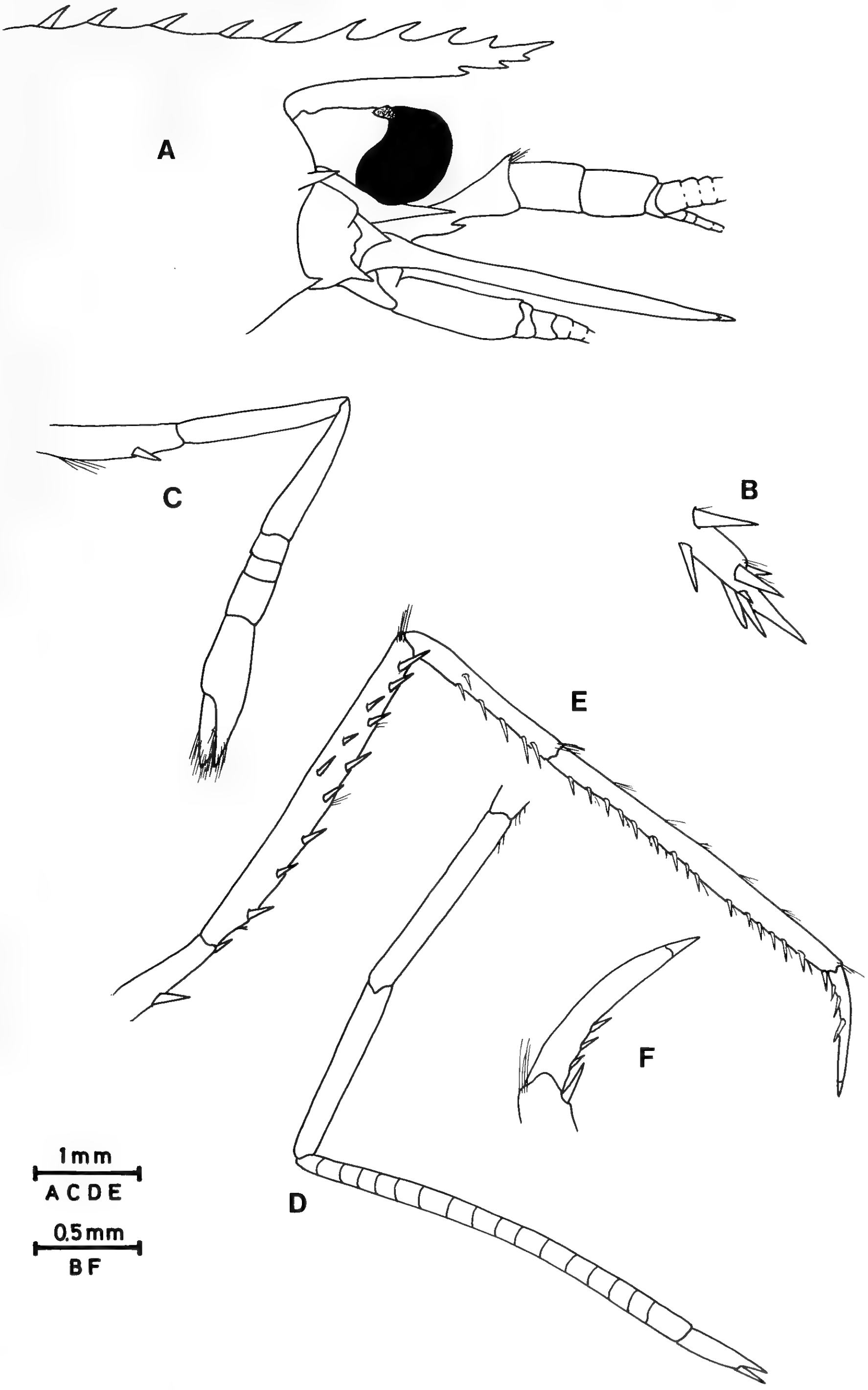


Fig. 1. *Pandalina modesta* (Bate, 1888), ♀, CL = 4.5 mm, SAM A13280. A, Anterior carapace and anterior appendages; B, Right third maxilliped, distal end; C, Second right pereopod; D, Second left pereopod; E, Third right pereopod; F, Same, dactylus.

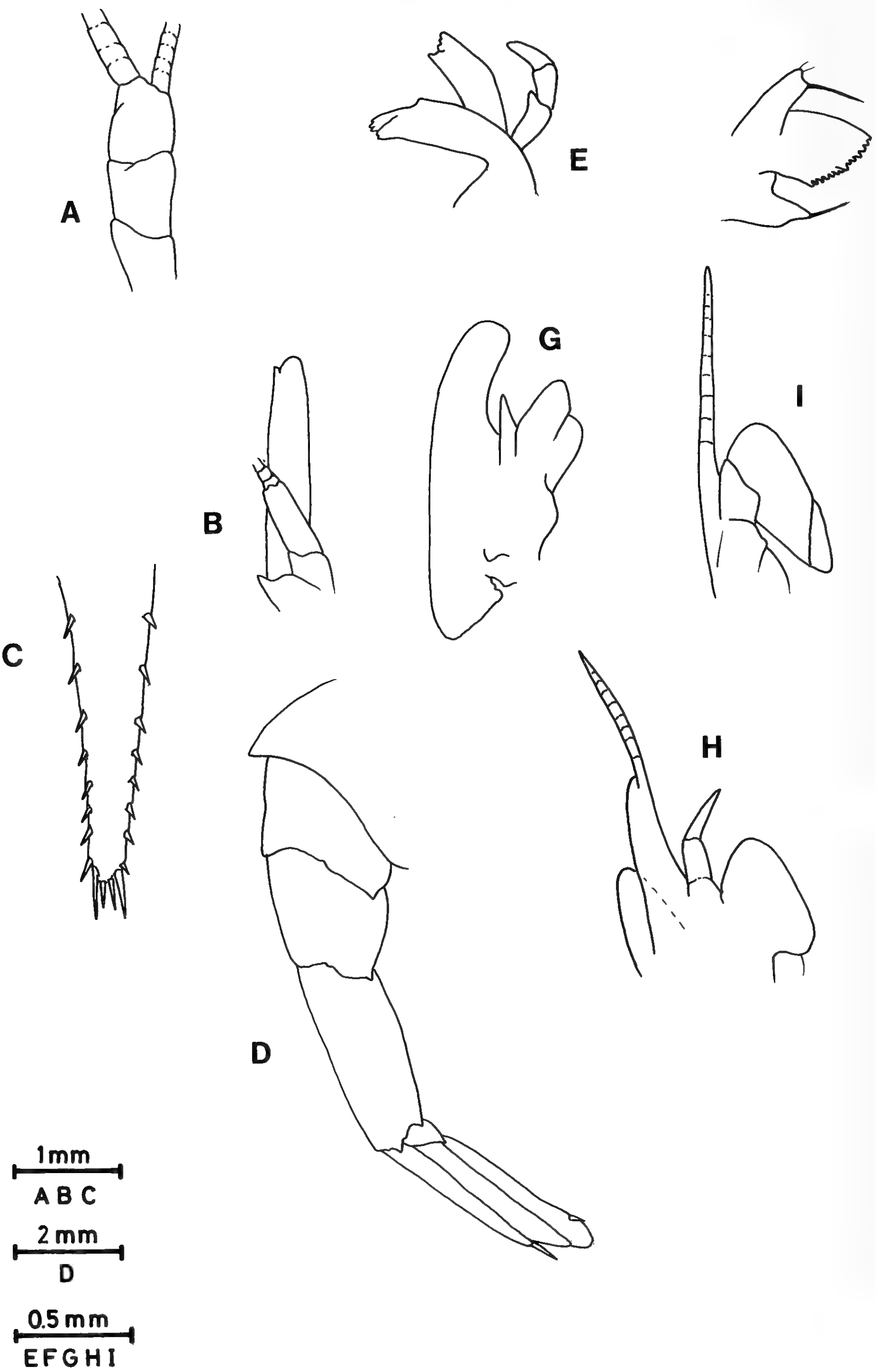


Fig. 2. *Pandalina modesta* (Bate, 1888). A–D, ♀, CL = 4.5 mm, SAM A13280. A, Right antennula; B, Right antenna, ventral view; C, Telson; D, Abdomen. E–I, ♀, 5.7 mm (SAM A8396–8398). E, Right mandible; F, Right first maxilla; G, Right second maxilla; H, Right first maxilliped; I, Right second maxilliped.

tylus is much shorter and the spines of the posterior margin always are regularly dispersed over the entire length (Holthuis 1946, Greve 1967, Zariquiey-Alvarez 1968).

Pandalina modesta has a long and slender dactylus, with spines only in the proximal half; thereby it resembles *P. profunda* (material examined of *P. profunda*: 1 ♀ [CL = 5.7 mm], Travailleur, st. 58, 440 m [MNHN Na1213].—2 ♀ [CL = 3.1–4.3 mm], 47°34.8′N, 07°18.1′W, 825 m [MNHN Na10319].—1 ♀ [CL = 3.2 mm], 48°40.8′S, 09°47.7′W, 373 m [MNHN Na10321].—4 ♀ [CL = 2.8–3.8 mm], 48°41.6′S, 09°52.9′W, 350 m [MNHN Na10322].—1 ♂ [CL = 3.8 mm], 7 ♀ [CL = 3.6–4.4 mm], 47°36′S, 07°16.8′W, 330 m [MNHN Na10320]). The comparative analysis of these specimens shows that they are easily distinguished by the length of the pereopods, clearly longer in *P. modesta* than in *P. profunda.*

The merus of the 2nd left pereopod of *P. modesta* almost reaches the end of the basal segment of the antennular peduncle, while in *P. profunda* it slightly overreaches the basicerite.

In *P. modesta* the 3rd pereopod has the merus reaching or overreaching the terminal border of the cornea. In *P. profunda* it reaches only to the level of the proximal border of the cornea.

The merus of the 4th pereopod in *P. modesta* reaches or overreaches the distal margin of the basicerite, while in *P. profunda* it only slightly overreaches the pterygostomian border.

Also, the carpus of the left second pereopods has generally more articles in *P. modesta* (16 to 21) than in *P. profunda* (14 to 16).

Distribution.—Southern Africa, from East London to Saldanha Bay and south of Namibia. Depth range: 265 to 360 m.

Acknowledgments

I am grateful to Dr. L. B. Holthuis (Rijksmuseum van Natuurlijke Historie, Leiden) for reading a draft of the manuscript. I thank Dr. F. A. Chace, Jr. (National Museum of Natural History, Washington) and Dr. A. Crosnier (Museum national d'Histoire naturelle, Paris) for the revision of the manuscript. Thanks are also extended to Dr. Forest (Museum national d'Histoire naturelle, Paris) and Mrs. M. van der Merwe (South African Museum, Cape Town) for the loan of the material of *Pandalina.*

Literature Cited

Barnard, K. H. 1947. Descriptions of new species of South African decapod Crustacea, with notes on synonymy and new records.—Annals and Magazine of Natural History, ser. 11, 13:361–392.

———. 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps).—Annals of the South African Museum 38:1–837.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. "Challenger" during the Years 1873–76, 24:1–942.

Crosnier, A., & J. Forest. 1973. Les crevettes profondes de l'Atlantique oriental tropical.—Faune Tropicale 19:1–409.

Greve, L. 1967. Notes on the genus *Pandalina* in Norwegian waters (Crustacea Decapoda).—Sarsia 26:1–5.

Holthuis, L. B. 1946. Note on the genus *Pandalina* (Crustacea Decapoda), with the description of a new species from European waters.—Zoologische Mededeelingen 26:281–286.

Kensley, B. 1981. On the zoogeography of southern African decapod Crustacea, with a distributional checklist of the species.—Smithsonian Contributions to Zoology 338:1–64.

Macpherson, E. 1983. Crustáceos Decápodos capturados en las costas de Namibia.—Resultádos Expediciones Científicas (supl. Investigación Pesquera) 11:3–79.

Stebbing, T. R. R. 1910. General catalogue of South African Crustacea (Part V of S.A. Crustacea, for the marine investigations in South Africa).—Annals of the South African Museum 6:281–593.

———. 1914. South African Crustacea (Part VII of S.A. Crustacea, for the marine investigations in South Africa).—Annals of the South African Museum 15:1–55.

Zariquiey-Alvarez, R. 1968. Crustáceos Decápodos Ibéricos.—Investigación Pesquera 32:i–xv + 1–510.

Instituto de Ciencias del Mar, P° Nacional s/n. 08003 Barcelona, Spain.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 358–363

GALATHEA CORALLIOPHILUS, A NEW DECAPOD CRUSTACEAN (ANOMURA: GALATHEIDAE) FROM SINGAPORE, GULF OF THAILAND, AND WEST IRIAN

Keiji Baba and Sang-Chul Oh

Abstract.—*Galathea coralliophilus,* a new galatheid crustacean, is described and illustrated. The new species is common in association with reef corals in Singapore and the Gulf of Thailand. *Galathea spinosorostris* reported by Johnson (1970:6) from Singapore and *Galathea* aff. *consobrina* described by Gordon (1935:5) from West Irian are synonymized with the present species.

During ecological studies on the coral communities of the Gulf of Thailand in 1984, Dr. Y. Nakasone collected galatheid crustaceans commensal with several species of reef corals and made them available to one of us (KB) for identification; they were immediately identified as an undescribed species of *Galathea.* Recently, Singaporean galatheids in the collection of the National University of Singapore (Zoological Reference Collection [ZRC]), taken mostly on coral reefs, rarely from crinoids or fouling rubbles on a ship or among fouling community, were made available for study. They comprise two species: one of them is *Allogalathea elegans* (Adams & White), a common crinoid associate in the Indo-West Pacific, and the other is identical with the Thailand species, as well as with the species reported by Johnson (1970:6) as *Galathea spinosorostris,* which, according to him, is the only shore galatheid in Singapore. However, Johnson's identification is incorrect, as the identity of *Galathea spinosorostris* Dana, 1852 has recently been established (Baba 1988:78). In addition, examination of the literature discloses that *Galathea* aff. *consobrina* from West Irian (Gordon 1935: 5) should also be merged with the new species.

Most of the material from Thailand is retained in the collection of Kumamoto University, and part will be sent to the Smithsonian Institution. Locations of stations where the Thailand survey was carried out can be found in Nakasone et al. (1986: fig. 1). The measurements of the specimens examined are given in parentheses under "Material," showing minimum and maximum carapace lengths in millimeters taken between the rostral tip and midpoint of the posterior margin of the carapace. The host corals from Thailand have been identified by Kazuhiko Sakai (see Nakasone et al. 1986:155), and those, as well as a host crinoid, from Singapore have been determined by Beverly Goh (Peter Ng, pers. comm.).

Galathea coralliophilus, new species
Fig. 1

Galathea aff. *consobrina.*—Gordon, 1935: 5, figs. 2, 3a, b.

Galathea spinosorostris.—Johnson, 1970:6, fig. 1b. [Not *G. spinosorostris* Dana, 1852.]

Material.—Thailand: Khang Khao Island, sta. B, 26 Oct 1984, on *Pavona frondifera* Lamarck: 1 ovig. ♀ (3.5); on *Pocillopora damicornis* Linnaeus: 4 ♂ (3.1–5.5), 2 ovig. ♀ (3.7, 5.1); 15 Nov 1984, on *P. damicornis*: 1 ♂ (4.5), 1 ovig. ♀ (3.8), 1 ♀ (3.2); sta. C, 25 Oct 1984, on *P. damicornis*: 1 ♂ (3.0). Samui Island, sta. 1, 10 Nov 1984, on *Acropora* sp.: 1 ♀ (3.5); on *Psammocora con-*

tigua (Esper): 4 ♂ (2.8–4.8). Singapore: Pulau Hantu, North, 12 Aug 1986, coll. B. Goh, on *Acropora* (*Acropora*) *tenuis* (Dana): 1 ♂ (4.7) (ZRC 1987.2555); Pulau Hantu, South, 19 Aug 1986, on *Pavona frondifera*: 2 ♀ (4.1, 4.3) (ZRC 1987.2558–2559); Pulau Hantu, West, 19 Sep 1986, on *Pocillopora damicornis*: 3 ♂ (3.7–5.3), 1 ♀ (4.9) (ZRC 1987.2582–2585). Cyrene Reef, 15 Aug 1986, coll. B. Goh, on *Pavona decussata* (Dana): 1 ovig. ♀ (4.3+), 1 ♀ (3.7+) (ZRC 1987.2556–2557). Pulau Semakau, 22 Aug 1986, coll. B. Goh, on *Pavona frondifera*: 1 ♂ (4.5), 2 ovig. ♀ (4.4, 4.1+), 1 ♀ (cephalothorax missing) (ZRC 1987.2560–2563); on *Cyphastrea serailia* (Forskål): 1 ♂ (3.9), 1 ♀ (carapace missing) (ZRC 1987.2564–2565); on *Pavona cactus* (Forskål): 1 ♂ (4.8) (ZRC 1987.2566); coll. G. Lim, on crinoid *Comaster gracilis* (Hartlaub): 1 ♂ (5.3) (ZRC 1987.2596). Pulau Jong, 26 Aug 1986, coll. B. Goh, on *Pocillopora damicornis*: 1 ovig. ♀ (4.4+) (ZRC 1987.2567). Pulau Jong, South, 24 Oct 1986, coll. B. Goh, on *Pavona frondifera*: 1 ovig. ♀ (5.5) (ZRC 1987.2595). Raffles Lighthouse, 2 Sep 1986, coll. B. Goh, on *Acropora* (*Acropora*) *willisae* Veron & Wallace: 1 ♂ (5.1) (ZRC 1987.2568); on *Pocillopora damicornis*: 3 ♂ (3.7–4.8), 1 ovig. ♀ (4.2), 1 ♀ (4.7) (ZRC 1987.2569–2573); 16 Oct 1986, on *Pocillopora damicornis*: 1 ♂ (4.9), 1 ovig. ♀ (5.9) (ZRC 1987.2586–2587); on *Pavona frondifera*: 3 ♂ (4.5–6.3), 1 ♀ (6.0) (ZRC 1987.2588–2591) [largest male is holotype]; on *Pavona decussata*: 2 ♂ (4.5, 5.6), 1 ovig. ♀ (4.5) (ZRC 1987.2592–2594). Terembu Pempang Laut, South, 9 Sep 1986, coll. B. Goh, on *Pocillopora damicornis*: 5 ♂ (4.0–6.4), 3 ovig. ♀ (3.7–5.2) (ZRC 1987.2574–2581). Southern Islands, Dec 1986, coll. J. B. Sigurdson, from fouling rubble on ship: 1 ♂ (6.4), 1 ovig. ♀ (4.8) (ZRC 1987.2597–2599). Sentosa Reef, Dec 1985, coll. P. Ng: 2 ♂ (3.7, 4.1), 2 ovig. ♀ (3.9, 4.1) (ZRC 1987.2600–2603). Pulau Busing, 1 May 1987, coll. J. B. Sigurdson, from fouling community: 2 ovig. ♀ (4.5, 5.2) (ZRC 1987.2604–2605).

Description of holotype.—Carapace excluding rostrum and lateral spines nearly as long as wide, dorsal surface with distinct transverse ridges as figured, cervical groove indistinct; first transverse ridge with pair of submedian spines, each spine accompanied by feathered seta mesial to it, also lateral to it on left side only; scale-like ridge present directly behind second transverse ridge, bearing 4 pits for roots of stiff feathered setae. Lateral margins convex, bearing 7 spines, first (anterolateral) pronounced, second small and somewhat dorsal in position, third to seventh located behind end of cervical groove, fifth largest. Another spine ventral to level of second lateral marginal spine and somewhat anterior to anterior end of linea anomurica. Outer angle of orbit strongly produced, ending in sharp point.

Rostrum broadly triangular, 1.4 times as long as wide when measured between incisions formed by 2 proximal teeth, dorsal surface with several pronounced feathered setae in addition to fine simple ones, lateral margin with 4 sharply incised teeth, basal lateral tooth smaller, ultimate lateral tooth terminating opposite midlength of rostral median spine.

Eyestalks with few feathered setae near mesial limit of terminal fringe of very fine setae proximal to cornea.

Abdominal segments sparsely provided with feathered setae as illustrated; second and third segments each with 4 transverse ridges, first (anterior) ridge elevated, second ridge medially interrupted by considerable space, third ridge uninterrupted, accompanying groove anterior to it, fourth ridge faint and medially interrupted.

Pterygostomian flap anteriorly ending in sharp spine, bearing small spine on second ridge.

Basal segment of antennule with 3 well developed terminal spines, distal segment with tuft of pronounced terminal setae. First (proximal) segment of antennal peduncle with rather long distomesial spine nearly reaching end of third segment; second segment with distomesial and distolateral spines of subequal size; third segment with small distomesial spine.

Third maxilliped having ischium with small distoventral and short but stout distodorsal spines, mesial ridge with 23 denticles; merus with 2 well developed ventral spines on distal half of length, distal one present at midlength of space between proximal spine and distal end of ventral margin; dorsal margin with distodorsal spine of small size and eminence proximal to it; carpus unarmed but with 3 eminences on dorsal margin; dactylus elongate.

Third thoracic sternum depressed below level of following sternum, anteriorly narrowed, anterior margin with distinct median notch.

Chelipeds 2.7 times as long as carapace, provided with coarse setae in moderate density and very spinose as illustrated; merus with 5 rows of spines, distal 2 of mesial marginal spines prominent; carpus with 5 rows of spines, penultimate of mesial marginal spines very strong; palm about 3 times as long as wide, with 4 rows of spines on dorsal surface and mesial and lateral margins; fingers gaping, touching each other with several intermeshing teeth at tip when closed; movable finger 0.57 as long as palm, bearing few spinules slightly dorsal to proximal mesial margin, opposable margin with prominent but short basal process proximal to opposing process at midlength of fixed finger.

Walking legs sparsely provided with pronounced feathered setae. First and second walking legs subequal in size, third one shorter; meri dorsally provided with 10 spines on first leg, 9 or 10 on second leg, 4 on third leg proximal to distodorsal spine, distolaterally with pronounced spine on all these legs, accompanying tiny one proximal and ventral to it on first and second legs; carpi with few tiny spines on dorsolateral surface parallel to 4 dorsal marginal spines. Dorsal margins of propodi with 2 proximal spines, ventral margins with 4 spinelets on first leg, 3 on second leg and 3 or 4 on third leg; dactyli ending in strongly curved sharp claw, ventrally bearing 5 teeth each with stiff seta at base, all these teeth and setae decreasing in size toward base of segment.

Epipods present on chelipeds, absent from walking legs.

Variation.—The scale-like ridge immediately behind the second transverse ridge is absent in only two of the 66 specimens examined. In these two, the second stria is interrupted at midpoint and both of their mesial limits are directed posteriad. The feathered seta mesial to each epigastric spine is consistently present, and an additional one lateral to it is present in two specimens including the holotype. The spine on the pterygostomian flap is usually very tiny, occasionally discernible only under high magnification, and very rarely obsolete (in two specimens). The propodal ventral spinelets vary from two to five (mostly four) on the first walking leg, two to four (mostly three) on the second walking leg, one to four (mostly three, occasionally two) on the third walking leg. The merus of the third walking leg bears three to five (mostly four) spines on the dorsolateral surface near dorsal margin, in addition to a distodorsal one. The dorsal margin of the merus of the third maxilliped bears at most three spines; the median one is mostly tiny and rarely missing; the proximal one tends to be obsolete; and the distal one is constantly present.

Habitat.—The specimens examined are mostly reef associates, very frequently taken from *Pocillopora damicornis* Linnaeus, occasionally from *Pavona frondifera* Lamarck, rarely from *Pavona decussata* (Dana), *P. cactus* (Forskål), *Acropora tenuis* (Dana), *A. willisae* Veron & Wallace, *Cyphastrea serailia* (Forskål) and *Psammocora contigua* (Esper); a few lots are taken from a crinoid *Comaster gracilis* (Hartlaub), fouling rubble on a ship, and among fouling community.

Parasites.—Six of the 50 specimens from

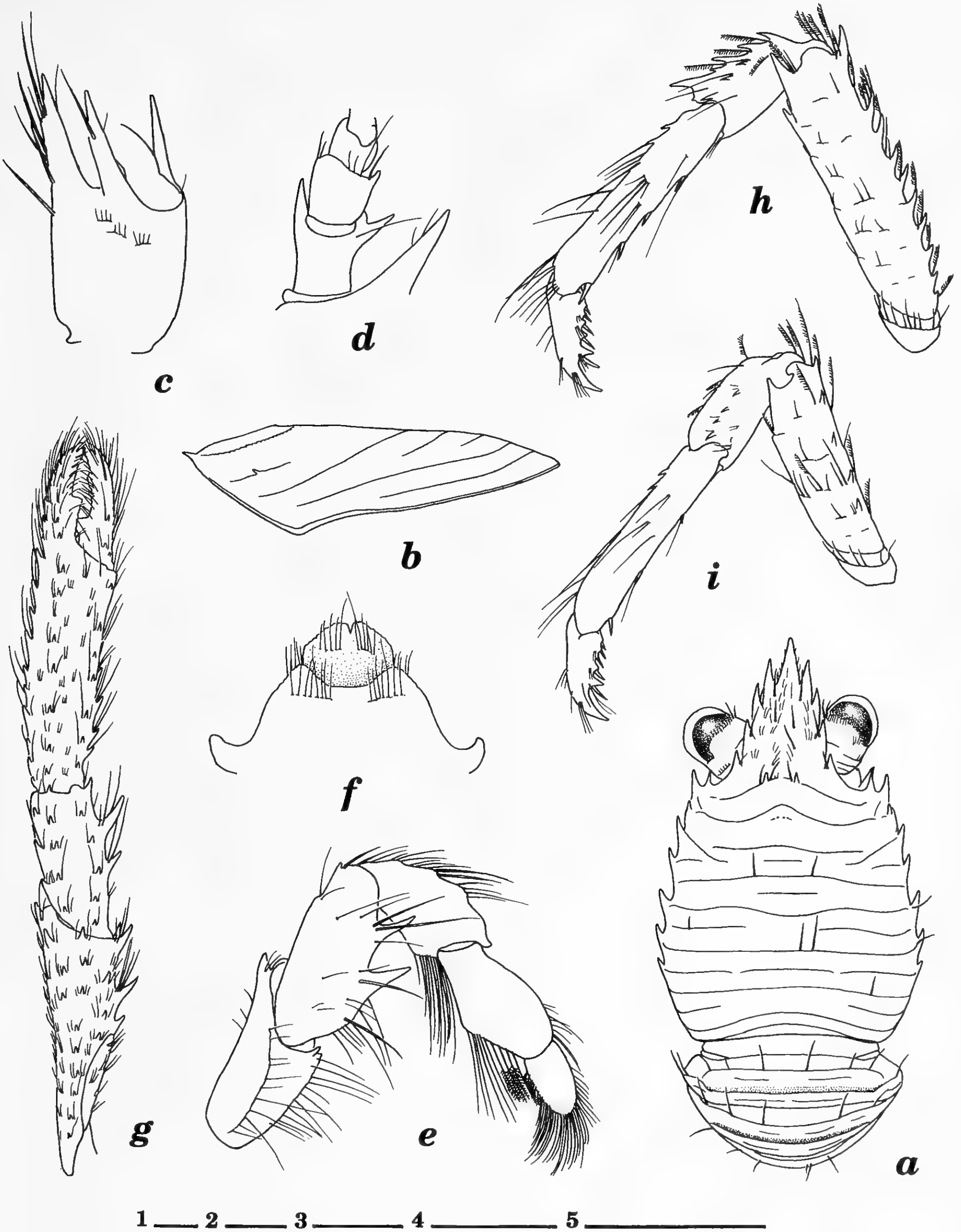


Fig. 1. *Galathea coralliophilus* new species, male holotype, ZRC1987.2588: a, Carapace and abdomen, dorsal view, fine setae on transverse ridges omitted; b, Left pterygostomian flap; c, Basal segment of right antennule, ventral view; d, Right antennal peduncle, ventral view; e, Endopod of right third maxilliped, lateral view; f, Anterior part of sternal segments; g, Left cheliped, dorsal view; h, Left first walking leg, lateral view; i, Left third walking leg, lateral view. Scales = 1 mm; scale 1 for g; scale 2 for a; scale 3 for b, h, i; scale 4 for f; scale 5 for c, d, e.

Singapore have externas of rhizocephalan parasites; no externas on the Thailand specimens.

Remarks.—*Galathea* aff. *consobrina,* reported by Gordon (1935:5) from West Irian, the identity of which was questioned because of a lack of two spinules on the hepatic region (Baba 1988:73), is in all probability identical with the present species. The rounded outer orbital angle in *G.* aff. *consobrina,* which Gordon stressed as one of the characteristics that differentiates her unique specimen from *G. consobrina,* is the only one that does not agree with the present specimens. Very possibly she must have overlooked a sharp tip, because, in my experience, such a sharply produced angle as illustrated by Gordon (1930:fig. 2) has not been observed in any of the known species that have a rounded outer orbital angle.

The differences between *G. coralliophilus* and *G. consobrina* De Man, 1902 are apparent in the following particulars that were verified by examination of both the male holotype in the collection of the Senckenberg Museum at Frankfurt am Main (SMF 4556) and additional specimens from the Philippines (Baba 1988:73) of *G. consobrina*: 1) the epipods on the chelipeds are present in *G. coralliophilus,* absent in *G. consobrina*; 2) the hepatic region bears two spinules other than the second of the seven lateral marginal spines of the carapace in *G. consobrina,* none in *G. coralliophilus*; 3) the third thoracic sternum is much wider in *G. consobrina* than in *G. coralliophilus* (see Baba 1988:fig. 30e); 4) a spine on the anterior surface of the pterygostomian flap is usually present though mostly tiny in *G. coralliophilus,* absent in *G. consobrina.*

Johnson (1970:6) mistakenly reported *G. spinosorostris* from Singapore. The true *G. spinosorostris* originally known from the Hawaiian Islands (Dana 1852:480) is characterized by scale-like ridges on the branchial region, the outer orbital angle unarmed, three hepatic spinules including the second lateral marginal spine of the carapace, and lack of a spine on the anterior portion of the pterygostomian flap (Baba 1988:78). The brief account of morphology with an illustration, as well as a note on the habitat, of *G. spinosorostris* provided by Johnson, suggests that his specimens should be referable to the present new species. He stated that the merus of the third walking leg bears seven or eight dorsal spines. This is the only one to be at variance with the present species. However, it is most likely that his note is based on the first or second walking leg, because most of the known species including the present new species has the third walking leg with at most four or five dorsal and one distolateral spines.

The presence of a spine on the anterior stria of the pterygostomian flap and two epigastric and seven lateral marginal spines on the carapace link the species to *Galathea orientalis* Stimpson, 1858 (see Miyake & Baba 1967:233). However, they differ in that: the carpus of the third maxilliped bears a few but usually distinct dorsal spines in *G. orientalis* but lacks them in *G. coralliophilus*; the scale-like ridge immediately behind the second transverse ridge is distinct in *G. coralliophilus,* absent in *G. orientalis*; and the rostrum has a few to several feathered setae on the dorsal surface in *G. coralliophilus* but lacks them in *G. orientalis.*

Etymology.—The specific name is a noun in apposition from the Greek, "corallion," coral, and "philos," loving or fond of, for the association of the species mostly with corals.

Acknowledgments

We thank Yukio Nakasone of the University of the Ryukyus and Peter Ng of the National University of Singapore, for making the interesting specimens available for study. We owe a special debt of gratitude to Raymond B. Manning and Fenner A. Chace, Jr. of the Smithsonian Institution for reviewing the manuscript. The holotype of *Galathea consobrina* De Man in the collection of the Senckenberg Museum was ex-

amined on loan by the courtesy of Michael Türkay.

Literature Cited

Baba, K. 1988. Chirostylid and galatheid crustaceans (Decapoda: Anomura) of the "Albatross" Philippine Expedition, 1907–1910.—Researches on Crustacea, Special Number 2:v + 203 pp.

Dana, J. D. 1852. Crustacea, Part 1. *In* United States exploring expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N.. 13:viii + 685 pp., C. Sherman, Philadelphia.

De Man, J. G. 1902. Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden.—Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft 25:467–929, pls. 19–27.

Gordon, I. 1935. Anomura (excluding Paguridea), *in* Résultats scientifiques du Voyage aux Indes orientales Néerlandaises de LL.AA.RR. le Prince et la Princesse Léopold de Bélgique. Volume III, Fascicule 15.—Mémoires du Musée Royal d'Histoire naturelle de Belgique, hors série, 12 pp.

Johnson, D. S. 1970. The Galatheidea (Crustacea, Decapoda) of Singapore and adjacent waters.—Bulletin of the National Museum Singapore 35(1):1–44.

Miyake, S., & K. Baba. 1967. Galatheids of the East China Sea (Chirostylidae and Galatheidae, Decapoda, Crustacea).—Journal of the Faculty of Agriculture, Kyushu University 14(2):225–246.

Nakasone, Y., M. Tsuchiya, V. Manthachitra, & M. Nishihira. 1986. Species composition of decapod crustaceans associated with living corals in the Gulf of Thailand.—Galaxea, Publications of Sesoko Marine Science Center, University of the Ryukyus 5:141–156.

(KB) Faculty of Education, Kumamoto University, Kumamoto, 860 Japan; (SO) Department of Natural Sciences, Cheju College of Education, Cheju, 590 Korea.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 364–371

CALYPTRAEOTHERES, A NEW GENUS OF PINNOTHERIDAE FOR THE LIMPET CRAB *FABIA GRANTI* GLASSELL, 1933 (CRUSTACEA, BRACHYURA)

Ernesto Campos

Abstract.—Fabia granti Glassell, 1933 is incorrectly assigned to the genus *Fabia* Dana, 1851. Its unique morphological features include: (1) lack of two longitudinal sulci on the carapace; (2) the anterolateral margins of the carapace are sharp-edged; (3) the third maxilliped has a palp of two articles, carpus longer and wider than propodus, and (4) abdomen, in both sexes, of seven free somites, and these support the placement of *F. granti* as type species of a new pinnotherid crab genus, *Calyptraeotheres.* In addition to the morphological differences, this genus is ecologically different from others in the Pinnotheridae, since it is a symbiont of gastropods, family Calyptraeidae.

Resúmen.—Fabia granti Glassell, 1933 ha estado incorrectamente asignada dentro del género *Fabia* Dana, 1851. Sus características exclusivas incluyen: (1) ausencia de dos surcos longitudinales sobre el caparazón; (2) márgenes del caparazón agudos; (3) tercer maxilipedio con su palpo formado de dos artejos, el carpus más ancho y largo que el propodus y (4) el abdomen, en el macho y la hembra, formado de siete somitos libremente articulados. Lo anterior apoya la asignación de *F. granti* como especie tipo de un nuevo género de cangrejo en la familia Pinnotheridae, *Calyptraeotheres.* Adicional a las características morfológicas, *Calyptraeotheres* es ecologicamente diferente de otros géneros en los Pinnotheridae dado que es simbionte de Mollusca—Gastropoda, familia Calyptraeidae.

The pinnotherid crab genus *Fabia* was established by Dana, 1851 with *F. subquadrata* Dana, 1851, from the northeastern Pacific, as its type species. Subsequently, eleven species were assigned within this genus (Schmitt et al. 1973, Rodrigues da Costa 1970, De Melo 1971, Cobb 1973, Dai 1980, Gore 1986). Of these, two species have been transferred to other genera. Pregenzer (1979) assigned *F. hickmani* to *Pinnotheres* Bosc, 1802, and Campos (1989a) included *F. unquifalcula* in *Orthotheres* Sakai, 1965. Recent examination of males and females of *F. granti* Glassell, 1933, and their comparison with specimens and descriptions of *F. subquadrata* (Rathbun 1918, Davidson 1968) revealed several morphological differences of taxonomic importance. In *F. subquadrata* two longitudinal sulci, which arise from the upper margin of the orbit, are present on the carapace of the female, the palp of the third maxilliped is composed of three articles in both sexes and the abdomen of the male has somites 3–5 fused (Rathbun 1918, pers. obs.). In contrast, *F. granti* does not show the sulci, the palp is composed of two articles in both sexes, and the abdomen of the male is formed by seven free somites. These morphological differences suggest that (1) *F. granti* should not be considered as congeneric with *F. subquadrata*; (2) its inclusion within genus

Fabia was incorrect; and (3) as *F. granti* is morphologically unique in the Pinnotheridae, a new genus should be proposed to receive this singular species.

Systematic Results

Family Pinnotheridae

Calyptraeotheres, new genus

Diagnosis.—Female: Carapace with anterolateral margin arcuate and sharp-edged, dorsal regions ill-defined. Third maxilliped obliquely placed in buccal cavity; ischium and merus indistinguishably fused, widening distally, inner margin concave, distal one almost straight; palp with two articles, carpus wider and longer than propodus, latter digitiform and obliquely truncated. Abdomen with seven free somites, covering sternum but not reaching to buccal area.

Male: Carapace subpentagonal, regions ill-defined, dorsal surface even and with short and separate setae; anterolateral margins with fringe of hair-like setae. Third maxilliped similar to that of female. Abdomen with seven free somites, widest at third somite and narrowing toward seventh.

Type species.—By present designation, *Fabia granti* Glassell 1933. The genus is monotypic.

Etymology.—*Calyptraeotheres* has been selected to emphasize the symbiotic relationship between the limpet-crabs and gastropods, family Calyptraeidae. Gender masculine.

Distribution.—East Pacific: Golfo de California and West coast of Baja California Sur at Bahía Magdalena (Glassell 1933, 1935).

Hosts.—Mollusca: Gastropoda: Calyptraeidae: *Crepidula* and *Crucibulum.* Acmaeidae: *Acmaea.*

Remarks.—At present five genera in the Pinnotheridae contain one or more species with the palp of the third maxilliped composed of two articles. These are, *Dissodactylus* (sensu Griffith 1987), *Durckheimia* (sensu Serène 1967), *Ostracotheres* (sensu Tesch 1918, Pregenzer 1988), *Pinnotheres* (sensu Roberts 1975), and *Xanthasia* (sensu Bürger 1895). The genus *Calyptraeotheres* can be distinguished from all of these genera because its carapace is smooth, with the regions ill-defined and the anterolateral margins sharp-edged, and the carpus of the third maxilliped being larger than the digitiform and obliquely truncated propodus. Furthermore, *Calyptraeotheres* is also different ecologically. This genus is an ecosymbiont of limpets, Gastropoda—Calyptraeidae, while the genera listed above are symbionts of echinoids, Bivalvia, and/or Tunicata, which suggest divergent evolutionary trends. Only one species is now included within *Calyptraeotheres*; however, two additional ones, *Pinnotheres politus* (Smith, 1870) and *P. garthi* Fennuci, 1975, possibly should be included in this new genus. The comparison between *C. granti* and descriptions and figures of *P. politus* and *P. garthi* recorded by Rathbun (1918), Garth (1957) and Fennuci (1975) suggest that both males and females of *C. granti* share a morphological similarity to the South American species which are symbionts of limpets, family Calyptraeidae, too. The major difference observed in *P. politus* and *P. garthi* is the presence of a minute and rounded dactylus on the palp of the third maxilliped (Fig. 2B, C). A decision on the status of these Austral species and whether they should be included in *Calyptraeotheres* awaits a revision of the type series or of voucher specimens.

Calyptraeotheres granti (Glassell, 1933), new combination

Figs. 1, 2A, D–F

Fabia granti Glassell, 1933:342, pl. 26, fig. 1–3; 1934:301; 1935:105; 1938:452, pl. 33, fig. 12.—Balss, 1957:1421.—De Melo, 1971:202.—Schmitt, McCain & Davidson, 1973:24.—Campos-González & Macías-Chávez, 1988:241.—Campos, 1989a: 1127.

Material examined.—Eighty-four males,

carapace width from 1.7 to 3.1 mm and 296 females (196 ovigerous), carapace width from 2.2 to 8.8 mm, collected between August 1983 to July 1984, Laguna Percebú, about 23 km south of San Felipe, Baja California, Mexico, (lat 30°49′00″N, long 114°41′40″W), E. Campos coll.

Distribution.—Golfo de California, and West coast of Baja California Sur at Bahía Magdalena (type locality), (Glassell 1933, 1935).

Female.—Carapace (Fig. 1A) with front little projected, anterior third arcuate, lateral margins subparallel and posteriorly convergent; posterior margin straight or little concave in middle. Carapace margins, specially of frontal and anterolateral regions, sharp-edged. Gastric, cardiac and intestinal regions ill-defined, limited by straight cervical depressions arising from orbital region. Antennular grooves large. Orbits small, completely filling sockets, cornea not visible in dorsal view. Buccal cavity crescentic. Third maxilliped placed obliquely, ischium and merus indistinguishably fused, widening distally, inner margin concave, distal margin straight; palp placed in outer angle of merus, with two articles, carpus longer and wider than propodus, latter obliquely truncated (Fig. 2A). Chelipeds stout, palm widening distally, outer and inner surfaces even; dactylus with proximal, small, blunt tooth, occasionally other smaller tooth present; propodus with two proximal blunt teeth separated by notch where tooth of dactylus fits. Fingers little deflexed, without gap when closed; ventral margin of palm almost straight, with fringe of hair arising from distal third reaching to end of pollex; both fingers curved inward to tip.

In decreasing order, relative length of walking legs 3 > 2 > 4 > 1. Third slightly longer then second, latter a little longer than fourth. Legs 1 to 3 of similar shape, their height increasing towards third leg, fourth being the most slender. First three pairs of walking legs with margins of propodi converging distally, those of fourth pair subparallel; relative length of above-mentioned propodi similar to those of walking legs. Dactyli acute and curved at tip, in decreasing order the relative length is 4 > 3 > 2 > 1.

Abdomen with seven free somites, covering the sternum and not reaching to buccal cavity, fourth somite widest, fifth longest.

Male.—Carapace subpentagonal (Fig. 1B), as long as wide, occasionally a little wider than long, regions ill-defined, dorsal surface even, with short, separate setae. With exception of posterior margin in small specimens, carapace margins with closely-set short hair-like setae. Frontal area from widely arcuate to subrectangular, with medial sulcus covered with setae. Cervical depressions similar to the female, but shallower. Eyes dorsally visible. Antennular grooves filling ventral surface of frontal region. Antenna small but visible.

Third maxilliped covered with feathery setae; similar to that of female except for relatively wider merus (Fig. 2D).

Chelipeds stout, longer than first leg, merus and carpus evenly, with hair; chela as long as, or longer than, the preceding articles together; palm widening suddenly in proximal third, dorsal margin almost convex, ventral one rather straight, both with fringe of hair-like setae; palm surfaces covered with scattered hair, inner surface inflated; dactylus curved, with dorsal fringe of hair and proximal, acute and triangular tooth on cutting edge; pollex without hair but with small blunt teeth along cutting surface. Fingers curved inwardly to tip.

Walking legs similar in shape, surface with small and scattered hair-like setae; dorsal and ventral margins of meri, propodi and dactyli with fringe of short and very close setae; legs 2 and 3 with an additional fringe of natatory setae. Propodus spatulate, dactylus curved, more slender than preceding articles. In decreasing order relative length

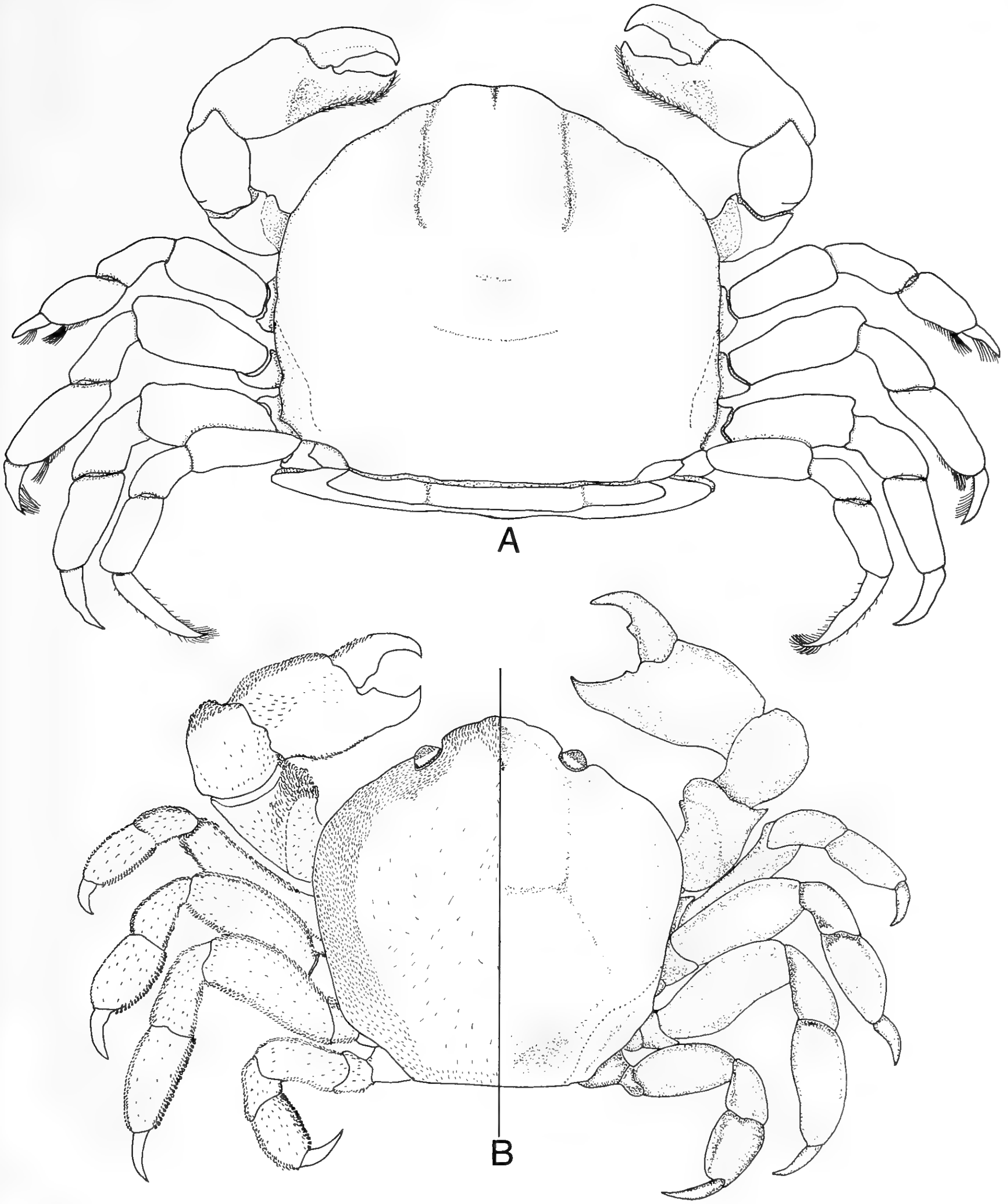
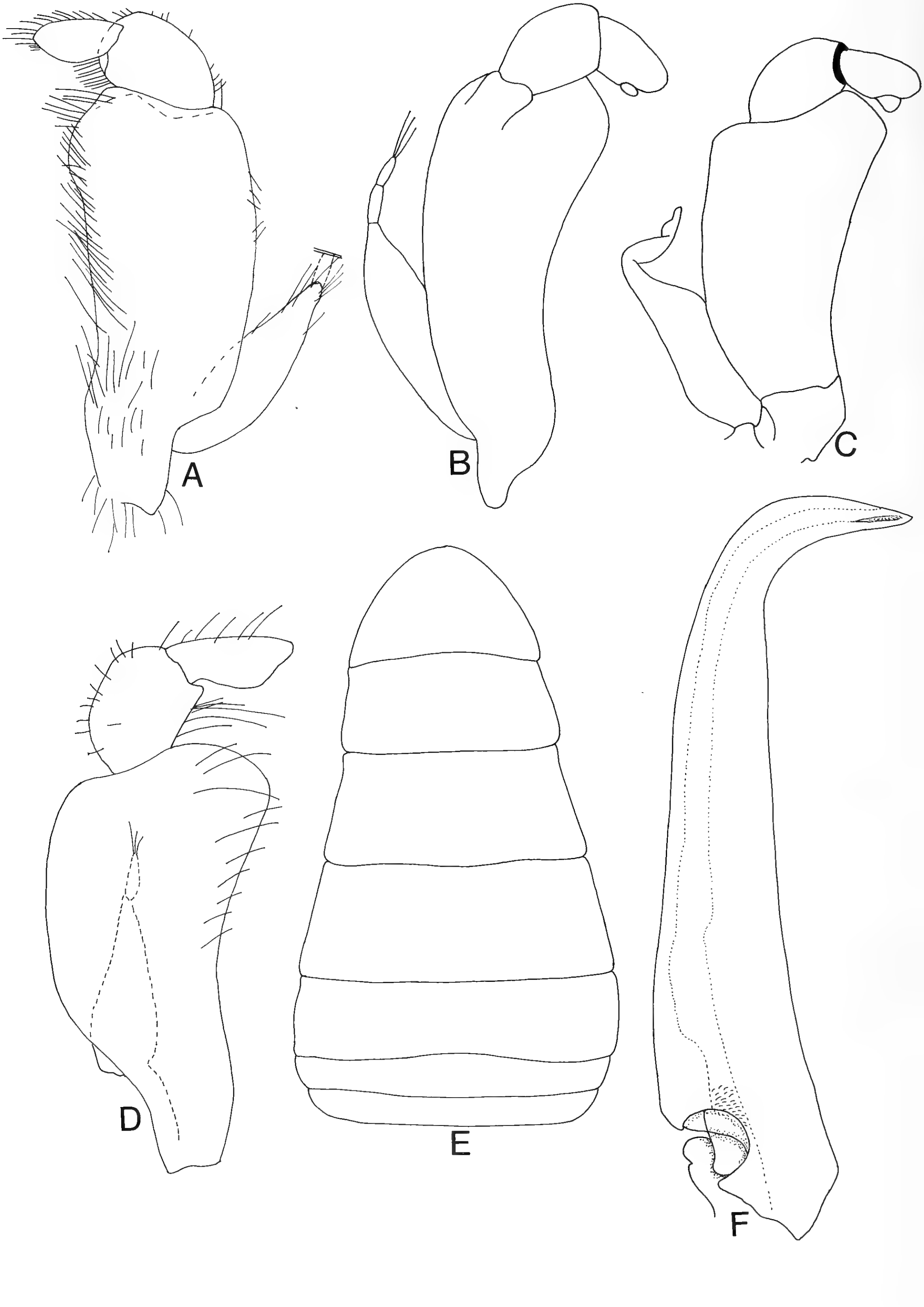


Fig. 1. *Calyptraeotheres granti* (Glassell, 1933): A, female; B, male, right side without hair-like setae.

of walking legs 2 > 3 > 4 > 1; fourth leg reaching to proximal third of propodus of leg 3.

Abdomen (Fig. 2E) with tomentum on margin, widest at third somite, narrowing towards triangular seventh somite; fourth somite longest. Gonopods (Fig. 2F) distolaterally acute, curved the tip, forming right angle.

Taxonomic remarks.—Calyptraeotheres


A
B
C
D
E
F

granti was incorrectly assigned to the genus *Fabia.* This species has two longitudinal depressions on the carapace arising behind the orbital margin. These differ from the longitudinal sulci of *Fabia,* which invariably arise from the upper margin of the orbit (see fig. 54a in Rathbun 1918). In *C. granti* the palp of the outer maxilliped is composed of two articles, the carpus being longer and wider than the digitiform propodus. In all species of *Fabia* the palp of the outer maxilliped has three articles, the carpus being shorter or subequal than the trapezoidal propodus and the dactylus inserted invariably in the middle of the ventral margin of the propodus. In addition, the abdomen of the male in *C. granti* has seven free somites. In contrast males of *Fabia* sensu stricto have two or more abdominal somites fused. As regards to the male's abdominal morphology in the genus *Fabia,* Gore (1986) pointed out that *F. subquadrata* and *F. concharum* have seven free abdominal somites. This supposition herein is considered as a misinterpertation of Davidson's (1968) figures. Rathbun (1918:86) describing the male and the hard stage female of *F. subquadrata* [as *Pinnotheres choncharum* (Rathbun), see Wells (1928) and Davidson (1968) for corrections] noted that the abdomen of both adult males and inmature females possesses the fourth and fifth somites partially fused, contradicting Gore's (1986) interpretation. With respect to *F. concharum,* examination of two hard stage females from the Allan Hancock Foundation (males were not found in the United States National Museum or elsewhere) revealed that abdominal somites 2–4 are fused. Previous accounts about the morphology of the stages of development in Pinnotheridae (Christensen & McDermott 1958, Pearce 1966, Jones 1977, Campos 1989b) have pointed out that an adult or hard stage male and an immature or hard stage female are almost identical morphologically; this applies to the male and inmature female of *Fabia subquadrata* (Rathbun, 1918:86). These observations permit me to infer that males of *F. concharum* have, like the hard stage female, the abdominal somites 2–4 fused. This inference, which must be confirmed, in my opinion is more believable than the interpretation made by Gore (1986). His are based neither on specimens nor in descriptions of the above-mentioned species of *Fabia* but on the Davidson's (1968) figures, which do not reflect adequately the morphology of the male abdomen in both *F. subquadrata* and *F. concharum.* Additional data that support my above-mentioned inference about the adbominal fusion in *F. concharum* is that males of *F. emiliai* (De Melo, 1971) (perhaps a junior synonym of *F. byssomiae* Say, 1818), *F. tellinae* Cobb, 1973 and a new species of *Fabia* from the Golfo de California have two or more abdominal somites fused. This is similar to the condition observed in males and females in the hard stage of *F. subquadrata* and females in the hard stage of *F. concharum.* The remaining four species of the genus *Fabia, F. canfieldi* Rathbun, 1918, *F. sebastianensis* Rodrigues da Costa, 1970, *F. obtusidentata* Dai, 1980, and *F. delderi* Gore, 1986 are incorrectly or questionably assigned to *Fabia* (Campos, in prep).

Ecological remarks.—*C. granti* is common on the intertidal area of the peninsular coast of the upper Golfo de California. However, the greatest number was found in Laguna Percebú area. There I have recorded

---

←

Fig. 2. A, D–F: *Calyptraeotheres granti* (Glassell, 1933). B: *Pinnotheres garthi* Fennuci, 1975, third maxilliped of male. C: *P. politus* (Smith, 1870), third maxilliped of male. A, third maxilliped of female; D, third maxilliped of male; E, Abdomen of male; F, first pleopod of male. A, slightly modified from Glassell (1933); B, redrawing from Fennuci (1975); C, redrawing from Garth (1957).

infestation up to 35%. According to Glassell (1935), *C. granti* was found as symbiont of *Crucibulum spinosum* (Sowerby, 1824), *Crepidula nieva* C. B. Adams, 1852 (= *C. striolata* Menke, 1851), and *Acmaea mesoleuca* Menke, 1851 [= *Nomaeopelta mesoleuca* (Menke, 1851)]. Although I have collected the above three species of limpets, I found *C. granti* living in *C. spinosum* only, a species that I consider as the preferred host. My conclusion is based on the fact that *C. spinosum* is the only of the above species of limpets that possesses a suitable space between the cephalic area and the shell for the growth and development of *C. granti.* The other two species, which have the cephalic-shell area very reduced, perhaps may harbor occasionally and temporarily very young stages of the crabs. This agrees with the observations recorded by Glassell (1935).

Acknowledgments

I am indebted to Raymond B. Manning and Alma Rosa de Campos for the support given to my work on systematics of Pinnotheridae. My great appreciation is due to Lon McClanahan, Roger Seapy and Lady Janie Yeo Kirk who helped me out during my stay at California State University, Fullerton. My gratitude is for George Steyskal who assisted me in the derivation of the generic name *Calyptraeotheres.* This investigation was sponsored by the project "Sistemática y Bioecología de los Arthropoda dominantes en áreas selectas del municipio de Ensenada" of the Escuela Superior de Ciencias, Universidad Autónoma de Baja California and by agreement SEP-UABC 089-01-0352. Voucher material has been deposited in the following institutions: Escuela Superior de Ciencias, Universidad Autónoma de Baja California (uncataloged); National Museum of Natural History (Smithsonian Institution); School of Zoology, University of New South Wales; and San Diego Museum of Natural History.

Literature Cited

Balss, H. 1957. Decapoda, VIII: Systematik, *in* H. G. Bronn, Klassen und Ordungen des Tierreichs, Band 5, Abteilung 1, 7(12):1505–1672.

Bürger, O. 1895. Ein Beitrag zur Kenntniss der Pinnotherinen.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 8:361–390.

Campos, E. 1989a. Comments on taxonomy of the genus *Orthotheres* Sakai, 1969 (Crustacea, Brachyura, Pinnotheridae).—Bulletin of Marine Science 44(3):1123–1128.

———. 1989b. *Tumidotheres,* a new genus for *Pinnotheres margarita* Smith, 1869 and *Pinnotheres maculatus* Say, 1818 (Brachyura, Pinnotheridae).—Journal of Crustacean Biology 9(4):672–679.

Campos-González, E., & L. J. Macías-Chávez. 1988. Fases posplanctónicas de *Petrolisthes armatus* (Gibbes) (Decapoda, Porcellanidae) comensales con la lapa *Crucibulum* (*Crucibulum*) *spinosum* (Sowerby) (Gastropoda, Caliptraeidae) en el alto Golfo de California, Mexico.—Revista de Biología Tropical 35(2):241–244.

Christensen, A. M., & J. J. McDermott. 1958. Life history and biology of the oyster crab, *Pinnotheres ostreum* Say.—Biological Bulletin 114(2): 146–179.

Cobb, S. P. 1973. *Fabia tellinae,* a new species of commensal crab (Decapoda, Pinnotheridae) from the northeastern Gulf of Mexico.—Crustaceana 25(1):70–74.

Dai, Ai-yun. 1980. *Fabia obtusidentata* Dai, sp. nov. *in* Ai-yun Dai, Zhong-qi Feng, Yu-zhi Sung, & Guo-xiao Chen, New species and new records of family Pinnotheridae from Hainan Island.—Acta Zootaxonomica Sinica 5(2):129–142 (In Chinese with English summary).

Davidson, E. S. 1968. The *Pinnotheres concharum* complex (Crustacea, Decapoda, family Pinnotheridae).—Bulletin Southern California Academy of Sciences 67(2):85–88.

De Melo, G. A. S. 1971. Duas novas espécies de Pinnotheridae (Crustacea, Brachyura) do litoral brasileiro.—Papeis Avulsos de Zoologia 23(22): 197–203.

Fennuci, J. L. 1975. Los cangrejos de la familia Pinnotheridae del litoral argentino (Crustacea, Decapoda, Brachyura).—Physis, seccion A 34(88): 165–184.

Garth, J. S. 1957. The Crustacea Decapoda Brachyura of Chile.—Reports of the Lund University Chile Expedition 1948–49 29:1–127.

Glassell, S. A. 1933. Description of five new species of Brachyura collected on the west coast of Mexico.—Transactions of the San Diego Society of Natural History 7(28):331–334.

———. 1934. Affinities of the brachyuran fauna of the Gulf of California.—Journal of the Washington Academy of Sciences 24(7):296–302.

———. 1935. New or little known crabs from the Pacific coast of northern Mexico.—Transactions of the San Diego Society of Natural History 8(14):91–106.

———. 1938. New and obscure decapod Crustacea from the west American coast.—Transactions of the San Diego Society of Natural History 8(33): 411–454.

Gore, R. H. 1986. *Fabia felderi* species novum, a new pinnotherid crab from the central eastern coast of Florida (Crustacea: Decapoda: Brachyura).—Northeast Gulf Science 8(2):143–148.

Griffith, H. 1987. Taxonomy of the genus *Dissodactylus* (Crustacea: Brachyura: Pinnotheridae) with description of three new species.—Bulletin of Marine Science 40(3):397–422.

Jones, J. B. 1977. Post-planktonic stages of *Pinnotheres novaezelandie* Filhol, 1886 (Brachyura: Pinnotheridae).—New Zealand Journal of Marine and Freshwater Research 11(1):145–158.

Pearce, J. B. 1966. The biology of the mussel crab, *Fabia subquadrata* from the waters of the San Juan Archipelago, Washington.—Pacific Science 20(1):3–35.

Pregenzer, C., Jr. 1979. A redescription of *Pinnotheres hickmani* (Guiler) and comparison with *Pinnotheres novaezelandiae* Filhol and *Pinnotheres pisum* (L.) (Decapoda Brachyura).—Crustaceana Supplement 5:22–30.

———. 1988. A redescription of *Pinnotheres holothuriensis* Baker, 1907 and *Pinnotheres subglobosus* Baker, 1907 with a reassignment to the genus *Ostracotheres* (Decapoda, Brachyura).—Crustaceana 55(1):17–28.

Rathbun, M. J. 1918. The grapsoid crabs of America.—United States National Museum Bulletin 97:1–461.

Roberts, M. H., Jr. 1975. Description of a pea crab, *Pinnotheres chamae,* sp. nov. from the jewel box, *Chama congregata.*—Chesapeake Science 16(4):238–241.

Rodrigues da Costa, H. 1970. As species brasileiras da familia Pinnotheridae (Crustacea, Reptantia) com descricao de uma nova espécie (*Fabia sebastianensis*).—Trabalhos Oceanograficos, Universidade Federal da Pernambuco (Recife), 9/11 [1967/1969]:255–264.

Schmitt, W. L., J. C. McCain, & E. S. Davidson. 1973. Decapoda I, Brachyura I. Family Pinnotheridae, *in* H.-E. Gruner & L. B. Holthuis, eds., Crustaceorum Catalogus, 3:1–160, W. Junk, Den Haag.

Serène, R. 1967. Sur deux espèces nouvelles de brachyoures (Crustacés Décapodes) et sur une troisième peu conne, récoltées dans la région Malaise.—Bulletin du Muséum National d'Histoire Naturelle, Paris 38(6):817–827.

Tesch, J. J. 1918. Goneplacidae and Pinnotheridae. The Decapoda of the Siboga Expedition II.—Siboga-Expeditie 39 c^1:1–295.

Wells, W. W. 1928. Pinnotheridae of Puget Sound—Publications Puget Sound Biological Station, University of Washington 6:283–314.

Department of Biological Sciences, California State University Fullerton, Fullerton, California 92634; (Postal address) Escuela Superior de Ciencias, Universidad Autónoma de Baja California, Apartado Postal 2300, Ensenada, Baja California, México.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 372–375

MESACTURUS DICRURUS, NEW SPECIES, AN UNUSUAL STOMATOPOD FROM MICRONESIA (STOMATOPODA: GONODACTYLIDAE)

Roy K. Kropp and Jane H. Dominguez

Abstract.—*Mesacturus dicrurus,* the third species in the genus, is described. The new species is distinguished from other species in the genus by having an apically bifurcate median projection of the telson that is about as long as the base of the telson and that is covered with relatively long setae. The apical bifurcation is V-shaped.

Manning (1969), in a discussion of the *Gonodactylus*-like stomatopods in the Gonodactylidae, presented a diagnosis and discussion of the genus *Mesacturus* and a key to species then included in the genus. He noted that there were two general types of telson morphology in the genus, in one the telson is similar to that of *Gonodactylus,* whereas in the other the telson is characterized by a median bifurcate process. Later, Manning (1978) erected a new genus, *Mesacturoides,* to include the species of *Mesacturus* having *Gonodactylus*-like telsons. Two species, *Mesacturus furcicaudatus* (Miers, 1880) and *M. kempi* (Odhner, 1923), remained in *Mesacturus.*

Among crustaceans collected from consolidated coralline algae at the seaward margin of an erosion bench at Guam, Mariana Islands, we found specimens of *Mesacturus* not referable to either known species. Further examination of stomatopods collected at Saipan, Mariana Islands, by the senior author revealed specimens of the new species. We examined stomatopods in the collection of the National Museum of Natural History, Smithsonian Institution (USNM) that were collected from Yap, Caroline Islands, and had been identified as *M. kempi* and found them to be referable to the new species.

Primary types have been deposited in the USNM, Bernice P. Bishop Museum, Honolulu (BPBM), and the Natural History Museum of Los Angeles County, Los Angeles (LACM), as indicated in the material examined.

We thank the University of Guam Marine Laboratory and the Division of Crustacea, USNM, for support and R. B. Manning for reviewing the manuscript. This is Contribution No. 278 from the University of Guam Marine Laboratory.

Family Gonodactylidae Giesbrecht, 1910
Mesacturus dicrurus, new species
Figs. 1, 2

Material.—Holotype: Mariana Islands: Guam; Pago Bay, Taogam Point [13°25′N, 144°48′E]; from consolidated coralline algae at seaward edge of erosion bench; 7 June 1986; 1 male (USNM).

Paratypes: Mariana Islands: Guam; same locality and habitat as holotype; 3 Sep 1984; 3 females (USNM, LACM). Saipan; sand + coral; 25 Dec 1945; Coll. A. H. Banner; 1 male, 1 female (USNM). Saipan; SSW side of island; in coral heads; 1945; Coll. A. H. Banner; 2 males (USNM). Saipan; Wing Beach, near Matuis [15°16′N, 145°48′E]; from reef rock bearing coralline algae collected just shoreward of reef margin; 0.5 m; 21 Nov 1980; 3 females (BPBM).

Caroline Islands: Yap; Ifalik (formerly Ifaluk) Atoll; south end of Falarik Islet

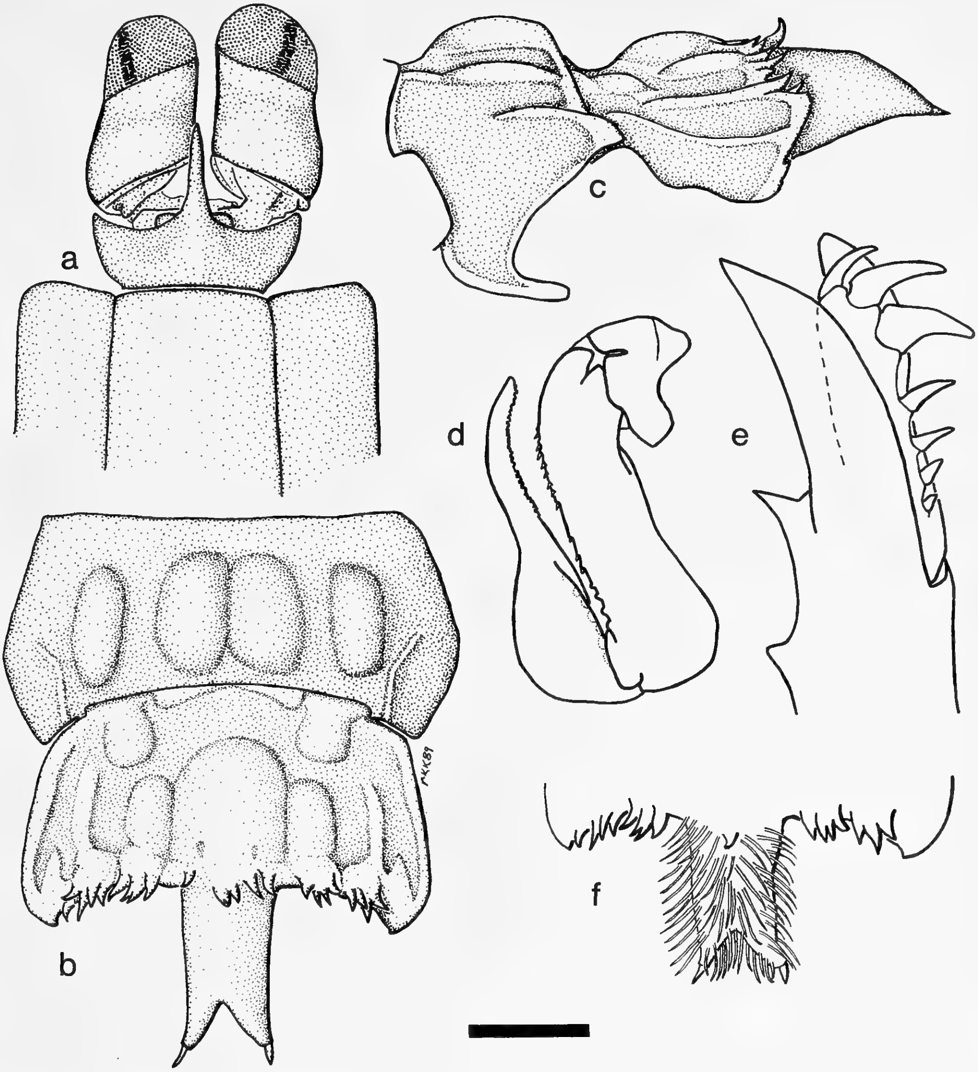


Fig. 1. *Mesacturus dicrurus,* male holotype: a, Anterior part of body; b, Sixth abdominal somite, telson (dorsal view); c, Same (lateral view); d, Left claw; e, Left uropod (ventral view); f, Median projection of telson, showing setae. Scale: 1 mm.

[07°15′N, 144°27′E]; Sta. 13-C-3, 14-B-1, 19-D, 20-C, 706; 25 Aug 1953; Coll. D. P. Abbott and Bates, 4th Pacific Atoll Survey Team, Pacific Science Board; 5 males, 2 females, 1 juvenile (USNM 104692, 104694–7). Ifalik Atoll; north end of Falarik; Sta. 359, 372, 638; 21, 22 Sep, 17 Oct 1953; Coll. F. M. Bayer; 3 males, 2 females (USNM 104689–91).

Description of holotype.—Eyestalks cylindrical, slightly inflated proximally, length about twice width. Ocular scale small, blunt, erect.

Anterior margin of rostral plate concave, anterolateral angles bluntly rounded or acute, but not spiniform, width of plate greater than median length, anterior spine twice as long as basal part of plate.

Dactylus of raptorial claw serrated on distal half of inner margin. Opposable margin

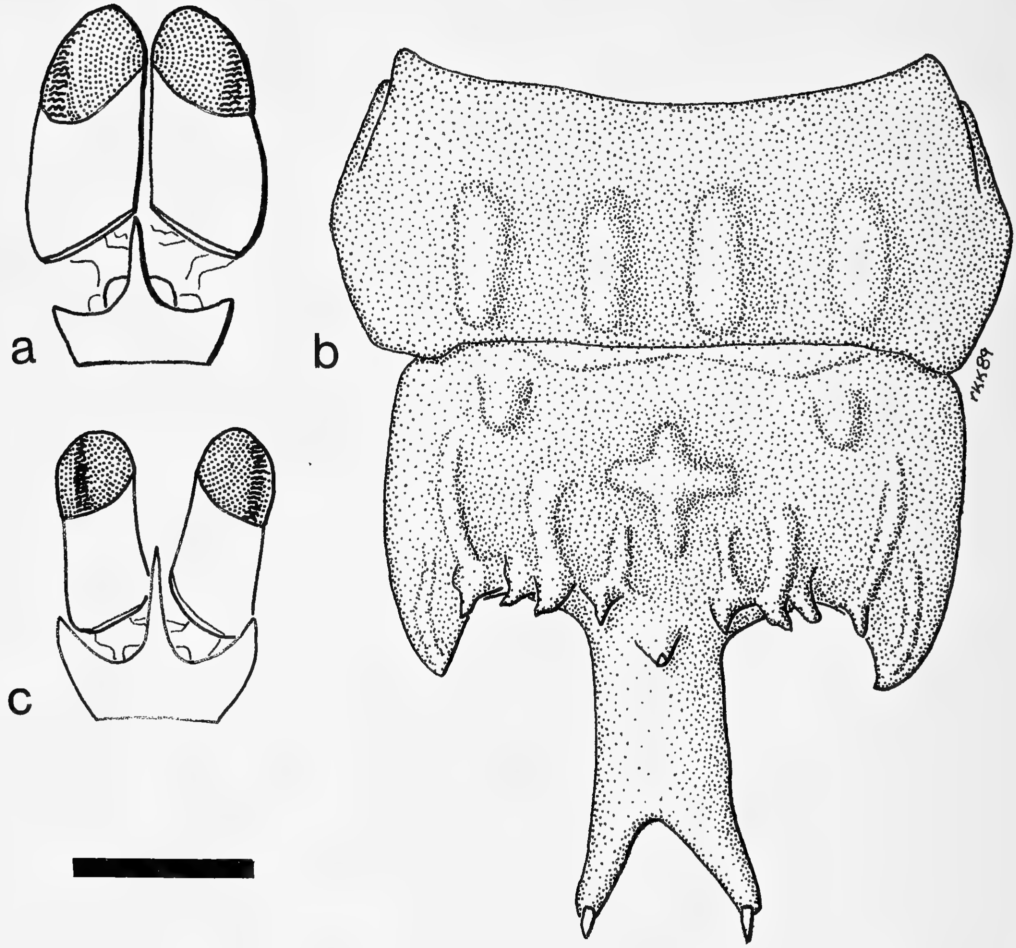


Fig. 2. *Mesacturus dicrurus,* juvenile paratype, total length 12.9 mm: a, Eyes, rostral plate; b, Sixth abdominal somite, telson (dorsal view). Female paratype, total length 33.3 mm (USNM 104692): c, Eyes, rostral plate. Scale: a = 1 mm, b = 0.5 mm, c = 2 mm.

of propodus with 10 articulated teeth along midlength, with 4 rounded bosses proximally fitting into corresponding sockets on dactylus.

Anterior 5 abdominal somites smooth. Dorsal surface of sixth abdominal somite with 4 swollen, unarmed carinae, submedian carinae confluent medially.

Telson slightly wider than long, posterior medial projection half total length of telson, narrowing slightly distally, with V-shaped fork at ⅗ projection length, surface covered with very stout simple setae. Dorsal surface of telson with 3 broadly inflated carinae, median largest. Posterior margin with 4 clusters of 4–5 dorsally curved teeth, base of median projection with 5 irregularly placed teeth.

Base of uropod with single lobe or spine distally near inner margin, outer margin of proximal segment of exopod with 7 spines, distal 3 recurved.

Variations.—Some of the paratypes differed slightly from the holotype. Variation was noticed in the shape of the rostral plate. In some specimens from Falarik the anterior margin of the plate was very concave and the anterolateral angles of the plate more sharply pointed than in specimens from the Marianas (compare Fig. 2c to Fig. 1a). The number of teeth on the margin of the propodus of the raptorial claw ranged from 6 to 13. Size-related variation in the development of carinae on the sixth abdominal segment and the telson, spination of the posterior margin of the telson, and the degree of setal development on the median projection of the telson was noticeable. In larger individuals the carinae were much more swollen than in small individuals (compare Fig. 1b to Fig. 2b). In large individuals the posterior margin of the telson had 4 clusters of 4–5 teeth, but in small individuals the posterior margin had 6 individual teeth. Small individuals had fewer setae on the median projection of the telson than large specimens. The number of teeth on the outer margin of the proximal segment of the uropod varied from 7 to 8. The larger number resulted from the presence of an additional very small tooth proximally.

Measurements.—Total length of males 11.4 to 33.2 mm, of females 10.7 to 33.3 mm. Measurements of holotype: total length 22.4 mm; carapace length 4.6 mm; eyestalk length 1.9 mm; cornea length 0.9 mm; rostral plate length 1.2 mm, width 1.6 mm; sixth abdominal somite width 3.6 mm; telson length (excluding median projection) 1.6 mm, width 3.6 mm; median projection of telson length 1.4 mm.

Color.—Body brown fading to tan at base of telson, median process of telson olive-green. Antennae, walking leg, maxillipeds, pleopods, and uropods pale olive-green. Meral spot clear with black spot anteriorly.

Habitat.—Guam specimens were collected from consolidated coralline algae at seaward edge of erosion bench. Saipan specimens were collected from coralline-encrusted reef rock just shoreward of fringing reef margin or from coral heads. Yap specimens from Station 706 (USNM 104692) were collected from inside coral heads on the outer slope of the reef platform. The bathymetric range of the new species is from the intertidal zone to 0.5 m.

Remarks.—The telson of *Mesacturus furcicaudatus* (Miers, 1880) differs from that of the new species and *M. kempi* (Odhner, 1923) by having a deeply bifurcate median projection; the median projection is shallowly bifurcate in the latter two species. The new species differs from *M. kempi* in the relative lengths of the base of the telson and the median projection. In *M. dicrurus* the median projection is about as long as the base of the telson, whereas in *M. kempi* the median projection is about twice the length of the base. Also, the median projection is covered by relatively long setae in the new species, but in *M. kempi* the projection is covered by relatively short setae. The bifurcation of the median projection of the telson is broadly concave in *M. kempi,* but V-shaped in the new species.

Etymology.—From the Greek *dikros,* meaning forked, in combination with *oura,* meaning tail, in reference to the forked median projection of the telson.

Distribution.—*Mesacturus dicrurus* is known only from Yap, Guam, and Saipan.

Literature Cited

Manning, R. B. 1969. Notes on the *Gonodactylus* section of the family Gonodactylidae (Crustacea, Stomatopoda), with descriptions of four new genera and a new species.—Proceedings of the Biological Society of Washington 82:143–166.

———. 1978. A new genus of stomatopod crustacean from the Indo-West Pacific region.—Proceedings of the Biological Society of Washington 91: 1–4.

Battelle Ocean Sciences, 1431 Spinnaker Drive, Ventura, California 93001.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 376–379

THE PRIMARY TYPES OF THE RICHARD M. BOHART MUSEUM OF ENTOMOLOGY, I. TARDIGRADA

R. O. Schuster, T. L. Tyler, J. A. Skinner, and E. A. Sugden

Abstract.—This paper lists the primary types of Tardigrada deposited in the Richard M. Bohart Museum of Entomology, University of California, Davis, California (UCD). A brief history of the museum is also given.

This is the first in a series of articles listing the primary type specimens in the collection of the Richard M. Bohart Museum, Department of Entomology, University of California, Davis, California (UCD).

All of the primary types listed here are holotypes. The Bohart Museum is presently responsible for 1438 primary types. Information was compiled from type labels, original descriptions, field notes and reexamination of type specimens.

Names listed for types and host species are as in the original description of the type. Changes in the name of a host species before original publication of the type are noted. Zoological or botanical synonomies are not established in this paper.

History of the Bohart Museum Collections

The research collections of the Department of Entomology, University of California, Davis were established in 1946. Mr. A. T. McClay, the first curator, enlarged the holdings from a Schmidt box each of Calliphoridae and honey bees to about 600,000 specimens, housed in California Academy style cabinets. The collection was particularly rich in Coleoptera donated from his personal collection.

Mr. McClay retired in 1966 and managerial responsibility was assumed by Mr. Robert O. Schuster. At that time the decision was made to maintain a type collection, and to broaden holdings of non-insectan arthropods because an invertebrate collection did not exist at the University of California, Davis. Prior to 1966 primary types were deposited with the California Academy of Sciences.

The collections have grown partly through active California-based field research programs, and the result is a rich selection of material from the Western United States and Mexico. In addition, the research interests of faculty and graduate students have led to significant cosmopolitan holdings in many taxonomic groups. In recognition of the rapid destruction of neotropical habitats, the collection and preparation of specimens from northern South America, Central America, and the West Indies is a high priority of the museum.

The various collections of insects and related arthropods were officially dedicated on 11 October 1983 as the Richard M. Bohart Museum of Entomology. The museum holds in excess of four million prepared specimens, includes from 50,000 to 100,000 uncataloged allotypes and paratypes, and is supported by the Department of Entomology and the Bohart Museum Society, founded in 1986. The acronym used for the Richard M. Bohart Museum of Entomology is UCD.

This list, the Tardigrada, contains 21 types resulting from the studies of Albert A. Grigarick, Robert O. Schuster, and Elizabeth C. Toftner at UC Davis, Donald S. (Woody) Horning, Jr., presently at Mcleay Museum, University of Sydney, Australia, the late Franz Mihelčič, and Diane R. Nelson at East Tennessee State University. The tardigrade collection comprises 60,000 slides and is cosmopolitan with specimens from all continents excluding Asia. We felt it appropriate to list the Tardigrada separately from the rest of the primary types, as these invertebrates are not currently thought to be arthropods.

The Bohart Museum Tardigrada Type Collection

Class Heterotardigrada
Family Oreellidae

Oreella breviclava Grigarick, Schuster, & Nelson, 1983:66. Holotype is a female, UCD 1269; type locality La Carbonera, Campo Elias, Merida, Venezuela, 2000 ft, collected by R. W. Brooks, A. A. Grigarick, J. McLaughlin, & R. O. Schuster on 30 Jun 1979.

Family Echiniscidae

Bryodelphax crossotus Grigarick, Schuster, & Nelson, 1983:69. Holotype is a female, UCD 1270, from Rancho Grande, Aragua, Venezuela, 1130 m, collected by R. W. Brooks, A. A. Grigarick, J. McLaughlin, & R. O. Schuster on 14 Jul 1979.

Echiniscus (*Bryodelphax*) *dominicanus* Schuster & Toftner, 1982:225. Holotype is a female, UCD 1215, from Constanza, La Vega Province, Dominican Republic, collected by R. O. Schuster on *Groutiella mucronifolia* (Hooker & Greville, 1824: 116) Crum & Steere 1950:146. Crum & Anderson 1981:738 state that "The type of *Orthotrichum mucronifolium* Hook. & Grev. 1824, collected by Guilding in the West Indies, is clearly the same as the Mexican type of *O. apiculatum* Hook. 1818, collected by Humboldt and Bonpland. It is obvious, therefore, that *Groutiella mucronifolia* belongs in the synonymy of *G. apiculata*." The label data for the host plant for *E.* (*Bryodelphax*) *dominicanus* is probably incorrect, and *Groutiella apiculata* (Hooker, 1818:plate 45) Crum & Steere 1950:146 is the appropriate name for this moss.

Echiniscus aliguantilus Grigarick, Schuster, & Nelson, 1983:73. Holotype is a female, UCD 1266, from La Carbonera, Campo Elias, Merida, Venezuela, collected by R. W. Brooks, A. A. Grigarick, J. McLaughlin & R. O. Schuster on 30 Jun 1979.

Echiniscus becki Schuster & Grigarick, 1966: 127. Holotype sex is uncertain, UCD 209, from Mountaineer Mine, south of Vidal Junction, Riverside Mountains, Riverside County, California, collected by A. J. Beck & R. O. Schuster.

Echiniscus cavagnaroi Schuster & Grigarick, 1966:321. Holotype sex is uncertain, UCD 94, from Old Bella Vista trail, Santa Cruz Island, Galápagos Islands, Ecuador, 90 m, collected by R. O. Schuster, on 4 Feb 1964, in mixture of *Frullania* sp., *Parmelia* sp., and *Ramalina* sp.

Echiniscus horningi Schuster & Grigarick, 1971:105. Holotype sex is uncertain, UCD 322, from Silver Falls State Park, Marion County, Oregon, collected by D. S. (Woody) Horning, Jr., on 10 Jan 1970.

Echiniscus knowltoni Schuster & Grigarick, 1971:109. Holotype sex is uncertain, UCD 401, from Black Pine, Oneida County, Idaho, collected by G. F. Knowlton on 29 Sep 1969.

Echiniscus kofordi Schuster & Grigarick, 1966:321. Holotype sex is uncertain, UCD 95, from Darwin Research Station, Santa Cruz Island, Galápagos Islands, Ecuador, less than 10 m, collected by R. O. Schuster on 21 Jan 1964, on *Ramalina* sp.

Echiniscus (*Echiniscus*) *laterculus* Schuster, Grigarick, & Toftner, 1980:265. Holotype is a female, UCD 1264, from Riverton, El Dorado County, California, collected by E. C. Toftner & R. O. Schuster, on 1 Feb 1974.

Echiniscus marginoporus Grigarick, Schuster, & Nelson, 1983:76. Holotype is a female, UCD 1268, from La Mucuy, Campo Elias, Merida, Venezuela, 2000 m, collected by R. W. Brooks, A. A. Grigarick, J. McLaughlin, & R. O. Schuster, on 30 Jun 1979.

Echiniscus mosaicus Grigarick, Schuster, & Nelson, 1983:76. Holotype is a female, UCD 1267, from La Carbonera, Campo Elias, Merida, Venezuela, collected by R. W. Brooks, A. A. Grigarick, J. McLaughlin, & R. O. Schuster, on 30 Jun 1979.

Echiniscus robertsi Schuster & Grigarick, 1965:56. Holotype sex is uncertain, UCD 93, from bog at Sand Point, Popof Island, Alaska, collected by Warren G. Roberts, in mid June 1963.

Parechiniscus armadilloides Schuster, 1975: 335. Holotype is a female, UCD 904, from Logan Canyon near Logan, Cache County, Utah, collected by D. R. Miller & A. S. Menke, on 5 Apr 1973.

Pseudechiniscus goedeni Grigarick, Mihelčič, & Schuster, 1964:5. Holotype sex is uncertain, UCD 90, from 6 mi SSW of Breitenbush Hot Springs, Marion County, Oregon, collected by K. Goeden, on 18 Oct 1962, in lichens on Douglas fir and cedar.

Pseudechiniscus raneyi Grigarick, Mihelčič, & Schuster, 1964:6. Holotype sex is uncertain, UCD 91, from 46 mi E of Fresno on Hwy 189, Tulare County, California, 4300 ft, collected by A. A. Grigarick, on 31 Oct 1962, in mixed lichen and moss on pine.

Class Eutardigrada

Family Hypsibiidae

Hypsibius (*Diphascon*) *iltisi* Schuster & Grigarick, 1965:32. Holotype sex is uncertain, UCD 92, from Mt. St. Helena, Napa County, California, collected by J. S. Buckett & M. E. Irwin, on 13 Mar 1962, on a rotting cone of *Pseudotsuga menziesii* (Mirbel, 1825:63,70) Franco 1950:74.

Isohypsibius saltursus Schuster, Toftner, & Grigarick, 1977:126. Holotype is a female, UCD 960, from Pope Beach, Lake Tahoe, El Dorado County, California, collected by R. O. Schuster & E. C. Toftner, on 10 Oct 1975.

Family Macrobiotidae

Macrobiotus grandipes Schuster, Toftner, & Grigarick, 1977:118. Holotype is a female, UCD 959, from Pope Beach, Lake Tahoe, El Dorado County, California, collected by R. O. Schuster & E. C. Toftner, on 12 Sep 1975.

Macrobiotus tridigitus Schuster, 1983:254. Holotype sex is uncertain, UCD 1217, from Sierra Martial, Tierra del Fuego, Argentina, 2000–2500 ft, collected by A. M. Shapiro, on 19 Jan 1979, at tree line, in cryptograms.

Pseudodiphascon dubium Schuster & Toftner, 1982:228. Holotype sex is uncertain, UCD 1216, from Cabrera, Sanchez Province, Maria Trinidad, Dominican Republic, collected by R. O. Schuster, on 1 Aug 1978, on *Lejeunea* sp.

Acknowledgments

The authors thank R. M. Bohart for comments on the manuscript, G. L. Webster and K. A. Chambers for assistance with botanical nomenclature.

Literature Cited

Crum, H. A., & L. E. Anderson. 1981. Mosses of eastern North America, volume 2. Columbia University Press, New York, New York, 663 pp.

———, & W. C. Steere. 1950. Additions to the moss flora of Panama.—The Bryologist 53(2):139–152.

Franco, J. D. A. 1950. *Cedrus libanensis* et *Pseudotsuga menziesii.*—Boletim da Sociedad Broteriana, 2 serie, 24:73–77.

Grigarick, A. A., F. Mihelčič, & R. O. Schuster. 1964. New Tardigrada from western North America: I. *Pseudechiniscus.*—Proceedings of the Biological Society of Washington 77:5–8.

———, R. O. Schuster, & D. R. Nelson. 1983. Heterotardigrada of Venezuela.—Pan-Pacific Entomologist 59(1–4):64–77.

Hooker, W. J. 1818. Musci exotici. Containing figures and descriptions of new or little known foreign mosses and other cryptogamic subjects, volume 1. Longman, Hurst, Rees, Orme and Brown, London, viii + pl. 1–96.

———, & R. K. Greville. 1824. Sketch of the characters of the species of mosses belonging to the genera *Orthotrichum* (including *Schlotheimia, Micromitrion* and *Ulota*), *Glyphomitrion* and *Zygodon.*—Edinburgh Journal of Science 1:110–133.

Mirbel, M. 1825. Essai sur la distribution géographique des conifères.—Mémoires du Muséum National d'Historie Naturelle, Paris 13:28–76.

Schuster, R. O. 1975. A new species of *Parechiniscus* from Utah (Tardigrada: Echiniscidae).—Memorie dell'Istituto Italiano di Idrobiologia–Verbania Pallanza 32(Supplemento):105–110.

———. 1983. A new species of *Macrobiotus* from Tierra del Fuego (Tardigrada: Macrobiotidae).—Pan-Pacific Entomologist 59(1–4):254–255.

———, & A. A. Grigarick. 1965. Tardigrada from western North America with emphasis on the fauna of California.—University of California Publications in Zoology 76:1–67.

———, & ———. 1966a. Tardigrada from the Galápagos and Cocos Islands.—Proceedings of the California Academy of Sciences 34:315–328.

———, & ———. 1966b. New Tardigrada from western North America: II. *Echiniscus.*—Proceedings of the Biological Society of Washington 79: 127–130.

———, & ———. 1971. Two new species of *Echiniscus* from the Pacific Northwest (Tardigrada: Echiniscidae).—Proceedings of the Entomological Society of Washington 73(1):105–110.

———, A. A. Grigarick, & E. C. Toftner. 1980. A new species of *Echiniscus* from California (Tardigrada: Echiniscidae).—Pan-Pacific Entomologist 56(4):265–267.

———, & E. C. Toftner. 1982. Dominican Republic Tardigrada. Pp. 221–236 *in* D. R. Nelson, ed., Proceedings of the Third International Symposium on Tardigrada, East Tennessee State University Press, Johnson City.

———, E. C. Toftner, & A. A. Grigarick. 1977. Tardigrada of Pope Beach, Lake Tahoe, California.—Wasmann Journal of Biology 35(1):333–336.

(ROS[1] & TLT) Department of Entomology, University of California, Davis, California 95616; (JAS) Department of Entomology and Plant Pathology, University of Tennessee, Knoxville, Tennessee 37901; (EAS) USDA-ARS Honeybee Lab, 507 W. 4th St., Weslaco, Texas 78596.

---

[1] Mr. Robert O. Schuster unexpectedly died on 15 August 1989, after this paper was submitted.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 380–426

TWO NEW SPECIES OF *MIMAGONIATES* (TELEOSTEI: CHARACIDAE: GLANDULOCAUDINAE), THEIR PHYLOGENY AND BIOGEOGRAPHY AND A KEY TO THE GLANDULOCAUDIN FISHES OF BRAZIL AND PARAGUAY

Naércio A. Menezes and Stanley H. Weitzman

Abstract.—Two new species of freshwater glandulocaudine characid fishes are described from coastal streams of eastern Brazil. The first, *Mimagoniates sylvicola,* is from southeastern Bahia, the second, *Mimagoniates rheocharis,* from southeastern Santa Catarina and northeastern Rio Grande do Sul. *Mimagoniates sylvicola* is hypothesized to form an unresolved trichotomy with *Mimagoniates lateralis* and a monophyletic line leading to the more derived *Mimagoniates microlepis* and *Mimagoniates rheocharis. Mimagoniates rheocharis* most parsimoniously appears to be a sister species of *M. microlepis* but its phylogenetic relationships may be quite complex and its possible introgression with *M. inequalis* and/or its origin by introgression between *M. inequalis* and *M. microlepis* is discussed. Solution to this problem awaits additional data based on more appropriate population samples than available to us and on genetic information. The biogeography of all these species is briefly discussed on the basis of the limited available phylogenetic information.

The descriptions of the new fish species herein continue a series of contributions to the knowledge of the fauna of the streams of the east coast of Brazil. As discussed by Weitzman et al. (1986:344–345), the freshwater fish fauna of the coastal or littoral streams of eastern Brazil appears to contain many new species, a fact unrecognized until the last 15 or 20 years. The descriptions provided here are a product of a continuing study by us of the Glandulocaudinae, a characid subfamily distributed from Costa Rica south to northern Argentina in Atlantic drainages and to the Guyas basin in Pacific drainages. We describe these new fishes here because we wish to have them available for a phylogenetic analysis of the Glandulocaudinae and especially the Glandulocaudini in progress.

The Glandulocaudini, one of apparently four tribes of the Glandulocaudinae (Weitzman et al. 1988:383, Weitzman et al. *in* Weitzman & Fink 1985:112–117), currently consists of two genera, *Glandulocauda* Eigenmann (1911) and *Mimagoniates* Regan (1907). Use of the generic names *Mimagoniates, Coelurichthys* Miranda-Ribeiro (1908) and *Glandulocauda* in the tribe has changed frequently, with little agreement among various authors. Weitzman & Fink (1985:1, 2, 109) reviewed some of the nomenclatural and phylogenetic problems regarding the generic names of the tribe. We follow their usage until ongoing studies allow us to evaluate the present preliminary phylogeny of the tribe based on more abundant data than shown in Fig. 1.

The Glandulocaudini contains eight known species, including the two described here. Schultz (1959), the last author to review the species of the Glandulocaudini in any detail, accepted five species. He considered *M. lateralis* (Nichols) a synonym of *M. inequalis* (Eigenmann). These two species

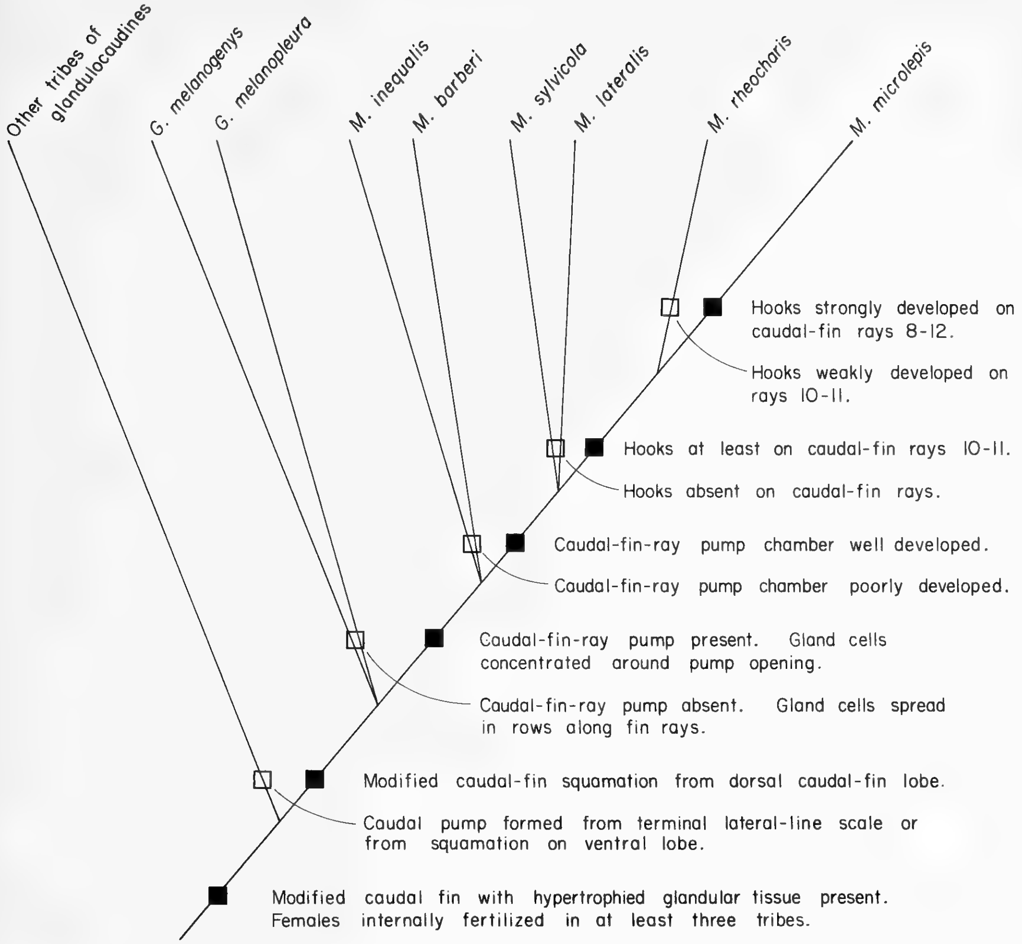


Fig. 1. Diagram of tentative phylogenetic relationships of the species of the Glandulocaudini based on an analysis of synapomorphies found in the caudal skeleton of males. Filled in squares = apomorphies and empty squares = plesiomorphies at the levels indicated.

are recognized as distinct and valid here. Géry (1966:228–230) constructed a key to the tribe and recognized seven species. He appeared doubtful that the group as presented by Schultz or himself was monophyletic. Six of the species tentatively included as valid by Géry are among those accepted here. Inclusion of Géry's seventh species, *Glandulocauda terofali* Géry (1964), would make polyphyletic the monophyletic Glandulocaudini as defined below. This species lacks the modified dorsal lobe caudal-fin squamation that is synapomorphic for the adults of both sexes of all species included by us in the Glandulocaudini. It also lacks the ventrally bowed form of caudal-fin rays 11 and 12 or the particular kind of modification into caudal fin-ray pump structures which form a synapomorphic morphological transformation series confined to members of this tribe. See the key below for a summary exposition of these glandulocaudin characters. We follow Weitzman & Fink (1985:103, 109) in assigning Géry's species to *Diapoma* Cope and accept *Diapoma terofali* (Géry) as a member of the glandulocaudine tribe Diapomini because it has the derived ventral lobe caudal-fin squamation in both sexes closely matching that of *Diapoma speculiferum* Cope. This squamation pattern (see Weitzman & Fink, 1985:fig. 15) is synapomorphic for the Diapomini, which also includes the species of *Acrobrycon* Eigenmann & Pearson and *Planaltina* Böhlke.

The keys to the species of the Glandulocaudini presented by Schultz (1959) and Géry (1966) were based on information from previous literature, some of the types and a few additional specimens. Because we are describing two new species and have examined all of the types and have new information from over 200 recently collected population samples, we provide an almost entirely new key to the species of the Glandulocaudini. See Weitzman et al. (1988:384–390, figs. 5, 6) for distribution maps and a summarized comparison of the collections available to Schultz and to us. A preliminary discussion of the Glandulocaudini, its phylogeny and biogeography were presented by Weitzman et al. (1988:384–419). See also Weitzman & Fink (1985:98–99) for a discussion of the morphology and possible function of the fin-ray pheromone pump mechanism of the species of *Mimagoniates.*

The two new species described below were designated as "new species A" (here = *M. sylvicola*) and "new species B" (here = *M. rheocharis*) in Weitzman et al. (1988). A third putative species, "new species C," recognized as possibly new by them, appears closely related to *M. microlepis* (Steindachner) and may be one of several relatively distinct populations of this species. The relationships among and distinctness of these populations is a complex problem and will require extensive analysis, research not undertaken here.

The importance of well-documented phylogenies to biogeographic hypotheses is emphasized by the changes noted below in the section on biogeography. A change in our tentative understanding of the phylogenetic relationships of *M. sylvicola* based on a population sample unavailable to Weitzman et al. (1988) resulted in a consequent change in our hypotheses regarding the biogeographic history of the species of *Mimagoniates.* Compare the tentative phylogenetic diagram presented here, Fig. 1, with that of Weitzman et al. (1988:fig. 10). The phylogenetic and biogeographic accounts by Weitzman et al. (1988:414–419) of *M. rheocharis* remain essentially unchanged, but questions are raised about of phylogenetic relationships of this species that could have extensive biogeographic consequences, depending on the nature of their answers. The phylogenetic relationships of all species of the Glandulocaudini need further investigation.

Methods and Materials

Counts and measurements are those described by Fink & Weitzman (1974:1–2). In the counts given in the text of the descriptions, the holotype is given first followed by the mean, range and number of paratypes counted given in parentheses. The posterior terminal ray of the dorsal fin is not divided to its base and is counted as one. However, the posterior terminal ray of the anal fin is so divided and thus the apparent two posteriormost rays of the anal fin are counted as one. Note that "branched rays" refers to all rays posterior to the anterior unbranched rays of a given fin even if, as with the posterior terminal ray of the dorsal and pectoral fins, the posterior rays are unbranched at their bases or their distal segments. Body depth was measured vertically (orthogonal to the longitudinal body axis) from the dorsal-fin origin. All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of the head which are recorded as a percentage of head length. Total vertebral counts (including the Weberian apparatus) were taken from radiographs and from cleared Alizarin red and Alcian blue stained preparations. These preparations are called "cleared and stained" in the text. The terminal "half centrum," hypural bones and associated vertebral elements, usually designated as PU_1+U_1, but not necessarily consisting only of those elements (Schultze & Arratia 1989:203) was counted as one vertebral element.

Statistical comparisons and basic statistics of characters taken from population samples were computed using SYSTAT (version 4.0, Systat, Inc., 1989) and BIOM-PC (version 2, Exeter Publishing Ltd, 1988). All hypotheses of statistical significance are two-tailed. Common logarithms were used for transformations of original data used in covariance analyses. In the morphometric scatter plots, both axes are logarithmic and the regression lines are based on log transformed data plotted in the figures. Regression equations given in the figure captions are based on logarithmic transformations of original data and correspond to their respective logarithmic transformed covariance analyses in the text. The regression lines and equations are given only to present a concept of the comparative approximations of the growth lines of sexually maturing and mature population samples within the limits of the data. In no instances are regression lines, regression equations or covariance analyses to be construed as predictors of body shape beyond the data shown in the appropriate plots. Logarithmic regression lines and semilogarithmic scatter plots were prepared using Sigma-Plot (version 3.10, Jandel Scientific, 1988). In cases where a value of a *t*-statistic was computed for comparisons of population means of counts, square-root transformations were utilized. In the key, and abbreviated parts of the diagnoses, the ranges, means and other statistical parameters that may be given are for all of the paratypes and the holotype of each respective new species. In the statistical comparisons (statistical hypotheses of differences), ranges, means and other statistical parameters are naturally limited to the population samples being compared.

In our discussions, comments on phylogeny are based on the concepts of phylogenetic systematics of Hennig (1966) as reviewed and discussed by Wiley (1981). Maddison et al. (1984) are followed for outgroup considerations. Biogeographic principals follow Humphries & Parenti (1986).

Specimens examined for this study are deposited in the Museu Anchieta, Porto Alegre (MAPA), Museu de Zoologia da Universidade de São Paulo (MZUSP); the Smithsonian Institution, National Museum of Natural History (USNM); Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul (MCP); Museum of Zoology, University of Michigan (UMMZ) and the California Academy of Sciences (CAS). Specimens examined in detail, other than those listed or cited here, were listed in Weitzman & Fink (1985:102–108.

Geographic entities (such as rivers) and place names (except those of countries) are in the language of the country of origin. Countries are in English because there is an English name for the various countries. Therefore rio (rio in Portuguese, río in Spanish) is not capitalized when referring to a river (thus rio Jordão and rio Grande), but it is capitalized when referring to a place name (thus Rio de Janeiro and Rio Grande do Sul). We do this because we are attempting to avoid the transferal of English style and grammar onto foreign localities and geographical units.

Key to the Species of the Glandulocaudini

Although this key employs many characters that are apparently synapomorphic at their level of use, the key is not a hypothesis of phylogeny for any of the included taxa except for the Glandulocaudini diagnosed in the first half (1a) of the first couplet. Because the primary purpose of this key is to identify species, we use any appropriate character that either clusters and/or distinguishes species. Thus, except for couplet 1a where the characters are synapomorphies, a given character may be either a plesiomorphy, a synapomorphy or an autapomorphy at its point of use. At this time we lack corroborated polarity hypotheses for many of the characters that are not associated with the secondary sexual features of adult males and our hypotheses for the secondary sexual characters cannot be considered well-supported. Homoplastic characters are used where they serve the purpose of the key. The reader should note that when using couplet 4, many maturing males of species of *Mimagoniates* that have a well-developed caudal pump chamber when fully mature, will key to 4a rather than 4b (where they belong) because of the incomplete development of the specimen's caudal fin-ray pump. This will often be the case in relatively small and some moderate sized specimens even in the presence of apparently active testes.

1a. Adult males and females with modified caudal-fin squamation extending posteriorly onto caudal fin from base of ventral portion of dorsal caudal-fin lobe; principal caudal-fin rays 11 and 12 of adult males somewhat bowed or curved ventrally, these and adjacent rays modified into a chamber or support for a chamber of a fin-ray pump organ in some species (compare Figs. 2–6) . . . . Glandulocaudini (2)

1b. Adult males and females without modified caudal-fin squamation or, if such scales present, then these derived from both caudal-fin lobes, only from ventral caudal-fin lobe or primarily from terminal lateral-line scale; principal caudal-fin rays 11 and 12 of adult males straight or if modified, not bowed ventrally (as in Fig. 6) or modified into a fin-ray pump organ (as in Figs. 2–5) although they may provide origins for muscular and ligamentous attachments to a scale-diaphragm pump mechanism . . . . other tetragonopterine or glandulocaudine characid groups

2a. Caudal fin-ray pump absent in all sexes at all ages (see Fig. 6); hypertrophied glandular tissue widespread along caudal-fin rays, especially those of ventral caudal-fin lobe, but most dense along proximal portions of rays 11 and 12; more than 1 hook on each anterior anal-fin ray that bears hooks . . . . *Glandulocauda* (3)

2b. Caudal fin-ray pump present in mature males, modified primarily from caudal-fin rays 10–12, sometimes relatively simple and represented by expanded, flattened anterior portions of ray halves, sometimes by an anterior fin-ray pump chamber; hypertrophied glandular tissue confined to area immediately around and on caudal pump region of gland (see Figs. 2, 5); no more than 1 hook on any anal-fin ray that bears hooks . . . . *Mimagoniates* (4)

3a. Branched anal-fin rays 20–23; perforated lateral line scales 11–21; scale rows between dorsal-fin origin and anal-fin origin 14–17; scale rows around caudal peduncle 17–18, usually 18; dorsal-fin origin somewhat anterior to vertical line drawn from anal-fin origin . . . . *Glandulocauda melanogenys* Eigenmann
(upper rio Tietê, in São Paulo, Brazil)

3b. Branched anal-fin rays 15–18; perforated lateral-line scales 4–6; scale rows between dorsal-fin origin and anal-fin origin 11–13; scale rows around caudal peduncle 16; dorsal-fin origin somewhat posterior to vertical line drawn from anal-fin origin . . . . *Glandulocauda melanopleura* Eigenmann

(upper rio Iguaçu, in Paraná and
Santa Catarina, Brazil)

4a. Caudal fin-ray pump little developed in males of completed sexual maturity and without obvious pump chamber enclosed by modified proximal portions of caudal-fin ray halves 11 and 12; ray halves of this region of these rays modified into expanded, flattened structures parallel to one another; these modified ray halves of each side of caudal fin developed so that a groove exists between them; groove and accompanying hypertrophied glandular tissue constitute a primitive pump organ (see Figs. 2, 3) (5)

4b. Caudal fin-ray pump well-developed in males of completed sexual maturity, consisting of bilateral chambers, one on each side of fin and each chamber enclosed by flattened expanded portions of ray halves of rays 11 and 12; pump chamber with an obvious posterior opening, lateral slit and anterior opening (see Figs. 4, 5) .... (6)

5. Branched anal-fin rays 23–29, usually 25–27, rarely 28 or 29; scales in lateral series (including lateral line scales) 36–41, usually 37–40; scale rows between dorsal-fin origin and anal-fin origin 16–18; dorsal-fin origin at vertical line drawn from base of second or third branched anal-fin ray; mid-lateral dark body stripe of adult males diffuse, poorly developed, often not apparent; body depth approximately 2.7 to 3.3 in SL ....
.... *Mimagoniates inequalis* (Eigenmann)
dos Patos and lagoa Mirim, in Rio
Grande do Sul, Brazil and
northeastern Uruguay)

5b. Branched anal-fin rays 30–36; scales in lateral series 41–48; scale rows between dorsal-fin origin and anal-fin origin 13–15; dorsal-fin origin at line drawn vertically from base of seventh to ninth branched anal-fin rays; lateral dark body stripe of adult males nearly black, clearly distinct; body depth at dorsal-fin origin about 4.0 to 4.5 times in SL ... *Mimagoniates barberi* Regan
(tributaries of rio Paraguay in
parts of Brazil and Paraguay)

6a. Hooks absent on all principal caudal-fin rays of adult males (see Figs. 3, 11, 12) .... (7)

6b. Hooks present on at least principal caudal-fin rays 10 and 11 of adult males, hooks also frequently present on ray 12 (see Figs. 5, 21) ... (8)

7a. Lateral series scales 49–56; scale rows between dorsal-fin and anal-fin origins 16–18; body depth of adult males 3.4–3.8 in SL; in wild caught specimens body silvery blue, when black horizontal stripe present, located at and partly dorsal to mid-lateral region of body from tip of snout to central caudal-fin rays, stripe diffuse and broad and often obscured by silvery blue coloration posteriorly and by silvery pigment anteriorly; stripe rarely clearly defined ....
.... *M. sylvicola,* new species
(tributaries of Atlantic Ocean in
southern Bahia, Brazil)

7b. Lateral series scales 37–44; scale rows between dorsal-fin and anal-fin origins 12–15; body depth of adult males 3.8–5.1 in SL; in wild caught specimens body mahogany brown, especially dorsally, with dark brown, nearly black, horizontal lateral body stripe below mid-region of body prominent and extending from tip of lower jaw, posteriorly ventral to eye, across opercle and body sides just ventral to mid body region onto caudal peduncle and across central portion

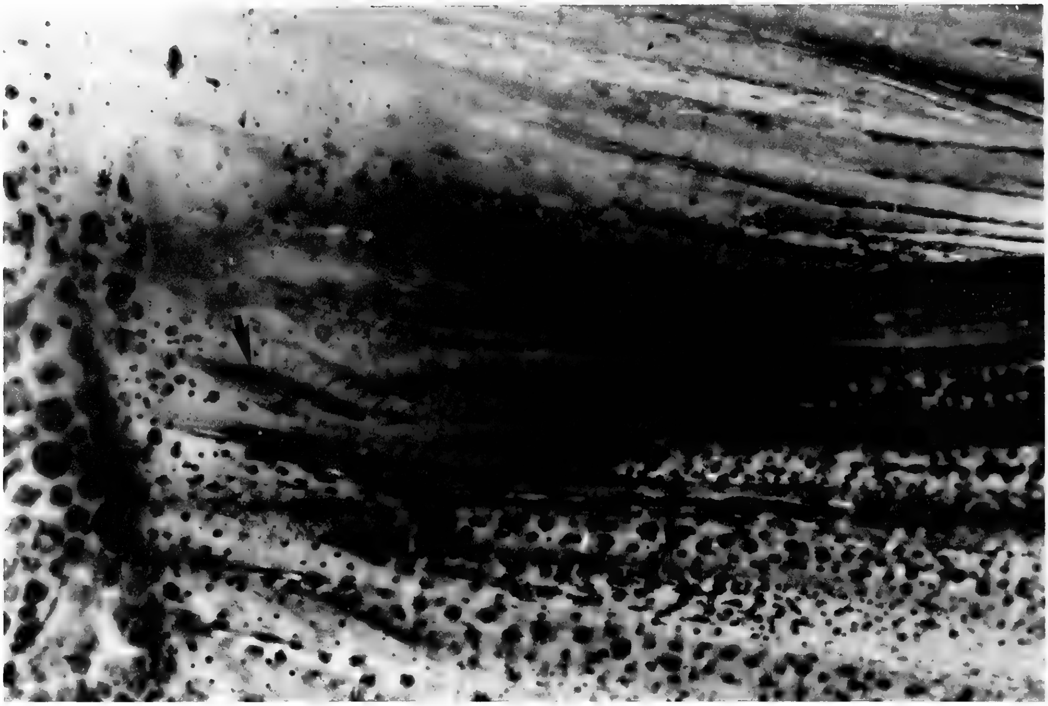


Fig. 2. *Mimagoniates barberi,* unstained central basal region of caudal fin adjacent to caudal peduncle of a preserved adult male, lateral view, left side, anterior at left. SL 32.7 mm, UMMZ 205420, Paraguay, río Aguarymi, tributary to río Paraguay, San Pedro. Illustrates external features of a caudal gland without complex pump chamber. Darkly pigmented glandular groove between principal rays 11 and 12 indicated by arrow. Modified dorsal caudal-fin lobe scales, although present, are transparent and not visible.

of caudal fin .... *Mimagoniates lateralis* (Nichols) (tributaries of Atlantic Ocean from Santos, São Paulo south to Joinville, Santa Catarina, Brazil)

8a. Branched anal-fin rays 23–29, usually 24–26; branched dorsal-fin rays 8–12, rarely 8; scale rows between dorsal-fin origin and anal-fin origin 17–22, usually 19–20; scale rows around caudal peduncle 19–23, usually 20–22; branched dorsal-fin rays 8–12, rarely 8; very small hooks on caudal-fin rays 11–12 of fully adult males (Fig. 21); dorsal-fin origin at vertical line drawn from anal-fin origin or from base of 2 to 4 rays posterior to anal-fin origin .... *Mimagoniates rheocharis,* new species (tributaries to Atlantic Ocean of southern Santa Catarina and northern Rio Grande do Sul, Brazil)

8b. Branched anal-fin rays 26–33, usually 28–31; branched dorsal-fin rays 7–9, rarely 9; scale rows between dorsal-fin origin and anal-fin origin 14–17, usually 15–16; scale rows around caudal peduncle 15–18; numerous strong hooks on at least caudal-fin rays 11–12 (sometimes 7–12) of fully adult males (see Fig. 5); dorsal-fin origin at a vertical line drawn from base of branched anal-fin rays 5 or 6 . ... *Mimagoniates microlepis* (Steindachner) (tributaries to

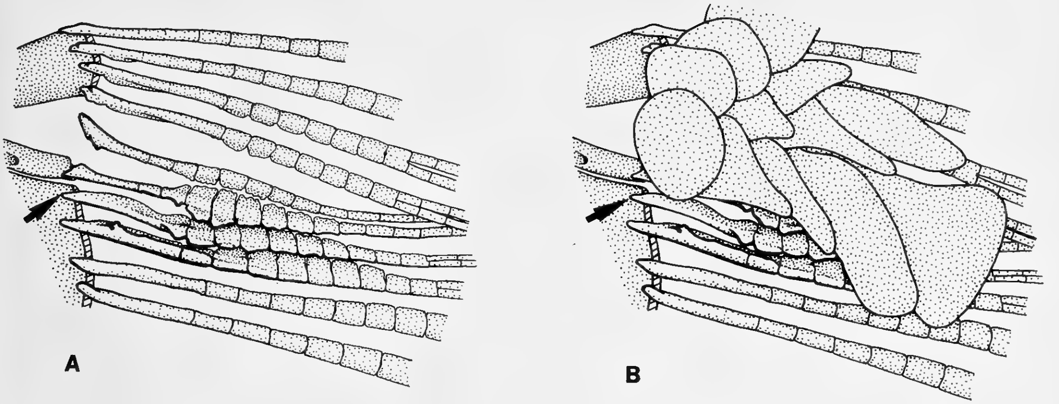


Fig. 3. *Mimagoniates barberi,* osteology of central basal region of caudal-fin skeleton, principal fin-rays 6–15, of adult male, lateral views, left side, anterior at left. SL 35.6 mm, UMMZ 205420, same locality as Fig. 2. Principal ray 12 indicated by arrow. (A) Illustrates glandular groove between rays 11 and 12. (B) Illustrates relationship of modified dorsal caudal-fin lobe squamation to glandular groove. Note that modified scales together with their epidermis form a movable flap just lateral to surface of rays and glandular groove. Free border of this flap occurs along ventral margin of ventral row of scales and at posterior edge of posterior scale of ventral scale row.

Atlantic Ocean from southern Bahia south to northern Rio Grande do Sul, also in upper rio Iguaçu, Paraná)

Mimagoniates sylvicola, new species

Figs. 7–16, Table 1

Species A.—Weitzman et al., 1988:figs. 6, 10 [phylogeny and biogeography].

Holotype.—MZUSP 36612, male, SL 30.2 mm, Brazil, Bahia, Município de Prado, forest stream tributary to Atlantic Ocean, near Fazenda Embaçuaba, approximately 8–9 km NW of Cumuruxatiba, 17°05′S, 39°13′W, 20 Mar 1985; N. Menezes, R. M. C. Castro, M. Weitzman, and S. Weitzman.

Paratypes.—Following 2 lots of immatures to adults collected with holotype: MZUSP 28817, spms. 42, SL 15.1–30.2 mm; USNM 276557, spms. 42, SL 14.7–33.5 mm, 1 male SL 29.3 mm and 1 female SL 26.6 mm [both cleared and stained]. Following lots of immature to adult paratypes all collected 20 Mar 1985 by N. Menezes and party unless otherwise noted: MZUSP 28815, spms. 77, SL 11.0–27.4 mm; USNM 276547, spms. 77, SL 14.4–27.4 mm, Brazil, Bahia, Município de Prado, first stream (locally called rio do Sul) south of rio Caí, on road between Cumuruxatiba and Itamaraju, 17°00′S, 39°12′W. MZUSP 28816, spms. 28, SL 12.7–25.1 mm; 6, spms. 25, SL 13.2–24.0 mm, Brazil, Bahia, Município de Prado, small stream NW of Cumuruxatiba, about 17°01′S, 39°12′W. USNM 300633, spms. 5, SL 22.3–31.3 mm and USNM 300634, spm. 1, cleared and stained, SL 31.8 mm, Brazil, Bahia, Município de Porto Seguro, riacho Ronca Água, tributary to right margin of rio Camurugi, tributary to rio João de Tiba drainage, 15 km NW of Porto Seguro, approximately 16°20′S, 30°07′W, 19 Feb 1986, I. Rosa and party.

Diagnosis.—*Mimagoniates sylvicola* may be separated from all other species of *Mimagoniates* by use of the key to the species provided above. It is distinguished from its morphologically most similar relative, *M. lateralis,* by the following characters: lateral series scales 49–56 (37–44 for *M. lateralis*), scale rows between dorsal-fin and anal-fin origins 16–18 (12–15 for *M. lateralis*). Certain body measurement ratios differ signif-

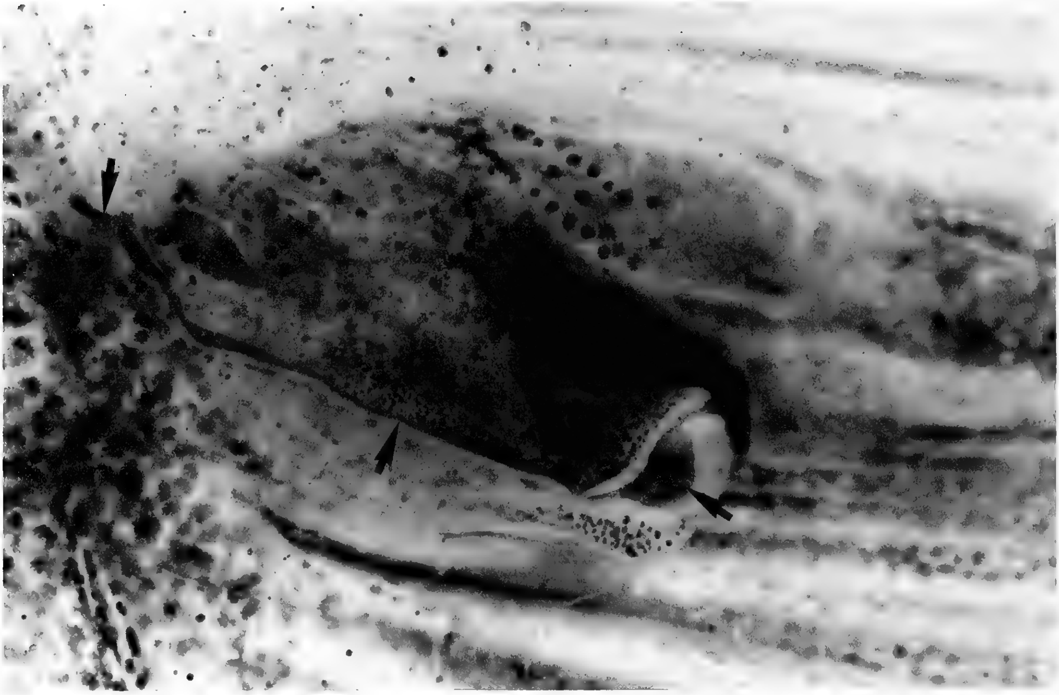


Fig. 4. *Mimagoniates microlepis,* unstained central basal region of caudal fin adjacent to caudal peduncle of a preserved adult male, lateral view, left side, anterior at left. SL 51.7 mm, USNM 279876, Brazil, Santa Catarina, rio Itapocú. Illustrates external features of a caudal gland with a complex pump chamber. Arrow at left indicates anterior intake opening, middle arrow indicates lateral slit of chamber and arrow at right designates posterior exit opening of chamber. These openings surrounded by glandular tissue, especially exit opening. Modified dorsal caudal-fin scales appear as rather poorly focused "ghost" images in upper half of picture, above main body of pump chamber.

icantly between adults of these species but overlap broadly in young and juveniles. For example, body depths in adult males and females of *M. sylvicola* diverge considerably from those in adult males and females of *M. lateralis* (body more elongate and slender). See "*Discussion*" below and Figs. 15, 16. Preserved and live colors differ between the species. Preserved males of *M. sylvicola* with dark lateral body stripe relatively pale and diffuse, occurring mostly at and partly dorsal to mid-lateral body region. Approximately dorsal half of opercle dark, nearly black (relatively pale in *M. lateralis*). *Mimagoniates lateralis* with a dark, relatively narrow, clearly defined lateral body stripe that lies mostly ventral to mid-lateral body region. Dark stripe continues onto ventral one-third of opercle. Males of *M. sylvicola* with distal one-fourth to one-fifth (less posteriorly) of anal-fin rays black (distal two-thirds to one-half black in *M. lateralis*). Males of *M. lateralis* with distal one-fourth of most elongate anterior unbranched ray and branched portions of anterior five to six branched rays hyaline or with a thin scattering of dark chromatophores, never black as in *M. sylvicola.* Numerous other, but less obvious, color differences occur in preserved males of both species. These best discerned by comparing respective color descriptions given below. Life color of these

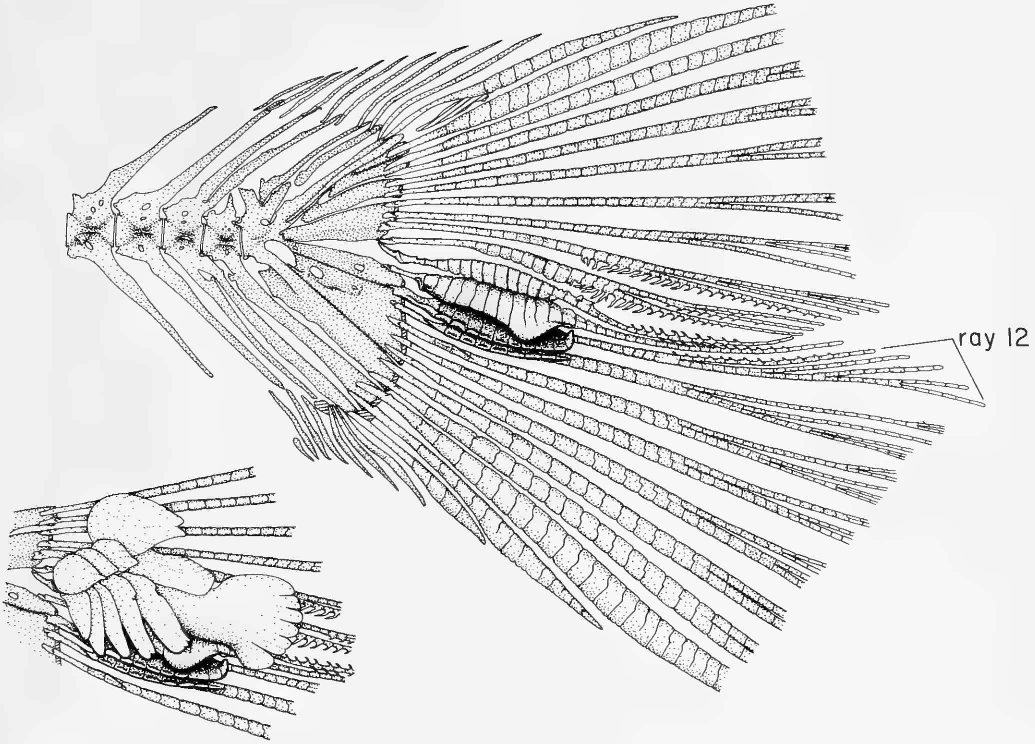


Fig. 5. *Mimagoniates microlepis,* osteology of central and basal region of caudal skeleton of adult male, lateral view, left side, anterior at left. SL 45.3 mm, USNM 236089, Brazil, Paraná, rio Nhundiaquara at Morretes. Relationship of modified dorsal lobe caudal-fin squamation to caudal gland shown in inset at left. Distal regions of ventral and posterior scales and their epidermis form a flap partly covering intake openings of pump chamber.

species quite different. Male *M. sylvicola* with dorsally located black lateral "stripe" obscured by silvery blue reflective color, especially anteriorly. Ventrally located black stripe of male *M. lateralis* deep black except at its mid-length ventral to dorsal-fin origin where partly obscured by blue to silvery pigment in some population samples. Wild caught males of *M. lateralis* with a yellow-orange stripe just ventral to black lateral stripe, absent in *M. sylvicola,* although both species often with anal-fin base yellow to orange. Note, in aquaria at least, *M. lateralis* loses yellow or orange coloration but black stripe always present. See live color descriptions below for a more complete account of *M. sylvicola.*

Description.—Table 1 presents morphometrics of holotype and paratypes. Except where noted, entire description refers to lots from near Cumuruxatiba. These collections are treated statistically as one population sample since no statistical differences were found among them and all lots were collected from only a few kilometers apart. Counts for specimens from rio Camurugi are given only when they differ from those from near Cumuruxatiba.

Body compressed, moderately elongate; body deepest about midway between snout tip and dorsal-fin origin, near anal-fin origin. Predorsal body profile gently convex to snout tip. Body profile slightly elevated at dorsal-fin origin, straight along dorsal-fin base and nearly straight to origin of dorsal procurrent caudal-fin rays. Dorsal-fin origin

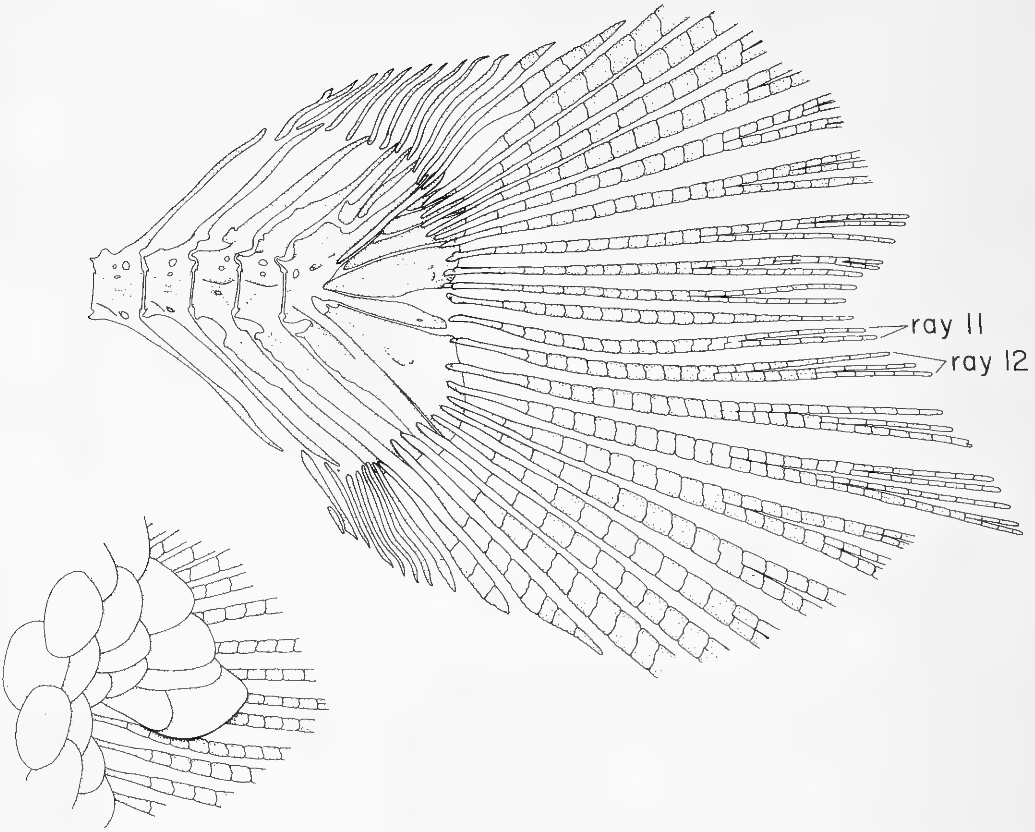


Fig. 6. *Glandulocauda melanogenys,* osteology of central and basal region of caudal skeleton of adult male, lateral view, left side, anterior at left. SL 40.2 mm, USNM 236093, Brazil, São Paulo, headwater stream of rio Tietê near Campo Grande (=Alto da Serra, type locality), about 3.5 km west of Paranapiacaba. Decurved principal caudal-fin rays 11 and 12 are labeled and inset at left illustrates relationship of modified dorsal caudal-fin squamation to rays 11 and 12. Note that modified caudal-fin squamation of females of in all species of *Glandulocauda* and *Mimagoniates* is very similar to that illustrated here but may reach only about half the relative dimensions depicted here.

nearer to caudal-fin base than to snout tip. Ventral body profile convex from anterior tip of lower jaw to point on abdomen about midway between pectoral- and pelvic-fin bases. Belly profile abruptly becomes concave and then straight to anal-fin origin. Body profile slightly convex along anal-fin base to anal-fin insertion. Ventral profile of caudal peduncle slightly convex, especially in adult males where profile formed by ventral procurrent caudal fin rays. In females and juveniles this profile nearly straight.

Head and snout of moderate size in proportion to body length. Lower jaw protruding, anterior to upper jaw. Lower jaw of males thick and heavy compared to that of females. Mouth angled posteroventrally from anterior tip of snout to posterior part of mandibular joint. Maxilla extending posteriorly to a point anterior of a vertical line drawn through anterior border of pupil of eye.

Dorsal-fin rays ii,8 (unbranched rays ii in all specimens, branched rays $\bar{x} = 8.0$ [3 spms. with 9], range = 8–9, $n = 90$); of 6 specimens from rio Camurugi (not included in $n = 90$)

Table 1. Morphometrics of *Mimagoniates sylvicola,* new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Specimens are from the area near Cumuruxatiba, Bahia, MZUSP 28815, 28816, 28817, 36612 and USNM 276547, 276556, 276557.

	Holotype	n	Range	$\bar{x}$
Standard length	30.2	88	14.5–30.2	20.9
Depth at dorsal-fin origin	—	88	20.7–29.3	24.9
Males	29.1	44	21.5–29.3	25.7
Females	—	44	20.7–27.2	24.0
Snout to dorsal-fin origin	61.6	88	57.1–63.8	60.1
Snout to pectoral-fin origin	28.1	88	24.3–29.0	26.3
Snout to pelvic-fin origin	43.4	88	39.8–46.9	43.3
Snout to anal-fin origin	55.6	88	54.4–61.0	57.1
Caudal peduncle depth	—	88	8.5–14.3	10.8
Males	13.2	44	8.7–14.3	11.6
Females	—	44	8.5–11.7	10.1
Caudal peduncle length	12.3	88	10.2–13.8	12.1
Pectoral-fin length	23.2	88	20.2–24.8	22.6
Pelvic-fin length	14.9	88	11.1–16.1	13.3
Dorsal-fin base length	14.2	88	11.8–16.6	13.8
Dorsal-fin height	19.2	88	14.4–21.0	18.1
Anal-fin base length	33.4	84	29.7–35.2	32.6
Anal-fin lobe length	19.2	87	17.2–22.6	20.1
Eye to dorsal-fin origin	46.4	88	42.9–51.0	46.3
Dorsal-fin origin to caudal-fin base	43.7	88	39.4–46.9	42.4
Bony head length	27.8	88	24.8–28.6	26.3
Horizontal eye diameter	35.7	90	33.7–47.4	40.6
Snout length	22.6	90	20.8–26.5	23.8
Least interorbital width	33.3	90	31.6–40.5	35.3
Upper jaw length	45.2	90	34.4–49.3	45.7

2 with 8 and 4 with 7 branched rays; posterior ray not split to its base and counted as 1. Adipose fin present, slender. Anal-fin rays iv,25 (unbranched rays iv in all specimens, branched rays $\bar{x} = 24.8$, range = 23–26, $n = 90$); posterior ray split to its base and counted as 1. Anal fin with moderately developed lobed anterior portion including fourth unbranched ray and first 5–6 branched rays. Anal fin of sexually mature males with bilateral blunt hooks on anterior 6 branched fin rays, 1 set of hooks for each ray (see Fig. 9). Pectoral-fin rays i,10 (unbranched rays i in all specimens, branched rays $\bar{x} = 9.7$, range = 9–11, $n = 90$); all 6 specimens from rio Camurugi with 10 branched rays. Posterior tips of longest pectoral-fin ray extend posteriorly beyond origin of pelvic fin; of about equal length in both sexes. Pectoral-fin rays without hooks. Pelvic-fin rays 8 (8 in all specimens except 1 with 9, $n = 90$). Pelvic fin with anterior most ray branched in all specimens (see Fig. 10). Adult males with total of over 100 small to tiny hooks present on rays of pelvic fin, distributed as in Fig. 10. Each ray bears 9 to over 40 hooks, depending on the maturity of the specimen and/or the fin ray examined.

Principal caudal-fin ray count 10/9 in all specimens ($n = 90$). Fin rays modified in association with caudal pheromone pump as in Figs. 11 and 12. Fig. 11 illustrates a relatively immature pump, while Fig. 12 shows a presumably mature pump in which pump chamber has well-developed water

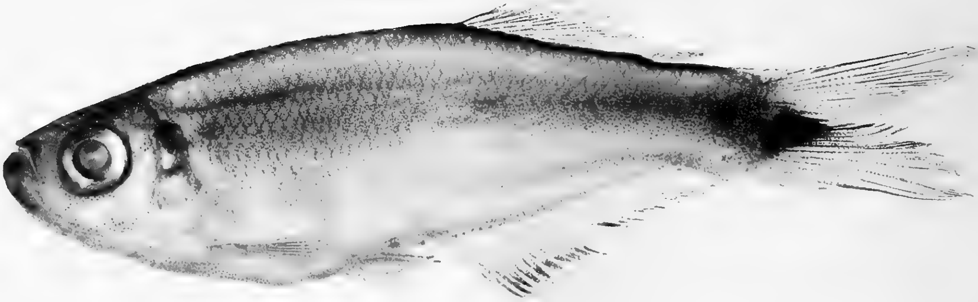


Fig. 7. *Mimagoniates sylvicola,* new species, holotype, MZUSP 36612, male, SL 30.2 mm; Brazil, Bahia, Município de Prado, unnamed forest rivulet near Fazenda Embaçuaba, 8–9 km northwest of Cumuruxatiba.

entrances and exit. Fin rays modified very much like those of *M. lateralis.* Caudal-fin rays without bony hooks. See also Weitzman & Fink (1985:98–99), Weitzman et al. (1988:384–413) and "*Discussion*" below, regarding phylogeny of *M. sylvicola* for hypothetical function of secondary sexual characters and phylogeny for glandulocaudins as indicated by their caudal pump morphology.

Scales cycloid, almost deciduous, with few radii along posterior border; smallest scales often nearly without or without radii. Terminal scale of modified caudal series with exaggerated radii appearing as incisions of posterior scale borders (see Figs. 11b, 12b).

Lateral line incomplete, perforated scales 8 ($\bar{x} = 7$, range = 6–8, $n = 34$); 2 specimens from rio Camurugi with 9 perforated scales. Lateral series scales 53 ($\bar{x} = 52.7$, range = 49–56, $n = 34$). Predorsal scales 25 ($\bar{x} = 25.9$, range = 24–28, $n = 39$). Scale rows between dorsal-fin origin and anal-fin origin 17 ($\bar{x} = 16.7$, range = 16–18, $n = 64$). Scale rows around caudal peduncle 20 ($\bar{x} = 19.7$, range = 19–20, $n = 21$); 1 specimen from rio Camurugi with 22 scale rows around caudal peduncle.

Premaxillary teeth in 2 distinct rows although this is not clear in Fig. 13. Larger teeth tricuspid, smaller teeth tricuspid or bicuspid, smallest ones unicuspid. Outer row teeth 6 ($\bar{x} = 5.4$, range = 3–7, $n = 90$). Inner row teeth 3 ($\bar{x} = 3.0$, range 2–5, $n = 90$). Outer and inner row premaxillary teeth somewhat compressed compared to most "tetragonopterine" characid teeth which often appear almost circular in cross section. Maxillary teeth 6 ($\bar{x} = 6.8$, range = 5–10, larger specimens usually with highest counts, $n = 90$); two specimens from rio Camurugi with 11 maxillary teeth. Maxillary teeth show an increase in number with increasing SL from a mean of 5.9 in 9 specimens between 15.5 and 16.5 mm SL to a mean of 7.6 in 14 specimens between 25.0 and 30.5 mm SL. Anterior 4–5 maxillary teeth tricuspid and larger than remaining teeth with 2 or 1 cusps. Dentary with 4 large tricuspid teeth in all specimens, $n = 90$; smaller posterior dentary series unicuspid except anterior tooth which is tricuspid, 10 ($\bar{x} = 8.9$, range = 6–12, $n = 90$); 1 specimen from rio Camurugi had 13 dentary teeth. Maxillary and dentary teeth shaped much like premaxillary teeth as described above. At any given SL considerable variation in tooth count occurs and nearly any tooth count within ranges given may be expected. No significant differences in tooth number found between males and females.

Vertebrae 40 ($\bar{x} = 39.9$, range = 39–41,

Fig. 8. *Mimagoniates sylvicola,* new species, paratype, USNM 276547, female, SL 25.7 mm, Brazil, Bahia, Município de Prado, rio do Sul.

$n = 88$). Dorsal limb gill-rakers 6 ($\bar{x} = 6.0$, range 6–7, $n = 90$, two specimens from rio Camurugi with 5 dorsal limb gill-rakers); ventral limb gill-rakers 12 ($\bar{x} = 11.7$, range $= 11$–13, $n = 90$). Branchiostegal rays 4 in 3 cleared and stained specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—See Figs. 7 and 8 for preserved color pattern in males and females. Body pale to medium brown, almost white ventrally, darkest dorsally. Lateral body stripe pale, diffuse, best developed in males. Stripe extending from darker opercular spot on dorsal half of opercle posteriorly to a dark, spot-like region on caudal peduncle. Immediately posterior to this spot, caudal gland region enveloped in black pigment forming triangular-shaped area with its posterior apex continuous onto ray 11 and to a certain extent ray 12. Remainder of caudal fin dusky due to scattering of dark chromatophores, especially along ventral border of 19th principal caudal ray. Dorsal body surface dark dusky, especially in area of predorsal scales.

Pectoral, pelvic, dorsal and anal fins dusky from scattered dark chromatophores along fin rays. Pelvic fins considerably darker than pectoral fins. Anal fin with a dark, elongate stripe running length of fin. Width of stripe about ¼–⅕ height of fin. Stripe borders distal ends of fin rays posteriorly; anterior portion of dark stripe separated from distal ends of first five or six fin rays by relatively hyaline area on anterior lobe of fin. Dorsal fin with horizontal dark stripe extending posteriorly from about mid-length of anterior elongate undivided ray to posterior tips of two terminal dorsal-fin rays. Adipose fin dusky with scattered dark chromatophores. Head dark brown around mouth and on dorsal surface of snout, between eyes, dorsum of cranium and nape. Iris dorsal to pupil dark brown to black, most of remainder of iris silvery with some dark brown or black areas ventrally. Circumorbitals pale brown or silvery with evenly scattered dark chromatophores. Ventral area of opercle, preopercle and posterior region of branchiostegal rays silvery, without much dark brown pigment.

Color in life.—Life color patterns taken from color slides and color notes made while collecting specimens listed above from clear and black waters near Cumuruxatiba. Sides of body silvery deep blue with back dark brown and abdominal area silvery white. All fins translucent, lemon yellow with dark brown pigment described above under preserved color description appearing brown to black. Females with similar color pattern

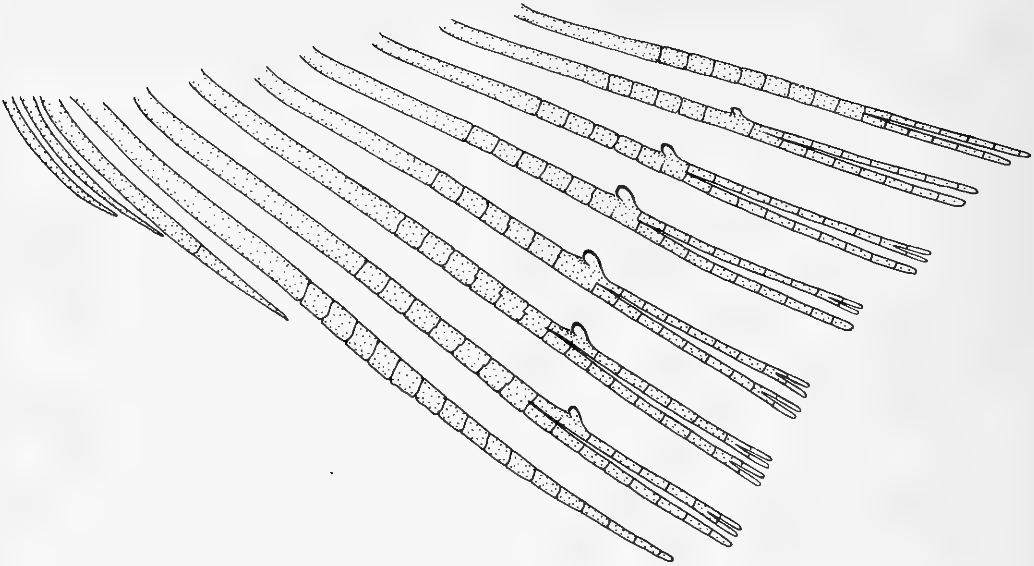


Fig. 9. *Mimagoniates sylvicola,* new species, paratype, anterior 11 anal-fin rays of an adult male, lateral view, left side, anterior at left, S1 32.5 mm, USNM 300634, Brazil, Bahia, riacho Ronca Áqua. For explanation see Description of *M. sylvicola.*

but blue, yellow, and dark pigment patterns much paler. In life caudal-fin rays 13 and 14 considerably darkened with black pigment. Some male specimens display a considerable but rather diffuse lateral dark brown stripe below lateral mid-region of body, suggesting elongate lateral stripe of *M. lateralis.* Specimens from rio do Sul, Cumuruxatiba area (USNM 276547), gold silvery in color and without blue coloration. Some of these specimens with black pigment considerably reduced, absent or covered in patches by guanine, especially on body sides. These specimens may have been infested by metacercaria of a trematode as noted for other similar appearing characids by Géry & Delage (1963).

Sexual dimorphism.—Females lack the caudal pheromone pump organ, anal-fin and pelvic-fin hooks of males (Figs. 9, 10) and display a more subdued live body coloration as noted above. Figure 14 presents graphic evidence that the caudal peduncle depth is usually deeper in adult males than in adult females and that males reach a greater adult length than females, so far as known. Below in covariance analyses we compare males and females of unequal length ranges, although the range of the females is included within that of the males. We do this because we believe these ranges are expressions of their natural differences. In our population samples of various species of *Mimagoniates* the length of the largest males always exceeds that of the largest females. If in nature the females reached the same lengths as the males our results could be biased, but longer females were not represented in our samples. We hypothesize that most of our samples fairly represent the adult lengths of both sexes. Figure 14 indicates that caudal peduncle depth divergence between males and females begins around 18 mm in SL. Even though we have few female specimens in the size range between 23.0 to nearly 28.0 or longer, we are inclined to accept that 28.0 mm SL may be the approximate adult size limit for females. Also, at least some glandulocaudine species undergo delayed sexual maturation in males,

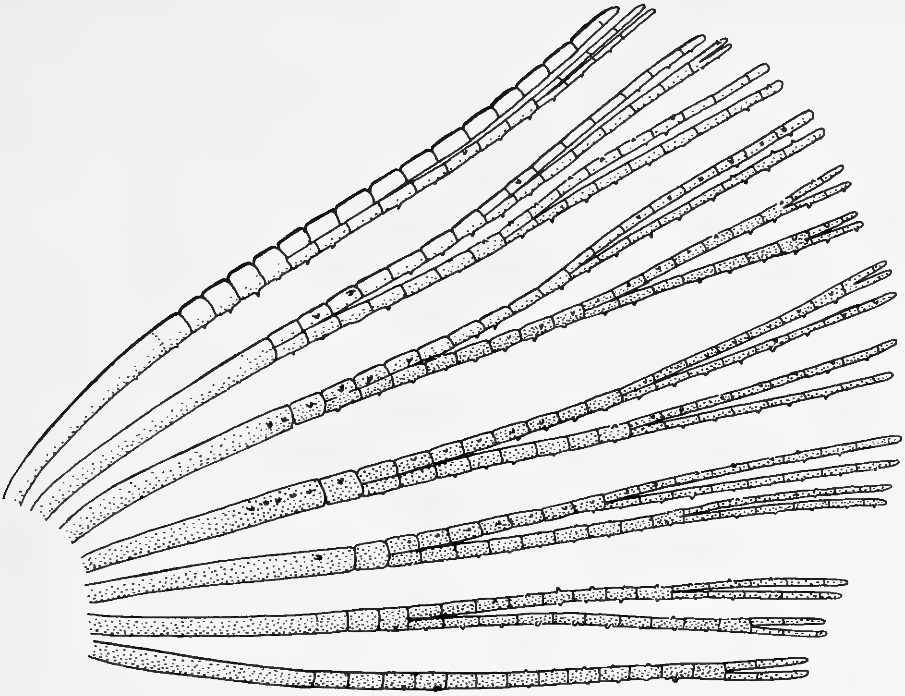


Fig. 10. *Mimagoniates sylvicola,* new species, paratype, pelvic-fin osteology of an adult male, ventral view, left side, anterior at left. SL 29.3 mm, USNM 276557, same locality data as holotype, Fig. 7. Medial fin-ray at bottom of picture.

Weitzman & Fink (1985:38, 42). If present in species of *Mimagoniates,* this kind of growth pattern might affect the regression slope shown for sexually maturing and sexually mature males towards that of the females in Fig. 14, if the large males of latent sexual maturity were included in the male population sample graphed and analyzed.

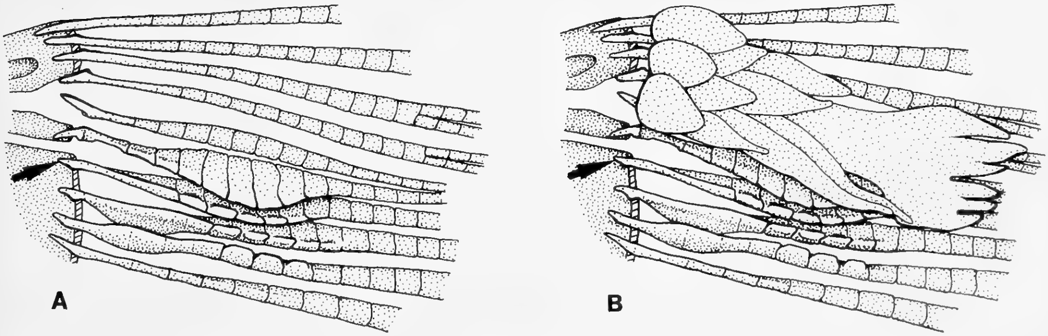


Fig. 11. *Mimagoniates sylvicola,* new species, paratype, osteology of central basal region of caudal-fin skeleton, principal rays 6–15, of an adult but still developing male, lateral views, left side, anterior at left. SL 29.3 mm, USNM 276557, same locality data as holotype, Fig. 7. Principal ray 12 indicated by arrow. (A) Illustrates area of developing rays associated with caudal pump. Note that pump chamber not yet fully developed. (B) Illustrates modified dorsal caudal-fin lobe squamation in natural position.

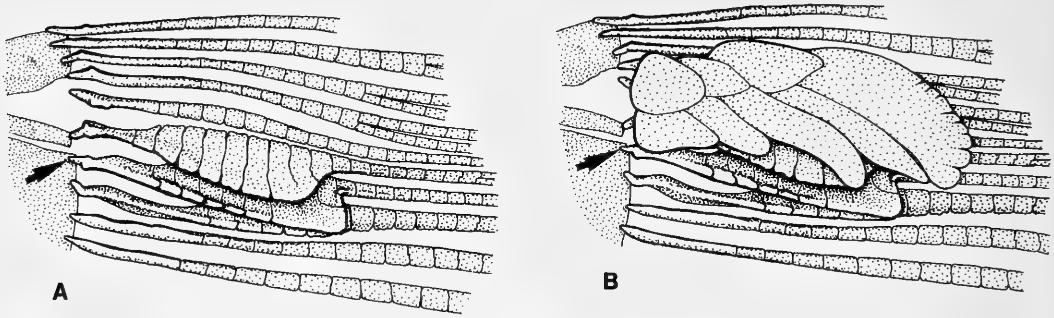


Fig. 12. *Mimagoniates sylvicola,* new species, paratype, osteology of central basal region of caudal-fin skeleton, principal rays 6–15, of an adult male, lateral views, left side, anterior at left. SL 32.5 mm, USNM 300634, Brazil, Bahia, riacho Ronca Áqua. Principal ray 12 indicated by arrow. (A) Illustrates area of fully developed caudal pump. (B) Illustrates relationship of modified dorsal caudal-fin lobe squamation to pump skeleton.

In the two slopes plotted in Fig. 14, latent males, if present, are included in that of the females. Thus Fig. 14 appears to demonstrate that as males mature sexually their caudal peduncles increase in depth at a faster rate relative to body length than it does in juveniles or females. With the above reservations and explanations in mind, we find that divergence in caudal peduncle depth on SL by apparent sex in an *F*-ratio test for homogeneity of slopes in an analysis of covariance were significantly different ($F_{0.05,(1,\ 86)} = 9.42$, $P < 0.002$) between 45 males and 45 females from the area near Cumuruxatiba (MZUSP 28815, 28816, 28817, 36612 and USNM 276547, 276556, 276557).

Etymology.—The name *sylvicola* is from the Latin *silva* (forest) and *colo* (dwell or inhabit) and is in reference to the forested nature of the streams in which this fish is found.

Discussion.—Weitzman et al. (1988:404, 414–419, fig. 10), as new species A, tentatively hypothesized that *M. sylvicola* was a relatively primitive species of *Mimagoniates* with respect to caudal-fin pump evolution. They placed *M. sylvicola* in an unresolved polytomy in their phylogenetic diagram along with *M. barberi* and *M. inequalis* and a monophyletic line leading to *M. lateralis, M. microlepis* and their new species B and C. This hypothesis was based on the information that apparently fully adult males of all three species, *M. barberi, M. inequalis* and their new species A (here = *M. sylvicola*), lack the more derived chambered, caudal-fin ray pump of the other four species. Compare caudal pump structures in Figs. 2 and 3 with those in Figs. 4 and 5.

Evidence taken from a specimen of *M. sylvicola,* USNM 300633, SL 32.5 mm, subsequently available to us from near Porto Seguro, Bahia, showed that the caudal gland matures with a well-developed pump chamber, (compare Figs. 11 and 12). However, this species lacks the caudal-fin hooks found in the more derived species, *M. rheocharis,* described below, and in *M. microlepis* (compare Figs. 5, 11, 12, and 24). This information would place *M. sylvicola* in a trichotomy, Fig. 1, with *M. lateralis* and a monophyletic line leading to the two species with caudal-fin hooks. This hypothesis would leave *M. inequalis, M. barberi* and a monophyletic line leading to the species of *Mimagoniates* with more derived caudal pumps in a trichotomy at a lower level in the phylogenetic diagram (Fig. 1). If this relationship can be supported by further phylogenetic evidence, then the biogeo-

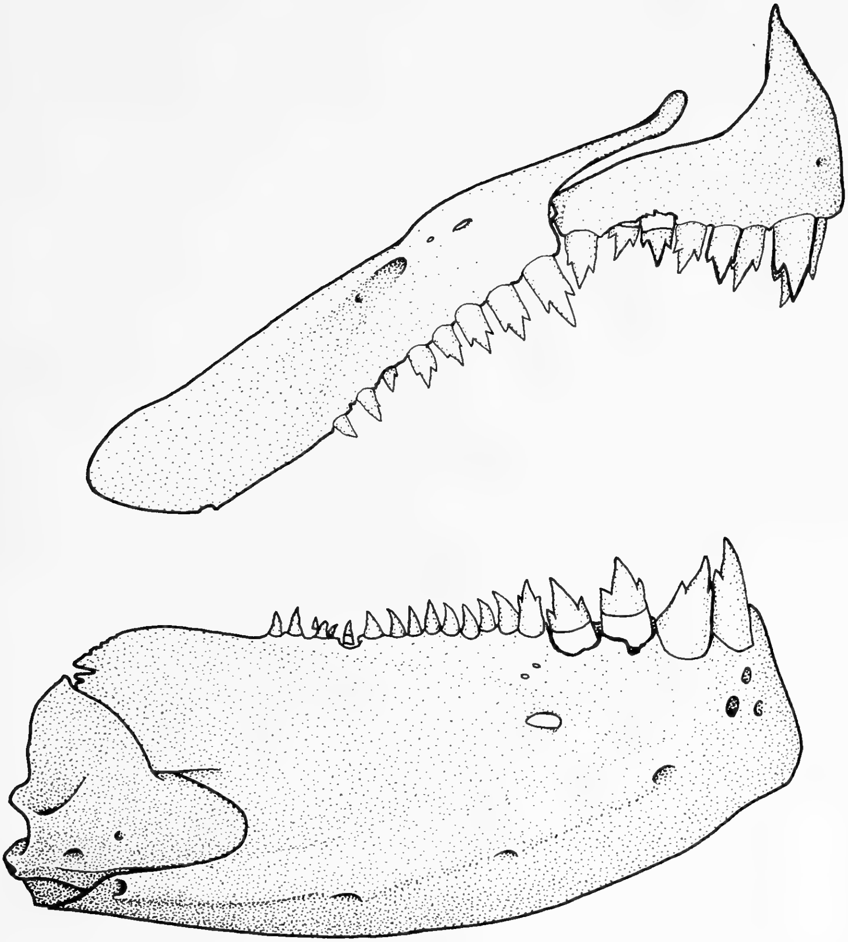


Fig. 13. *Mimagoniates sylvicola,* new species, paratype, jaws and dentition of an adult male, lateral view, right side, anterior at right. SL 29.3 mm, USNM 276557, same locality data as holotype, Fig. 7. For explanation see text under Description of *M. sylvicola.*

graphic comments of Weitzman et al. (1988: 412, 413) need some alteration (see section on biogeography below).

It was noted in the diagnosis above that adult males and females of *M. sylvicola* from Cumuruxatiba (MZUSP 28815, 28816, 28817, 36612 and USNM 276547, 276556, 276557), differ in body depth from adult males and females of *M. lateralis* from the Santos region (CAS 36634, MZUSP 40276, 40277, USNM 226468, 254268, 257200, and 257202). Forty five males of *M. sylvicola* and 22 males of *M. lateralis* were significantly different ($F_{0.05,(1,63)} = 49.75$, $P < 0.000$) in an analysis of covariance for body depth on SL in an F-ratio test for homogeneity of slopes, Fig. 15. Body depth ratios of SL useful for identification of fully or near fully mature males (at or above 23.0 mm SL) are as follows: $n = 12$ specimens of *M. sylvicola* from Cumuruxatiba and near Porto Seguro, $\bar{x} = 3.6$, range $= 3.4$–3.8 and $n = 23$ specimens of *M. lateralis* from near Santos and Município de Cananéia, $\bar{x} = 4.3$,

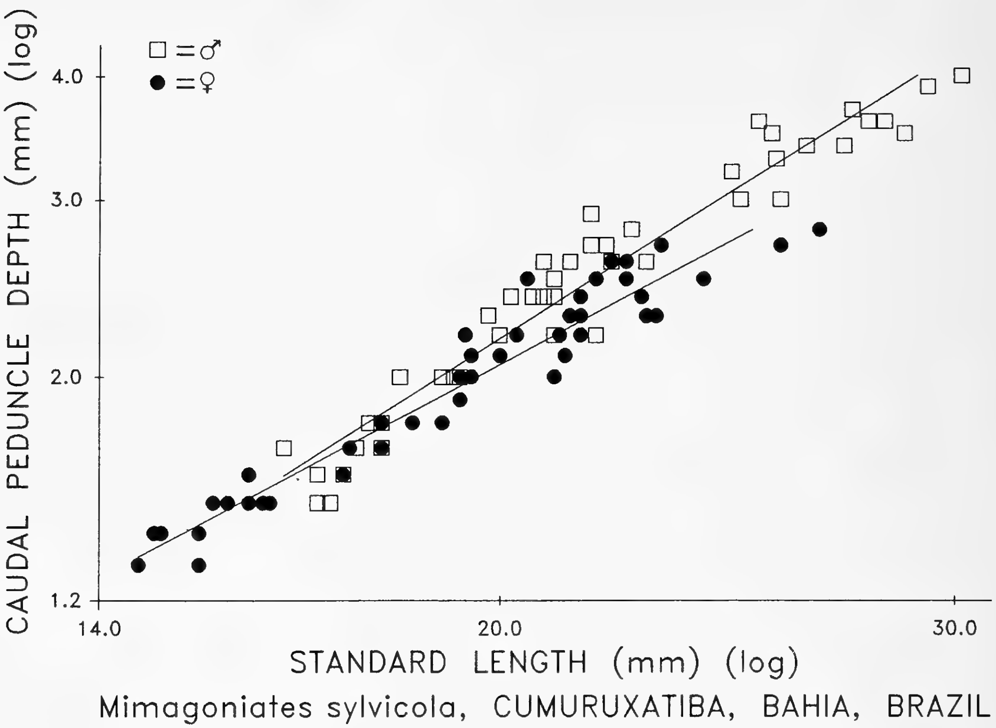


Fig. 14. *Mimagoniates sylvicola,* new species, caudal peduncle depth as a function of SL by sex. Plot axes are logarithmic. Logarithmic regression equation for 45 males: ($Y = -4.089 + 1.625X$), for 45 females: ($Y = -3.377 + 1.368X$). Immature males and juveniles may be included in the category designated female. For explanation see under Sexual dimorphism in text of *M. sylvicola.*

range = 3.8–5.1. The shorter males in these size ranges accounted for most of the overlap.

In a similar covariance analysis for slopes, 45 adult females of *M. sylvicola* and 26 females of *M. lateralis* from the same population samples as the males discussed above, also displayed significant difference in body depth ($F_{0.05, (1, 67)} = 16.3$, $P < 0.001$) (Fig. 16).

The number of branched anal-fin rays in the two species was significantly different ($t = 22.012$, $P < 0.00$ in a two-sample, two-tailed t-test), although there was some overlap in counts: $n = 90$ specimens of *M. sylvicola* from near Cumuruxatiba (same lots as listed above), range = 23–26, $\bar{x} = 24.8$, SD = 0.7728 and $n = 91$ specimens of *M. lateralis* from near Santos and Município Cananéia (same lots as listed above), $\bar{x} = 27.9$, range = 25–31, SD = 1.0899.

Ecology.—Little is known about the ecology of this species. Most of the streams in which it was captured were relatively slow moving, with little gradient. They were approximately 4 to 6 meters wide, to 1.5 meters deep and surrounded by vegetation, usually trees of a few to many meters high. The water varied from clear to black (tea color). The fish occurred in depths of 0.1 to about 0.5 meters usually in areas of little current over white sandy, rocky or dark mud bottoms. They occurred in both sunlight or shaded areas, most often near shore, especially near emergent or submerged vegetation where almost immediate cover could

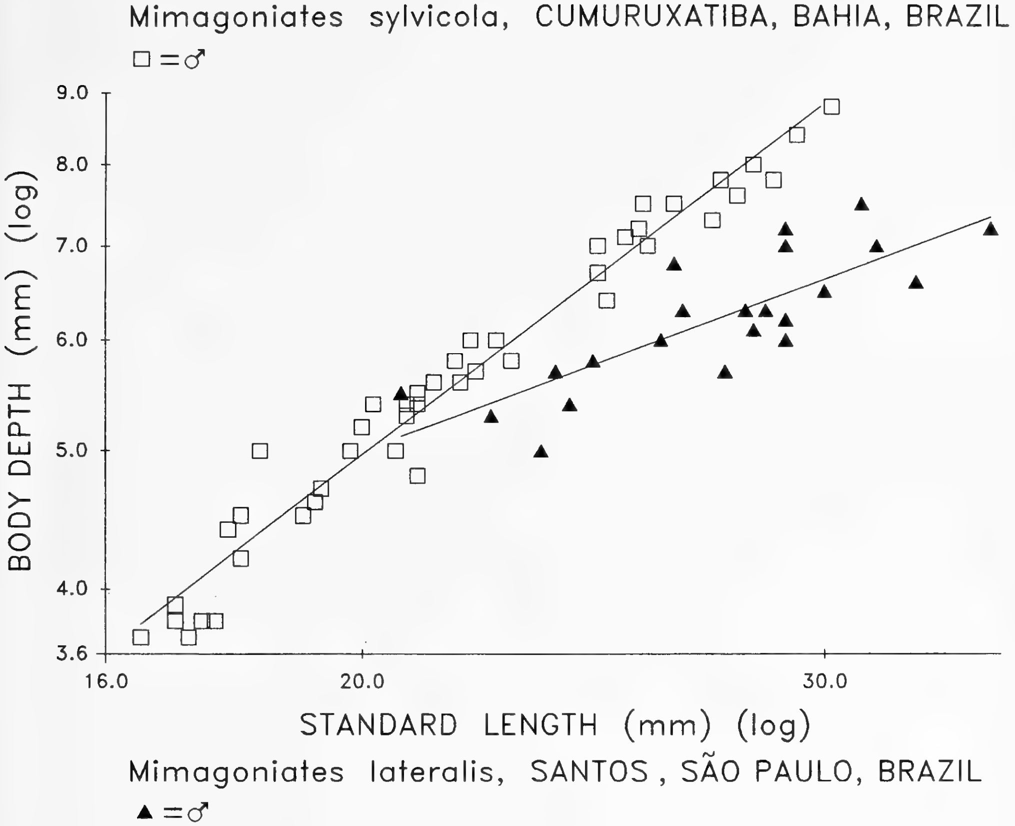


Fig. 15. *Mimagoniates sylvicola* and *Mimagoniates lateralis,* body depth as a function of standard length for young to adult males. Plot axes are logarithmic. Logarithmic regression equation for 45 males of *M. sylvicola*: ($Y = -2.650 + 1.420X$) and 22 males of *M. lateralis*: ($Y = 0.473 + 0.695X$). For explanation see Discussion under *M. sylvicola.*

be taken from predators such as large cichlids or the characid *Oligosarcus.*

Specimens of *M. sylvicola,* now MZUSP 28817 and USNM 276557, were collected 22 March 1985 in a well-shaded forest rivulet less than 1 meter wide and about 20–30 cm deep in most places. This creek was in a ravine of a mostly uncut, undisturbed tall forest, 1 or 2 km from the Atlantic coast, about 17 km from Cumuruxatiba, Bahia. The stream bottom consisted of forest litter, rocks, soil and sand with a mild nearly 0° to 30° gradient, well covered by riparian vegetation in many places. The water was tea colored. Other fish species taken at this site were *Rachoviscus graciliceps,* species of *Astyanax, Characidium, Aspidoras, Heptapterus,* a gobiid and a hypoptopomine loricariid catfish.

Mimagoniates rheocharis, new species
Figs. 17–28, Table 2

Species B.—Weitzman et al., 1988:figs. 6, 10, 23 [phylogeny and biogeography].

Holotype.—MZUSP 40278, male, SL 47.3 mm, Brazil, Santa Catarina, Município de Praia Grande, rio Faxinalzinho at Mãe dos Homens, near Praia Grande, approximately

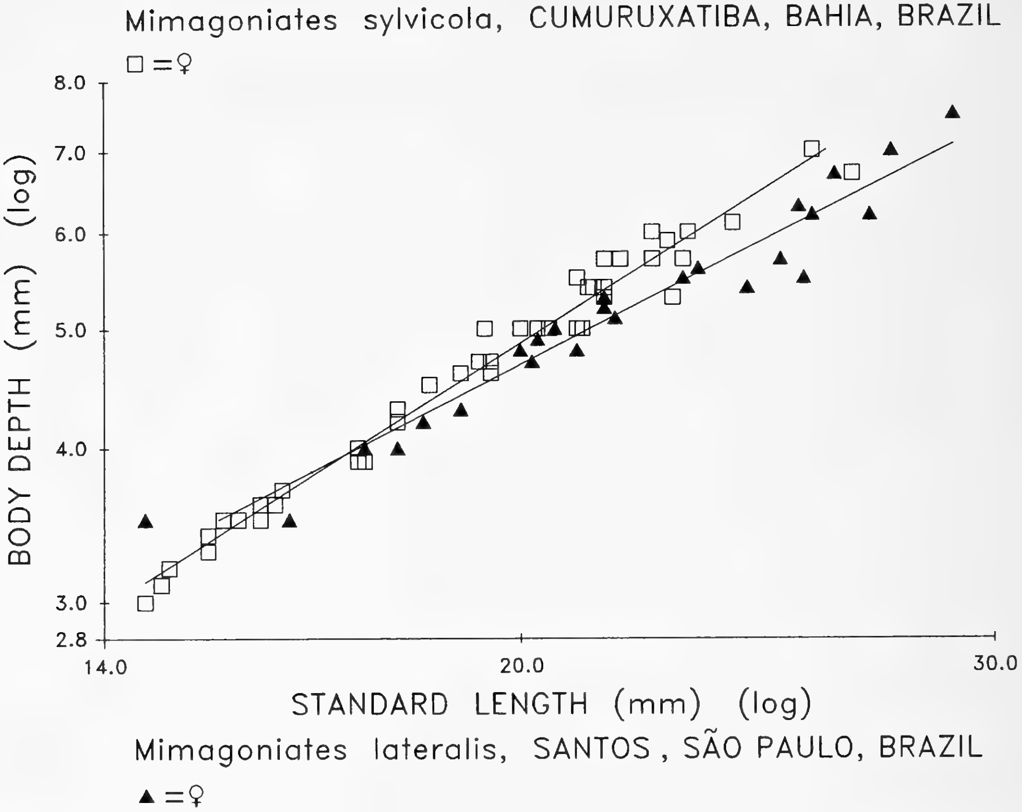


Fig. 16. *Mimagoniates sylvicola* and *Mimagoniates lateralis,* body depth as a function of standard length for young to adult females. Plot axes are logarithmic. Logarithmic regression equation for 45 females of *M. sylvicola*: $(Y = -2.567 + 1.385X)$ and 26 females of *M. lateralis*: $(Y = -1.807 + 1.118X)$. For explanation see Discussion under *M. sylvicola.*

29°20′S, 14°40′W, 9 Jun 1985; C. A. S. de Lucena, R. E. Reis, and L. R. Malabarba.

Paratypes.—Following 2 lots of immatures to adults collected with holotype: MCP 13616, spms. 3, SL 24.3–40.8 mm; USNM 279878, spms. 3, SL 33.3–47.8 mm. Following 3 lots of immature to adult paratypes all collected 7 Jun 1985 by C. A. S. de Lucena and party: Brazil, Santa Catarina, Município de Nova Veneza, rio Jordão at Jordão Alto, approximately 28°36′S, 49°28′W, MCP 13617, spms. 83, SL 21.9–39.0 mm; MZUSP 40279, spms. 81, SL 22.4–42.8 mm; USNM 270879, spms. 89, SL 22.8–49.0 mm. Following 3 lots of immature to adults all collected by R. M. C. Castro 13 Feb 1988: Brazil, Santa Catarina, Município de Praia Grande, tributary of rio Grande approximately 29°20′S, 49°40′W, MZUSP 40280, spms. 29, SL 13.5–38.4 mm; USNM 306339, spms. 18, SL 17.0–40.0; spms. 2 to R. M. C. Castro, SL 28.0–31.30 mm. MZUSP 40281, SL 41.8 mm (mature male), Brazil, Rio Grande do Sul, Município de Osório, arroio das Pedras, approximately 29°52′S, 50°19′W, 11 Feb 1988, R. M. C. Castro. MCP 13613 spms. 7, SL 27.5–31.3 mm, Brazil, Município de Osório, arroio Água Parada, tributary to rio Maquiné, in Maquiné, approximately 29°40′S, 50°11′W, 10 Oct 1989, R. E. Reis, S. O. Kullander, L. R. Malabarba and J. Pozzi. MCP 10806, SL 39.5 mm (mature male), Brazil, Rio Grande do Sul, Município de

Torres, tributary of rio Três Furquilhas, Chapéu, approximately 29°19′S, 49°44′W, 25 May 1986, C. A. S. Lucena, R. E. Reis, and L. R. Malabarba.

Diagnosis.—*Mimagoniates rheocharis* may be separated from all other species of *Mimagoniates* by use of the key provided above and the characters described and discussed below. *Mimagoniates rheocharis* is sympatric with and apparently at least partly syntopic with *M. microlepis* in south coastal Santa Catarina. It is also sympatric and syntopic with *M. microlepis* in the rio Maquiné drainage. The southern distribution of *M. rheocharis* (rio Maquiné drainage and streams immediately surrounding Osório in Rio Grande do Sul) is adjacent to the northeastern limit (rio Gravataí drainage) of *M. inequalis* where these two species abut and appear to be allopatric (see the Biogeography section and phylogenetic discussion in the Discussion section below). The possible relationships of *M. rheocharis* to *M. inequalis* or *M. microlepis* is uncertain and perhaps complex but the following series of characters distinguish *M. rheocharis* from one or the other of these species or, in some cases, both of them. Because the comparisons are somewhat complex, for clarity the two compared species are treated separately.

Mimagoniates rheocharis may be distinguished from *M. microlepis,* by the following characters (see also the statistical analyses of overlapping characters under Statistical Comparisons below). Scale rows around caudal peduncle 19–23 (15–18 for *M. microlepis*); scale rows between dorsal-fin and anal-fin origins 17–22, rarely 17 (14–17, rarely 17 for *M. microlepis*); total lateral series scale count shows broad overlap between both species, 41–48 (42–49 for *M. microlepis*) but in at least one population comparison of *M. rheocharis* and *M. microlepis* showed a statistically significant difference (see the statistical comparisons below); branched dorsal-fin ray count 8–12, usually 9–10, rarely 8 (7–9, rarely 9 for *M. microlepis*); branched anal-fin ray count 23–29, usually 24–26 and rarely 28 or 29 (26–33, usually 28–31 and rarely 26 or 27 for *M. microlepis*); total vertebral count 35–40, usually 36–38, rarely 39 or 40 (38–41, usually 39–40, rarely 38 in *M. microlepis*); tenth and eleventh principal caudal-fin rays of adult males with small, little developed hooks posterior to caudal organ but with sturdy hooks on ray 11 along ventral border of expanded ray segments of caudal organ, Fig. 24 (adult male *M. microlepis* with well-developed hooks on caudal-fin rays 7–12 and no sturdy hooks on principal ray 11 along ventral border of expanded ray segments of caudal organ, note, some populations with few or no hooks on rays 7 and/or 12); preserved and live colors in part different between both species, but variation in live colors among various population samples of *M. microlepis* make comparisons difficult.

A few life color characters appear consistently different in fully mature males: pelvic-fin rays and membranes of adult males distally white (adult male *M. microlepis* with yellow and/or black pigment of pelvic fins continuous to edge of fin where fin bordered by narrow band of white); anal fin posterior to anterior lobe bordered by broad band of deep yellow pigment, very little to no black pigment on fin (adult male *M. microlepis* with posterior portion of anal fin ventrally bordered by narrow band of black pigment, none or very little yellow pigment).

As treated below in the Discussion, there are some, perhaps plesiomorphic, body shape similarities shared between *M. rheocharis* and *M. inequalis.* Furthermore, *M. rheocharis* appears to have the caudal peduncle and body depths for both sexes intermediate between those of *M. microlepis* and *M. inequalis*; see Figs. 17 and 27. Certain aspects of the caudal pump morphology of *M. rheocharis* could also be interpreted as intermediate. This suggests the possibility that *M. rheocharis* might be closely related to *M. inequalis* rather than to *M. mi-*

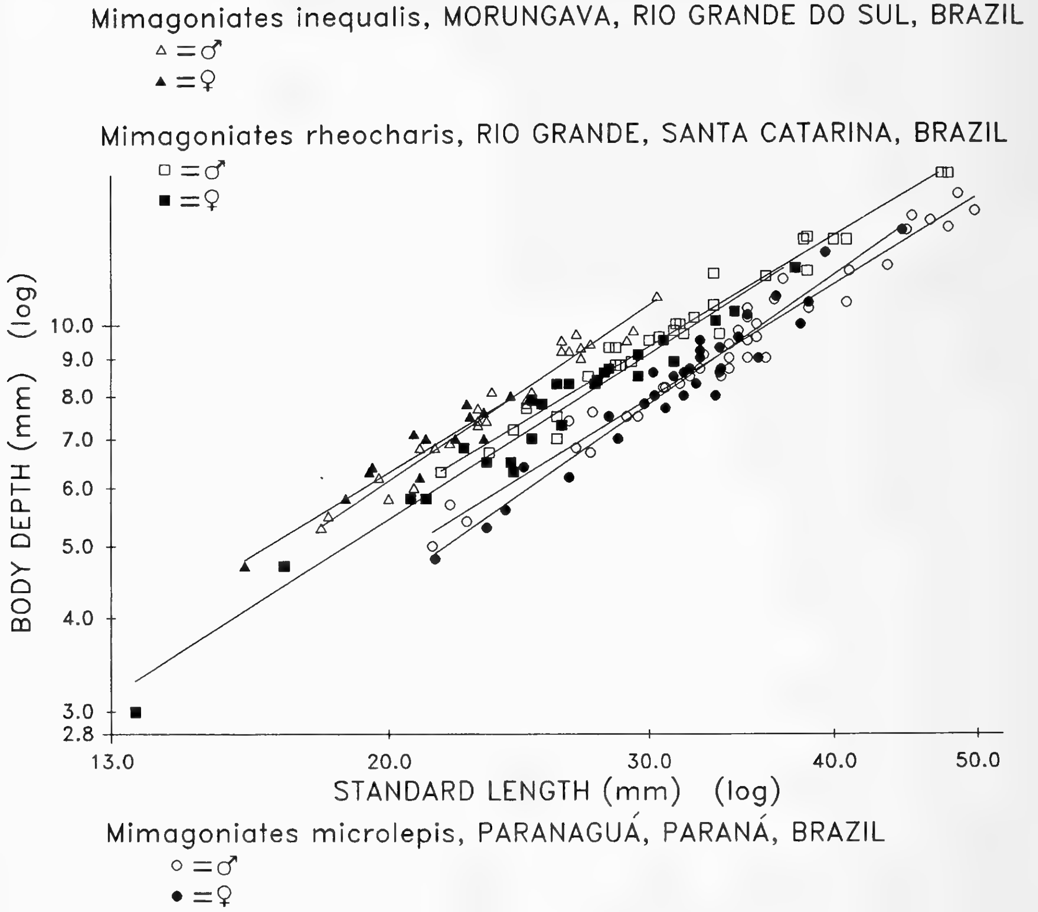


Fig. 17. *Mimagoniates rheocharis, M. microlepis* and *M. inequalis,* body depth as a function of SL by species and sex. Plot axes are logarithmic. Logarithmic regression equation for 31 males of *M. rheocharis*: (Y = −1.846 + 1.199X), 25 females or this species: (Y = −2.115 + 1.271X); for 39 males of *M. microlepis*: (Y = −2.130 + 1.235X) and for 31 females of the later species: (Y = −2.705 + 1.399X); and for 26 males of *M. inequalis*: (Y = −2.230 + 1.3499X), 14 females of this species: (Y = −1.812 + 1.2187X). For explanation see Diagnosis, Sexual dimorphism, Discussion and Description under *M. rheocharis.*

crolepis or even derived by introgression from ancestral sympatric populations of *M. microlepis* and *M. inequalis* in a manner suggested by Hubbs (1955:19) for freshwater fishes in North America. However, not all counts or body proportions of *M. rheocharis* are intermediate between the two species and we question the intermediacy of *M. rheocharis* based on tentative polarity and parsimony analyses of the available data (see Discussion below). In any case, the similarities of many features, especially of immature or just maturing specimens, shared between *M. rheocharis* and *M. inequalis* makes it a practical necessity to describe the differences in some detail between the population samples at hand of these two species. The phylogenetic polarities of most of these characters are relatively uncertain for those species possessing them. Therefore their use as synapomorphies suggesting relationships to and/or among species of *Mimagoniates* that may share them remains to be more fully investigated. Tentatively, many of these

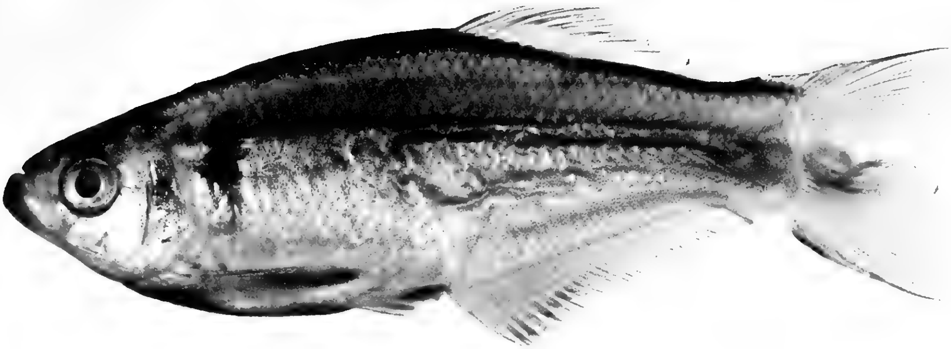


Fig. 18. *Mimagoniates rheocharis,* new species, holotype, MZUSP 40278, male, SL 47.3 mm; Brazil, Santa Catarina, rio Faxinalzinho at Mãe dos Homens, near Praia Grande.

characters appear plesiomorphic for *M. inequalis* when the latter is compared to *M. rheocharis* or *M. microlepis.*

For convenience the following same characters as those treated above to separate *M. rheocharis* and *M. microlepis* are considered for comparison between *M. rheocharis* and *M. inequalis* even though not all these characters are diagnostic for separation of the latter two species (see also the section below on Statistical Comparisons). Scale rows around caudal peduncle = 19–23 for *M. rheocharis* (16–19 for *M. inequalis*) (both species commonly with a count of 19); scale

Fig. 19. *Mimagoniates rheocharis,* new species, paratype, USNM 306339, female, SL 34.3 mm; Brazil, tributary to rio Grande, Santa Catarina.

Fig. 20. *Mimagoniates rheocharis,* new species, paratype, MZUSP 40281, male, SL 41.8 mm; Brazil, Rio Grande do Sul, arroio das Pedras, near Osório.

rows between dorsal-fin and anal-fin origins = 17–22 (16–18 for *M. inequalis*); lateral series scale count = 41–48, rarely 41 (36–41 for *M. inequalis,* 41 being uncommon); branched dorsal-fin ray count 8–12, usually 9 or 10, only occasionally 8 (8–9, rarely 9 for *M. inequalis*); branched anal-fin ray count 23–29, usually 24–26, rarely 28 or 29 (24–30, rarely 24 for *M. inequalis*), these counts significantly different statistically between some population samples but not in others (see statistical analyses below); total vertebral count 35–40, rarely 39–40 (36–39 for *M. inequalis*); principal caudal-fin rays 10 and 11 of adult males with small, little developed hooks posterior to caudal-fin organ, see Fig. 24 (adult male of *M. inequalis* without hooks on caudal-fin rays 10 and 11); preserved color patterns essentially indistinguishable between the two species and we have not been able to study the live color patterns of adult males where differences between the species would most likely be present.

Description.—Table 2 presents morphometrics of the holotype and paratypes. Except where noted, the entire description refers to the population sample from near Praia Grande, southern Santa Catarina. These collections were treated statistically as one population sample in an attempt to represent the species as a whole from this area. Counts and ratios of measurements for other population samples taken from a tributary of the rio Grande are given only when they differ from those from near Praia Grande.

Body compressed, relatively deep, especially near dorsal-fin origin; body deepest at vertical line through anal-fin origin. Predorsal body profile relatively arched in adult males, less so in adult females and immatures which have predorsal profile gently convex to tip of snout. Body profile elevated at dorsal-fin origin, still strongly arched in males, less so in females and juveniles. Dorsal body profile nearly straight along dorsal-fin base to adipose fin. Body profile posterior to adipose fin somewhat concave dorsal to caudal peduncle, ending at origin of procurrent caudal-fin rays. Dorsal-fin origin nearer to caudal-fin base than to snout tip.

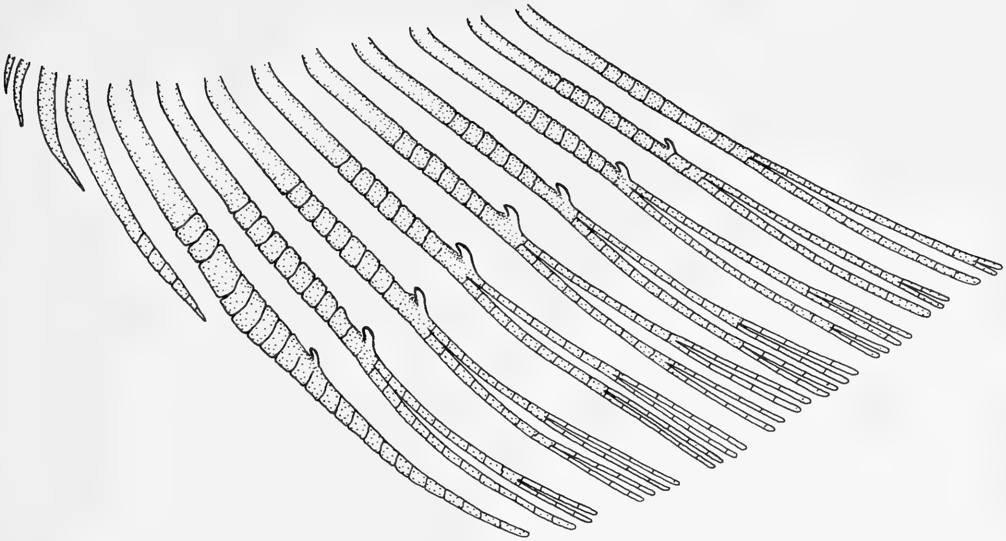


Fig. 21. *Mimagoniates rheocharis,* new species, paratype, anterior 13 anal-fin rays of an adult male, lateral view, anterior is at left. USNM 279879, SL 45.4 mm; Brazil, Santa Catarina, rio Jordão at Jordão Alto. For explanation see Description under *M. rheocharis.*

Ventral body profile strongly convex in adult males from anterior tip of lower jaw to origin of pelvic fins, less strongly convex in females and juveniles. Belly profile in adult males slightly concave to anal-fin origin, straight or nearly so in females and juveniles. Body profile along anal-fin base in males slightly concave at anterior base in region of anterior lobe of anal fin; straight along base of remainder of fin in males and along entire anal-fin base in females and juveniles. Ventral profile of caudal peduncle convex in adult males when anterior 5 or 6 strongly developed procurrent ventral caudal-fin rays are included in that profile; slightly concave or nearly straight in females and juveniles.

Head and snout of moderate size in proportion to body length. Lower jaw protruding, slightly anterior to upper jaw. Lower jaw of adult males thick and heavy compared to that of females and juveniles. Mouth angled posteroventrally from anterior tip of snout to posterior part of mandibular joint. Maxilla long, extending to a point ventral to a horizontal line drawn from ventral border of eye in juveniles and adults of both sexes. Maxilla extends posteriorly to a point anterior to vertical line drawn through anterior border of pupil of eye.

Dorsal-fin rays ii,9 (unbranched rays ii in all specimens, branched rays $\bar{x} = 8.9$, range $= 8–10$, $n = 56$); posterior ray not split to its base and counted as 1. Adipose fin present, slender. Anal-fin rays iv,26 (iv or v, usually iv, $\bar{x} = 26.8$ for branched rays, range $= 25–29$, $n = 56$); posterior ray split to its base and counted as 1. Anal fin with moderately developed lobe anteriorly (Figs. 18, 19). Lobe includes fourth or fifth undivided ray and first 3 divided rays. Anal fin of sexually mature males with bilateral hooks, 1 on each side, on anterior unbranched ray iv or v, whichever occurs just before branched rays (Fig. 21). Usually anterior 7 branched fin rays with bilateral hooks, 1 set for each ray. Pectoral-fin rays i,10 (unbranched ray i in all specimens, branched rays $\bar{x} = 10.1$, range 10–11, $n = 56$). Posterior tips of longest pectoral-fin rays extend posteriorly beyond origin of pelvic fins; fins of about equal extent in both sexes. Pectoral-fin rays with-

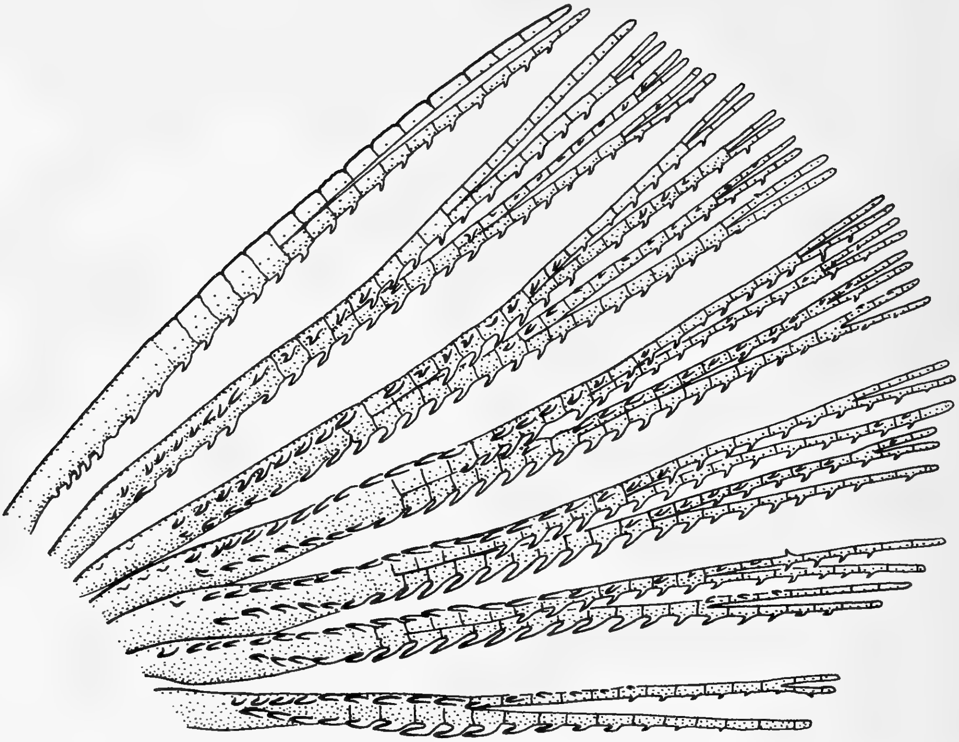


Fig. 22. *Mimagoniates rheocharis,* new species, paratype, pelvic fin of adult male, ventral view, left side, anterior at left, medial fin ray at bottom. USNM 279879, SL 45.4 mm; same locality data as specimen in Fig. 21.

out hooks. Pelvic fin rays 8 in all specimens. Pelvic fin with anterior (first) ray branched once, branches remaining close together and entire ray tapering as in most characiforms that have anterior ray unbranched (Fig. 22). Sexually mature, large adult males with over 400 hooks on each pelvic fin.

Principal caudal-fin ray count 10/9 in all specimens, (n = 56). Fin rays modified in association with caudal pheromone pump as in Figs. 23 and 24. Fin rays modified more like those in *M. microlepis* than any other species of *Mimagoniates* (Fig. 5). Caudal-fin rays 10 and 11 with small bony hooks. Ventral borders of 4 anterior expanded ray segments of ray 11, which form anterior external wall of dorsal portion of pump chamber, with about 4 short but large hooks, 2 middle hooks often bicornate, others 1 hooked.

Scales cycloid, with few radii along posterior border. Terminal scale of modified caudal-fin series without exaggerated radii (Fig. 24b).

Lateral line incomplete, perforated scales 7 ($\bar{x}$ = 6.7, range 5–9, n = 48). Lateral series scales 45 ($\bar{x}$ = 44.3, range = 41–48, n = 48). Predorsal scales = 22 ($\bar{x}$ = 22.3, range = 21–24, n = 46). Scale rows between dorsal-fin and anal-fin origins 19 ($\bar{x}$ = 18.8, range = 17–21, n = 55). Scale rows around caudal peduncle 20 ($\bar{x}$ = 19.7, range = 19–22, n = 46).

Premaxillary teeth in 2 distinct rows, Fig. 25. Larger and smaller teeth tricuspid in all large specimens, sometimes in smaller specimens small teeth bicuspid or conical. Outer row teeth 5 ($\bar{x}$ = 6.2, range 5–8, n = 55). Inner row teeth few, 3 ($\bar{x}$ = 2.1, range = 1–3, n = 55). Outer and inner row premaxil-

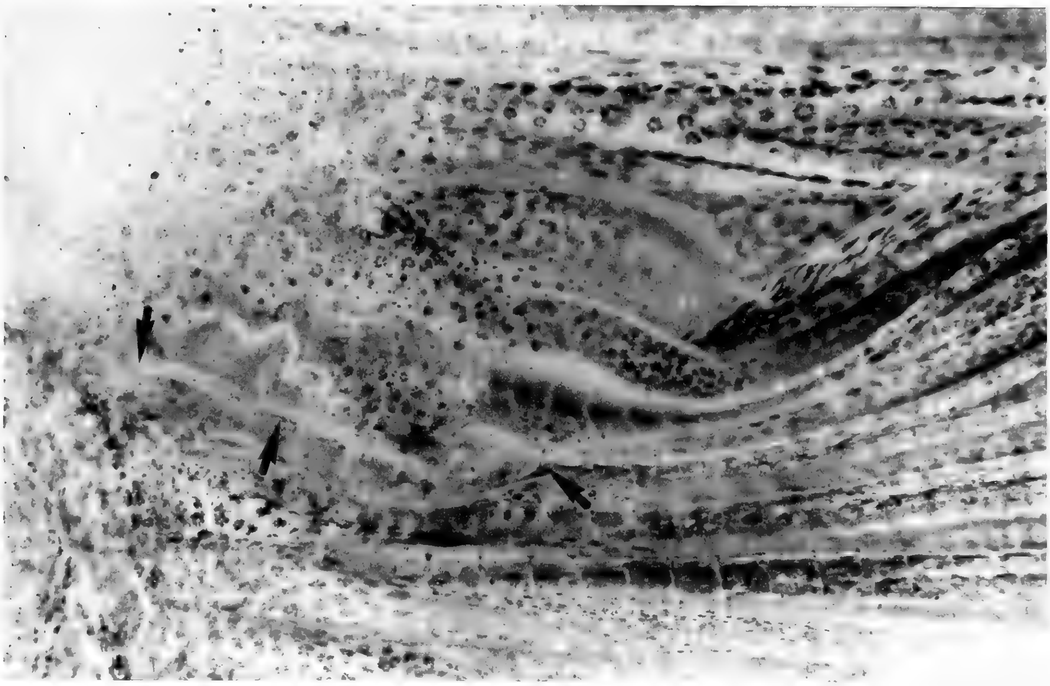


Fig. 23. *Mimagoniates rheocharis,* new species, paratype, unstained central basal region of caudal fin and adjacent caudal peduncle of adult male, lateral view, left side, anterior at left. USNM 279879, SL 49.0 mm; same locality data as specimen in Fig. 21. Arrow at left indicates anterior intake region of pump chamber. Middle arrow indicates region of lateral slit with ray half of principal ray 11 just dorsal to arrow tip. Arrow at right points to opening of posterior exhaust vent of pump chamber. Note that in this species pump chamber not formed into an obvious cylindrical tube as that of *M. microlepis,* Fig. 3. Glandular tissue surrounding chamber openings in this photograph obscure details of pump.

lary teeth somewhat compressed compared to most "tetragonopterine" characid teeth which are often circular in cross section. Maxillary teeth 8 ($\bar{x}$ = 5.4, range = 3–8, larger specimens usually with higher counts, n = 55). All maxillary teeth usually tricuspid in large sepcimens; small specimens with posterior maxillary teeth often conical. Dentary with 4 large tricuspid teeth in all specimens, smaller posterior teeth 12 ($\bar{x}$ = 8.4, range = 5–12, almost always greater number of teeth in largest specimens, anterior small maxillary teeth tricuspid, posterior ones conic, n = 54). Maxillary and dentary teeth shaped much like premaxillary teeth described above. No significant difference in tooth number found between males and females.

Vertebrae 38 ($\bar{x}$ = 38, range = 37–40, n = 107). Dorsal limb gill rakers 7 ($\bar{x}$ = 6.6, range = 6–8, n = 54); ventral limb gill rakers 12 ($\bar{x}$ = 11.7, range = 11–13, n = 54). Branchiostegal rays 4, in 3 cleared and stained specimens, 3 rays originating on anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—See Figs. 18–20 for preserved color pattern of males and females. Body pale to medium brown, pale yellowish brown ventrally, much darker dorsally. Lateral body stripe diffuse in both sexes, especially anteriorly. Stripe extending from vertical humeral spot posteriorly to caudal fin and onto dorsal region of ventral caudal-fin lobe and small part of dorsal caudal-fin lobe. Lateral stripe extends over all

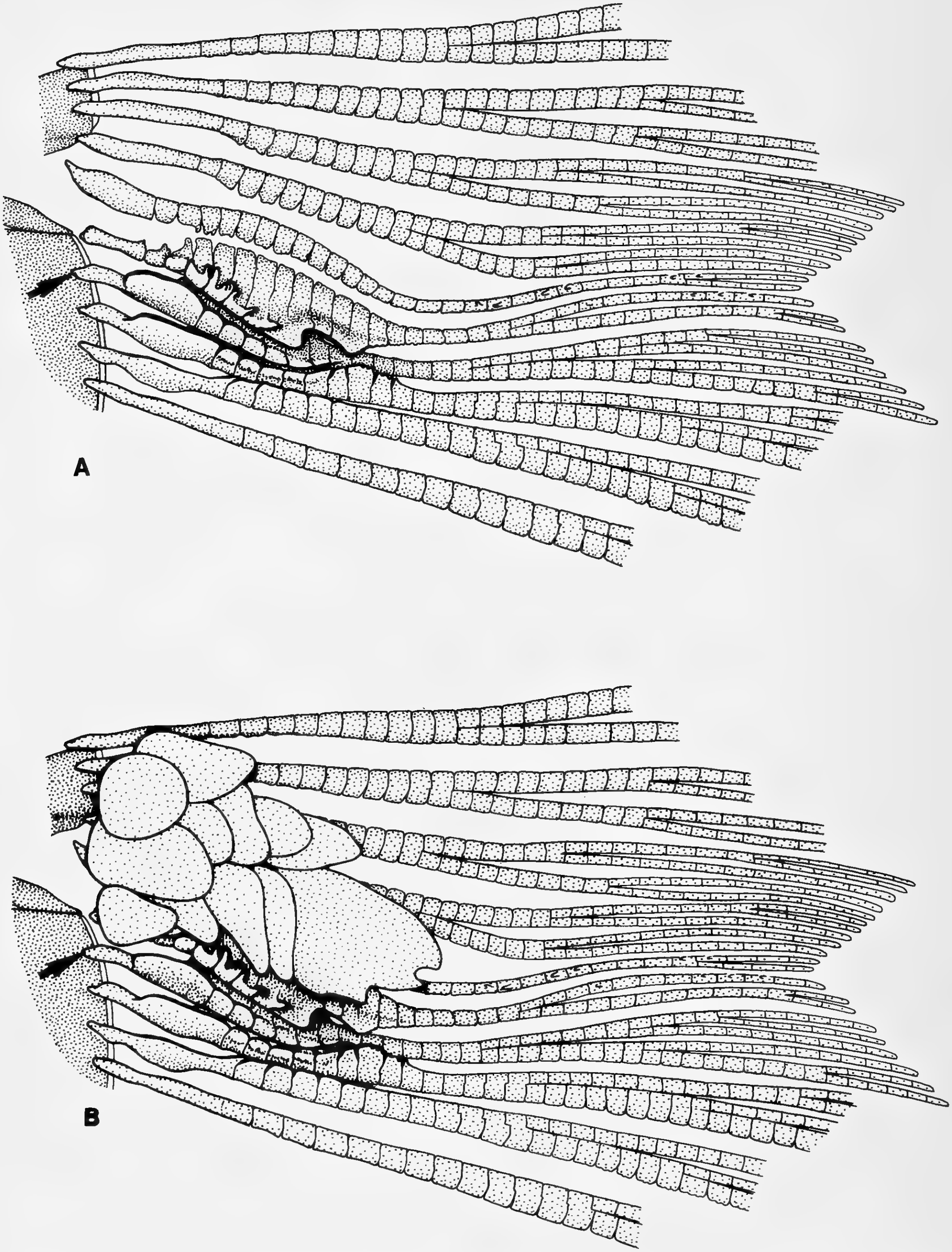


Fig. 24. *Mimagoniates rheocharis,* new species, paratype, osteology of central basal region of caudal skeleton, principal fin rays 6–15, of an adult male, lateral views, left side, anterior at left. USNM 279879, SL 45.4 mm, same locality data as specimen in Fig. 21. Principal ray 12 indicated by arrow. (A) Illustrates caudal pump region. (B) illustrates relationship of modified dorsal caudal-fin lobe squamation to caudal pump.

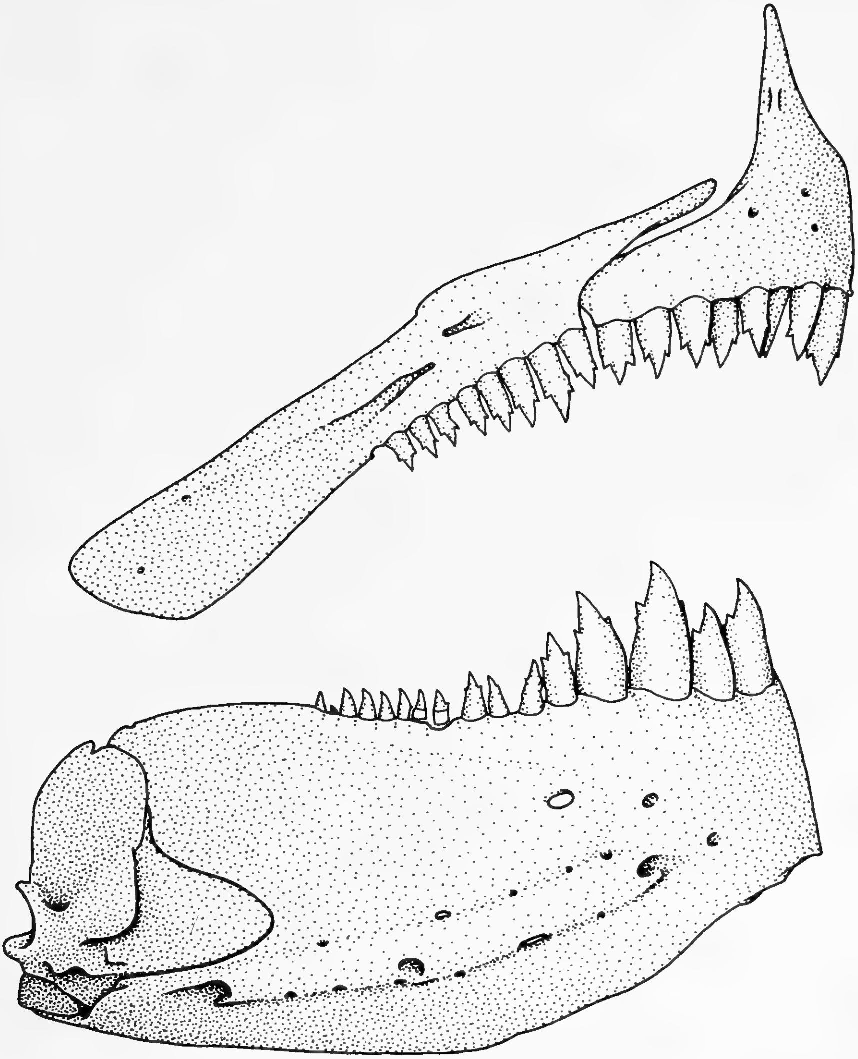


Fig. 25. *Mimagoniates rheocharis,* new species, paratype, jaws and dentition of adult male, lateral view, right side, anterior at right. USNM 279879, SL 45.4 mm, same locality data as in Fig. 21. For explanation see text Description under *M. rheocharis.*

caudal gland structures, including those derived from dorsal caudal-fin lobe such as modified caudal squamation. Stripe especially dark on principal rays 10, 11 and 12, less so on ray 13. Humeral spot vertically elongate, especially in sexually mature males. Remainder of caudal fin dusky because of scattered dark chromatophores. Dorsal border of first principal caudal-fin ray and ventral border of nineteenth principal caudal-fin ray black. Utmost dorsal body surface black, forming a narrow stripe extending from supraoccipital region to base of dorsal procurrent rays of caudal fin. Remainder of dorsal body surface ventral to lateral body stripe pale brown.

Pectoral, pelvic, dorsal and anal fins dusky with scattered dark chromatophores along fin rays and membranes. Anal fin with a dark elongate stripe running length of fin.

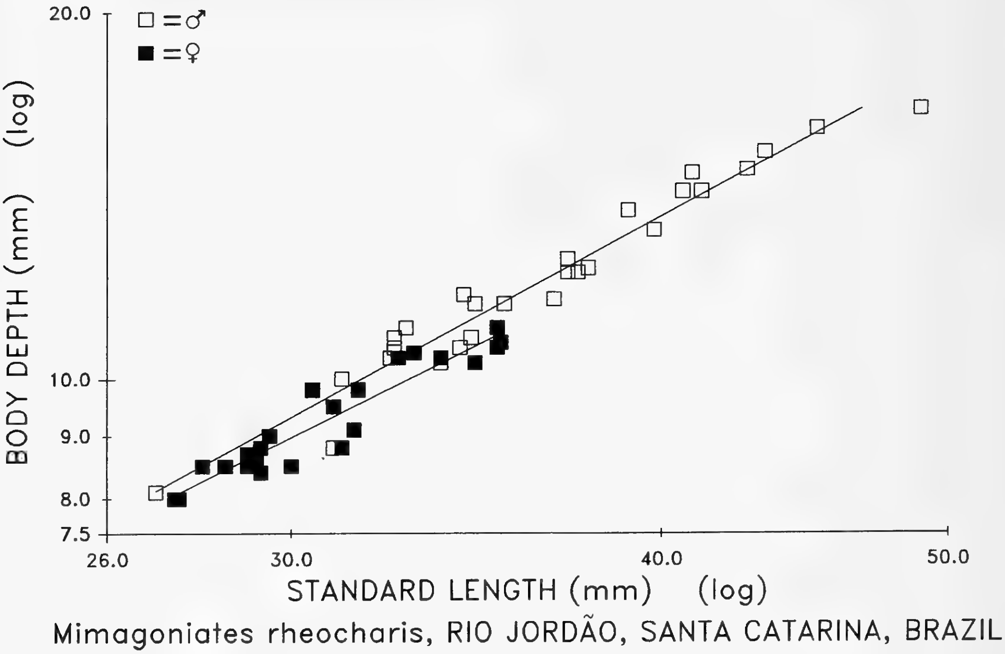


Fig. 26. *Mimagoniates rheocharis,* new species, paratypes, body depth as a function of SL by sex. Plot axes are logarithmic. Logarithmic regression equation for 27 males of *M. rheocharis*: ($Y = -2.190 + 1.300X$) and for 23 females of this species: ($Y = -1.831 + 1.183X$). For explanation see Sexual dimorphism under *M. rheocharis.*

Stripe width about one-fourth height of anal fin anteriorly and about one-half fin's height posteriorly. Stripe of nearly uniform width throughout its length, but fin height changes, being considerably shorter posteriorly. In sexually mature males stripe considerably darker anteriorly, especially dorsal to anterior anal-fin lobe which appears relatively hyaline. Dorsal-fin with a horizontal dark stripe in adult males and females extending posteriorly from about mid-length of anterior elongate undivided ray to posterior tips of terminal two dorsal-fin rays. Stripe usually narrow, less than one-eighth height of dorsal fin at latter's longest measurement. Width and density of stripe variable depending on sex and sexual maturity. Preserved males sometimes with posterior portion of stripe diffuse. Adipose fin dusky with scattered dark chromatophores.

Head dark brown around mouth and on dorsal surface of snout, between eyes, dorsum of cranium and nape. Mental area of lower jaw dark brown. Head area posterior to circumorbitals and extending ventrally from parietal region, across dorsal opercular region dark brown. Dark area continues ventrally across posterior region of opercular bone to just reach interopercular bone; looks like an anteriorly misplaced humeral spot. Iris dorsal to pupil dark brown, most of remainder of iris silvery. Circumorbitals silvery if guanine preserved, pale yellowish brown if guanine destroyed by formalin. Dark brown chromatophores scattered evenly through circumorbital area. Anterior area of opercle, all of preopercle, and branchiostegal rays silvery or pale brown, without much dark brown pigment.

Color in life.—Life colors described here taken from a 35 mm color slide made by Ricardo M. C. Castro of an adult male 41.8 mm SL (MZUSP 40281). See also black and white photograph of this specimen in pre-

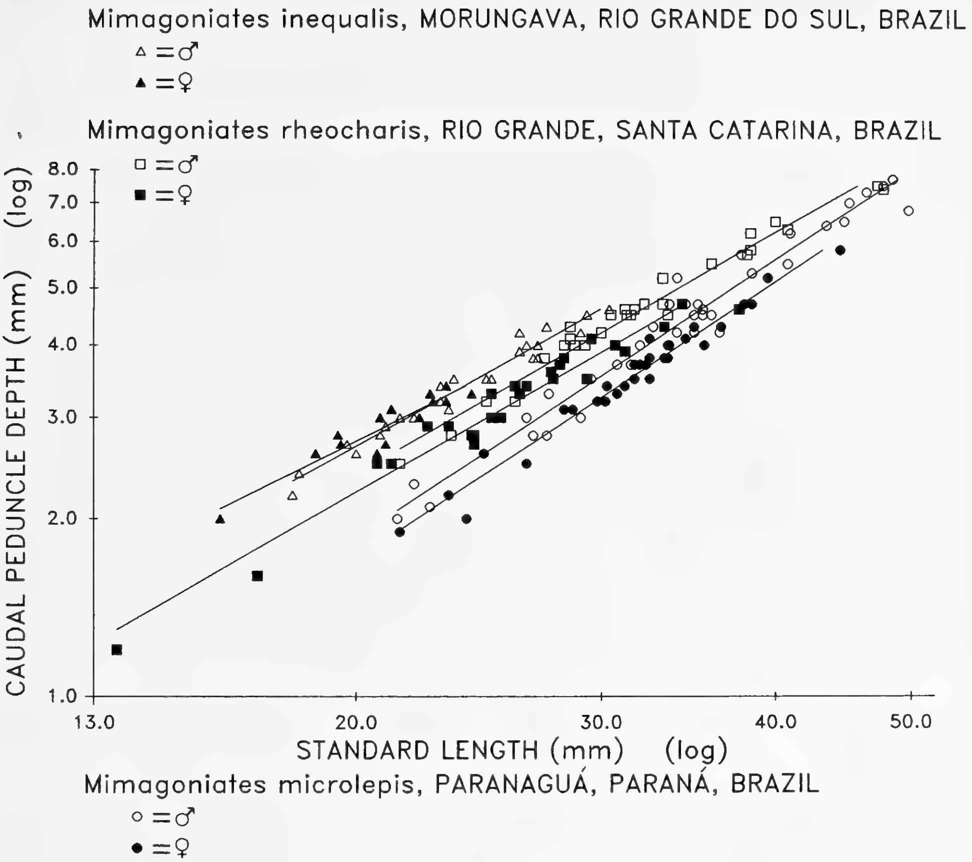


Fig. 27. *Mimagoniates rheocharis, M. microlepis* and *M. inequalis* caudal peduncle depth as a function of SL by species and sex. Plot axes are logarithmic. Logarithmic regression equation for 31 males of *M. rheocharis*: (Y = −4.222 + 1.588X), for 26 females of the same species: (Y = −3.311 + 1.374X); for 40 males of *M. microlepis*: (Y = −4.151 + 1.592X) and for 30 females of the later species: (Y = −3.239 + 1.374X); and for 26 males of *M. inequalis*: (Y = −3.021 + 1.3375X), 14 females of this species; (Y = −2.625 + 1.2116X). For explanation see Diagnosis, Sexual dimorphism, Discussion and Description under *M. rheocharis*.

servative, Fig. 20. Specimen photographed just after capture from a clear water stream surrounded by vegetation. Site located immediately north of city of Osório, Rio Grande do Sul. Sides of body pale silvery blue. Broad lateral body stripe somewhat deeper silvery blue from humeral spot to caudal peduncle termination. Just dorsal to silvery blue color of body sides, back with a narrow dark brown line extending from parietal region of head to just ventral to adipose fin. Lateral portion of back between narrow brown line and dorsomedian narrow dark brown line extending across dorsalmost portion of back, a brownish yellow green color. Dorsal region of caudal peduncle nearly yellow. Ventral abdominal area, most of lower jaw, ventral opercular area, branchiostegal rays and their membranes silvery white. Dark pigment of head similar to that described for preserved specimens except that dorsal region of opercle appears silvery blue. Dorsal caudal-fin lobe and principal caudal-fin rays 14–16 on ventral caudal-fin lobe bright yellow, except for black proximal half of ray 14. This black pigment continuous with black pigment surrounding structures of caudal phero-

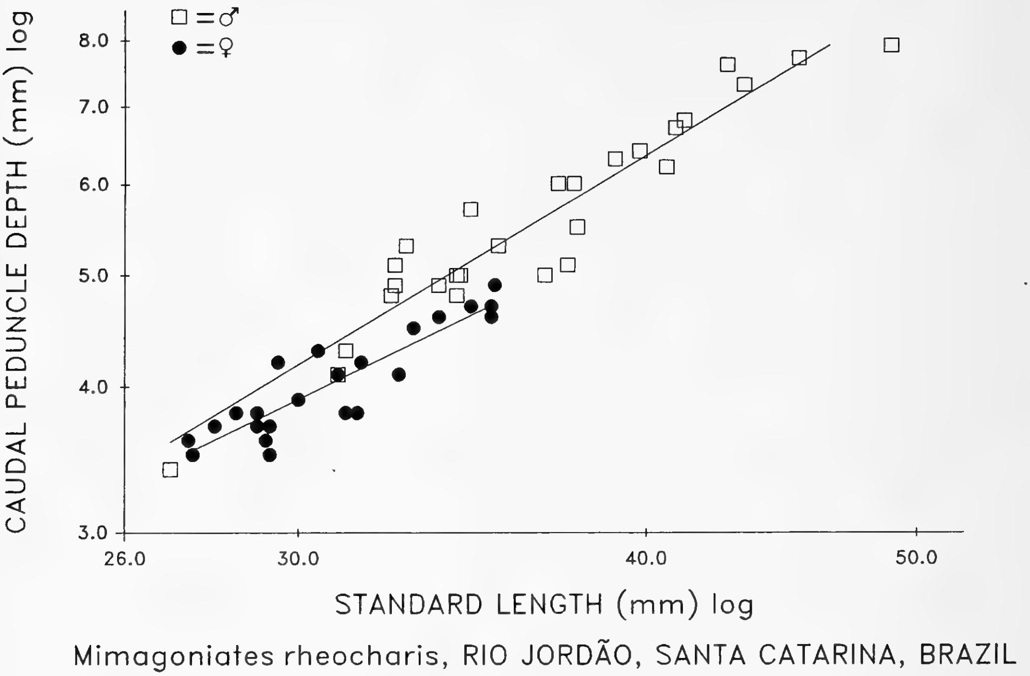


Fig. 28. *Mimagoniates rheocharis,* new species, paratypes caudal peduncle depth as a function of SL by sex. Plot axes are logarithmic. Logarithmic regression equation for 27 males of *M. rheocharis*: ($Y = -3.490 + 1.447X$) and for 23 females of *M. rheocharis*: ($Y = -2.606 + 1.167X$). For explanation see Sexual dimorphism under *M. rheocharis.*

mone organ. Rays 17–19 (ventral caudal-fin lobe) hyaline or nearly hyaline except ray 17 which is somewhat yellow. Remainder of black pigment of caudal fin as described above for preserved specimens.

Anal fin with distal portion of fin rays posterior to anterior anal-fin lobe lemon yellow, forming a stripe along ventral border of fin. Distal region of anterior anal-fin lobe hyaline to white, proximally bordered by black pigment described above for preserved specimens. This black pigment mixed with yellow. Basal half of anal fin hyaline with some scattered brown chromatophores and a small amount of yellow anteriorly. Posterior portion of narrow horizontal black line of anal fin pale. Approximately distal half of pelvic fin white; a black and yellow band proximal to this; remaining proximal portion of fin hyaline. Distal half of pectoral fins yellow, proximal half with black rays and yellow membranes. Dorsal fin hyaline to white distal and proximal to longitudinal black and brown longitudinal stripe.

Sexual dimorphism. —Females lack a caudal pheromone pump organ and pelvic-fin and anal-fin hooks described above for males. Live color of females is unknown but undoubtedly more subdued than that of sexually mature males. Figure 17 graphically indicates that according to these population samples, males and females of *M. rheocharis* and *M. microlepis* respectively show no significant sexual dimorphism in body depth. In an *F*-ratio test for homogeneity of slopes in an analysis of covariance for body depth on SL of *M. rheocharis,* no significant difference was found for 31 males and 25 females from Praia Grande (MZUSP 40270, 40280, MCP 13616, and USNM 279878, 306339. The above sample included very young as well as fully adult speci-

Table 2. Morphometrics of *Mimagoniates rheocharis,* new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Specimens are from near Rio Grande, Santa Catarina, MZUSP 40278, 40280, MCP 13616, and USNM 279878, 306339.

	Holotype	n	Range	$\bar{x}$
Standard length	47.3	57	13.5–47.8	29.5
Depth at dorsal-fin origin	—	57	22.2–35.2	30.5
Males	33.8	31	26.9–35.2	31.4
Females	—	26	22.2–32.9	29.4
Snout to dorsal-fin origin	57.9	57	54.6–60.7	58.0
Snout to pectoral-fin origin	26.6	57	24.2–29.6	26.3
Snout to pelvic-fin origin	43.4	57	40.4–47.6	45.0
Snout to anal-fin origin	58.8	57	52.3–58.8	56.9
Caudal peduncle depth	—	57	8.9–16.3	13.4
Males	16.0	31	11.5–16.3	14.2
Females	—	26	8.9–14.2	12.4
Caudal peduncle length	11.4	57	7.1–13.3	9.9
Pectoral-fin length	21.6	57	18.5–24.9	22.7
Pelvic-fin length	12.3	57	11.1–15.1	13.4
Dorsal-fin base length	17.3	57	12.7–19.1	15.8
Dorsal-fin height	26.0	57	20.7–28.0	23.7
Anal-fin base length	34.5	57	33.7–38.7	36.0
Anal-fin lobe length	19.0	57	15.6–22.6	19.9
Eye to dorsal-fin origin	45.9	57	41.5–48.3	45.2
Dorsal-fin origin to caudal-fin base	46.5	57	39.3–49.2	45.4
Bony head length	25.6	57	24.2–28.1	25.5
Horizontal eye diameter	33.1	56	33.1–48.1	39.5
Snout length	24.8	56	20.0–26.2	22.5
Least interorbital width	33.9	56	28.9–40.4	36.0
Upper jaw length	43.8	56	42.9–50.0	45.7

mens. Juveniles of undetermined sex were entered as females since young females are indistinguishable from juveniles in body depth.

In another sample of *M. rheocharis* consisting of only adults from rio Jordão (MZUSP 40279, MCP 13617 and USNM 279879), Fig. 25, the same statistical test for body depth as a function of SL in 27 males and 23 females demonstrated no significant difference between slopes but does show a significant difference ($F_{0.05,\ (1,\ 47)} = 18.67$, $P < 0.001$) in adjusted means. Both Figs. 25 and 26 indicate considerable sexual dimorphism in body length for *M. rheocharis.*

Figures 27 and 28 provide graphic evidence that there appears to be a divergence in caudal peduncle depth between males and females of *M. rheocharis* as they become sexually mature and increase in length. We have few females over 33.0 mm in SL so the nature of caudal peduncle depth divergence between males and females remains unsampled if females reach the same SL as males. We doubt that happens, because in all the population samples of various species of *Mimagoniates* examined by us, the males reach a greater adult length than females. Thus, again in our analyses of sexual dimorphism our comparison of males and females of unequal body lengths is probably an expression of reality rather than of missing data for females. In *F*-ratio tests of an analysis of covariance for caudal peduncle depth on SL, no significant difference was found for the homogeneity of slopes between 30 male specimens and 25 females although a significant difference ($F_{0.05, (1, 52)} = 22.33$, $P < 0.001$) in adjusted means was evident; see also Fig. 27. This population sample is from the specimens reported above from near Praia Grande. In another population sample, the same one reported above regarding body depth as a function of SL from rio Jordão, the slopes of the females versus males were not significantly different in caudal peduncle depth as a function of SL (Fig. 28) but the adjusted means are significantly different ($F_{0.05, (1, 47)} = 18.67$, $P < 0.001$) and are similar to those reported above from near Praia Grande rio Grande region, Santa Catarina.

Statistical comparisons.—As noted in the Diagnosis above and the Discussion below of *M. rheocharis,* comparisons testing hypotheses of significant statistical difference between *M. rheocharis* and two species, *M. microlepis* and *M. inequalis,* were necessary because many of their characters overlap and because of the need to examine, in a preliminary way, the possibilities of introgression among these species.

Body depth as a function of SL in an *F*-ratio test for homogeneity of slopes (Fig. 17) showed no significant differences in an analysis of covariance between 31 males of *M. rheocharis* from rio Grande region, Santa Catarina (MZUSP 40280, USNM 306339) and 39 males of *M. microlepis* from the area near Paranaguá, Paraná (MZUSP 40288, USNM 306378) but did show a significant difference ($F_{0.05, (1, 67)} = 188.05$, $P < 0.000$) in adjusted means. Same analysis for 24 and 31 females respectively from same localities also showed no significant difference in slopes but did show such a difference ($F_{0.05, (1, 53)} = 82.97$, $P < 0.000$) in adjusted means.

Caudal peduncle depth as a function of SL in an *F*-ratio test for homogeneity of slopes (Fig. 27) showed no statistically significant difference in an analysis of covariance between 30 males of *M. rheocharis* from near Praia Grande, rio Grande region, Santa Catarina (MZUSP 40280, USNM 306339) and 40 males of *M. microlepis* from area near Paranaguá, Paraná (MZUSP 40288, USNM 306378) but did show a significant difference ($F_{0.05, (1, 67)} = 94.36$, $P = 0.000$) in adjusted means. Same analysis for 26 and 31 females respectively from same localities also showed no significant differences in slopes but did show such a difference ($F_{0.05, (1,54)} = 106.03$, $P < 0.000$) in adjusted means.

Number of scale rows between dorsal-fin origin and anal-fin origin of *M. rheocharis* (17–22) and *M. microlepis* (14–17) overlaps somewhat but is statistically significantly different. Forty-two specimens of *M. rheocharis* ($\bar{x} = 19.6$, range = 18–22, SD = 0.8211) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 58 specimens of *M. microlepis* ($\bar{x} = 15.2$, range = 14–17, SD 0.6702) do not overlap but 53 specimens of *M. rheocharis* ($\bar{x} = 18.8$, range = 17–21, SD = 0.8905) from the rio Grande region of Santa Catarina do overlap with the specimens of *M. microlepis* just noted. These last two samples are significantly different ($t = 24.959$, $P = 0.00$).

Lateral series scale counts, as noted above broadly overlap but one case of 48 specimens of *M. rheocharis* ($\bar{x} = 44.2$, range = 41–48, SD = 1.7704) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 45 specimens of *M. microlepis* ($\bar{x} = 45.0$, range = 42–49, SD = 1.5948) from Paranaguá and rio Nhundiaquara (MZUSP 40281, USNM 249886, 249890, 249894, 249897, 257114, 257115, 257198) showed a significant difference ($t = 2.459$, $P = 0.015$).

Branched dorsal-fin ray count higher (8–12, $\bar{x} = 9.4$) for *M. rheocharis* than any other species in tribe Glandulocaudini (branched dorsal-fin rays almost always 8, rarely 7 or 9) and constitutes an autapomorphy for the species. Two sampled populations differed considerably from one another in this count. Fifty specimens of *M. rheocharis* ($\bar{x} = 9.8$, range = 9–12, SD = 0.6701) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879 and 56 specimens of this species ($\bar{x}$

$= 8.9$, range $= 8–10$, SD $= 0.4615$) from rio Grande region of Santa Catarina (MZUSP 40280, USNM 306339) were significantly different ($t = 7.901$, $P = 0.00$). Both of these population samples of *M. rheocharis* differed significantly from that of 70 specimens of *M. microlepis* ($\bar{x} = 8.0$, range $= 7–9$, SD $= 0.1703$) from area near Paranaguá and rio Nhundiaquara, Paraná (MZUSP 40281, 40288, USNM 249886, 249890, 249894, 24897, 257114, 257115, 257198, 306378). Thus, $t = 22.490$, $P = 0.00$ for rio Jordão sample and $t = 9.472$, $P = 0.00$ for rio Grande sample of *M. rheocharis.*

Branched anal-fin ray counts, although overlapping for these two species are statistically different ($t = 19.402$, $P = 0.00$) in 50 specimens of *M. rheocharis* ($\bar{x} = 25.3$, range $= 23–27$, SD $= 1.1073$) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 70 specimens of *M. microlepis* ($\bar{x} = 29.7$, range $= 26–33$, SD $= 1.2471$) from near Paranaguá and rio Nhundiaquara at Morretes, Paraná, (MZUSP 40281, 40288, USNM 306378, 249886, 249890, 249894, 249897, 257114, 257115). A second population sample of 56 specimens of *M. rheocharis* ($\bar{x} = 26.8$, range $= 25–29$, SD $= 1.3088$) from area of rio Grande, Santa Catarina (MZUSP 40278, 40280, MCP 13616, USNM 279878, 306339) also differed significantly in a similar test from the Paranaguá and rio Nhundiaquara samples ($t = 12.1510$, $P = 0.00$).

Vertebral counts of *M. rheocharis* and *M. microlepis* overlap somewhat, but they are significantly different ($t = 12.528$, $P < 0.00$): $\bar{x} = 38.0$, range $= 37–40$, SD $= 0.6558$, $n = 87$ for *M. rheocharis* from rio Jordão (MZUSP 40279, USNM 270879) and $\bar{x} = 39.3$, range $= 38–41$, SD $= 0.6532$, $n = 70$ for *M. microlepis* from rio Nhundiaquara (MZUSP 40281, USNM 249886, 249890, 249894, 249897, 257114, 257115, and 257198).

In the following statistical comparisons of *M. rheocharis* and *M. inequalis,* specimens of the latter species from an arroio near Morungava, Município de Gravataí, Rio Grande do Sul (MAPA 115), were chosen for comparison because they came from the rio Gravataí system, a drainage adjacent to the streams around Osório which contain *M. rheocharis.* See also in the *Discussion* below comparison of our few specimens of *M. rheocharis* from the adjacent streams around Osório and the rio Maquiné just to the north of Osório.

Body depth as a function of SL in an F-ratio test for homogeneity of slopes (Fig. 17) showed no significant difference in an analysis of covariance between 31 males of *M. rheocharis* from rio Grande region, Santa Catarina (MZUSP 40280, USNM 306339) and 26 males of *M. inequalis* from Morungava, Rio Grande do Sul (MAPA 115) but did show a difference ($F_{0.05,(1,54)} = 50.03$, $P < 0.000$) in adjusted means. Same analysis for 25 females and 14 females of each species respectively from same localities showed a significant difference ($F_{0.05,(1,36)} = 42.41$, $P < 0.000$) in body depth on SL only for adjusted means.

Caudal peduncle depth as a function of SL in an F-ratio test for homogeneity of slopes (Fig. 27) showed no statistically significant difference in an analysis of covariance between 30 males of *M. rheocharis* from rio Grande, Santa Catarina (MZUSP 40280, USNM 306339) and 26 males of *M. inequalis* from Morungava, Rio Grande do Sul (MAPA 115) but did show a significant difference ($F_{0.05\,(1,53)} = 43.95$, $P < 0.000$) in adjusted means. Some test for 26 females and 14 females respectively from same localities showed a significant difference ($F_{0.05,(1,37)} = 69.18$, $P < 0.000$) only in adjusted means.

Number of scale rows around caudal peduncle of *M. rheocharis* (19–22) and *M. inequalis* (16–19) overlaps slightly but is significantly different. No overlap for present 17 specimens of *M. rheocharis* ($\bar{x} = 21.5$, range $= 20–22$, SD $= 0.7174$) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 34 specimens of *M. inequalis*

($\bar{x}$ = 17.6, range 16–19, SD = 0.8170) from Morungava, Rio Grande do Sul (MAPA 115). Number of scale rows around caudal peduncle overlaps slightly in 46 specimens of *M. rheocharis* ($\bar{x}$ = 19.7, range = 19–22, SD = 0.7520) from rio Grande region of Santa Catarina (MZUSP 40280, USNM 306339) and those just listed just above of *M. inequalis,* but counts significantly different (t = 12.011, P = 0.00).

Number of scale rows between dorsal-fin origin and anal-fin origin of *M. rheocharis* (17–22) and *M. inequalis* (16–18) also overlaps somewhat but again is statistically significantly different. There is an overlap in 42 specimens of *M. rheocharis* ($\bar{x}$ = 19.6, range = 18–22, SD = 0.8211) from the rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 40 specimens of *M. inequalis* ($\bar{x}$ = 16.5, range = 16–18, SD = 0.6405) from Morungava, Rio Grande do Sul (MAPA 115), but these counts are significantly different (t = 19.565, P = 0.00).

Lateral series scale count of *M. rheocharis* (41–48) and *M. inequalis* (36–41) overlaps somewhat but is significantly different statistically. No overlap occurs in 26 specimens of *M. rheocharis* ($\bar{x}$ = 45.5, range = 43–48, SD = 1.4760) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 38 specimens of *M. inequalis* ($\bar{x}$ = 38.3, range = 36–41, SD = 1.1455) from Morungava, Rio Grande do Sul (MAPA 115). Lateral series scale count overlaps slightly in 48 specimens of *M. rheocharis* ($\bar{x}$ = 44.2, range = 41–48, SD = 1.7704) from rio Grande region of Santa Catarina (MZUSP 40280, USNM 306339) and those just listed of *M. inequalis,* but these counts are significantly different (t = 17.922, P = 0.00).

Branched dorsal-fin ray count in 50 specimens of *M. rheocharis* ($\bar{x}$ = 9.8, range = 9–12, SD = 0.6701) from rio Jordão (MZUSP 40279, USNM 270879) differed significantly from a sample of 40 specimens of *M. inequalis* ($\bar{x}$ = 8.125, range = 8–9, SD = 0.3349) from Morungava, Rio Grande do Sul (MAPA 115) (t = 14.951, P = 0.00). Same comparison for 56 specimens of *M. rheocharis* ($\bar{x}$ = 8.9, range = 8–10, SD = 0.4615) with same sample of *M. inequalis* just mentioned was also significantly different (t = 9.472, P = 0.00).

Branched anal-fin ray counts overlap for both species but are statistically significantly different (t = 6.336, P = 0.00) in 50 specimens of *M. rheocharis* ($\bar{x}$ = 25.3, range = 23–27, SD = 1.2471) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 40 specimens of *M. inequalis* ($\bar{x}$ = 26.7, range = 24–30, SD = 0.9443) from Morungava, Rio Grande do Sul (MAPA 115). These not significantly different in a second population sample of 56 specimens of *M. rheocharis* ($\bar{x}$ = 26.8, range = 25–29, SD = 1.3088) from rio Grande, Santa Catarina (MZUSP 40278, 40280, MCP 13616, USNM 279878, 306339) from that of *M. inequalis* just described.

Vertebral counts, $\bar{x}$ = 38.0, range = 37–40, SD = 0.6558, n = 87, for *M. rheocharis* from rio Jordão (MZUSP 40279, USNM 27879) and, $\bar{x}$ = 37.9, range = 36–39, SD = 0.7055, n = 70, for *M. inequalis* from Morungava, Rio Grande do Sul (MAPA 115) are not significantly different statistically.

Etymology.—The name *rheocharis* is from the Greek *rheos* (= current or stream) and *charis,* also Greek, (= loveliness, grace or charming) and is in reference to the streams in which this fish has been taken and to the beauty of the fish itself.

Discussion.—The phylogenetic relationships of *M. rheocharis* are uncertain but fully mature males, as noted above, have a caudal fin-ray pump chamber, a putative synapomorphy uniting that species with *M. sylvicola, M. lateralis,* and *M. microlepis. Mimagoniates inequalis* and *M. barberi* are not included in this group because they lack a caudal pump chamber, having only a groove in its place.

Weitzman et al. (1988:412) tentatively hypothesized that *M. rheocharis,* as new species B, is a sister species of *M. microlepis* because these species share caudal-fin hooks (absent in other species of *Mimagoniates*) distal to the pump area on principal caudal-fin rays 10 and 11. These hooks are not nearly as numerous or as large in *M. rheocharis* as they are in *M. microlepis* (compare Figs. 5 and 24). We found no other synapomorphy uniting these two species. *Mimagoniates rheocharis* and *M. microlepis* thus may still be hypothesized as one another's closest relatives (Fig. 1). However, Fig. 1 is presented primarily as a visual aid to the discussion that follows. We accept the hypothesis it presents with reservations because the relationships of *M. rheocharis* may be quite complex due to a possible hybrid origin or at least some introgression with other species. Furthermore a considerable amount of character conflict exists among all the species of *Mimagoniates* making acceptance of many of the relationships suggested in Fig. 1 quite questionable.

A number of differences, outlined in the key and diagnosis above, were found among *M. rheocharis* and *M. microlepis* and *M. inequalis.* Although these differences indicate these species are divergent, many of these characters cannot at present be used to corroborate hypotheses of phylogenetic relationship with other species of *Mimagoniates* because so far they have not been identified as synapomorphies shared among other species. Certain of these characters are continuously variable between at least some species, for example between *M. rheocharis* and *M. inequalis,* possibly limiting their use as characters suitable for phylogenetic analyses, Chappill (1989) and Pimentel & Riggins (1987). Some of the states of these characters as shared by *M. rheocharis* and *M. inequalis* are plesiomorphic with respect to their condition in other species of *Mimagoniates,* making their use as synapomorphies for these two species impossible. For example, outgroup comparison with species of *Glandulocauda* and species in other tribes of the Glandulocaudinae indicates that relatively short overall body shape and central median fin position of *M. rheocharis,* shared with *M. inequalis,* is plesiomorphic with respect to the more elongate body and posterior dorsal-fin position in *M. microlepis, M. lateralis, M. sylvicola* and *M. barberi* (see also comments below). Relatively elongate body shapes might be considered synapomorphic for the latter four species but use of this character for corroboration of phylogenetic hypotheses in the Glandulocaudini is still in need of further study and may be difficult to use at some nodes because of continuous variability. The high number of dorsal-fin rays (8–12 in *M. rheocharis* versus 7–9 in other species of *Mimagoniates*) appears autapomorphic for that species, but, again the character is continuously variable between *M. inequalis, M. rheocharis* and other species of *Mimagoniates.*

If these and other similar characters can be used as synapomorphies at some nodes, then character conflict and complex homoplasies will need to be resolved using parsimony with enough corroborated evidence to be convincing. For example, at present at least three characters or character complexes appear in conflict with one another in regard to their possible significance in suggesting phylogenetic relationships. These are relative body length, relative derivation of the caudal pump and the presence or absence of a prominent lateral mid-side dark stripe. For example, if elongate body, present in *M. sylvicola, M. lateralis, M. barberi* and *M. microlepis,* were hypothesized to have evolved only once then these four species would form a monophyletic line based on this character. Then the caudal fin-ray pump chamber might have evolved twice, once in *M. rheocharis* and again in a clade including *M. lateralis, M. sylvicola* and *M. microlepis.* On the other hand, monophyly based in part on elongate body could result in a phylogeny wherein *M. lateralis* was the sister species to all of the other species just mentioned and *M. rheocharis* regained a relatively short body shape.

Again, *M. lateralis* and *M. barberi* share the possession of a dark brown or black broad lateral stripe extending from the lower jaw tip posteriorly across the body sides to the region of the caudal gland on the caudal fin. A hypothesis that considers this character synapomorphic for these two species requires that the pump chamber evolved more than once, independently in *M. lateralis,* and in a clade consisting of *M. sylvicola, M. rheocharis* and *M. microlepis,* a phylogenetic configuration different from those noted above for acceptance of elongate body as a synapomorphy for four species of *Mimagoniates.* Finally, if one hypothesizes that a fully derived caudal fin-ray pump chamber evolved only once in a clade consisting of *M. sylvicola, M. lateralis, M. rheocharis* and *M. microlepis,* then both the lateral stripe and elongate body would have evolved twice each and in a phylogenetic configuration different from any of those above. At this time the above speculations and others like them are fruitless and we mention them only to point out the current complexities regarding the phylogeny of the species of *Mimagoniates.* As yet we have not fully investigated the possible phylogenetic significance of many of the characters putatively available for phylogenetic analysis of the Glandulocaudini. The matter is quite complex and the use of parsimony to propose acceptable phylogenetic hypothesis and resolve the problems of character polarities will naturally still result in numerous homoplasies. We might add that the use of any "method" other than parsimony to resolve character conflict will not eliminate all homoplasies but only subjectively delete some rather than others.

As noted above, we tentatively hypothesize that *M. rheocharis* and *M. microlepis* are sister species based on fin-ray secondary sexual characters which do not appear to be continuously variable and may be synapomorphic if the character conflicts mentioned above can be resolved in a form that favors the secondary sexual fin-ray structures. However, as one might expect, there are complications and possible alternative hypotheses of phylogenetic relationships other than those mentioned above. For various reasons some of these should be briefly discussed.

In searching for possible alternate hypotheses of phylogenetic relationship for *M. rheocharis* we note that this species and *M. inequalis* look remarkably alike in general body shape, fin position, body color and the counts recorded above as separating the species are not remarkably different. Both species lack the distinct mid-lateral body stripe found in *M. lateralis* and *M. barberi.* Furthermore, both species have closely similar vertebral counts that are not significantly different, $n = 39$ for specimens of *M. inequalis* from Arroio Fiuza near Passo Fiuza, Municipio de Viamão, south east of Porto Alegre, Rio Grande do Sul, (USNM 254273), $\bar{x} = 38.0$, range = 35–39, SD = 0.6489 and $n = 87$ for specimens of *M. rheocharis* from rio Jordão, (MZUSP 40279, USNM 279879), $\bar{x} = 38.0$, range = 37–40, SD = 0.6288. See also the nearly identical results of a different comparison of vertebral numbers and other counts given in the section labeled Statistical Comparisons. These vertebral counts are relatively low when compared with those of the more elongate species of *Mimagoniates* such as *M. rheocharis* but broad overlap occurs, again see section above labeled *Statistical Comparisons,* and we are unable to show that shared vertebral counts by *M. rheocharis* and *M. inequalis* are shared derived characters. We discuss such characters only to point out the difficulties in attempting to study the relationships of the species of *Mimagoniates* based on characters other than those directly associated with their secondary sexual characteristics.

Our preliminary analysis suggests that these character similarities are unlikely to be synapomorphic for *M. rheocharis* and *M. inequalis* because these features are also found in immediate outgroups down the tree, for example species of *Glandulocauda* and certain of the apparently less derived glandulocaudine species belonging to tribes that are possibly sister groups to the Glandulocaudini. However, our analysis is incomplete and alternate hypotheses suggesting that *M. inequalis* and *M. rheocharis* are sister species or related in some way cannot be confidently rejected at this time.

The intermediacy of the *M. rheocharis* between *M. inequalis* and *M. microlepis* in body depth and caudal peduncle depth (Figs. 17, 27) was noted above in the Diagnosis and the Statistical Comparison section of *M. rheocharis.* The relatively modest development of the fin-ray pump chamber and of the small and few caudal-fin spines on rays 10 and 11 in *M. rheocharis,* rather than being considered plesiomorphic relative to the state of these structures in *M. microlepis,* could be considered intermediate between the state in *M. inequalis* (no spines, no pump chamber) and that in *M. microlepis* (many well developed spines, and a highly developed fin-ray pump chamber). This suggests a possible origin of *M. rheocharis* by introgression between *M. microlepis* and *M. inequalis.* However, a hypothesis of hybrid origin for *M. rheocharis* might be rejected because it does have autapomorphies that are absent in both *M. inequalis* and *M. microlepis.* Even then, it cannot be discounted that *M. rheocharis* might have originated through introgression in a geographical range once shared by the ancestors of the current populations of *M. inequalis* and *M. microlepis* and that the autapomorphies of *M. rheocharis* evolved subsequent to that introgression at a time when *M. rheocharis* became isolated from its parent populations. The current geographical ranges of these species would be congruent with such a biogeographical hypothesis but in our view this hypothesis, just as any hypothesis of species origin by introgression, unless corroborated by genetic data as well as much statistical data on morphology from pertinent natural populations, is less parsimonious than that of sister status, in this case between *M. rheocharis* and *M. microlepis.* Because we lack such data, we currently reject this introgression hypothesis. If *M. rheocharis* did evolve in part through introgression, according to our hypotheses of phylogeny among the species of *Mimagoniates* this introgression would have taken place between two of the more distantly related members of the genus, something we view as possible but in need of study by breeding experiments and intensive statistical analyses of the characters of the three species from population samples in the areas of their contingency and sympatry.

It might be proposed that specimens of *M. rheocharis* are simply hybrid individuals between *M. inequalis* and *M. microlepis* but several factors argue against this. First, only one of the putative parent species occurs in the present range of *M. rheocharis,* that is *M. microlepis* which is sympatric and syntopic with *M. rheocharis. Mimagoniates inequalis,* as explained above, is so far as known allopatric with *M. rheocharis,* preventing it from being a parent of current specimens of *M. rheocharis.* Furthermore, *M. rheocharis* has autapomorphic characters not present in either putative parent.

Another hypothesis of phylogenetic relationship, one that is less parsimonious than sister species status for *M. rheocharis* and *M. microlepis,* could be put forward and we mention this one only because of its implications regarding the dangerous practice of assuming biogeographical significance for geographically adjacent similar looking species, done by some biogeographers. One could hypothesize that *M. rheocharis* and *M. inequalis* are sister species. This hypothesis is not out of the realm of possibility even though current character polarity hypotheses for secondary sexual characters indicate that other features shared by these latter two species are plesiomorphic at this level of relationship. Nevertheless, if such a hypothesis were true the current distributions of these two species would make good historical biogeographical sense. *Mimagoniates inequalis* is found in the freshwater biogeographical South Coastal Subregion of Menezes (1988:300) and *M. rheocharis* is found in the adjacent southern part of his Central Coastal Subregion. A simple vicariance or dispersion event historically separating two parts of an ancestral population for the two species could have been responsible for initiating their evolution. However, the phylogenetic evidence, in all its current uncertain status, does not support such a hypothesis of phylogeny and therefore does not support this historical biogeographical pattern. This example provides one reason why we refuse to use current distributional patterns of species as either evidence of relationships among organisms or as direct indicators of historical biogeographic events. Most distribution patterns may correlate with a variety of phylogenetic and biogeographic scenarios and cannot be used as primary evidence for any given one.

Another problem with some of our data remains to be discussed. Given the current limitations of our population samples and the small adult lengths of most of our specimens of *M. inequalis,* it is difficult to place too much confidence in certain aspects of the above phylogenetic discussions based on some secondary sexual characteristics. This is true because at least one, caudal pump morphology, of the phylogenetically important characters currently available for *M. rheocharis* and its possible relatives such as *M. inequalis,* is based on a character that may be juvenile, that is not representing a character state attained in fully mature adults of that species. Such juvenile character states may then be compared incorrectly with homologous but fully adult characters in another species, leading to invalid conclusions regarding the relative apomorphy of these characters. This kind of problem affects both of the very separate tasks of studying phylogenetic relationships and of distinguishing species from one another, witness our caution about couplet four in our key above and our mistake in Weitzman et al. (1988) regarding the relative apomorphy of the caudal gland in *M. sylvicola* (see the Discussion above of that species). Regarding *M. inequalis* in the current treatment, perhaps our collections contain no fully adult males of this species and at the completion of sexual maturity, males have a caudal fin-ray pump chamber similar to that found in males of *M. rheocharis.* If this were true the phylogenetic relationships we have presented based on caudal morphology would be drastically altered. The evidence we have bearing on this problem is as follows. A male specimen of each of the two species of nearly equal length (one, *M. inequalis,* SL 38.8 mm, MCP 9892, from rio Caí drainage, Rio Grande do Sul, and the other, *M. rheocharis,* SL 39.5 mm, MCP 10806, from rio Três Furquilhas, Rio Grande do Sul), indicate that *M. rheocharis* has a well-developed caudal-fin ray pump chamber as well as tiny hooks on principal caudal fin-rays 10 and 11 and that *M. inequalis* only has a groove and no hooks. Also, two old aquarium specimens of male *M. inequalis* (USNM 94310, originally imported from Porto Alegre and grown to "old age" in an aquarium by Herman Meinken) have standard lengths of 38.2 and 41.0 mm. The latter specimen is the largest we have of this species. These specimens show no evidence of a caudal pump chamber or hooks on fin-rays 10 and 11 but do have a groove. Furthermore, three smaller (SL 28.5–31.3 mm) sexually mature males of *M. rheocharis* (MCP 13613, from arroio Água Parada, a tributary of the rio Maquiné from near Maquiné, Rio Grande do Sul) have well-developed pump chambers as well as tiny hooks present on caudal-fin rays 10 and 11. These facts reinforce our hypothesis that *M. rheocharis* is a derived species distinct from the more plesiomorphic *M. inequalis.*

The specimens of *M. rheocharis,* MCP 13613, three males and four females, from arroio Água Parada plus a single large specimen (SL 41.8 mm, MZUSP 40281, Fig. 20, from a nearby locality, arroio das Pedras near Osório), are interesting in light of the introgression hypotheses discussed above. The meristic characters that help distinguish *M. inequalis* and *M. rheocharis* are all within the overlapping range of the two species (9 branched dorsal-fin rays, 16–17 scale rows between the dorsal-fin and anal-fin origins, 18–19 scale rows around the caudal peduncle and 42–43 scales in a lateral series). Although these counts fall well within the range of those of other population samples of *M. rheocharis* to the north, they do fall closer to those counts of *M. inequalis* than any of our other population samples of *M. rheocharis.* Compare the counts just given with those presented in the comparative section of the Diagnosis of *M. rheocharis* above. We also note that these localities for *M. rheocharis* near Osório lie adjacent to the rio Gravataí drainage just to the west which is occupied by *M. inequalis.* We are unsure of the real significance of these counts but they could imply some gene flow between *M. rheocharis* and *M. inequalis* in this region at some time in the past. We are unaware of any current sympatry of these two species in this region but the area is not well sampled.

In summary, the phylogenetic relationships of *M. rheocharis* are uncertain. It could simply be a sister species of *M. microlepis* with a somewhat more plesiomorphic state of the caudal pheromone origin, a somewhat derived sister species of *M. inequalis,* a species derived by introgression between *M. inequalis* and *M. microlepis* with subsequent evolution of some autapomorphic characters, or, for example, a sister species of *M. microlepis* which may be introgressing with *M. inequalis.* Other hypotheses of phylogenetic relationship could be suggested but these examples are sufficient to indicate the possible complexities of the phylogeny of *M. rheocharis.* Because the shared characters of *M. rheocharis* and *M. inequalis* have been hypothesized to be pleisomorphies in the context of the entire phylogeny of the Glandulocaudini, we, at least for now, accept the evidence that the male caudal secondary sexual characters represent synapomorphies and tentatively propose sister species status for *M. rheocharis* and *M. microlepis.* The other hypotheses of possible phylogenetic relationship await considerable additional evidence for possible corroboration.

Ecology.—We do not have extensive notes on the ecology of this species but the following information is taken from notes by Carlos Lucena from two localities (one the type locality) and by Ricardo M. C. Castro from two localities.

Specimens collected by C. A. S. de Lucena and party from rio Faxinalzinho at Mãe dos Homens, rio Mampituba drainage, near Praia Grande, the type locality, MZUSP 40278, MCP 3616, USNM 279878, were removed from a clear-water stream 2–6 m wide, 0.1–1.0 m deep, with a moderate current. There was a moderate amount of (unspecified) marginal vegetation present. The substrate consisted of rubble, rocks, stones, and gravel. *Mimagoniates microlepis* and a species of each of *Rhamdia, Rhamdella, Heptapturus, Ancistrus, Rhineloricaria, Pseudotocinclus, Pareiorhyna, Corymbophanes, Trichomycterus, Characidum,* an unspecified species of tetragonopterine characid, two species of *Astyanax,* and a species of *Jenynsia* were present.

The second locality collected by Carlos Lucena and party was rio Jordão near Jordão Alto, MCP 13617, MZUSP 40279, and USNM 270879. This was the upper region of the rio Jordão where the stream was 1–5 m wide and 0.1–0.7 m deep. The current was slow, there was a small amount of (unspecified) marginal vegetation, and the substrate consisted of rubble, rocks, stones, gravel, sand and mud. The fishes that were collected at the same locality were species of *Rhamdia, Heptapterus, Ancistrus,* two loricariids unidentified to genus, *Rhineloricaria, Pseudotocinclus,* two species of *Tri-*

chomycterus, Characidium, Hoplias, Astyanax, an unidentified tetragonopterine characid, *Phalloceros, Jenynsia, Geophagus brasiliensis* and *Cichlasoma facetum.*

The first locality collected by Ricardo Castro is from near Osório, Rio Grande do Sul, MZUSP 40281. The specimen was collected in a small clear-water stream about 1.5 m wide and 20 cm deep, surrounded by shrubs and small trees. The water was clear, with very little suspended matter. Algae covered rocks were common on the substrate. Other fishes collected in the area were species of *Astyanax, Oligosarcus, Rhamdia,* and a small unidentified catfish.

Specimens of *M. rheocharis* from a tributary of the rio Grande, Santa Catarina, MZUSP 40280 and USNM 306339, were collected from a slow moving clear water stream about 1.5 m wide and 30 cm deep. Not far away the stream flowed into the larger river. Rocks, sand, soil and twigs fallen from nearby trees were the main substrate components. The rocks and twigs were densely covered with algae. The stream was bordered by rocks, mud, grass and small trees in many places.

Biogeography

Weitzman et al. (1988:404) tentatively hypothesized that *M. inequalis, M. barberi* and *M. sylvicola* (as new species A) were less derived than the remaining species of *Mimagoniates* and that they might form a natural group although the three species shared no synapomorphies. This hypothesis was used to make the statement that species with a relatively primitive pump morphology are distributed peripheral to the other, more derived species. The evolution of those species with derived caudal pumps was hypothesized to have taken place where they now live, the central area of the north to south coastal stream distribution of *Mimagoniates,* roughly from southern Bahia to northern Rio Grande do Sul. We suggested that at one time a species of *Mimagoniates* with a relatively simple, primitive caudal-fin pheromone pump may have been distributed throughout the current range of *Mimagoniates* and that subsequent vicariance and/or dispersion events associated with changes in sea level may have played a major role in speciation and the evolution of the complex fin-ray pump. Evidence for dispersion by stream capture or other means of migration was considered because some of the species were found to be in part or wholly sympatric (in some cases allotopic and in others syntopic). Weitzman et al. (1988:414) also hypothesized that the most derived species, *M. microlepis,* distributed in coastal stream from southern Bahia to northern Rio Grande do Sul, reached the upper rio Iguaçu drainage by stream capture or possibly was introduced by man.

As indicated above in the present Discussion of *M. sylvicola,* this species has a well-developed caudal pump chamber and therefore there is no direct evidence that a primitive species ever existed at the northern end of the current known range of the species of *Mimagoniates.* This does not mean that one never existed there, since it could have been replaced by the more derived species currently in that location, a hypothesis only testable by fossil evidence. If the phylogenetic relationships hypothesized here for *M. sylvicola* are correct, we might assume that caudal pump chamber evolution took place throughout the coastal stream distribution of *Mimagoniates* in Brazil north of the current distribution of *M. inequalis* in the state of Rio Grande do Sul.

If the phylogenetic hypothesis that *M. rheocharis* and *M. microlepis* are sister species can be accepted, then at one time in the past a vicariance or perhaps a dispersion event isolated two populations of the parent species, possibly in or at least near the current range of *M. rheocharis.* Subsequently further evolution of the caudal organ took place in *M. microlepis.* It would appear that subsequent dispersion of *M. microlepis* into the range of *M. rheocharis* resulting in their present sympatry is the at least one likely scenario but the reverse could also be true at least in part. Speculations about patterns of dispersion other than the mention of their existence are often sterile because data bearing directly on the problem are limited to fossil evidence. If any one of the alternate hypotheses of introgression or sister species relationship with *M. inequalis* for *M. rheocharis* represent reality, it would alter the above biogeographical hypothesis. However, currently there is no reason to discuss such an alteration beyond a brief mention of its possibility. See also the comments concerning biogeography in the Discussion above on the relationships of *M. rheocharis,* especially those on the possible sister species status between *M. rheocharis* and *M. inequalis.*

The problem of speciation as it bears on the biogeography of *Mimagoniates* is quite complex because ecological adaptations, climatic and geomorphological change in association with either vicariance, dispersion, and/or introgression may have played major roles in the evolution of some its species. See especially our comments above regarding introgression and sister species status in the Discussion above of *M. rheocharis.* The biogeographical problems associated with ecological adaptations in species of *Mimagoniates* are little understood but we have enough information to indicate that they cannot be ignored.

For example, of the two species hypothesized above to be sister species, the distribution of *M. rheocharis* is sympatric with that of *M. microlepis.* The information we have so far indicates that *M. rheocharis* is a clear water species. *Mimagoniates microlepis* occurs rarely, if ever, in black acid waters and all our collections of this species came from clear somewhat acid waters. However, these two species apparently are separated (allotopic) at least in some places but we have no information about possible ecological factors preventing syntopy. Furthermore, they have been taken together (syntopic) in two localities, rio Faxinalzinho at Mãe dos Homens, Praia Grande, Santa Catarina, (MZUSP 40278, MCP 13616 and USNM 279878, all *M. rheocharis,* and MCP 13766, *M. microlepis*) and arroio Água Parada, tributary of the rio Maquiné Município de Osório, Rio Grande do Sul, (MCP 13613), *M. rheocharis* and MCP 13625, *M. microlepis*). Thus, in this case black acid waters may have played no role in their speciation although such waters could have formed a barrier in a vicariance event.

At least one species, *Mimagoniates inequalis,* is found in clear and black water streams. This species is often taken in relatively small clear water tributary streams (for example the arroio Paradiso, rio Caí drainage, Rio Grande do Sul, MZUSP 19942, USNM 254275), and we have taken it a few times in small blackwater streams (for example the banhado do Tigre south of Taim, Rio Grande do Sul USNM 254270). The greater adaptability of this species could more easily allow it to introgress with species of more limited ecological tolerance and we have some reason to believe that it may be involved or may have been involved in the past with introgression with either *M. rheocharis* and/or *M. microlepis.* See the Discussion above under *M. rheocharis.*

In another example, the distribution of *M. lateralis,* although geographically completely within (sympatric) that of *M. microlepis,* appears ecologically distinct and therefore allotopic. *Mimagoniates lateralis* appears completely confined to acid black waters and we have never taken *M. lateralis* and *M. microlepis* together even when their respective habitats are contingent. A species such as *M. lateralis* would thus seemingly have limited chances for introgression and we have not found any evidence for this in the populations we have examined. Whatever the ecological adaptations of the various species of *Mimagoniates,* the data indicate that at least broad geographical sympatry occurs in some cases, making the probability of dispersion subsequent to speciation high and producing a possibility of introgression.

Restrictive ecological adaptations, often based on climate, geomorphology and the associated biota, affect speciation in fishes through vicariance, dispersion and/or introgression in very complex ways. We suggest that the species of the Glandulocaudini have been subject to such complexities and that their biogeographical history will not soon be clarified in any detail.

Resumo

Mimagoniates sylvicola e *Mimagoniates rheocharis,* duas espécies de caracídeos brasileiros da tribo Glandulocaudini, subfamília Glandulocaudinae, são descritas como novas. A primeira foi coletada no sul da Bahia, em riachos costeiros de água escura situados ao norte de Cumuruxatiba e em um pequeno tributário do rio Camurugi, perto de Porto Seguro. A segunda é originária de riachos costeiros do sul de Santa Catarina e norte do Rio Grande do Sul. Admite-se que *M. sylvicola* pertence a uma tricotomia não resolvida juntamente com uma linhagem filogenética constituída por *Mimagoniates microlepis* e *M. rheocharis. Mimagoniates lateralis,* conhecida de riachos costeiros de água escura da Costa Atlântica desde as proximidades de Santos, São Paulo até pelo menos próximo de Joinvile, Santa Catarina, ao sul, é morfologicamente mais semelhante a *M. sylvicola.* Estas duas espécies se diferenciam por vários caracteres mencionados na diagnose de *M. sylvicola* e resumidos em uma nove chave para as espécies de Glandulocaudini.

As relações filogenéticas de *M. rheocharis* são incertas e possivelemente complexas. Possíveis hipóteses alternativas de relações filogenéticas desta espécie são discutidas. Com base na presença de uma bomba de feromônio complexa na caudal que representa uma condição derivada e especialmente de espinhos nos raios principais da caudal 10 e 11 distalmente ao complexo de bombeamento de feromônio tanto em *M. rheocharis* como em *M. microlepis,* sugere-se que a primeira seja espécie-irmã da segunda, que distribui-se nos riachos costeiros desde o sul da Bahia até o nordeste do Rio Grande do Sul. *Mimagoniates microlepis* ocorre também na parte alta do rio Iguaçu que drena para oeste, no Paraná. Esta condição de relacionamento filogenético de *M. rheocharis* parece ser a hipótese mais parcimoniosa, mas esta espécie tem a forma do corpo, algumas contagens e proporções corporais e o padrão de colorido pelo menos em exemplares conservados, semelhantes a *M. inequalis.* Também possui alguns caracteres sexuais secundários intermediários entre *M. inequalis* e *M. microlepis.* Assim, não está excluída a possibilidade de *M. rheocharis* ter-se originado de ancestrais de *M. inequalis* e *M. microlepis* por introgressão ou ela pode ser uma espécie-irmã de *M. microlepis* atualmente recebendo fluxo gênico por introgressão com *M. inequalis.* Também é discutida a possibilidade de relacionamento ao nível de espécies-irmãs entre *M. rheocharis* e *M. inequalis,* esta última ocorrendo em riachos costeiros no nordeste do Uruguai e em quase toda a região costeira do Rio Grande do Sul onde ela ocupa uma área adjacente ao limite sul da distribuição de *M. rheocharis* no nordeste do Rio Grande do Sul. Outras hipóteses de relacionamento são apresentadas e algumas discutidas simplesemente para mostrar a natureza possivelmente muito complexa das relações filogenéticas de *M. rhoecharis. Mimagoniates rheocharis* distinguese de *M. microlepis* e *M. inequalis* por características apresentadas na chave e na diagnose de *M. rheocharis.*

As relações filagenéticas e biogeografias filagenéticas das novas espécies são reavaliadas a luz de novos dados e então comparadas com as considerações feitas previamente em um estudo de biogeografia filogenética de Glandulocaudini. Dúvidas são levantadas sobre a filogenia das espécies de Glandulocaudini, mas corroboração de hipóteses alternativas da filogenia dessas espécies depende da análise de novos dados tanto dentro como fora do grupo.

Acknowledgments

Most of the field work for this study was supported by funding from the Neotropical Lowland Research Program of the International Environmental Science Program of the Smithsonian Institution. This program also supported travel for laboratory research in São Paulo and Washington, D.C. The Bacon Fund, Smithsonian Institution provided funds for part of the field work in Rio Grande do Sul and Santa Catarina. Field research was also supported in part by a grant from the National Geographic Society. The following individuals and institutions have contributed much support for this study either by loan of specimens, support for collecting or by personal collecting efforts or both: Reeve M. Bailey and William L. Fink, UMMZ; Heraldo A. Britski and Paulo E. Vanzolini, MZUSP; Ricardo M. C. Castro, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo; Carlos A. Gonçalves da Cruz and Oswaldo L. Peixoto, Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro; Julio C. Garavello, Universidade Federal de São Carlos; Leda F. A. Jardim, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul; Carlos and Margarete Lucena, Luiz R. Malabarba and Roberto Reis, MCP; Gustavo W. Nunan, Museu Nacional de Rio de Janeiro; William Eschmeyer and Pearl Sonoda, California Academy of Sciences; and Ierecê and Ricardo Rosa, Universidade de Federal da Paraiba, João Pessoa. Marilyn Weitzman prepared Fig. 1. Sara V. Fink prepared Figs. 3, 5, 6, 9–13, 21, 22, 24 and 25 with funds provided by the Department of Vertebrate Zoology, Smithsonian Institution. Field assistance especially concerned with this contribution and not mentioned above was provided by Rosario LaCorte, Viggo Schultz, Paulo Buckup, Labbish N. Chao, Luiz E. Macedo Cordoso, Alicido Witeck and especially Marilyn Weitzman and Luis Pinni Netto. Laboratory assistance in preparation of x-ray negatives and propagation of glandulocaudines and other characids were provided by Lisa Palmer. Ray Carthy and Jeffrey Clayton provided curatorial assistance. Richard P. Vari, G. David Johnson, Richard E. Strauss, Scott A. Schaefer, and Marilyn Weitzman provided constructive comments on the manuscript.

Literature Cited

Chappill, J. A. 1989. Quantitative characters in phylogenetic analysis.—Cladistics 5:217–234.

Eigenmann, C. H. 1911. III: New characins in the collections of the Carnegie Museum.—Annals of the Carnegie Museum 8(1):164–181.

Fink, W. L., & S. H. Weitzman. 1974. The so-called cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae).—Smithsonian Contributions to Zoology 172:1–46.

Géry, J. 1964. *Glandulocauda terofali* sp. nov., un nouveau poisson characoïde de la République Argentine, avec une note sur la "glande" caudale des Stevardiidi.—Opuscula Zoologica 78:1–12.

———. 1966. A review of certain Tetragonopterinae (Characoidei), with the description of two new genera.—Ichthyologia/the Aquarium Journal 37(5):211–236.

———, & J. Delage. 1963. Origine pathologique du *stratum argenteum* chex certaines variétés phénotypiques de Characidae, les "brass-tetras."—Vie et Milieu 14(1):169–182.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Chicago, 203 pp.

Hubbs, C. L. 1955. Hybridization between fish species in nature.—Systematic Zoology 4(1):1–20.

Humphries, C. J., & L. R. Parenti. 1986. Cladistic biogeography. Oxford Monographs on Biogeography, Clarendon Press, Oxford, 98 pp.

Maddison, W. P., M. J. Donoghue, & D. R. Maddison. 1984. Outgroup comparison and parsimony.—Systematic Zoology 33:83–103.

Menezes, N. A. 1988. Implications of the distribution patterns of the species of *Oligosarcus* (Teleostei, Characidae) from central and southern South America. Pp. 295–304 *in* P. E. Vanzolini & W. R. Heyer, ed., Proceedings of a Workshop on

Neotropical Distribution Patterns, Academia Brasileria de Ciências, 488 pp.

Miranda-Ribeiro, A. de. 1908. Peixes da Ribeira: Resultados de excursão do Sr. Ricardo Krone, membro correspondente do Museu Nacional do Rio de Janeiro.—Kosmos, Revista Artistica, Scientifica e Litteraria (Rio de Janeiro) 5(2):5 unnumbered pages.

Pimentel, R. A., & R. Riggens. 1987. The nature of cladistic data.—Cladistics 3:201–209.

Regan, C. T. 1907. Description of two new characinid fishes from South America.—Annals and Magazine of Natural History, ser. 7, 20:402–403.

Schultz, L. P. 1959. Generic status of *Mimagoniates* and *Glandulocauda,* South American characid fishes.—Tropical Fish Hobbyist 8(2):6–10, 63, 64.

Schultze, H., & G. Arratia. 1989.. The composition of the caudal skeleton of teleosts (Actinopterygii: Osteichthyes).—Zoological Journal of the Linnean Society 97:189–231.

Weitzman, S. H., & S. V. Fink. 1985. Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae).—Smithsonian Contributions to Zoology 421:1–121.

———, N. A. Menezes, & H. A. Britski. 1986. *Nematocharax venustus,* a new genus and species of fish from the rio Jequitinhonha, Minas Gerais, Brazil (Teleostei: Characidae).—Proceedings of the Biological Society of Washington 99(2):335–346.

———, ———, & M. J. Weitzman. 1988. Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distributions of other freshwater fishes in eastern and southeastern Brazil. Pp. 379–427 *in* P. E. Vanzolini & W. R. Heyer, ed., Proceedings of a Workshop on Neotropical Distribution Patterns, Academia Brasileira de Ciências, 488 pp.

Wiley, E. O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. John Wiley and Sons, New York, 439 pp.

(NAM) Museu de Zoologia, Universidade de São Paulo, Caixa Postal 7172, CEP 01051, São Paulo, Brazil and pesquisador do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNP$_q$); (SHW) Department of Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 427–431

THE TADPOLE OF A DART-POISON FROG *PHYLLOBATES LUGUBRIS* (ANURA: DENDROBATIDAE)

Maureen A. Donnelly, Craig Guyer, and Rafael O. de Sá

Abstract.—The tadpole of *Phyllobates lugubris* is described based on specimens collected from male nurse frogs in northeastern Costa Rica and northwestern Panama. *Phyllobates lugubris* tadpoles undergo ontogenetic changes in mouthparts, spiracle location, and vent tube location. The tadpole of *Phyllobates lugubris* is similar to those of *P. aurotaenia, P. terribilis* and *P. vittatus,* although absolute size varies among species.

The monophyletic genus *Phyllobates* is comprised of five neotropical species (*P. aurotaenia, P. bicolor, P. lugubris, P. terribilis,* and *P. vittatus*) that produce steroidal alkaloids (batrachotoxins) in granular skin glands (Myers et al. 1978, Myers 1987). *Phyllobates lugubris* inhabits humid lowland forests along the Atlantic versant of Costa Rica and western Panama (Silverstone 1976). Altig & Johnston (1986) summarized larval characteristics of *Phyllobates lugubris* based on a description provided by Savage (1968). Savage (1968) considered *Phyllobates vittatus* to be conspecific with *P. lugubris,* and described the tadpole based on material collected from the Golfo Dulce region of southwestern Costa Rica (J. M. Savage, pers. comm.). Silverstone (1976) considered *Phyllobates vittatus* to be a distinct taxon restricted to southwestern Costa Rica; therefore, the tadpole of *P. vittatus* has been described twice (Savage 1968, Silverstone 1976) and the tadpole of *P. lugubris* has not been described (Savage & Villa 1986). Here we describe the tadpole of *Phyllobates lugubris* based on material collected in northeastern Costa Rica and northwestern Panama.

Two male nurse frogs transporting tadpoles were captured by CG and MAD at the La Selva Biological Reserve (2.6 km SE of Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica). Two of five tadpoles collected on 25 May (stage 25 of Gosner, 1960) and four of six collected on 16 June (stage 25) were preserved on the data of capture. The remaining tadpoles were reared in the laboratory on a diet of algae; these were killed and fixed in 10% formalin at various stages of development following techniques described by Starrett (1960). The nurse frogs were released after the tadpoles were removed. The tadpoles were deposited in the Costa Rican Expeditions (CRE) collection at the University of Miami (CRE 6696, 6714).

Three lots of *Phyllobates lugubris* tadpoles and male nurse frogs, housed in the American Museum of Natural History (AMNH), were collected in Bocas del Toro, Panama by Charles W. Myers and his associates. One lot of four tadpoles (AMNH 86642) and the nurse frog (AMNH 86642) were collected on 21 January 1971 on the mainland about 5 km W Almirante (30–40 m), one lot of five tadpoles (AMNH 102253) and the nurse frog (AMNH 102246) were collected on 5 May 1977 on Isla Colón (near La Gruta, 10 m), and one lot of three tadpoles (AMNH 107237) and the nurse frog (AMNH 107231) were collected in forest on a ridge near Río Changuinola (near Quebrada El Guabo, 200 m) on 15 April 1980. All the Panamanian tadpoles taken from the

Fig. 1. Lateral view of a tadpole of *Phyllobates lugubris* in stage 37 (Gosner 1960) (CRE 6714). Bar = 10.0 mm.

backs of nurse frogs are in stages 24 or 25 (Gosner 1960).

We also examined tadpoles of *Phyllobates vittatus* (CRE 900, 903, 3152, 7234), *P. aurotaenia* (AMNH uncatalogued), and *P. terribilis* (AMNH 88979–88981). All tadpoles were measured to the nearest tenth of a millimeter under a dissecting scope with an ocular micrometer. The description of the tadpole of *Phyllobates lugubris* is based on two stage 37 specimens (CRE 6714).

Description of the Tadpole

Values are means. Body depressed (body width/body depth = 1.58); snout rounded in dorsal and lateral profiles (Fig. 1). Nostrils dorsal, directed laterally, opening 0.76 mm behind snout; internarial distance 1.75 mm. Eyes dorsal, directed dorsolaterally; diameter 0.95 mm; interocular plane 1.9 mm behind snout; interorbital distance 1.75 mm. Spiracle sinistral, low, opening 6.0 mm behind snout. Vent tube dextral to ventral fin.

Caudal musculature moderately robust anteriorly, gradually tapering posteriorly to near tail tip; height adjacent to body 2.0 mm, height at mid-tail 1.7 mm. Tail length 58% of total length. Tail height 15% of total length. Fins subequal in height; dorsal fin height 0.85 mm at mid-tail, not extending onto body; ventral fin height 1.0 mm at mid-tail. Tip of fin rounded (Fig. 1).

Mouth directed ventrally. Oral disc emarginate (Fig. 2); oral disc width 2.35 mm. Labial teeth in two anterior and three posterior rows; tooth row formula 2(2)/3. Anterior rows equal in length, extending to marginal papillae; second row interrupted medially (A-2 gap = 0.35 mm). First and second posterior rows equal in length, slightly longer than third row. Upper jaw sheath moderately robust forming a broad arch with slender lateral processes; large pointed serrations present. Lower jaw sheath V-shaped, moderately robust; large pointed serrations present. Posterior lip bordered by one row of marginal papillae; one row marginal papillae extend onto lateral margins of anterior lip, one row submarginal papillae on lateral margins of oral disc.

In preservative, dorsal body color dark brown, lateral body color light brown, ventral body surface light brown with scattered white spots. Caudal musculature light brown. Fins transparent with brown blotches dorsally near musculature; ventral fin with brown spots near tail tip.

Ontogenetic Changes

The mouthparts of *Phyllobates lugubris* tadpoles undergo changes similar to those described for *P. terribilis* (Myers et al. 1978). Stage 24, 25, and 28 *Phyllobates lugubris* larvae have one row of submarginal papillae and one row of papillae on the posterior labium. In the stage 37 tadpole, there is a single row of papillae on the posterior la-

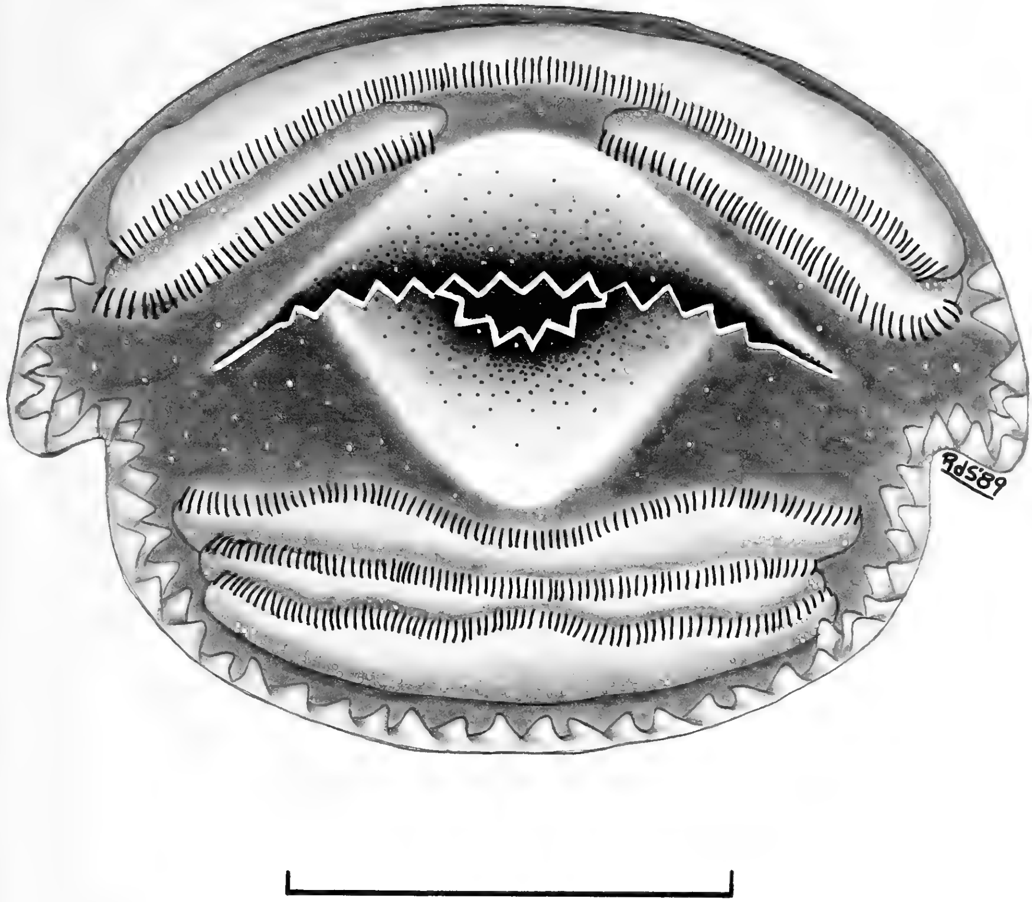


Fig. 2. Oral disc of a tadpole of *Phyllobates lugubris* in stage 37 (CRE 6714). Bar = 1.0 mm.

bium; the papillae alternate in orientation and it appears to be two rows rather than one. The jaw sheath edges are smooth in several stage 24 and 25 tadpoles, but they are serrated by stage 28. The labial tooth rows are not all keratinized at hatching; in many stage 24 and 25 larvae, the second anterior and the third posterior rows are not keratinized. The sequence of tooth row keratinization appears to be: P1 → A1 → P2 → A2 → P3. By stage 28, all tooth rows are keratinized. In our single stage 41 specimen, the A2 and P3 rows are reduced in length. The tail comprises 56% of the total length in stage 24 larvae and 60% of the total length in stage 41. The ratio of tail height to total length changes from 17% in stage 24 to 13% in stage 41. In the early stages (24 and 25), the vent tube is medial and the spiracle is located at mid-body; in later stages, the vent tube is dextral and the spiracle is low on the left side of the body. Changes in body length, body depth, body width, tail length, and total length are summarized in Table 1.

Comparisons Among Species

We have not examined the tadpole of *Phyllobates bicolor* but we can compare the tadpole of *P. lugubris* to tadpoles of the remaining species in the genus. All *Phyllobates* tadpoles examined have: depressed bodies (width > depth), sinistral spiracles, dorsal eyes and nostrils, low-finned tails with

Table 1. Measurements (mm) of various stages of tadpoles of *Phyllobates lugubris* collected in Costa Rica and Panama. Values are means ± one standard deviation.

Stage	n	Body length	Body depth	Body width	Tail length	Total length
24	3	4.30 ± 0.361	2.00 ± 0.300	2.73 ± 0.252	5.47 ± 0.611	9.77 ± 0.379
25	15	4.16 ± 0.519	1.80 ± 0.288	2.82 ± 0.459	6.23 ± 0.466	10.39 ± 0.844
28	2	7.10 ± 0.566	2.95 ± 0.071	4.60 ± 0.141	—	—
37	2	10.30 ± 0.000	4.35 ± 0.212	6.90 ± 0.141	14.05 ± 0.636	24.35 ± 0.636
41	1	9.0	4.0	6.5	13.7	22.7

rounded tips, emarginate oral discs, two anterior and three posterior labial tooth rows, with the second anterior row interrupted medially, serrated jaw sheaths, and rounded papillae on the posterior and lateral margins of the oral disc.

The mouthparts of *Phyllobates* tadpoles we examined undergo ontogenetic changes similar to those observed in *P. lugubris* and *P. terribilis.* In some stage 25 larvae of *P. vittatus,* the third posterior row of labial teeth is not keratinized and the jaw sheaths lack serrations. Although Silverstone (1976) stated that *Phyllobates vittatus* larvae have two rows of labial papillae, all stage 25 tadpoles we examined have a single row of marginal papillae. By stage 28, *Phyllobates vittatus* larvae have two rows of papillae and all labial tooth rows are keratinized. In stage 25 *Phyllobates aurotaenia* tadpoles, the labial tooth rows are not keratinized, the jaw sheath edges are smooth, and there is one row of marginal papillae on the posterior labium and one row of submarginal papillae. By stage 37, *Phyllobates aurotaenia* tadpoles have keratinized labial teeth, serrated jaw sheaths, and two rows of papillae. Ontogenetic changes in oral papillae have been reported for some hylids (Donnelly et al. 1987, Zweifel 1961).

The vent tube location changes ontogenetically in the four species. In early stages (24 and 25) the vent tube is medial; it becomes dextral in *Phyllobates lugubris* and *P. vittatus* by stage 28. The developmental series of *P. aurotaenia* and *P. terribilis* lack specimens in stage 28; both species have dextral vent tubes by stage 37.

Myers et al. (1978) described changes in the relationship between tail height and total length for *Phyllobates terribilis*; tail height equals 12–15% of total length in stages 24–27 and increases to a maximum of 20% of total length in later stages. Similar changes in tail height relative to total length occur in *Phyllobates aurotaenia* and *P. vittatus.* In *Phyllobates lugubris,* tail height does not increase relative to increasing total length.

Phyllobates tadpoles collected from male nurse frogs have been in stage 24 or 25; at this stage of development, the mouthparts of the species we examined were not completely developed. Measurements of stage 25 larvae for *P. aurotaenia, P. terribilis,* and *P. vittatus* are summarized in Table 2. The tadpole of *P. vittatus* is larger than tadpoles

Table 2. Measurements (mm) of stage 25 *Phyllobates* tadpoles. The following abbreviations identify the species: Pa = *P. aurotaenia,* Pt = *P. terribilis,* Pv = *P. vittatus.* Values are means ± one standard deviation.

Species	n	Body length	Body depth	Body width	Tail length	Total length
Pa	6	3.75 ± 0.138	1.57 ± 0.103	2.37 ± 0.121	6.73 ± 0.175	10.48 ± 0.306
Pt	12	4.38 ± 0.175	1.89 ± 0.131	2.98 ± 0.171	7.30[a] ± 0.258	11.65[a] ± 0.334
Pv	7	4.40 ± 0.883	2.04 ± 0.395	3.07 ± 0.170	8.08[b] ± 0.898	12.70[b] ± 1.138

[a] n = 10.
[b] n = 5.

Table 3. Tadpole size (mean total length) at stage 25 and adult mean snout–vent length (SVL) in *Phyllobates.* Body size data for *P. terribilis* from Myers et al. (1978), for all other species from Silverstone (1976).

Species	Tadpole total length (mm)	Male SVL (mm)	Female SVL (mm)
P. aurotaenia	10.48	26.9	30.4
P. lugubris	10.39	19.2	22.2
P. terribilis	11.65	41.1	43.2
P. vittatus	12.70	24.4	27.7

of the other species (Tables 1, 2); and its oral disc is wider (*P. vittatus,* 1.22 mm; *P. aurotaenia,* 0.80 mm; *P. lugubris,* 1.17 mm; *P. terribilis,* 1.09 mm). Although absolute size varies among the stage 25 tadpoles, the relationship between body width and body depth is similar (body width/body depth = 1.51 in *Phyllobates aurotaenia,* 1.57 in *P. lugubris,* and 1.58 in *P. terribilis* and *P. vittatus*). The relationship between tail length and total length in stage 25 tadpoles is also similar among species; the tail accounts for 64% of total length in *Phyllobates aurotaenia* and *P. vittatus,* 60% of total length in *P. lugubris,* and 63% in *P. terribilis.* No clear relationship exists between tadpole size and adult body size in *Phyllobates* (Table 3). Our observations agree with those of Myers et al. (1978); accurate identification of *Phyllobates* tadpoles in early (stage 24 or 25) developmental stages requires nurse frog identification. *Phyllobates* tadpoles in these stages exhibit little variation in larval characteristics other than absolute size. We expect that the tadpole of *Phyllobates bicolor* will resemble those of the other species.

Acknowledgments

We thank the Organization for Tropical Studies for supporting our research through Jessie Smith Noyes pre-doctoral fellowships granted to MAD and CG. We thank C. W. Myers for permission to report on *Phyllobates* tadpoles he raised in the laboratory and those he collected in Panama and Colombia. We thank J. M. Savage for allowing us to examine tadpoles of *Phyllobates vittatus.* R. Altig, B. I. Crother, D. M. Hillis, C. W. Myers, J. M. Savage, and two anonymous reviewers read and commented on the manuscript.

Literature Cited

Altig, R., & G. F. Johnston. 1986. Major characteristics of free-living anuran tadpoles.—Smithsonian Herpetological Information Service 67: 1–75.

Donnelly, M. A., C. Guyer, D. M. Krempels, & H. E. Braker. 1987. The tadpole of *Agalychnis calcarifer* (Anura: Hylidae).—Copeia 1987:247–250.

Gosner, K. 1960. A simplified table for staging anuran embryos and larvae with notes on identification.—Herpetologica 16:183–190.

Myers, C. W. 1987. New generic names for some Neotropical poison frogs (Dendrobatidae).—Papeis Avulsos de Zoologica 36:301–306.

———, J. W. Daly, & B. Malkin. 1978. A dangerously toxic new frog (*Phyllobates*) used by Emberá indians of western Colombia, with discussion of blowgun fabrication and dart poisoning.—Bulletin American Museum Natural History 161: 307–366.

Savage, J. M. 1968. The dendrobatid frogs of Central America.—Copeia 1968:745–776.

———, & J. Villa. 1986. Introduction to the herpetofauna of Costa Rica/Introduccion a la Herpetofauna de Costa Rica.—Contributions to Herpetology. Number 3. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, 220 pp.

Silverstone, P. A. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron *in* Sagra (family Dendrobatidae).—Los Angeles County Museum of Natural History Science Bulletin 27:1–53.

Starrett, P. 1960. Descriptions of tadpoles of Middle American frogs.—Miscellaneous Publications Museum Zoology University Michigan 110:1–37 + 1 plate.

Zweifel, R. G. 1961. Larval development of the tree frogs *Hyla arenicolor* and *Hyla wrightorum.*—American Museum Novitates 2056:1–19.

(MAD) Department of Herpetology and Ichthyology, American Museum of Natural History, New York, New York 10024-5192; (CG) Department of Zoology and Wildlife Science, Auburn University, Auburn, Alabama 36849; (ROS) Department of Zoology, University of Texas, Austin, Texas 78712-1064.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 432–451

TAXA OF NORTH AMERICAN BIRDS DESCRIBED FROM 1957 TO 1987

M. Ralph Browning

Abstract.—Ninety-nine names proposed from 1957 to 1987 for North American birds are evaluated. Of these, 35 are judged taxonomically distinct; seven are recognized provisionally; 54 are considered synonyms of established names; and three forms cannot be identified positively. Five names are taxonomic changes, providing new names for forms previously described.

Since the publication of the fifth edition of the A.O.U. Check-list (American Ornithologists' Union 1957), more than 800 forms of birds, world-wide, have been newly described; 99 of these are from North America (sensu A.O.U. 1957). About half the names of these North American forms already have been considered, by various authors, to be synonyms of previously existing names, but others have received little or no taxonomic attention.

In the following accounts I summarize the taxonomic status of the taxa of North American birds for which names have been proposed since 1957. With minor exceptions I evaluated each form using the comparative material available to the original author, including, where possible, the holotypes and paratypes. In evaluating the forms I emphasized the range of variation more than the average difference in any given character. My standard for recognizing subspecies primarily on color has been more stringent than the so-called "75 percent rule"; statements in the accounts that a population differs from another means that at least 95 percent of the specimens I compared could be identified.

Each account includes the original name with the authority and year; complete citations are given in the Literature Cited. The type locality, modified when required, follows. The depository of holotypes or syntypes, when known, is abbreviated and appears in parentheses if I examined the specimens or in brackets if not. Abbreviations are: California Academy of Sciences (CAS); Cleveland Museum of Natural History (CMNH); Delaware Museum of Natural History (DMNH); Field Museum of Natural History (FM); Louisiana State University Museum of Natural Science (LSUMNS); National Museum of Canada (NMC); private collection of Amadeo Rea (AMR); Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); Royal Ontario Museum (ROM); San Diego Museum of Natural History (SDMNH); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); James Ford Bell Museum of Natural History, University of Minnesota (UMM); University of Michigan Museum of Zoology (UMMZ); Utah Museum of Natural History (UMNH); and U.S. National Museum of Natural History (USNM).

The present taxonomic status of each new name is next. References with the present name include sources that have provided data or an opinion on the taxonomic status of that name. I summarize characters and ranges, including a more detailed characterization as warranted by my study. Comments are omitted for forms discussed in my earlier papers (Browning 1974, 1977, 1978, 1979a). Names of genera (except *Pi-*

coides) and species, and sequence of the families, follow the sixth edition A.O.U. check-list (1983) and A.O.U. (1989).

Podicipedidae

Aechmophorus clarkii transitionalis Dickerman, PBSW 99(3), p. 436, 17 Oct 1986.—Silver Lake, Lake County, Oregon (USNM).
=*Aechmophorus clarkii transitionalis.*

Birds from northern North America are larger (Dickerman 1986a) than nominate *clarkii* of Mexico (Dickerman 1963, 1973).

Hydrobatidae

Oceanodroma leucorhoa cheimomnestes Ainley, 1980.—Guadalupe Island, Mexico (USNM).
=*Oceanodroma* (?*leucorhoa*) *cheimomnestes.*

The birds breeding on Guadalupe Island during the summer were assigned to *socorroensis* by Ainley (1980), who differentiated *cheimomnestes,* the subspecies breeding there during winter, by physiological, morphological, and vocal characteristics. Bourne & Jehl (1982) synonymized *cheimomnestes* with *O. l. beali.* Power & Ainley (1986) further demonstrated temporal and morphological differences between the summer (*socorroensis*) and winter (*cheimomnestes*) birds breeding on Guadalupe Island. I agree with Jehl & Everett (1985) that further study is required to determine the status of the two Guadalupe Island populations.

Ardeidae

Leucophoyx thula arileuca Oberholser, 1974.—mouth of Bear River, North Bay (=Bear River Bay), Great Salt Lake, Box Elder Co., Utah (USNM).
=*Egretta thula brewsteri* Thayer & Banks, 1909 (see Browning 1974, Behle 1985).

Anatidae

Anser albifrons elgasi Delacour & Ripley, 1975.—"Sacramento, California" = Sacramento National Wildlife Refuge, California (USNM).
=*Anser albifrons elgasi* (see Cramp 1977, Krogman 1979).

This subspecies differs from *A. a. gambelli* (sensu Delacour and Ripley 1975) and *frontalis* by its larger size and darker coloration. *Anser a. elgasi* winters in the Sacramento Valley, California. The breeding range was not known at the time of the description, but birds conforming to the description of *elgasi* breed in Alaska's Cook Inlet (Timm et al. 1982). Palmer (1976) and Bellrose (1976) synonymized *elgasi* with *gambelli* but Johnsgard (1979) and Godfrey (1986) recognized the subspecies.

Anas platyrhyncha neoboria Oberholser, 1974.—Athabaska River, La Lasine, Alberta (USNM).
=*Anas platyrhynchos platyrhynchos* Linnaeus, 1758 (see Browning 1974, 1978).

Falconidae

Falco peregrinus tundrius White, 1968.—near NW Sherman Basin, Adelaide Peninsula, Northwest Territories, Canada [NMC].
=*Falco peregrinus tundrius* (see Palmer 1988, White & Boyce 1988).

This widely accepted, northern subspecies differs most from *F. p. anatum* by its smaller size, paler color, narrower malar stripe and in immatures by the narrower ventral linear stripes (White 1968). It breeds on the tundra from Alaska to Labrador and western Greenland and migrates as far south as Argentina.

Phasianidae

Callipepla squamata hargravei Rea, 1973.—Pepper Ranch, 7 miles N, 32 miles E of

Folsom, Union Co., New Mexico [LSUMNS, ex G. M. Sutton].
=*Callipepla squamata hargravei.*

The population from the northeastern portion of the range of *pallida* was described as paler than other examples of the species. I examined over 100 specimens from the range of *pallida* (sensu A.O.U. 1957) and 9 specimens from Rea's (1973) comparative series. I found that the throat and sides of the head of eastern specimens are paler gray and less brownish and the belly is paler and usually less buffy than specimens from Arizona and western New Mexico. In fresh fall plumage specimens of *hargravei* also differ ventrally from *pallida* by having the terminal bars of the "scaled" areas more brownish and less black.

Post-mortem color changes and birds possibly introduced from the western population (Rea 1973) complicated comparisons of specimens from the range of *hargravei. Callipepla s. hargravei* is resident from southeastern Colorado to western Oklahoma, southwestern Kansas, northern New Mexico and northwestern Texas.

Gruidae

Grus canadensis rowani Walkinshaw, Jul–Aug 1965.—10 miles west of Fawcett, Alberta [FM].
=*Grus canadensis rowani* (see Johnson & Stewart 1973, Aldrich 1979).

This northern interior subspecies is intermediate in size to nominate *canadensis* and the more southern *tabida* (see Johnson & Stewart 1973). Color of the primary shafts, described by Walkinshaw (1965) as paler than in nominate *canadensis* is subject to individual variation (Aldrich 1979). *Grus c. rowani* breeds from the Mackenzie District to central Alberta, Saskatchewan, northern Ontario, and possibly central British Columbia; it winters in New Mexico, Oklahoma, and Texas.

Grus canadensis pulla Aldrich, 1972.—Captive bird hatched from egg taken 7 miles northwest of Fontainebleau, Jackson Co., Mississippi (USNM).
=*Grus canadensis pulla* (see Walkinshaw 1973).

This taxon was described as the darkest subspecies of *Grus canadensis.* It is similar in overall size to *pratensis,* smaller (except tarsus) than *tabida,* larger than nominate *canadensis,* and has longer tarsi than *rowani. Grus c. pulla* formerly occurred on the Gulf Coastal Plain of Louisiana, Mississippi, and Alabama (see Aldrich 1972), but it is now resident only in Jackson County, Mississippi.

Scolopacidae

Actitis macularia rava Burleigh, 1960.—Lewiston, Nez Perce Co., Idaho (USNM).
=*Actitis macularia* (Linnaeus, 1766).

Burleigh (1960a) described *rava,* from the western range of *A. macularia,* as darker gray (less brown) above, with the ventral spots more intensely black and less densely distributed than in eastern specimens of *macularia.* Although *rava* was recognized by Wetmore (1965a, b) and Sutton (1967), both authors characterized the form as paler above (*contra* Burleigh 1960a). My examination of 52 specimens from the breeding grounds of *A. macularia* revealed no geographic variation.

Laridae

Larus californicus albertaensis Jehl, 1987.—Frog Lake (53°55′N, 110°15′W), Alberta [UMMZ].
=*Larus californicus albertaensis.*

Although only four adults from the northern population of this species were examined, I found them easily distinguishable from 24 adults of nominate *californicus* to the south by its greater overall size, especially the bill, and paler gray mantle. It nests from the Northwest Territories to Alberta, Saskatchewan, and North Dakota. The winter distribution is presumably throughout the species' range, mainly along the Pacific coast from British Columbia to Baja California (Jehl 1987).

Columbidae

Zenaida asiatica grandis Saunders, 1968.—Near Ruidosa, Presidio Co., Texas, altitude about 3000 ft (USNM).
=*Zenaida asiatica mearnsi* (Ridgway, 1915).

Saunders (1968) described this population from western Texas as larger than *mearnsi* of the northwestern range of the species, *asiatica* of southern Texas and northern Mexico, and *monticola* Saunders, 1968 (type locality 11 miles S Acatan, Pueblo, Mexico). He also described *grandis* as paler than nominate *asiatica,* and slightly browner on the back and head than *monticola.* The subspecies *monticola,* from the interior plateau of Mexico, was described by Saunders (1968) as having a longer wing chord and tail than *asiatica* and *mearnsi,* and to be grayer with a shorter bill than the latter.

This species is subject to considerable individual variation in color and size (Aldrich 1981). Some populations measured by Saunders are statistically different in some characters, but overlap is nearly complete in the mensural ranges. Most of the specimens I compared were collected by Saunders including about 60 specimens of *mearnsi,* 22 *monticola,* 15 *grandis,* and 50 nominate *asiatica.* I found that both dorsal and ventral coloration varies individually. I place *grandis* and *monticola* in the synonymy of *mearnsi.* Saunders (1968) also named other subspecies of *Z. asiatica* from regions geographically beyond the scope of this paper.

Cuculidae

Geococcyx californianus dromicus Oberholser, 1974.—Brownsville, Cameron Co., Texas (USNM).
=*Geococcyx californianus* (Lesson), 1829 (see Browning 1978, but see Rea 1983).

Rea (1983) suggested that the overlap in measurements of *dromicus* and birds from California and Arizona given by Oberholser (1974) might be the result of the latter's use of missexed specimens and that *dromicus* might prove to be a "useful" subspecies. I find no reason to believe that Oberholser's series were missexed.

Strigidae

Otus flammeolus borealis Hekstra, 1982.—Penticton, Okanagan Valley, shore of Okanagan Lake, British Columbia [MVZ].
=*Otus flammeolus idahoensis* Merriam, 1892.

Hekstra (1982) described *borealis* as slightly larger, duller gray, and less white than *idahoensis* (type locality Ketchum, Blaine Co., Idaho). Specimens from the stated range of *borealis,* from interior British Columbia (east of the Cascade Mountains) to northeastern California, are within the range of individual variation of *idahoensis* in size and plumage characters (J. T. Marshall, pers. comm.).

Otus flammeolus frontalis Hekstra, 1982.—Estes Park, Larimer Co., Colorado (USNM).
=*Otus flammeolus frontalis.*

This subspecies was described as much darker with more extensive chestnut brown facial discs than *O. f. flammeolus,* the subspecies found to the south. Differences between *frontalis* and other populations of the species were not given. My series consisted of 11 specimens of *frontalis* and 10 specimens of *idahoensis* Merriam. The new subspecies differs from *flammeolus* and *idahoensis* by its wider ventral streaks and darker facial discs (J. T. Marshall, pers. comm.). The range of *frontalis* extends from the Rocky Mountains and, probably, most of the Great Basin.

Bubo virginianus scalariventris Snyder, 1961.—Elsas, on the upper Kapsuskasing

River, in Algoma District, Ontario [ROM].
=*Bubo virginianus* subsp.?

Snyder (1961) proposed *scalariventris* for the population from part of the eastern range of *subarcticus* Hoy, 1852 (=*wapacuthu* Gmelin of A.O.U. [1957] but see Manning [1952]). He distinguished *scalariventris* as "more coldly grey with bolder bars below" than *subarcticus* and that it differs from nominate *virginianus* by the lack of rufous and "virtual lack of large, vague, finely vermiculated spots superimposed over the barred ventral pattern. . . ." Johnsgard (1988) recognized *scalariventris,* but he stated that it "possibly should be included in *subarcticus.*" I join Godfrey (1986), who stated that he was unable to express an opinion on the validity of *scalariventris.*

Caprimulgidae

Chordeiles minor divisus Oberholser, 1974.—Loveland, Larimer Co., Colorado (USNM).
=*Chordeiles minor hesperis* Grinnell, 1905 (see Browning 1978).

Trochilidae

Phasmornis mystica Oberholser, Texas birds, 1974:485.—Boot Springs, Chisos Mountains, Texas (holotype unknown).
=hybrid or abberant individual (see Browning 1978, Mayr & Vuilleumier 1983).

Lampornis clemenciae phasmorus Oberholser, 1974.—northeastern side of Chisos Mountains, Pine Canyon, 6000 ft, Brewster Co., Texas (USNM).
=*Lampornis clemenciae phasmorus* (see Browning 1978).

Picidae

Dendrocopos scalaris soulei Banks, 1963.—Ruffo's Ranch, Cerralvo Island, Baja California, Mexico [CAS].
=*Dendrocopos scalaris soulei.*

The form was described as similar in size to *lucascanus* of southern Baja California, and intermediate to *eremicus* of northern Baja California and *sinaloensis* of mainland Mexico. *Dendrocopos s. soulei* was described as more grayish ventrally and more extensively black on the three outer rectrices and with larger and more abundant ventral spots than *lucasanus.* From *cactophilus* of the southwestern United States, the subspecies was diagnosed as darker above with spotted rather than streaked flanks.

Eight specimens of the endemic population from Cerralvo Island are distinctly paler and less buffy below than larger series of other subspecies of this species. Also, the ventral spots are more rounded than those of *sinaloensis.* I did not detect the described differences in the amount of black on the three outer rectrices between *lucasanus* and *soulei.* The feathers immediately above the bill are blackish in *soulei* and brownish in *lucasanus.* Short (1968) reviewed the species' southwestern forms but neglected to mention the birds from Cerralvo Island, and later he (Short 1982) synonymized *soulei* with *lucasanus. Dendrocopos s. soulei* is endemic to Cerralvo Island, Baja California.

Dendrocopos pubescens parvirostris Burleigh (1960) = 1961.—Moscow. Latah Co., Idaho (USNM).
=*Dendrocopos pubescens leucurus* (Hartlaub. 1852) (see Short 1982).

Burleigh (1961) separated birds from southern British Columbia to eastern Oregon and most of Idaho from the wide ranging *leucurus.* He characterized *parvirostris* as smaller, or similar in size to the darker western *turati.* The characters given for *parvirostris* are within the range of individual variation of *leucurus* (sensu Short 1982).

Tyrannidae

Contopus sordidulus amplus Burleigh, 1960[b].—Havre, Hill Co., Montana (USNM).

=*Contopus sordidulus vieilei* Coues, 1866 (see Browning 1974).

Contopus sordidulus siccicola Burleigh, 1960[b].—Potlatch, Latah Co., Idaho (USNM).
=*Contopus sordidulus vieilei* Baird, 1866 (see Browning 1974).

Empidonax oberholseri spodius Oberholser, 1974.—Gray, Bonneville Co., Idaho (USNM).
=*Empidonax oberholseri* Phillips, 1939 (see Browning 1974, 1978).

Hirundinidae

Progne subis arboricola Behle, 1968.—Payson Lakes, 8300 ft elevation, 12 miles southeast Payson, Utah Co., Utah [UMNH].
=*Progne subis arboricola* (see Phillips 1986).

Behle (1968) gave the range of *arboricola* as Utah, northern Arizona, and northern Mexico. According to Phillips (1986), *arboricola* breeds from southwestern British Columbia to central Baja California, locally in northwestern Mexico, and to the Trans-Pecos region of Texas, and winters in South America.

I compared 43 specimens from the eastern United States, 15 from Arizona, and 9 from Utah and conclude that specimens of *arboricola* are larger than those of *hesperia* and nominate *subis,* and, in females, usually whiter than nominate *subis.* Hubbard (1972) considered birds from southeastern Arizona to be intermediate between *arboricola* and nominate *subis.* I agree with Hubbard (1972) that a broader review is necessary to establish the validity of this subspecies, but I recognize *arboricola* provisionally.

Hirundo albifrons ganieri Phillips, 1986.—Swallow Bluff, Decatur Co., Tennessee [LSU].
=*Hirundo pyrrhonota ganieri.*

Phillips (1986) briefly described *ganieri* as shorter in wing chord than nominate *pyrrhonota* (=*albifrons* of Phillips), but he did not otherwise differentiate the two taxa. My evaluation of *ganieri* was based on 20 specimens collected before the reported (Phillips 1986:33; see also A.O.U. 1931, 1957) spread of this species to the southeastern United States. There is overlap in wing chord (see Phillips 1986) between *pyrrhonota* and *ganieri.* I found that the extent of black on the throat and the pale chestnut wash of the upper breast are noticeably reduced in *ganieri.* The chestnut of the undertail coverts is also darker than in *pyrrhonota.* In females the rump of *ganieri* averages paler than in *pyrrhonota. Hirundo p. ganieri* breeds west of the Appalachians from Tennessee to south-central Texas and migrates to Mexico and Middle and South America.

Corvidae

Cyanocitta cristata burleighi Bond, 1962.—South Brook, Newfoundland (USNM).
=*Cyanocitta cristata cristata* (Linnaeus, 1758) (see Phillips 1986).

The darker northern birds described by Bond (1962) represent the end of a cline, and many northern individuals are similar in coloration to populations to the south.

Aphelocoma coerulescens suttoni Phillips, 1965.—Scroogs' Arroyo, 35 km S Pueblo, Colorado (DMNH).
=*Aphelocoma coerulescens suttoni* (Phillips) (see Browning 1974, 1978).

Aphelocoma coerulescens mesolega Oberholser, 1974.—Fort Davis, Jeff Davis Co., Texas (USNM).
=*Aphelocoma coerulescens suttoni* Phillips, 1964 (see Browning 1978, Phillips 1986).

Corvus cryptoleucus reai Phillips, 1986.—3 km NE Nogales, southern-most Arizona.
=*Corvus cryptoleucus* Couch, 1854.

This subspecies was described as differing from nominate *cryptoleucus* of the Laredo region of Texas and adjacent northeastern Mexico by having a greater wing chord and longer tail. Most of the range of the species (see A.O.U. 1983) was included in *reai.* Phillips' (1986) brief description shows overlap in wing chord and tail for the two forms and included specimens that he stated might not be correctly sexed and fully adult. A study of the variation among definitely sexed and aged birds is needed before subspecies can be recognized.

Paridae

Parus rufescens caliginosus Burleigh, 1959.—Twenty miles northeast of Moscow, Latah Co., Idaho (USNM). Preoccupied by *Parus wollweberi caliginosus* van Rossem, 1947.

Parus rufescens levyi Burleigh, 1968. New name for *P. r. caliginosus* Burleigh, 1959.

=*Parus rufescens rufescens* Townsend, 1837 (see Phillips 1986).

Burleigh (1959) characterized the populations from the southeastern part of the range of nominate *rufescens,* which he later renamed *levyi,* as darker and less reddish than the northwestern populations. I agree with Phillips (1986) that the considerable individual variation of *rufescens* (sensu A.O.U. 1957) precludes recognition of *levyi.*

Parus wollweberi vandevenderi Rea, *in* Phillips 1986.—Sycamore Creek, 1.2–3.3 miles (1.9–5.3 km) N Sunflower, NE Maricopa Co., Arizona [SD].

=*Parus wollweberi vandevenderi.*

Based on examination of over 150 specimens of the species, I conclude that specimens of *vandevenderi* are darker and duller than *phillipsi* of southeastern Arizona and New Mexico. The subspecies is resident from central (Yavapai Co.) and eastern counties in Arizona to southwestern (Catron Co.) and western (Grant Co.) New Mexico but occasionally occurs in winter in the Lower Sonoran Zone of its range and to southern Arizona.

Sittidae

Sitta canadensis clariterga Burleigh, 1960[a].—Headquarters, Clearwater Co., Idaho (USNM).

=*Sitta canadensis* Linnaeus, 1766 (see Banks 1970, Phillips 1986).

Banks (1970) found that the supposed variation between eastern and western specimens compared by Burleigh (1960a) was the result of seasonal differences between the series, sooting of birds in eastern industralized areas, and variation in the quality of the prepared specimens.

Certhiidae

Certhia americana alascensis Webster, *in* Phillips 1986.—Ft. Wainwright, Fairbanks, Alaska (USNM, ex Univ. Alaska).

=*Certhia americana alascensis.*

Eight available specimens from south-central Alaska are paler dorsally with larger grayish white streaks on the back than examples of *montana* from the northwestern interior and than *occidentalis,* the western coastal subspecies. Webster (*in* Phillips 1986) believed that specimens from the southern coast of Alaska are intermediate to *alascensis* and *occidentalis,* but I regard this as an area of intergradation between *occidentalis* and *montana.*

Certhia americana stewarti Webster, *in* Phillips 1986.—Masset, Queen Charlotte Is., British Columbia [FM].

=*Certhia americana stewarti.*

The population from the Queen Charlotte Islands, separated from *occidentalis,* was described as "more orange or brighter orange dorsally than any other race." I examined 29 specimens of *occidentalis* and found that dorsal coloration appears to be clinal. Seven specimens from coastal British Columbia and a specimen from Juneau are dorsally browner than the three available specimens of *stewarti* but those from western Washington are slightly more orange. Specimens from western Oregon are less orange dorsally than those from Washington and also differ from those to the north by their darker heads. Specimens from the central coast of California are similar to those from western Oregon, but are buffy below (Webster, *in* Phillips 1986:200).

Certhia americana idahoensis Webster, *in* Phillips 1986.—Coolin, N Bonner Co., Idaho [FM].
=*Certhia americana montana* Ridgway, 1882.

Webster's description of *idahoensis* (*in* Phillips 1986) did not provide a clear comparison with the adjoining subspecies. The breeding range of *idahoensis* was given as central Alberta, extreme northern Idaho, and northwestern Montana. I found that the bill length and color of 50 specimens of *idahoensis* from Idaho and northwestern Montana are similar to other specimens of *montana.*

I agree with Webster that the northern limits of *zelotes* include the eastern slope of the Cascade Mountains in Oregon. However, the name *caurina* Aldrich, 1946 (type locality Mt. Adams, Yakima County, Washington), listed as a synonym of *montana* by Webster, may refer to pale individuals of *zelotes* of California. The name *leucosticta,* synonymized with *montana* by Webster, is a recognizable subspecies (*contra* Johnson 1965, see Austin & Rea 1976) and, according to Behle (1985), ranges as far north as west-central Utah.

Certhia familiaris iletica Oberholser, 1974.—The Bowl, Guadalupe Mountains, Culberson Co., Texas (USNM).
=*Certhia americana montana* Ridgway, 1882 (see Browning 1978, Webster, *in* Phillips 1986).

Troglodytidae

Campylorhynchus brunneicapillum sandiegense Rea, *in* Phillips 1986.—3.7 km W San Pasqual, west-central San Diego Co., California [SD].
=*Campylorhynchus brunneicapillus sandiegensis.*

This geographically isolated subspecies has overall coloration somewhat intermediate to *anthonyi* of east-central California and the subspecies of Baja California, and differs from other subspecies as characterized by Rea (*in* Phillips 1986). *Campylorhynchus b. sandiegensis* is a resident subspecies found from coastal Orange, Los Angeles and Ventura counties of California south to northwestern Baja California (Carrizo Val., Val. Palmas).

Catherpes mexicanus pallidior Phillips, 1986.—Green River, Wyoming [CM].
=*Catherpes mexicanus pallidior.*

Comparisons of ten available specimens from the range of *pallidior* and a larger series of other *C. mexicanus* revealed that the subspecies is the palest taxa of the species. *Catherpes m. pallidior* breeds from eastern Montana to northwestern Colorado and northeastern Utah; the winter range is not known.

Catherpes mexicanus croizati Phillips, 1986.—La Laguna, Sierra Laguna, Baja California.
=*Catherpes mexicanus croizati.*

This resident subspecies of southern Baja California was described by Phillips (1986) as "like the preceding races" but the "reddest" brown dorsally, and the "warmest," especially ventrally, form of the species. I compared 60 specimens from the southwestern range of the species and found that *croizati* is darker dorsally than *conspersus* from southern California and central Baja California and *pallidior,* and is similar in this character to the northwestern subspecies, *griseus,* and *punctulatus* Ridgway, 1882 (type locality Forest Hill, Placer Co., California). Below, *croizati* approaches *pallidior* in paleness, and is paler ventrally than the other northern subspecies.

Thryothorus ludovicianus nesophilus Stevenson, 1973.—Dog Island, Franklin Co., Florida (USNM).
=*Thryothorus ludovicianus nesophilus* (see Phillips 1986).

Known only from limited topotypical material, *nesophilus* was described by Stevenson (1973) as intermediate to *burleighi* and nominate *ludovicianus* in color. I recognize it provisionally.

Troglodytes bewickii pulichi Phillips, 1986.—Dallas, Texas.
=*Thryomanes bewickii pulichi.*

As characterized, this south-central form is paler than *calophonus,* less reddish brown than nominate *bewickii* and more reddish below than the other southern and western forms of the species. *Thryomanes b. pulichi* is resident in Oklahoma and most of Kansas, and also winters south to south-central Texas.

Troglodytes bewickii anthonyi Rea, *in* Phillips 1986. New name for *Thryothorus leucophrys* Anthony, 1895, preoccupied by *Troglodytes leucophrys* Tschudi, 1844 (=*Henicorhina leucophrys*).
=*Thryomanes bewickii leucophrys* (Anthony, 1895).

This new name is necessary only if the genus *Thryomanes* is merged with *Troglodytes* as by Phillips (1986).

Troglodytes troglodytes ochroleucus Rea, *in* Phillips 1986.—near Killisnoo, Admiralty Island, SE Alaska (USNM).
Troglodytes troglodytes muiri Rea, *in* Phillips 1986.—Navarro River, 7 km inland, Mendocino Co., California [AMR].
Troglodytes troglodytes obscurior Rea, *in* Phillips 1986.—North Fork Cosumnes River, 977 m, Grizzly Flats area, El Dorado Co., California [SD].
=*Troglodytes troglodytes pacificus* Baird, 1864.

These three forms were named from the range of *pacificus* (sensu A.O.U. 1957). Rea (*in* Phillips 1986) confined the range of *pacificus* to Prince of Wales Island, southeastern Alaska, and probably the Queen Charlotte Islands, British Columbia. My review of the variation in some of Rea's material suggests that these taxa are valid. However, recognition of these putative subspecies cannot be confirmed until a thorough analysis of the geographic variation of the western populations is presented.

Troglodytes troglodytes salebrosus Burleigh, 1959.—Dismal Lake, Shoshone Co., Idaho (USNM).
=*Troglodytes troglodytes salebrosus* (see Rea, *in* Phillips 1986).

This northern interior subspecies is less rufescent (Burleigh 1959) than *pacificus* (sensu A.O.U. 1957; Rea, *in* Phillips 1986). *Troglodytes t. salebrosus* breeds from southern British Columbia, east of the coast range, to southwestern Alberta, northeastern Washington, eastern Oregon, northern Idaho, and western Montana. It winters in its breeding range and casually southward.

Telmatodytes palustris canniphonus Oberholser, 1974.—4 miles N Sandusky, Bay Point, Ottawa Co., Ohio (CMNH).
=*Cistothorus palustris dissaeptus* (Bangs) 1902 (see Browning 1978, Phillips 1986).

Telmatodytes palustris cryphius Oberholser, 1974.—Blackmer, Richland Co., North Dakota (USNM).
=*Cistothorus palustris iliacus* Ridgway, 1903 (see Browning 1978, Phillips 1986).

Cistothorus palustris browningi Rea, *in* Phillips, Known birds, 1986:114.—Pitt Meadows, SW British Columbia [DMNH].
=*Cistothorus palustris browningi.*

This is the grayest and least rufescent of the Pacific Northwest coastal subspecies. Thirty-three specimens of *browningi* are darker throughout than an equal number of *paludicola* of the southern coast of Washington and central coast of Oregon. The black of the crown of *browningi* is greatly reduced to nearly obsolete. It breeds from southwestern British Columbia, including Vancouver Island (formerly ?), to the Puget Sound region and to Thurston Co. in central western Washington, and winters southward to northwestern Pacific County in southwestern Washington.

Cistothorus palustris deserticola Rea, *in* Phillips 1986.—New River, 3.2 km NNW Seeley, Imperial Co., central-southern California [SD].
=*Cistothorus palustris deserticola.*

This subspecies of the southwestern U.S. is distinguished from the coastal subspecies by its wider dorsal streaks. Based on 7 specimens, I conclude that *deserticola* is more rufescent than *aestuarinus* of central California and is less intensely brown than *paludicola* of coastal Washington and Oregon. *Cistothorus p. deserticola* is resident in the Salton Sea area of southeastern California and south-central Arizona (extirpated from the Gila River drainage, Rea in litt.), and north along the lower Colorado River to southern Nevada. I provisionally recognize *deserticola.*

Muscicapidae
Regulinae

Regulus calendula arizonensis Phillips, 1965.—vicinity of Phelps Ranger Station, White Mountains, Arizona (DMNH).
=*Regulus calendula calendula* Linnaeus, 1766 (see Hubbard & Crossin 1974, Browning 1979a).

Turdinae

Hylocichla fuscescens subpallida Burleigh and Duvall, 1959.—Moscow, Latah Co., Idaho (USNM).
=*Catharus fuscescens subpallidus* (see Wetmore et al. 1984).

Based on comparisons of over 500 specimens of the species, I conclude that *subpallidus* is somewhat duller and more gray above than other forms of the species, and further differs from *salicicola* by its slightly darker crown. The buff of the throat is slightly paler than in other subspecies. *Catharus f. subpallidus* breeds from northern Washington east of the Cascades to northeastern Oregon, northern and central Idaho, and western Montana. The winter range is not known. When naming *subpallidus,* Burleigh and Duvall (1959) restricted the type locality of *salicicola* to Fort Garland, Colorado.

Catharus guttatus munroi Phillips, 1962.—Nulki Lake, British Columbia (DMNH).
=*Catharus guttatus munroi.*

Phillips (1962) described *munroi* from northwestern Canada as differing from the "small" western subspecies by the distinct hue of brown on the sides and flanks, and the more reddish and paler dorsal color. The range of *munroi* was said to include most of that of *euborius* Oberholser, 1956, from Yukon Territory. Aldrich (1968) synonymized *munroi* with *euborius* and the A.O.U. (1957) synonymized both names with nominate *guttatus.* Ripley (1964) synonymized *munroi* with *nanus* of coastal Alaska and western British Columbia.

I compared 800 specimens of *C. guttatus* in fresh fall plumage and agree with Phillips (1962) that *munroi* is distinguishable. Dorsally, *munroi* is darker than *nanus,* paler and grayer than *faxoni,* the northeastern subspecies. The sides and flanks are paler than in nominate *guttatus.*

I also compared the type of *euborius* to specimens of *munroi.* Although the type is a worn individual collected in July, I disagree with Phillips (1962) that it is useless for subspecific identification. The holotype of *euborius* differs from eastern specimens by lacking the buffy coloration typical of *faxoni,* and it is darker above than either *munroi, faxoni,* or nominate *guttatus.* The sides of the holotype of *euborius,* although very worn, are also grayer than those of *munroi.* Five USNM migrants identified by Phillips in 1987 as "*euborius*" are similar to the holotype of *euborius.* The range of *euborius* appears to be restricted to central southern Yukon. The range of *C. g. munroi* is central and northern British Columbia, and, according to Phillips (1962), possibly the extreme northeastern part of British Columbia and probably extreme southwestern Yukon.

Catharus guttatus jewetti Phillips, 1962.—Hurricane Ridge and Elwha River, Olympic Mountains, Clallam Co., Washington (USNM).
=*Catharus guttatus jewetti* (see Phillips et al. 1964 and below).

The population of the Olympic Peninsula, Washington, was described as more reddish brown and less gray than *oromelus* Oberholser, 1932 (type locality 15 miles NE Lakeview, N base of Crook Peak, Warner Mountains, Lake Co., Oregon) of the mountains from southern British Columbia through the Cascades to northern California, and as darker than *sleveni* Grinnell, 1901 (type locality Point Sur, Monterey Co., California) of coastal Washington, Oregon, and California (Phillips 1962). Specimens of *jewetti* were characterized as paler than nominate *guttatus* and *verecundus* (type locality Queen Charlotte Islands) of southeastern Alaska and coastal British Columbia.

Aldrich (1968) considered the size and coloration of the Olympic Peninsula birds intermediate between *sleveni* and *oromelus.* I found that the immature syntype of *jewetti* is indistinguishable from specimens from southeastern Alaska. However, on the basis of the adult syntype and other specimens, I conclude that *jewetti* is a recognizable subspecies as described by Phillips (1962). Judged from less than a dozen specimens, *jewetti* migrates or winters to southern California and Nevada, northern Arizona (Monson & Phillips 1981), and New Mexico.

Turdus migratorius aleucus Oberholser, 1974.—South Yollo Bolly Mountain, Trinity Co., California (USNM).
=*Turdus migratorius propinquus* Ridgway, 1877 (see Browning 1974, 1978).

Mimidae

Toxostoma lecontei macmillanorum Phillips, 1965.—13 km E Buttonwillow, Kern Co., California (DMNH).
=*Toxostoma lecontei macmillanorum.*

Specimens in fresh fall plumage from the isolated population in the San Joaquin Valley, California, were described as darker than other populations of the species. Although my series of *macmillanorum* was small, I found that it differs from specimens of *arenicola* as described.

Dumetella carolinensis meridianus Burleigh (1959) = [1960].—Athens, Clarke Co., Georgia (USNM).
=*Dumetella carolinensis carolinensis* (Linnaeus, 1766) (see Monroe 1968, Phillips 1986).

Birds from the southern range of the species named *meridianus* by Burleigh (1960c) are within the range of variation of nominate *carolinensis.*

Bombycillidae

Bombycilla cendrorum larifuga Burleigh, 1963.—Headquarters, Clearwater Co., Idaho (USNM).
=*Bombycilla cedrorum larifuga* (see Behle 1985, and below).

Burleigh (1963) divided *B. cedrorum* and described the population from southwestern and central Canada and the western United States as paler than the other populations of the species.

I examined 45 specimens from the western range of *B. cedrorum* and found that the palest specimens from the type series of *larifuga* are those Burleigh collected and prepared. In the description of *larifuga,* Burleigh (1963) remarked that specimens from Oregon and Washington are darker brown than birds from Idaho. All but one of the specimens from Oregon and Washington were collected earlier than Burleigh's series from Idaho. The exceptional bird, from Washington, was collected by Burleigh and resembles his Idaho series in pallor. Specimens collected by persons other than Burleigh from Idaho, Washington, Oregon, and Montana, although darker than Burleigh's series of *larifuga,* are noticeably grayer and less reddish brown above and on the upper breast, and have paler crowns than specimens from the eastern range of the species. These western specimens are more similar to the Idaho series prepared by Burleigh than to specimens collected elsewhere. I provisionally agree with Oberholser (1974) and Behle (1985) that the population named *larifuga* should be recognized.

Bombycilla cedrorum aquilonia Burleigh, 1963.—Searston, Newfoundland (USNM).
=*Bombycilla cedrorum cedrorum* Vieillot, 1808.

Burleigh (1963) named the population from Newfoundland to northern Canada and Alaska *aquilonia* and described it as the grayest subspecies. I examined 23 of the specimens studied by Burleigh; except for the holotype of *aquilonia,* I lacked males from Canada. I conclude that there is too much individual variation to recognize an additional eastern subspecies (*contra* Behle 1985).

Vireonidae

Vireo solitarius jacksoni Oberholser, 1974.—16 miles south of Roundup, Musselshell Co., Montana (USNM).
=*Vireo solitarius plumbeus* Coues, 1866 (see Browning 1978).

Vireo gilvus petrorus Oberholser, 1974.—Fort Steele, Carbon Co., Wyoming (USNM).
=*Vireo gilvus brewsteri* (Ridgway, 1903).

In an earlier paper (Browning 1974) I concluded that the population from southern British Columbia to Sonora and the Trans-Pecos region of Texas, named *petrorus,* belonged to the western subspecies *leucopolius.* Allan R. Phillips (pers. comm.) suggested that *petrorus* is a northward extension of *brewsteri* from Mexico. Upon reexamination, I find that specimens of *petrorus* are slightly darker crowned than *swainsoni, leucopolius,* and, especially, nominate *gilvus.* A series of 21 specimens from the Rocky Mountains are darker and duller on their upper parts than a larger series of the other northern forms, are larger than *leucopolius* (see Browning 1974), and are most similar to *brewsteri* in size and coloration. I now consider *petrorus* to be a synonym of *brewsteri,* the subspecies breeding from Nayarit north to the Sierra Madre Occidental, southern Arizona (Phillips et al. 1964), and the Rocky Mountains to at least Montana.

Vireo olivaceus caniviridis Burleigh, 1960[a].—Moscow, Latah Co., Idaho (USNM).
=*Vireo olivaceus caniviridis* (see Wetmore et al. 1984, Behle 1985).

This pale subspecies breeds in Washington, Idaho, and northern Oregon. The winter range is unknown.

Emberizidae
Parulinae

Dendroica petechia hypochlora Oberholser, 1974.—3 miles N Fort Whipple (near Prescott), 3000 ft, Yavapai Co., Arizona (USNM).
=*Dendroica petechia sonorana* Brewster, 1888 (see Browning 1974).

Dendroica dominica axantha Oberholser, 1974.—Lucasville, Scioto Co., Ohio (CMNH).
=*Dendroica dominica albilora* Ridgway, 1873 (see Browning 1978).

Oporornis formosus umbraticus Oberholser, 1974.—1.25 miles down Ohio River from Vanport, near mouth of Four-mile Run, Beaver Co., Pennsylvania (USNM).
=*Oporornis formosus* (Wilson, 1811) (see Browning 1978).

Icteria virens danotia Oberholser, 1974.—20 miles W Mountain Home, Kerr Co., Texas (USNM).

=*Icteria virens virens* (Linnaeus, 1758) (see Browning 1978).

Thraupinae

Piranga ludoviciana zephyrica Oberholser, 1974.—Santa Rita Mountains, Madera Canyon, Santa Cruz Co., Arizona (USNM).
=*Piranga ludoviciana* (Wilson, 1811) (see Browning 1978).

Piranga rubra ochracea Phillips, 1966.—Trout Creek just above its mouth, near Cane Springs, lat. 34°57′N, long. 113°37′W, western Arizona (DMNH).
=*Piranga rubra ochracea.*

Females in first basic plumage from northwestern Arizona were described by Phillips (1966) as similar in size but darker and duller (less yellow) than the large-billed western subspecies *cooperi* and as paler and less green than nominate *rubra.* Adult males of *ochracea* were described as more purple and less orange than *cooperi.*

Nine specimens, including adult females and immatures from the type series of *ochracea,* are brighter green above than the dull grayish-backed *cooperi,* and the dark olive backed nominate subspecies. Adult females also differ from the other subspecies by their ochraceous rumps and heads and grayish ochraceous sides and flanks. Immature males are intermediate to nominate *rubra* and *cooperi* in back color. *Piranga r. ochracea* is known to breed in the central part of Big Sand Valley in Mojave County, Arizona, and to winter in Sinaloa and Colima, Mexico.

Cardinalinae

Richmondena cardinalis clintoni Banks, 1963.—Ruffo's Ranch, Cerralvo Island, Baja California, Mexico [CAS].
=*Cardinalis cardinalis clintoni.*

Described as similar in size to *ignea* of southern Baja California but smaller than *superba* of the southwestern U.S. and northwestern Mexico, the males of *clintoni* were characterized as less intensely red with paler gray edges to the dorsal feathers than *ignea.* Compared to *superba,* the red areas of *clintoni* were described as more pink and not orangish. Females of *clintoni* were characterized as grayer dorsally and less brown than *ignea.*

I agree with Banks (1963) and also found the crown coloration of four males of *clintoni* is more orange (less red) than the aforementioned forms. The population of central Baja California, *seftoni,* was not mentioned by Banks (1963). I compared two males of *seftoni* and found they are ventrally similar to 26 specimens of *ignea* and 27 of *clintoni,* and dorsally similar to *clintoni* in the gray edges of the back feathers, but the red feathers of the back and crown are more similar to *superba.* Paynter (1970b) recognized *clintoni* only provisionally.

Guiraca caerulea mesophila Oberholser, 1974.—Lipscomb, Lipscomb Co., Texas (USNM).
=*Guiraca caerulea caerulea* (Linnaeus, 1758) (see Browning 1978).

Emberizinae

Hortulanus fuscus aimophilus Oberholser, 1974.—Fort Davis, Jeff Davis Co., Texas (USNM).
=*Pipilo fuscus texanus* van Rossem, 1934 (see Browning 1978).

Use of the specific name follows Zink (1988) and A.O.U. (1989).

Pipilo aberti voorhiesi Phillips, 1962.—ca. 15 km S Tucson, Pima Co., Arizona [DMNH].
=*Pipilo aberti dumeticola* van Rossem, 1946 (see Hubbard 1972).

Baird's (1852) description of *P. aberti* could apply to either the western (*dumeticola*) or the eastern (nominate *aberti*) population. Phillips (1962), believing that the holotype of *aberti* was collected from the western population, renamed the eastern population. Evidence presented by Hubbard (1972) and McKlevey (1955) concerning the itineraries of the possible collectors of the type of *P. aberti* does not support Phillips' (1962) speculation (*contra* Paynter 1970a).

Spizella pusilla perissura Oberholser, Texas birds, 1974:941.—Valentine, Cherry Co., Nebraska (USNM).
Spizella pusilla vernonia Oberholser, 1974.—Japonica, Kerr Co., Texas (USNM).
=*Spizella pusilla arenacea* Chadbourne, 1886 (see Browning 1978).

Pooecetes gramineus altus Phillips, *in* Phillips, Marshall, & Monson 1964.—no type designated.
Pooecetes gramineus altus Phillips, 1965.—extreme southern part of Kenrick Park, San Francisco Mountains, Arizona (DMNH).
=*Pooecetes gramineus altus* Phillips, 1964 (see Rea 1983).

This dorsally dark brown subspecies was described as less buffy than *affinis* and similar in size to *confinis.* Paynter (1970a) synonymized *altus* with *confinis.* It occurs from northern Arizona to southern Utah, western Colorado, and New Mexico.

The authorship of *altus* has been questioned by Parkes (1966) because Marshall (who was not specifically given as the author of the name) may have written the section on *P. gramineus* in Phillips et al. (1964); he suggested that the author of this subspecies be given as "Phillips" =Marshall, *in* Phillips, Marshall, & Monson. Monson & Phillips (1981) cited Marshall as the author for the taxon, but Rea (1983) believed that Phillips is the true author of *altus.* It is specifically noted in Phillips, Marshall, & Monson (1964:ix) that Phillips "is responsible for the scientific names and classification used." According to Phillips (pers. comm.), he submitted the manuscript describing *altus* before 1964, but its publication (Phillips 1965) was delayed.

Chondestes grammacus quillini Oberholser, 1974.—Cotulla, La Salle Co., Texas (USNM).
=*Chondestes grammacus strigatus* Swainson, 1827 (see Browning 1978).

Amphispiza bilineata dapolia Oberholser, 1974.—Chisos Mountains, Pine Canyon, 6000 ft, Brewster Co., Texas (USNM).
=*Amphispiza bilineata opuntia* Burleigh & Lowery, 1939 (see Browning 1978).

Amphispiza bilineata belvederei Banks, 1963.—east side Cerralvo Island, Baja California, Mexico [CAS].
=*Amphispiza bilineata belvederei.*

This form was characterized as darker dorsally than *bangsi* of southern Baja California, and more gray (less brown) than *deserticola* of central Baja California and mainland Mexico. The maxilla of *belvederei* was described as slightly curved compared to the straighter maxilla of *bangsi.*

Paratypes of *belvederei* are noticeably dark vinaceous above, a color lacking in 20 specimens of *bangsi* and a larger series of *deserticola.* The crown of *belvederei* is also grayer than in *bangsi.* I did not compare the shape of the maxilla. Paynter (1970a), who did not examine specimens from Cerralvo Island, provisionally recognized *belvederei.* Banks (1963) suggested that *carmenae* van Rossem, 1945, from Carmen Island, Baja California, may also warrant recognition. A single specimen from Carmen Island examined by me is paler dorsally than *bangsi* and *belvederei.*

Ammodramus henslowi houstonensis Arnold, 1983.—south-central Houston, Harris County, Texas [TCWC].
=*Ammodramus henslowi henslowi* (Audubon, 1829).

This local population was described as

darker than the eastern subspecies, *susurrans,* and the western nominate *henslowi.*

All but the holotype of *houstonensis* were available to me for comparison. The male paratype collected in June is actually browner (not more black) dorsally than most specimens of the nominate subspecies, and two worn July males from the type series are indistinguishable in this characteristic. Nine specimens of nominate *henslowi* from Wisconsin, Ohio, and Missouri are blacker, and therefore, agree with the description of *houstonensis* in dorsal coloration. The nape of the new form was described as duller than nominate *henslowi,* but this character is not useful in separating the two populations. The yellow lore was said to be absent in *houstonensis.* This character is subject to individual variation in the nominate subspecies, and, in fact, the lores of the June male from Houston are yellow. Rump coloration, not mentioned by Arnold (1983), is darker and more richly chestnut in *susurrans* than in nominate *henslowi* and *houstonensis.* The amount of individual variation in coloration within the western form precludes recognition of additional subspecies.

Passerella iliaca chilcatensis Webster, 1981.—near Tsirku River, about 250 m elevation, 7 miles (airline) SSW Klukwan, Alaska [CAS].
=*Passerella iliaca chilcatensis.*

Swarth (1922) was the first to notice that birds from the southern part of the range of *fuliginosa,* as then recognized, differ from those to the north, but he declined to name the population for lack of sufficient specimens. Webster (1981) characterized *chilcatensis* as similar below but more reddish and duller above than *fuliginosa.*

I found that *chilcatensis* differs from the holotype and 30 other specimens of *fuliginosa,* including one bird from Vancouver Island, as described and that the subspecies is blacker and less reddish both dorsally and on the ventral spots than 35 specimens of *townsendi,* the form breeding farther to the north. The new subspecies breeds from the Chilkat River area of southeastern Alaska to the Stewart area of British Columbia and winters on the coasts of Oregon and California south to San Francisco.

Melospiza melodia callima Oberholser, 1974.—West Point, Orange Co., New York (USNM).
=*Melospiza melodia melodia* (Wilson, 1810) (see Browning 1978).

Melospiza melodia melanchra Oberholser, 1974.—Bay Point, 3 miles N Sandusky, Ohio (CMNH).
=*Melospiza melodia euphonia* Wetmore, 1936 (see Browning, 1978).

Zonotrichia leucophrys aphaea Oberholser, 1974.—Caribou Mountain, Bonneville Co., Idaho (CMNH).
=*Zonotrichia leucophrys leucophrys* (Forster) 1772 (see Browning 1974, 1978).

Junco hyemalis henshawi Phillips, 1962.—Bennett, British Columbia (USNM).
=*Junco hyemalis cismontanus* Dwight, 1918.

The name *henshawi* is a new name for the population that the A.O.U. (1957) called *cismontanus* Dwight, 1918. The name *cismontanus* was originally proposed by Dwight (1918) for convenience to discuss hybrids between the *oreganus* and *hyemalis* groups. It was later applied by Miller (1941: 343, 402) as the name of the stabilized hybrid population that breeds from south-central Yukon to central interior British Columbia and west-central Alberta, but Miller proposed that it should be applied to similar appearing hybrids as well as for the true subspecies. The name *cismontanus* is valid as applied to that breeding population (Miller 1941; *contra* Phillips 1962, Browning 1974, Rea 1983).

Junco hyemalis simillima Phillips, 1962.—Pringle Falls, 4245 ft, Experiment Station (Deschutes National Forest), Deschutes Co., Oregon (DMNH).

=*Junco hyemalis simillimus* (see Browning 1974, 1978, 1979b).

Junco oreganus eumesus Oberholser, 1974.—Blue Mountains, 3500 ft, ridge on east fork of Touchet River, 21 miles SE Dayton, Columbia Co., Washington (USNM).
=*Junco hyemalis shufeldti* Coale, 1887 (sensu Phillips 1962, see Browning 1974, 1978).

Calcarius pictus roweorum Kemsies, 1961.—Anaktuvik, Alaska (USNM).
=*Calcarius pictus* (Swainson), 1832 (see Jehl 1968).

Calcarius pictus mersi Kemsies, 1961.—Little Cape, Ontario [NMC].
=*Calcarius pictus* (Swainson), 1832 (see Jehl 1968).

Kemsies' (1961) descriptions of the two forms of *C. pictus* were based on comparisons of inadequate samples and characterizations of geographic variation using seasonally incomparable specimens (Jehl 1968).

Icterinae

Agelaius phoeniceus stereus Oberholser, 1974.—Barr, Adams Co., Colorado (USNM).
=*Agelaius phoeniceus stereus* (see Browning 1978).

I recognize *stereus* provisionally.

Agelaius phoeniceus zastereus Oberholser, 1974.—Boise, 2700 ft, Ada Co., Idaho (CMNH).
=*Agelaius phoeniceus zastereus* (see Browning 1974, 1978).

I recognize *zastereus* provisionally.

Agelaius phoeniceus heterus Oberholser, 1974.—Fort Wingate, McKinley Co., New Mexico (USNM).
=*Agelaius phoeniceus fortis* Ridgway, 1901 (see Browning 1978).

Rea (1983) stated that *heterus* may prove to be recognizable.

Quiscalus major alabamensis Stevenson, 1978.—4.5 km E Mobile, Baldwin Co., Alabama (USNM).
=*Quiscalus major alabamensis.*

Stevenson (1978) recognized four subspecies of *Quiscalus major: torreyi* from New Jersey to northeastern Florida, *westoni* on the Florida Peninsula, *alabamensis* along the coast of Alabama and southeastern Mississippi, and nominate *major* from southwestern Mississippi to Texas. The subspecies *westoni* Sprunt, 1934 (type locality St. Johns River marshes, Indian River Co., Florida), was included in nominate *major* by the A.O.U. (1957) as was the range attributed to *alabamensis.*

The eye is dark in *westoni* and nominate *major,* but it is pale in *torreyi* and *alabamensis* (Stevenson 1978). I compared three males and four females of *alabamensis* and about 15 specimens each of the other subspecies. I found that males of *westoni* are slightly larger than *torreyi* and *alabamensis,* with measurements of the wing chord averaging less than in nominate *major.* The subspecies *alabamensis* differs in size from the other taxa as implied. Females of *alabamensis* are similar to *torreyi* in color, and paler than *westoni* and nominate *major.*

Icterus bullockii eleutherus Oberholser, 1974.—Del Rio, Val Verde Co., Texas (USNM).
=*Icterus galbula bullockii* (Swainson, 1827) (see Browning 1978).

Carduelinae

Leucosticte tephrocotis irvingi Feinstein, 1958.—Anaktuvuk Pass, Brooks Range, Alaska (USNM).
=*Leucosticte arctoa tephrocotis* (Swainson, 1832).

Feinstein (1958) divided the subspecies *tephrocotis* and named the population of Alaska's Brooks Range, confining *tephrocotis* to the northern Rocky Mountains. He described *irvingi* as similar in size, but more brightly colored, above and below. The reddish regions of *irvingi* were described as averaging deeper red and more purplish than in *tephrocotis.* Specimens of *irvingi* were described as showing "a slight inclination towards *littoralis* in coloration" (Feinstein 1958:12), but with less gray in the malar and auricular region than in typical examples of that subspecies.

The type series of *irvingi* was reported by Feinstein (1958) to consist of 7 males and 5 females. These, and five other specimens from the Brooks Range are well within the range of individual variation in size and color found in 40 specimens of *tephrocotis* from the Rocky Mountains and bear no resemblance to *littoralis.* The characters of *irvingi* are attributable to individual variation, and I fully agree with R. E. Johnson (in litt.) that *irvingi* does not warrant recognition.

Erythrina mexicana anconophila Oberholser, 1974.—Chinati Mountains, Presidio Co., Texas (USNM).
=*Carpodacus mexicanus frontalis* (Say, 1823) (see Browning 1978).

Loxia curvirostra vividior Phillips, *in* Monson and Phillips 1981.—in "El Paso Co.," Colorado [=about 8–15 km from Monument] (sic) (USNM).
=*Loxia curvirostra vividior.*

This subspecies was described as overall similar in size to *neogaea* Griscom, 1937, but often having a thinner bill. Phillips (*in* Monson & Phillips 1986) also described *vividior* as more ochraceous than *neogaea* and gave its range as "usually the high mountains of the western United States from Montana to Colorado and probably west to Deschutes Co., Oregon. . . ." For the use of the name *neogaea* see Dickerman (1986b, 1987). I provisionally recognize *vividior.*

Loxia curvirostra reai Phillips, *in* Monson & Phillips 1981.—Dismal Lake, SE Shoshone Co., Idaho [AMR].
=*Loxia curvirostra reai* (but see Payne 1987).

This subspecies was described as having a bill often heavier than the otherwise similarly sized *minor.* Males were described as less reddish, and females as rich yellow on the rump and more deeply ochraceous below than *minor.* The range of *reai* was given as the mountains of northern Idaho (typical series) to southern British Columbia and Sheridan, Wyoming, and casually in western Oregon and Arizona, Minnesota, Michigan, and Kansas.

Payne (1987) considered *reai* indistinguishable from *minor,* but he (1987:28) based his conclusion mainly on a comparison of the holotypes of *pusilla* and *minor.* Payne designated AMR 3627 as the lectotype of *reai* but this specimen is not from the original series (Rea, pers. comm.). For the correct use of *minor* see Dickerman (1986b, 1987). Although Dickerman listed both *vividior* and *reai* in his summary, he did not comment on the validity of either name. My acceptance of *reai* and *vividior* is provisional, recognizing that the taxonomy of *L. curvirostra* still requires a comprehensive review.

Passeridae

Passer domesticus plecticus Oberholser, 1974.—Gray, Bonneville Co., Idaho (USNM).
=*Passer domesticus domesticus* Linnaeus, 1758 (see Browning 1978).

Acknowledgments

I thank Allan R. Phillips for the many useful discussions about the taxonomy of North American birds and for the opportunity to examine the long series of specimens available to him during his visits to the U.S. National Museum. I thank the California Academy of Sciences, Delaware Museum of Natural History, Field Museum of Natural History, Texas A&M University, and San Diego Museum of Natural History for loaning specimens, and extend appreciation to the many museums that loaned specimens to Dr. Phillips. Appreciation is extended to David Niles for his encouragement and assistance in locating some of the types described by Phillips. I am grateful to Robert W. Dickerman, Allan R. Phillips and Amadeo M. Rea for their critical reading of an earlier draft of the manuscript. I thank Burt L. Monroe, Jr., James V. Remsen, Jr., Storrs L. Olson, and especially Richard C. Banks for their many useful comments for the improvement of the manuscript.

Literature Cited

Ainley, D. G. 1980. Geographic variation in Leach's Storm-Petrel.—Auk 97(4):837–853.

Aldrich, J. W. 1968. Population characteristics and nomenclature of the Hermit Thrush.—Proceedings of the U.S. National Museum 124. 33 pp.

———. 1972. A new subspecies of Sandhill Crane from Mississippi.—Proceedings of the Biological Society of Washington 85(5):63–70.

———. 1979. Status of the Canadian Sandhill Crane.—Proceedings of the 1978 Crane Workshop, Rockport, Texas. Published by the National Audubon Society, pp. 139–148.

———. 1981. Geographic variation in White-winged Doves with reference to possible source of new Florida populations.—Proceedings of the Biological Society of Washington 94(3):641–651.

American Ornithologists' Union. 1931. Check-list of North American birds. Fourth edition. American Ornithologists' Union, Lancaster, Pennsylvania, 372 pp.

———. 1957. Check-list of North American birds. Fifth edition. American Ornithologists' Union, Baltimore, Maryland, 691 pp.

———. 1983. Check-list of North American birds. Sixth edition. American Ornithologists' Union, Washington, D.C., 877 pp.

———. 1989. Thirty-seventh supplement to the American Ornithologists' Union check-list of North American birds.—Auk 106(3):532–538.

Arnold, K. A. 1983. A new subspecies of Henslow's Sparrow (*Ammodramus henslowii*).—Auk 100(2):504–505.

Austin, G. T., & A. M. Rea. 1976. Recent southern Nevada bird records.—Condor 78(3):405–408.

Baird, S. F. 1852. Appendix C. Zoology. *In* H. Stansbury, Exploration and survey of the valley of the Great Salt Lake, Utah. U.S. Senate Special Session, March 1851, Executive Document Number 3:307–379.

Banks, R. C. 1963. New birds from Cerralvo Island, Baja California, Mexico.—Occasional Papers of the California Academy of Sciences No. 37, 5 pp.

———. 1970. Molt and taxonomy of Red-breasted Nuthatches.—Wilson Bulletin 82(2):201–205.

Behle, W. H. 1968. A new race of the Purple Martin from Utah.—Condor 70(2):166–169.

———. 1985. Utah birds: Geographic distribution and systematics.—Utah Museum of Natural History, Occasional Publication Number 5, 147 pp.

Bellrose, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania, 544 pp.

Bond, G. M. 1962. A new Blue Jay (*Cyanocitta cristata*) from Newfoundland.—Proceedings of the Biological Society of Washington 75:205–206.

Bourne, W. R. P., & J. R. Jehl, Jr. 1982. Variation and nomenclature of Leach's Storm-Petrel.—Auk 99(4):793–797.

Browning, M. R. 1974. Taxonomic remarks on recently described subspecies of birds that occur in the northwestern United States.—Murrelet 55(3):32–38.

———. 1977. Geographic variation in *Contopus sordidulus* and *C. virens* north of Mexico.—Great Basin Naturalist 37(4):453–456.

———. 1978. An evaluation of the new species and subspecies proposed in Oberholser's *Bird Life of Texas*.—Proceedings of the Biological Society of Washington 91(1):85–122.

———. 1979a. A review of geographic variation in continental populations of the Ruby-crowned Kinglet (*Regulus calendula*).—Nemouria Number 21, 9 pp.

———. 1979b. Type specimens of birds collected in Oregon.—Northwest Science 53(2):132–140.

Burleigh, T. D. 1959. Two new subspecies of birds from western North America.—Proceedings of the Biological Society of Washington 72:15–18.

———. 1960a. Three new subspecies of birds from western North America.—Auk 77(2):210–215.

———. 1960b. Geographic variation in the Western Wood Pewee (*Contopus sordidulus*).—Proceedings of the Biological Society of Washington 73(22):141–146.

———. 1960c. Geographic variation in the catbird *Dumetella carolinensis*.—Oriole 24(3–4):29–32.

———. 1961. A new subspecies of Downy Woodpecker from the Northwest.—Murrelet 41(3):42–44.

———. 1963. Geographic variation in the Cedar Waxwing (*Bombycilla cedrorum*).—Proceedings of the Biological Society of Washington 76:177–180.

———, & A. J. Duvall. 1959. A new subspecies of Veery from the northwestern United States.—Proceedings of the Biological Society of Washington 72:33–36.

Cramp, S. (ed.). 1977. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 1. Oxford University Press, Oxford, 716 pp.

Delacour, J., & S. D. Ripley. 1975. Description of a new subspecies of the White-fronted Goose *Anser albifrons.*—American Museum Novitates No. 2565, 4 pp.

Dickerman, R. W. 1963. The grebe *Aechmophorus occidentalis clarkii* as a nesting bird of the Mexican Plateau.—Condor 65(1):66–67.

———. 1973. Further notes on the Western Grebe in Mexico.—Condor 75(1):131–132.

———. 1986a. Two hitherto unnamed populations of *Aechmophorus* (Aves: Podicipitidae).—Proceedings of the Biological Society of Washington 99(3):435–436.

———. 1986b. A review of the Red Crossbill in New York state. Part 1. Historical and nomenclatural background.—Kingbird 36(2):73–78.

———. 1987. The "old northeastern" subspecies of Red Crossbill.—American Birds 41(2):189–194.

Dwight, J. 1918. The geographical distribution of color and other variable characters in the genus *Junco*: A new aspect of specific and subspecific values.—Bulletin of the American Museum of Natural History 38:296–309.

Feinstein, B. 1958. A new Gray-crowned Rosy Finch from northern Alaska.—Proceedings of the Biological Society of Washington 71:11–12.

Godfrey, W. E. 1986. The birds of Canada. Revised edition. National Museum Natural Science (Canada), Ottawa, 595 pp.

Hekstra, G. P. 1982. Description of twenty-four new subspecies of American owls (Aves:Strigidae).—Bulletin Zoologisch Museum Universiteit Amsterdam 9(7)49–63.

Hubbard, J. P. 1972. Notes on Arizona birds.—Nemouria Number 5, 22 pp.

———, & R. S. Crossin. 1974. Notes on northern Mexican birds.—Neumoria Number 14, 41 pp.

Jehl, J. R., Jr. 1968. Geographic and seasonal variation in Smith's Longspur, *Calcarius pictus.*—Transactions of the San Diego Society of Natural History 15(1):1–5.

———. 1987. Geographic variation and evolution in the California Gull (*Larus californicus*).—Auk 104(3):421--428.

———, & W. T. Everett. 1985. History and status of the avifauna of Isla Guadelupe, Mexico.—Transactions of the San Diego Society of Natural History 20(17):313–336.

Johnsgard, P. A. 1979. Order Anseriformes. Pp. 425–506 *in* E. Mayr & G. W. Cottrell, eds., Check-list of birds of the World. Volume 1, Second edition. Museum of Comparative Zoology, Cambridge, Massachusetts.

———. 1988. North American owls. Smithsonian Institution Press, Washington, D.C., 295 pp.

Johnson, D. H., & R. E. Stewart. 1973. Racial composition of migrant populations of Sandhill Cranes in the northern plains states.—Wilson Bulletin 85(2):148–162.

Johnson, N. K. 1965. The breeding avifaunas of the Sheep and Spring ranges in southern Nevada.—Condor 67(2):93–124.

Kemsies, E. 1961. Subspeciation in the Smith's Longspur, *Calcarius pictus.*—Canadian Field-Naturalist 75(3):143–149.

Krogman, B. D. 1979. A systematic study of *Anser albifrons* in California. Pp. 22–43 *in* R. L. Jarvis & J. C. Bartonek, eds., Management and biology of Pacific Flyway geese. Oregon State University Book Stores, Corvallis.

Manning, T. H. 1952. Birds of the west. James Bay and southern Hudson Bay coasts.—National Museum of Canada Bulletin no. 125, 114 pp.

Mayr, E., & F. Vuilleumier. 1983. New species of birds described from 1966 to 1975.—Journal für Ornithologie 124(3):217–232.

McKlevey, S. D. 1955. Botanical exploration of the Trans-Mississippi west 1790–1850. Arnold Arboretum, Harvard University, Jamaica Plain, Massachusetts, 1144 pp.

Miller, A. H. 1941. Speciation of the avian genus *Junco.*—University of California Publication in Zoology 44:173–434.

Monroe, B. L., Jr. 1968. A distributional survey of the birds of Honduras.—American Ornithologists' Union Ornithological Monograph No. 7, 458 pp.

Monson, G., & A. R. Phillips. 1981. Annotated checklist of the birds of Arizona. Second edition. University of Arizona Press, Tucson, 240 pp.

Oberholser, H. C. 1974. The bird life of Texas. University of Texas Press, Austin, 1068 pp.

Palmer, R. S. (ed.). 1976. Handbook of North American birds. Vol. 2. Yale University Press, New Haven, Connecticut, 521 pp.

———. 1988. Handbook of North American Birds. Vol. 5. Yale University Press, New Haven, Connecticut, 465 pp.

Parkes, K. C. 1966. [Review of] The birds of Arizona, by A. Phillips, J. Marshall, & G. Monson.—Auk 83(3):484–487.

Payne, R. B. 1987. Populations and type specimens of a nomadic bird: Comments on the North American crossbills *Loxia pusilla* Gloger 1834 and *Crucirostra minor* Brehm 1845.—Occasional Papers of the Museum of Zoology, University of Michigan, No. 714, 37 pp.

Paynter, R. A., Jr. 1970a. Subfamily Emberizinae. Pp. 3–214 *in* R. A. Paynter, Jr., ed., Check-list of birds of the world. Vol. 13. Museum of Comparative Zoology, Cambridge, Massachusetts.

———. 1970b. Subfamily Cardinalinae. Pp. 216–245 *in* R. A. Paynter, Jr., ed., Check-list of birds of the world. Vol. 13. Museum of Comparative Zoology, Cambridge, Massachusetts.

Phillips, A. R. 1962. Notas sistematicas sobre aves Mexicanas. 1.—Anales del Instituto de Biología México 32(1,2):333–381.

———. 1965. Notas sistematicas sobre aves Mexicanas 3.—Revista de la Sociedad Mexicanas de Historia Natural 25:217–242.

———. 1966. Further systematic notes on Mexican birds.—Bulletin of the British Ornithologist's Club 86(8):148–159.

———. 1986. The known birds of North and Middle America. Part 1. Privately published, Denver, 259 pp.

———, J. T. Marshall, Jr., & G. Monson. 1964. The birds of Arizona. University of Arizona Press, Tucson, 220 pp.

Power, D. M., & D. G. Ainley. 1986. Seabird geographic variation: Similarity among populations of Leach's Storm-Petrel.—Auk 103(3):575–585.

Rea, A. M. 1973. The Scaled Quail (*Callipepla squamata*) of the Southwest: Systematic and historical considerations.—Condor 75(3):322–329.

———. 1983. Once a river. University of Arizona Press, Tucson, 285 pp.

Ripley, S. D. 1964. Subfamily Turdinae. Pp. 13–227 *in* E. Mayr & R. A. Paynter, Jr., eds., Checklist of birds of the world. Volume 10. Museum of Comparative Zoology, Cambridge, Massachusetts.

Saunders, G. B. 1968. Seven new white-winged doves from Mexico, Central America, and southwestern United States.—North American Fauna Number 65, 30 pp.

Short, L. L., Jr. 1968. Variation of Ladder-backed Woodpeckers in southwestern North America.—Proceedings of the Biological Society of Washington 81:1–10.

———. 1982. Woodpeckers of the world. Delaware Museum of Natural History Monograph Series No. 4, 676 pp.

Snyder, L. L. 1961. On an unnamed population of the Great Horned Owl.—Royal Ontario Museum Contribution No. 54, 7 pp.

Stevenson, H. M. 1973. An undescribed insular race of the Carolina Wren.—Auk 90(1):35–38.

———. 1978. The populations of Boat-tailed Grackles in the southeastern United States.—Proceedings of the Biological Society of Washington 91(1):27–51.

Sutton, G. M. 1967. Oklahoma birds: Their ecology and distribution, with comments on the avifauna of the southern Great Plains. University of Oklahoma Press, Norman, 674 pp.

Swarth, H. S. 1922. Birds and mammals of the Sitkine River region of northern British Columbia and southeastern Alaska.—University of California Publications in Zoology 24(2):125–314.

Timm, D. E., M. L. Wege, & D. S. Gilmer. 1982. Current status and management challenges for Tule White-fronted Geese.—Transactions of the North American Wildlife and Natural Resource Conference 47:453–463.

Walkinshaw, L. H. 1965. A new Sandhill Crane from central Canada.—Canadian Field-Naturalist 79(3):181–184.

———. 1973. Cranes of the world. Winchester Press, New York, 370 pp.

Webster, J. D. 1981. A new subspecies of Fox Sparrow from Alaska.—Proceedings of the Biological Society of Washington 96(4):664–668.

Wetmore, A. 1965a. Additions to the list of birds of the Republic of Colombia.—L'Oiseau 35(special):156–162.

———. 1965b. The birds of the Republic of Panamá.—Smithsonian Miscellaneous Collections 150, part 1, 483 pp.

———, R. Pasquier, & S. L. Olson. 1984. The birds of the Republic of Panama.—Smithsonian Miscellaneous Collections 150, part 4, 670 pp.

White, C. M. 1968. Diagnosis and relationships of the North American tundra-inhabiting Peregrine Falcons.—Auk 85(2):179–191.

———, & D. A. Boyce, Jr. 1988. An overview of Peregrine Falcon subspecies. Pp. 789–810 *in* T. J. Cade, J. H. Enderson, C. G. Thelander, & C. M. White, eds., Peregrine Falcon populations, their management and recovery. The Peregrine Fund, Inc., Boise, Idaho.

Zink, R. M. 1988. Evolution of Brown Towhees: Allozymes, morphometrics and species limits.—Condor 90(1):72–82.

U.S. Fish and Wildlife Service, National Ecology Research Center, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, p. 452

ERRONEOUS EMENDATIONS TO NAMES PROPOSED BY HEKSTRA (STRIGIDAE: *OTUS*)

M. Ralph Browning

Abstract.—Four emendations (Browning 1989) of names of New World owls proposed by Hekstra (1982) are incorrect subsequent spellings. The spelling "*uruguaii*" of the proposed subspecific name of *Otus choliba* (sensu Hekstra) is chosen as correct.

I earlier (Browning 1989) misinterpreted Articles 31c and 32 d (ii) and applied Appendix D, IV, of the International Code of Zoological Nomenclature (ICZN 1985) to four subspecific names of New World owls proposed by Hekstra (1982). According to Article 32, the four emendations (Browning 1989) are incorrect subsequent spellings and have no nomenclatural standing.

The correct names as proposed by Hekstra (1982) and the incorrect emendations (in parentheses) are:

Otus atricapillus morelius (not *moreliensis*)
Otus atricapillus inambarii (not *inambariensis*)
Otus guatemalae peteni (not *petenensis*)
Otus choliba urugaii [sic] (not *uruguaiensis*)

Hekstra (1982) first used *Otus choliba uruguaii* [sic] as a nomen nudum in a list of species (1982:54). He spelled the subspecific name "*urugaii*" in the formal proposal, but again as *uruguaii* in a discussion of the etymology, from the Arroyo Urugua-i. The repeated use of *uruguaii* indicates his intended spelling, and as first revisor (ICZN 1985, Art. 24[b] and [c]) I select *uruguaii* as the correct spelling. König & Straneck (1989:3) listed this taxon as *uruguaii* and did not refer to other spellings.

Acknowledgments

I thank S. L. Olson, J. M. Savage, and G. C. Steyskal for pointing out the erroneous emendations and for reading the manuscript. I also thank R. C. Banks, who read a later version and offered helpful suggestions.

Literature Cited

Browning, M. R. 1989. The type specimens of Hekstra's owls.—Proceedings of the Biological Society of Washington 102:515–519.

Hekstra, G. P. 1982. Descriptions of twenty-four new subspecies of American owls (Aves: Strigidae).—Bulletin Zoologisch Museum Universiteit Amsterdam 9(7):49–63.

ICZN. 1985. International code of zoological nomenclature. 3rd ed. International Trust for Zoological Nomenclature, British Museum (Natural History), London, 338 pp.

König, C., & R. Straneck. 1989. Eine neue Eule (Aves: Strigidae) aus Nordargentinien.—Stuttgarter Beiträge zur Naturkunde, Series A (Biologie) Nr. 428, 205:1–20.

Biological Survey, National Ecology Research Center, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 453–463

SUBSPECIES OF *STENELLA LONGIROSTRIS* (MAMMALIA: CETACEA: DELPHINIDAE)

William F. Perrin

Abstract.—Three subspecies of *Stenella longirostris* are named, described and compared: *S. l. longirostris* from the world's tropical oceans, *S. l. orientalis* from tropical oceanic and coastal waters of the eastern Pacific, and *S. l. centroamericana* from Pacific coastal waters of Central America.

In a review of variation in *Stenella* spp. in eastern Pacific and Hawaiian waters (Perrin 1975a) I provisionally delineated four forms of the spinner dolphin:

1. "Costa Rican Spinner Porpoise, *Stenella longirostris* subsp. A (unnamed?),"
2. "Eastern Pacific Spinner Porpoise, *Stenella longirostris* subsp. B (unnamed?),"
3. "Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed?)," and
4. "Hawaiian Spinner Porpoise, *Stenella longirostris* subsp. D (unnamed?)."

I did not assign trinomial names to the forms because of a lack of data for spinner dolphins in other parts of the world and uncertainty about the affinities of the holotype specimen of the species. (The holotype is a skull from an unknown locality.) Sufficient data have now accumulated to allow formal description and naming of three subspecies. Two of the subspecies correspond to Nos. 1 and 2 above, and the third includes No. 4. No. 3, the "whitebelly spinner," has proved to be a highly variable hybrid/intergrade between Nos. 2 and 4.

Skull measurements summarized below were taken as described in Perrin (1975a).

Museum acronyms.—ANSP, Philadelphia Academy of Natural Sciences, Pittsburgh, Pennsylvania; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; DKC, personal collection of D. K. Caldwell, Marineland of Florida, St. Augustine; EDM, collection of Edward D. Mitchell; LACM, Los Angeles County Museum of Natural History; LSUMZ, Louisiana State University Museum of Zoology, Baton Rouge; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MMBL, National Marine Mammal Laboratory, Seattle, Washington; MNHN, Museum National d'Histoire Naturelle, Paris; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; NSM, National Science Museum, Tokyo; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SDMNH, San Diego Museum of Natural History, San Diego, California; SWFC, Marine Mammal Synoptic Collection, Southwest Fisheries Center, La Jolla, California; TCWC, Texas Cooperative Wildlife Collection, Texas A&M University, College Station; UCMP, Museum of Paleontology, University of California, Berkeley; UF, Florida State Museum, University of Florida, Gainesville; USNM, National Museum of Natural History, Washington, D.C.; ZMA, Zoologisch Museum, University of Amsterdam.

Stenella longirostris longirostris (Gray, 1828)

Holotype.—RMNH 8676, skull only, unknown locality.

Referred specimens.—Hawaiian Islands: CAS 10529, 16455, 16456, 16457, 16458; LACM 27093, 27095, 54049, 54050, 54056,

54057, 54060, 72296; SWFC WFP605, WFP606, WFP623, WFP669, WFP670, WFP671; MCZ 51700; MMBL 1194; NSM 24615, 24815; USNM 339649, 504140, 504470. Christmas Island (Central Pacific): ANSP 19194, 19195. Washington Island: USNM 504251. Rangiroa (Tuamoto Islands): USNM 504252. Hiva Oa (Marquesa Islands): USNM 504253. Enewetok (Marshall Islands): USNM 395404. Western Pacific between 1 and 9°S, 147 and 160°E: NSM M24928, M24929, M24930, M24931, M24933, M24934, M25373. Western Pacific between 3 and 5°N, 142 and 150°E: NSM M25376, M24932. Japan: NSM M05100, M24800. Sri Lanka: BMNH 1891.10.13.2, 1948.4.20.1, 1949.10.27.1 and 2. Maldive Islands: BMNH 1959.7.9.1, 1959.7.9.3, 1959.7.9.4, 1959.7.9.5 and 1959.7.9.6. Ivory Coast: USNM 470557. Liberia: RMNH 21.720. Senegal: ZMA 12.263, 13.146, 13.147, IFAN2; EDM 784. North Carolina: USNM 291352, 504525. South Carolina: USNM 500859. Florida: DKC R-4-SLS; UF 7861, 18719; LSUMZ 17017; Texas: TCWC 28286, 29035; USNM 504224, 504233, 504433–504456. St. Vincent (Lesser Antilles): UF 18720–18724. Venezuela: ZMA 15.138.

Diagnosis.—A subspecies of *Stenella longirostris* characterized by distinct tripartite color pattern (Fig. 1), erect (in adult male) to falcate dorsal fin, relatively small postanal hump, relatively large adult size (to about 215 cm; average about 180–190 cm) and relatively long (394–464 mm) and broad (zygomatic width 150–170 mm) adult skull.

Distribution.—Tropical and subtropical waters of the world. Replaced in the eastern Pacific by *S. longirostris orientalis* and *S. longirostris centroamericana* (described below) and possibly in Southeast Asia/northern Australasia by an undescribed dwarf subspecies (Perrin et al. 1989) with lower average tooth and vertebral counts and in the northwestern Indian Ocean/Red Sea by another locally adapted form (Robineau & Rose 1983). Most common near coasts and islands (Gilpatrick et al. 1987).

Description of holotype.—Measurements (in mm) of the holotype skull: condylobasal length 426, length of rostrum 277, width of rostrum at base 76, width of rostrum at ½ length 48, width of rostrum at ¾ length 36, greatest preorbital width 142, greatest postorbital width 159, zygomatic width 156, parietal width 125, length of left temporal fossa 50, height of left temporal fossa 43, length of left upper toothrow 241, length of left ramus 368, height of left ramus 57. Teeth: upper left 54, upper right 53, lower left 52, lower right 54. External size, shape and coloration unknown.

Variation.—The color pattern is stable except in a broad zone of hybridization/intergradation with *S. longirostris orientalis* in the offshore eastern tropical Pacific (range of the "whitebelly spinner"—Perrin et al. 1985), where coloration and shape may be intermediate between those of the two forms (Fig. 1; Perrin 1972, Perrin, Sloan & Henderson 1979). In these specimens, the cape may be less distinct and the ventral margin of the dorsal overlay (terminology of Perrin 1972) stepped, ragged or grading into ventral spots.

Adult size may vary geographically (Perrin et al. 1989). The largest individual known was from Hawaii (CAS 16456, 213 cm). An adult male hybrid/intergrade from the eastern Pacific (SWFC BGB008) was 235 cm long, but this may have been a case of endocrinally induced gigantism; the next largest in the sample of 262 specimens from the population (including several from the same school) was over 30 cm shorter (Perrin & Gilpatrick 1990). The largest body of external measurements from a single region is from the tropical Atlantic (Perrin et al. 1981): 17 adult females ranged from 177 to 204 cm (average 188.9 cm) and 17 males from 173 to 208 cm (average 192.5 cm); four physically mature males were 192–208

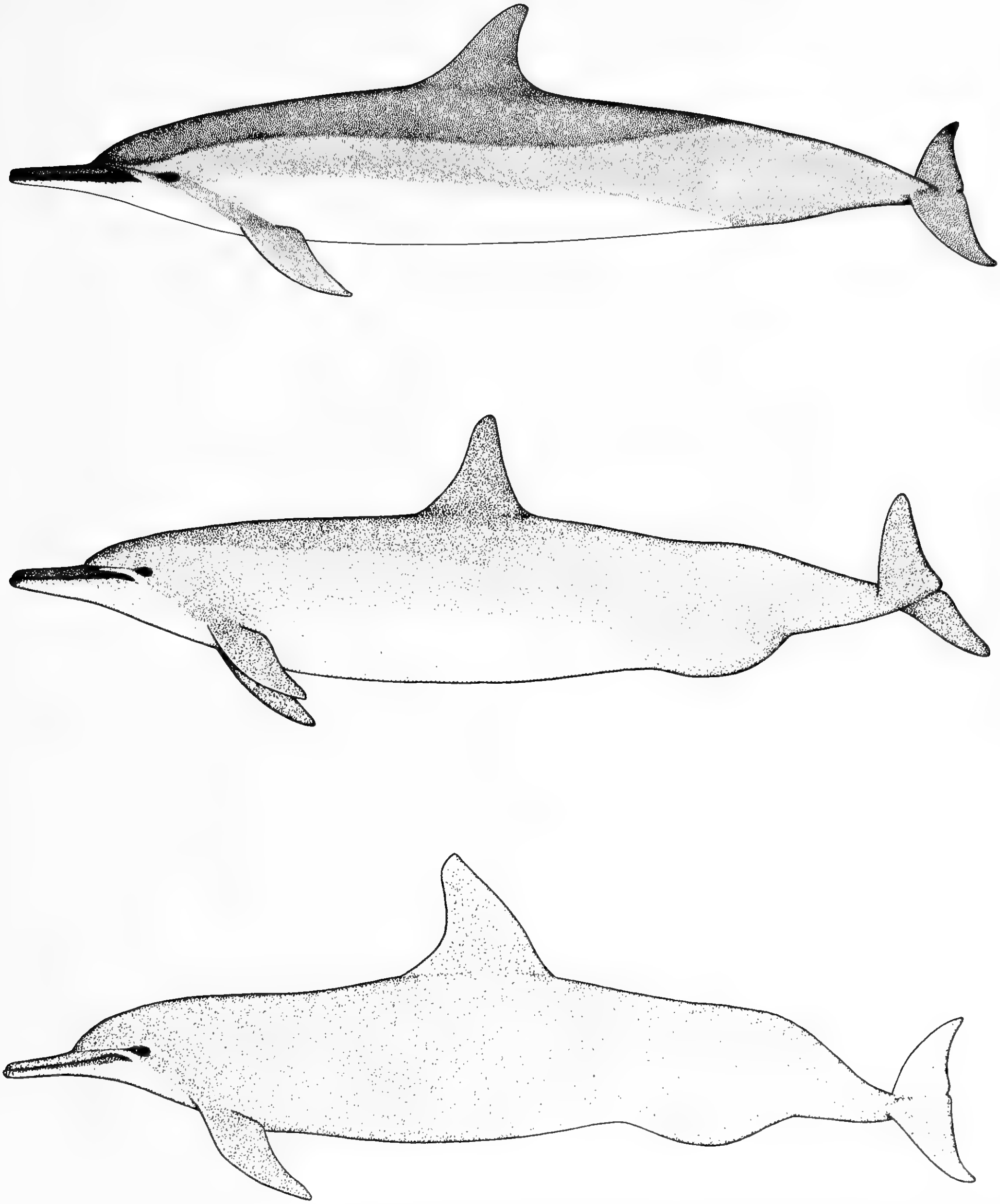


Fig. 1. Typical appearance of adult males of *Stenella longirostris longirostris* (top), *S. l. orientalis* (bottom) and a hybrid/intergrade (center). *S. l. centroamericana* is not illustrated, because the color pattern is not well known.

cm long and two females 196 and 201 cm long.

Skull size may also vary geographically (Table 1), but larger series from more localities will be necessary to demonstrate this adequately. The same is true of tooth counts (Table 1). Skulls from the hybrid/intergradation zone discussed above may be inter-

Table 1.—Means, standard deviations (for sample sizes ≥30), sample sizes (in parentheses), and maximum and minimum values for selected skull measurements and tooth counts for geographical series of cranially adult specimens of *Stenella longirostris longirostris* (from Perrin et al. 1989). Specimens of dwarf form from Southeast Asia excluded.

	Indian Ocean	Western Pacific	Central Pacific	Atlantic
Condylobasal length	409.2 (7) 394–430	420.1 (7) 411–431	436.9 (24) 417–464	427.0 ± 13.10 (41) 395–458
Length of rostrum	264.9 (7) 250–281	272.1 (7) 262–281	282.6 (24) 263–304	276.8 ± 11.00 (41) 251–304
Width of rostrum:				
At base	74.0 (7) 71–76	78.3 (7) 73–84	79.3 (24) 74–86	76.6 ± 3.41 (42) 68–83
At ½ length	43.3 (7) 42–45	47.9 (7) 44–54	47.0 (24) 42–56	44.4 ± 2.30 (41) 41–50
At ¾ length	31.0 (7) 28–34	31.4 (5) 26–36	32.3 (24) 27–37	31.9 ± 2.63 (39) 25–39
Width of PMXs at ½ length	19.4 (7) 18–20	21.0 (6) 19–23	21.1 (24) 17–23	21.0 ± 2.32 (37) 17–32
Preorbital width	141.6 (7) 135–146	144.6 (5) 140–150	150.8 (24) 140–158	145.6 ± 3.86 (42) 137–153
Postorbital width	155.4 (7) 153–160	160.8 (6) 155–169	165.2 (25) 158–172	161.1 ± 4.03 (41) 152–169
Zygomatic width	154.0 (7) 151–160	156.2 (5) 152–161	163.5 (25) 154–171	159.2 ± 3.92 (40) 150–167
Parietal width	128.7 (7) 122–133	127.6 (5) 125–131	131.4 (25) 122–140	130.5 ± 4.25 (41) 121–140
Length of temporal fossa	50.0 (7) 46–58	47.4 (5) 44–51	53.3 (25) 45–61	48.1 ± 3.30 (42) 42–56
Height of temporal fossa	41.4 (7) 39–45	41.0 (5) 36–44	42.9 (25) 37–50	38.3 ± 3.52 (42) 30–49
Length of upper toothrow	232.3 (7) 224–242	237.2 (6) 219–246	245.6 (24) 224–263	243.5 ± 10.30 (41) 221–265
Length of ramus	352.0 (7) 366–370	366.3 (7) 360–371	372.4 (23) 352–399	368.4 ± 11.68 (40) 343–399
Height of ramus	55.9 (7) 55–57	55.8 (6) 55–57	58.4 (23) 53–64	56.4 ± 2.28 (41) 51–61
Upper teeth (per row)	52.9 (15) 49–59	53.3 (12) 48–61	55.0 (29) 50–62	55.4 ± 3.01 (41) 48–64
Lower teeth (per row)	50.6 (8) 42–49	51.4 (15) 45–58	52.5 (29) 48–57	53.9 ± 3.32 (43) 47–62

mediate in size and form between those in this subspecies and in *S. l. orientalis* (Perrin 1975a, Perrin, Sloan & Henderson 1979).

Remarks.—This subspecies includes the "Hawaiian Spinner Porpoise, *Stenella longirostris* subsp. D (unnamed?)" (Perrin 1975a). Hybrids/intergrades with *S. l. orientalis* (described below) correspond to the "Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed)" (Perrin 1975a).

Genetic as well as morphological evidence support the hypothesis that the highly variable "northern whitebelly spinner" and "southern whitebelly spinner" (Perrin, Sloan & Henderson 1979, Perrin et al. 1985) represent a zone of hybridization or intergradation between the two distinct forms to the west and the east; "whitebelly spinners" possessed no unique mitochondrial DNA haplotypes when compared with animals to the east (Dizon & Perrin 1987).

Hewitt (1988) noted that the width of many hybrid zones is about one hundred times the estimate of dispersal for the individual organisms. The zone of hybridization/intergradation for *S. l. longirostris* and *S. l. orientalis* (described below) is about 2000 km wide (Perrin et al. 1985). The former tends to inhabit coastal waters and waters around islands (Gilpatrick et al. 1987, Perrin et al. 1983), but tagged oceanic spinner dolphins in the eastern Pacific have moved at least 400 km (Perrin, Evans & Holts 1979). However, as pointed out by Hewitt, gene dispersal rate is likely to vary greatly with population density, structure and patchiness, and more information is needed on these before the significance of the relatively great dispersal distance of individuals relative to the width of the hybridization/intergradation zone can be weighed.

The holotype specimens of two junior synonyms of *S. longirostris* are probably of this form; both are relatively long and broad skulls from unknown localities. These are the holotypes of *Delphinus alope* Gray, 1846 (BMNH 847a; condylobasal length 412 mm, zygomatic width 166 mm) and *D. stenorhynchus* Gray, 1866 (BMNH 1471a; condylobasal length ca. 447 mm, zygomatic width ca. 167 mm). A third holotype specimen, that of *D. microps,* also from an unknown locality (BMNH 349a), is at the lower end of the known range of adult skull length (394 mm) and below (at 147 mm) the range of skull width (150 mm) for this subspecies, suggesting that it belongs to a different form.

It seems likely that the very broadly distributed populations of this form will eventually prove to include several additional locally adapted races sufficiently distinct to merit recognition as subspecies. This seems to almost certainly be the case in Southeast Asia (Perrin et al. 1989) and is possibly the case in the northwestern Indian Ocean (Robineau & Rose 1983). The problem is simply one of material; cetacean specimens are very costly and difficult to collect, prepare and store. In the case of *S. longirostris* the species is known from several very large regions from only a single or a very few specimens; these areas include the Atlantic coast of South America, both coasts of Africa and the South Pacific.

If, as seems very likely, there proves to be a distinct (dwarf) form of the species in Southeast Asia, the name [*Delphinus*] *roseiventris* Wagner, 1846 may apply; the probable holotype specimen[1] MNHN 1882-104 is a small skull (condylobasal length 384 mm, zygomatic width 153 mm) from the Moluccas.

Use of the common name "Gray's spinner dolphin" is proposed for this, the nominate subspecies of *S. longirostris.*

Specimens examined.—In addition to the specimens designated as referred specimens above, the specimens listed in Perrin (1972, 1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989).

Stenella longirostris orientalis,
new subspecies

Holotype.—SDNHM 21427, physically mature male, total length 186 cm, from 12°20′N, 92°53′W (ca. 120 km off the coast

---

[1] The holotype specimens of Delphinidae at the MNNH are currently under review by D. Robineau of the Centre National d'Étude des Mammifères Marins.

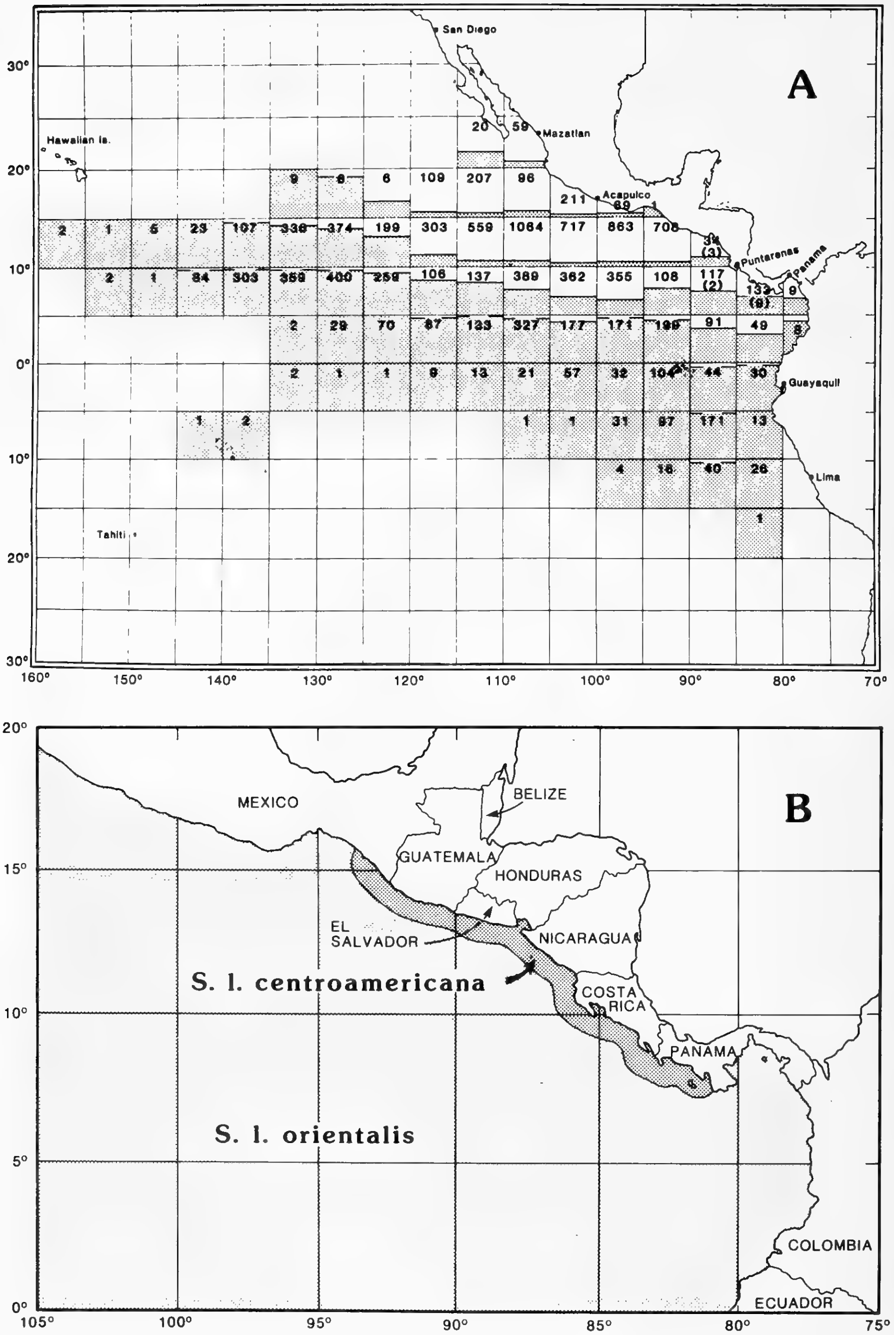


Fig. 2. Distribution of subspecies of *Stenella longirostris* in the eastern Pacific. Modified from Perrin et al. (1985). A. Schools sighted from tuna seiners and research vessels, identified to subspecies on the basis of predominant appearance of dolphins in school. Numbers indicate total number of schools sighted in square. Open portion of square = proportion of total sightings in the square that were of schools of the eastern spinner, *S. l. orientalis* or (on Central American coast, listed in parentheses) *S. l. centroamericana.* Shaded portion = *S. l. longirostris* (in west, southwest, and far south) and intergrades/hybrids between *S. l. longirostris* and *S. l. orientalis.* B. Approximate distributions of *S. l. orientalis* and *S. l. centroamericana* in Central American waters, based on records with voucher specimens.

of Guatemala in the eastern tropical Pacific), 10 Mar 1968, killed incidentally in tuna purse-seine fishery, complete skeleton, cast and external photographs. External photograph in Perrin (1972:989, fig. 9) and Leatherwood et al. (1988:151, fig. 191).

Referred specimens.—USNM 395396, 395531, 39533–34 from 12°51′N, 93°18′W; USNM 395260, 395270–73, 395526, 395593, 7°11′N, 90°32′W; USNM 395274–75, SWFC 0025 (CV245), SWFC 0027 (CV240), UF18726, 7°20′N, 92°30′W; LACM 54052 (WAW50), ca. 21°16′N, 106°16′W; LACM 54036 (WAW54), ca. 18°N, 102°12′W; LACM 54039 (WAW60), 14°30′N, 99°35′W; LACM 64062 (RLB405), ca. 14°20′N, 107°20′W; USNM 324974–75, 12°32′N, 91°4′W; USNM 395930, 16°15′N, 98°55′W; CAS 15665, 13°30′ to 14°6′N, 98° to 100°56′W; CAS 15666, 13°30′ to 14°2′W, 99°47′ to 102°2′W; MVZ 140641, 13°33′ to 14°2′N, 99° to 108°W; CAS 15667–69, MVZ 140642 and 140645, UCMP 86287, 9°50′ to 10°36′N, 99°47′ to 102°2′W; USNM 395026, ca. 3°N, 87°W; USNM 396169, 7°21′N, 87°14′W; USNM 23302, Pacific Ocean between Panama and Galapagos Islands; USNM 88976, ca. 21°35′N, 106°40′W; LACM 54038 (WAW58), ca. 17°N, 100°45′W; SDMNH 21200, ca. 18°20′N, 106°40′W; CAS 13821, 13828, ca. 12°22′N, 80°50′W; MMBL 1967-102, ca. 21°43′N, 10°47′W.

Diagnosis.—A subspecies of *Stenella longirostris* characterized by uniform gray coloration dorsally and laterally (Fig. 1), with patches of white in axillary and genital areas, erect to forward-canted dorsal fin in adult male, relatively large post-anal hump, relatively small adult size (to 199 cm in adult males and 193 cm in adult females), and relatively short (351–407 mm) and narrow (zygomatic width 139–153 mm) skull.

Distribution.—Tropical coastal and oceanic waters of the eastern Pacific (Fig. 2) in a large triangular region, with the base of the triangle extending from about the tip of Baja California (ca. 24°N) in the north to ca. 10°S off the coast of Peru and the tip of the triangle at about 145°W, 10°N. Most common off Mexico and Central America, in a region extending about 1000 km offshore (Perrin et al. 1985). Replaced south of the Gulf of Tehuantepec and north of the Bay of Panama in inshore coastal waters of extreme southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua and Costa Rica by *Stenella longirostris centroamericana* (described below).

Description of holotype.—The holotype specimen, a physically mature 186-cm male (all vertebral epiphyses fused to the centra) was dark gray dorsally and laterally, with the gular region slightly lighter gray and with patches of white in the axillary and genital regions (photograph in Perrin 1972:989, fig. 9). The dorsal fin was large and canted forward, and the post-anal hump was prominent; these features are preserved in the cast of the specimen in the SDMNH collection. Measurements (in mm) of the holotype skull: condylobasal length 401, length of rostrum 259, width of rostrum at base 74, width of rostrum at ½ length 46, width of rostrum at ¾ length 33, greatest preorbital width 133, greatest postorbital width 152, zygomatic width 150, parietal width 129, length of left temporal fossa 54, height of left temporal fossa 39, length of left upper toothrow 226, length of left ramus 346, height of left ramus 54. Teeth: upper left 49, upper right 48, lower left 52, lower right 52.

Variation.—The white axillary and genital patches may be confluent, with dark spots or patches between them. In a broad zone of hybridization/intergradation with *S. l. longirostris* in the offshore eastern tropical Pacific (the range of the "whitebelly spinner"—Perrin et al. 1985), coloration may be intermediate between those of the two forms (Fig. 1; Perrin 1972, 1975a; Perrin, Sloan & Henderson 1979).

Range in total length in 431 adult males (right testis ≥100 g) was 160–199 cm (average 176.1 cm, standard deviation 6.12 cm); 697 adult females (at least one corpus in the ovaries) were 152–193 cm long (average 171.3 cm, standard deviation 5.99 cm) (Per-

Table 2.—Means, standard deviations (for sample sizes ≥30), sample sizes (in parentheses), and maximum and minimum values for selected skull measurements and tooth counts for *Stenella longirostris orientalis* and *S. l. centroamericana.* From Perrin et al. (1989).

	S. l. orientalis	*S. l. centroamericana*
Condylobasal length	386.5	428.6
	(26) 351–407	(5) 416–439
Length of rostrum	245.5	279.0
	(26) 218–262	(5) 268–288
Width of rostrum		
At base	72.1	72.4
	(29) 66–77	(5) 70–77
At ½ length	41.6	42.0
	(26) 37–47	(5) 39–43
At ¾ length	30.5	29.8
	(26) 26–36	(5) 28–32
Width of PMXs at ½ length	19.6	21.4
	(26) 16–22	(5) 21–22
Preorbital width	132.3	134.2
	(29) 127–138	(5) 131–138
Postorbital width	148.1	151.2
	(29) 140–154	(5) 149–152
Zygomatic width	146.4	150.4
	(29) 139–153	(5) 149–152
Parietal width	125.9	128.8
	(29) 119–132	(5) 127–130
Length of temporal fossa	48.5	49.6
	(29) 41–57	(5) 46–57
Height of temporal fossa	36.6	36.4
	(29) 29–47	(5) 34–42
Length of upper toothrow	212.2	245.0
	(25) 192–299	(5) 238–255
Length of ramus	329.1	369.6
	(27) 301–348	(5) 358–379
Height of ramus	52.3	55.2
	(29) 47–57	(5) 53–57
Upper teeth (per row)	52.6 ± 3.18	55.3
	(32) 46–61	(5) 50–59
Lower teeth (per row)	50.5 ± 2.39	56.3
	(37) 45–56	(5) 51–59

rin et al. 1985). Ranges and averages for skull measurements and tooth counts are given in Table 2.

Additional data on ontogenetic, sexual, individual and geographic variation in size, shape, coloration and skeleton are given in Perrin (1972, 1975a, b), Perrin, Sloan & Henderson (1979), Perrin et al. (1985), Schnell et al. (1982, 1985), Douglas et al. (1986), and Leatherwood et al. (1988).

Remarks.—This subspecies corresponds to the "Eastern Spinner Porpoise, *Stenella longirostris* subsp. B (unnamed?)" (Perrin 1975a). Hybrids/intergrades with *S. l. longirostris* correspond to the "Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed?)" (Perrin 1975a).

Two alternative hypotheses have been proposed for the origin of this distinctive dolphin in the eastern Pacific: differentiation during isolation of a portion of the tropical eastern Pacific by a temperate-water barrier extending across the equator during a glacial period, or parapatric differentiation due to the peculiar oceanographic structure of the eastern Pacific (very shallow mixed layer and thick oxygen minimum layer that create an unique oceanic dolphin habitat—Au & Perryman 1985) and facilitated by complex social structure (Perrin et al. 1985).

The holotype specimen of the junior synonym *Delphinus microps* Gray, 1846 (BMNH 349a) is a small adult skull from an unknown locality; its measurements are within the range for *S. l. orientalis.* It may have come from the eastern Pacific, or it may have come from a different region where spinner dolphins are relatively small, e.g., Southeast Asia (Perrin et al. 1989). If future analyses were to determine that it came from the eastern Pacific, then the subspecies would bear the name *microps* rather than *orientalis.*

Continued use of the common name "eastern spinner dolphin" is proposed for this subspecies.

Specimens examined.—In addition to the specimens designated as referred specimens above, the specimens listed in Perrin (1972, 1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989).

Stenella longirostris centroamericana, new subspecies

Holotype.—USNM 395933, skull and external measurements, adult male, one of three specimens collected at 9°47′N, 85°42′W (Gulf of Nicoya, Pacific coast of Costa Rica) on 26 Mar 1963 by D. W. Waller; original field number BCFBL,SD XIII-9.

Paratypes.—USNM 395931 and 395932 (same collection data as holotype).

Referred specimens.—USNM 395934 from 9°58′N, 86°3′W (outer side of Peninsula de Nicoya, Pacific coast of Costa Rica); SWFC 0025 (DAB100), 14°19′N, 93°10′W (ca. 80 km off coast of southern Mexico near border with Guatemala, at southern end of Gulf of Tehuantepec over continental shelf).

Diagnosis.—A subspecies of *Stenella longirostris* characterized by uniform gray coloration dorsally and laterally (ventral coloration poorly known, but photographs of animals in the wild and sketches by field observers do not show the well-defined axillary and genital white patches typical of *S. l. orientalis*), erect to forward-canted dorsal fin in adult male, relatively large post-anal hump, relatively large adult size (to 216 cm), and relatively long (416–439 mm) and narrow (zygomatic width 149–152 mm) skull.

Distribution.—Coastal waters to ca. 80 km offshore over the continental shelf south of the Gulf of Tehuantepec and north of the Bay of Panama off extreme southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua and Costa Rica (Fig. 2). Replaced to the north, south and west by *S. l. orientalis.*

Description of holotype.—Measurements (in mm) of the holotype skull: condylobasal length 416, length of rostrum 269, width of rostrum at base 71, width of rostrum at ½ length 43, width of rostrum at ¾ length 30, greatest preorbital width 135, greatest postorbital width 152, zygomatic width 152, parietal width 129, length of left temporal fossa 48, height of left temporal fossa 36, length of upper left toothrow 239, length of left ramus 358, height of left ramus 56. Teeth: upper left 58, upper right 57 (estimated), lower left 57, lower right 57. External measurements (taken in field by D. W. Waller, following Norris 1961, in cm) of the carcass: total length 216.4, beak tip to melon 14.3, to angle of gape 28.3, to center of eye 32.0, to blowhole 32.1, to origin of flipper 46.3, to tip of dorsal fin 100.0, to umbilicus 99.7, axillary girth 69.2, posterior length of flipper 16.8, span of flukes 39.9.

Variation.—Three adult males (testis weight ≥100 g) were 212–216 cm long and 12 adult females (at least one corpus in ovaries) 193–211 cm (average 198.8 cm) (Perrin et al. 1985). Ranges and averages for skull measurements and tooth counts are given in Table 2. Additional data on osteological variation are given in Douglas et al. (1986), Perrin (1975a, b), Perrin et al. (1985), and Schnell et al. (1982, 1985).

Remarks.—This subspecies corresponds to the "Costa Rican spinner porpoise, *Stenella longirostris* subsp. A (unnamed?)" (Perrin 1975a). It differs from *S. l. orientalis* primarily in its relatively greater body size and its relatively long and narrow skull.

The few skulls available for this form can be easily discriminated from skulls of the other forms, based on simple scatterplots of length and width measurements or on scatterplots of scores for discriminant functions (Perrin 1975a), but it can be expected that overlap will be encountered when larger series of specimens become available.

The paucity of specimens is due to an apparent ecological difference between this form and *S. l. orientalis.* Large numbers of the latter are killed by tuna purse seiners because they are captured to catch yellowfin tuna (*Thunnus albacares*) that accompany them (Perrin 1975b); the former do not often "carry fish" and thus are only very rarely captured and killed.

The common name "Costa Rican spinner

dolphin" has been used for this form since 1975, but its range is now known to include the coastal waters of several nations. Therefore it is proposed that this subspecies be called the "Central American spinner dolphin."

Specimens examined.—In addition to the specimens designated above as paratypes, the specimens listed in Perrin (1972, 1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989).

Acknowledgments

I wish to thank R. L. Brownell, Jr., J. G. Mead, C. W. Potter, D. Robineau, G. D. Schnell and I. Barrett for reading the manuscript and suggesting useful changes. Curators who provided access to specimens in their charge are listed in Perrin (1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989); I also thank C. W. Potter for assistance with specimens at the USNM.

Literature Cited

Au, D. W. K., & W. L. Perryman. 1985. Dolphin habitats in the eastern tropical Pacific.—Fishery Bulletin 83:623–643.

Dizon, A. E., & W. F. Perrin. 1987. Genetic distances among and within species, populations, and schools of spinner and spotted dolphins.—Abstracts of the Seventh Biennial Conference on the Biology of Marine Mammals, December 5–9, 1987, Miami, Florida, p. 17.

Douglas, M. E., G. D. Schnell, & D. J. Hough. 1986. Variation in spinner dolphins (*Stenella longirostris*) from the eastern tropical Pacific Ocean: Sexual dimorphism in cranial morphology.—Journal of Mammalogy 67:537–544.

Gilpatrick, J. W., Jr., W. F. Perrin, S. Leatherwood, & L. Shiroma. 1987. Summary of distribution records of the spinner dolphin, *Stenella longirostris,* and the pantropical spotted dolphin, *S. attenuata,* from the western Pacific Ocean, Indian Ocean and Red Sea.—U.S. Department of Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-89, 42 pp.

Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies.—Trends in Ecology and Evolution 3:158–167.

Leatherwood, S., R. R. Reeves, W. F. Perrin, & W. E. Evans. 1988. Whales, dolphins, and porpoises of the eastern North Pacific and adjacent Arctic waters. A guide to their identification. Dover Press, New York, 245 pp.

Norris, K. S. (ed.). 1961. Standardized methods for measuring and recording data on the smaller cetaceans.—Journal of Mammalogy 42:471–476.

Perrin, W. F. 1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation.—Fishery Bulletin 70:983–1003.

———. 1975a. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii.—Bulletin of the Scripps Institution of Oceanography 21:206 pp.

———. 1975b. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific.—Journal of the Fisheries Research Board of Canada 32:1059–1067.

———, & J. W. Gilpatrick, Jr. 1990. Spinner dolphin *Stenella longirostris* (Gray, 1828). *In* S. H. Ridgway & R. J. Harrison, eds., Handbook of marine mammals, volume 5. Academic Press, New York (in press).

———, W. E. Evans, & D. B. Holts. 1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–76.—U.S. Department of Commerce, NOAA Technical Report, NMFS SSRF-737, 14 pp.

———, N. Miyazaki, & T. Kasuya. 1989. A dwarf form of the spinner dolphin (*Stenella longirostris*) from Thailand.—Marine Mammal Science 5:213–227.

———, P. A. Sloan, & J. R. Henderson. 1979b. Taxonomic status of the 'southwestern stocks' of spinner dolphin *Stenella longirostris* and spotted dolphin *S. attenuata.*—Report of the International Whaling Commission 29:175–184.

———, M. D. Scott, G. J. Walker, & V. L. Cass. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific.—U.S. Department of Commerce, NOA Technical Report, NMFS SSRF-28, 28 pp.

———, E. D. Mitchell, J. G. Mead, D. K. Caldwell, & P. J. H. van Bree. 1981. *Stenella clymene,* a rediscovered tropical dolphin of the Atlantic.—Journal of Mammalogy 62:583–598.

———, M. D. Scott, G. J. Walker, F. M. Ralston, & D. W. K. Au. 1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, with an annotated catalog of data sources.—U.S. Department of

Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-38, 65 pp.

Robineau, D., & J.-M. Rose. 1983. Note sur le *Stenella longirostris* (Cetacea, Delphinidae) du golfe d'Aden.—Mammalia 47:237–245.

Schnell, G. D., M. E. Douglas, & D. J. Hough. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Southwest Fisheries Center Administrative Report LJ-82-15C, 213 pp., Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

———, ———, & ———. 1985. Further studies of morphological differentiation in spotted and spinner dolphins (*Stenella attentuata* and *S. longirostris*) from the eastern tropical Pacific. Southwest Fisheries Center Administrative Report LJ-85-04C, 30 pp., Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

National Marine Fisheries Service, Southwest Fisheries Center, 8604 La Jolla Shores Drive, La Jolla, California 92038.

PROC. BIOL. SOC. WASH.
103(2), 1990, pp. 464–498

STUDIES IN THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE)
VII. THE GENUS *LEPIDAPLOA*

Harold Robinson

Abstract.—The Neotropical Vernonian genus *Lepidaploa* is recharacterized, nomenclaturally clarified, and its 116 species are listed. *Lepidaploa* has seriate-cymose inflorescences and lophate pollen surfaces of a type found in the related genera of the *Lepidaploa* Complex. *Lepidaploa* is distinct in the Complex by the sessile heads, the heads with 1.3–3.0 times as many involucral bracts as flowers, nodular style bases, sometimes glanduliferous achenes, and lack of glands on the anther appendages. Variations in exine patterns in *Lepidaploa* are compared with the three other genera of the Complex with rhizomatous crests, *Echinocoryne, Stenocephalum* and *Chrysolaena,* and the two genera with non-rhizomatous crests, *Lessingianthus* and *Mattfeldanthus.* New combinations are provided for 114 species, and two species, *L. beckii* and *L. solomonii* are described as new.

The present paper concludes a series of papers aimed at the resolution of the Neotropical *Lepidaploa* group in the tribe Vernonieae. Previous papers in the series have dealt with the five closely related genera of the informally defined *Lepidaploa* Complex, *Stenocephalum, Echinocoryne, Lessingianthus, Chrysolaena* and *Aynia* (Robinson 1987a, b, 1988a, b, c) that differ from *Vernonia* s. str. by having consistently lophate pollen, and with two less closely related genera, *Cyrtocymura* and *Eirmocephala* (Robinson 1987c), that usually have true scorpioid cymes. The remaining genus *Lepidaploa* of the *Lepidaploa* Complex having lophate pollen is treated in the present paper.

Lepidaploa was named originally by Cassini (1817b) as a subgenus of *Vernonia* with brief comments on distinctions from the other two subgenera accepted at that time. Six species were mentioned in association with the subgenus, *Vernonia glauca, V. fasciculata, V. arborescens, V. divaricata, V. scorpioides* and *V. albicaulis,* in that order.

The genus was treated more fully five years after the original description (Cassini 1823), but was still referred to as a subgenus. Generic status of *Lepidaploa* is sometimes erroneously dated from the 1823 treatment (Gleason 1906:174) because of the combinations under *Lepidaploa* included in that treatment. *Lepidaploa* was not given generic status until it was listed in a series of genera by Cassini (1825) in his treatment of the genus *Oliganthes.* The latter listing mentioned no included species.

The proper characterization of *Lepidaploa* dates from the treatment of the subgenus by Cassini in 1823. The subgenus was given the alternative French name *Lépidaple,* and was described as having involucral bracts "régulierement imbriquées, appliquées, subcoriaces, lancéolées, acuminées et presque spinescentes au sommet; les intérieures étrécies de bas en haut, terminées en pointe, nullement élargies, arrondies, ni colorées au sommet." Cassini (1823) clearly distinguished his subgenus from typical *Vernonia* by the lack of a subulate appendage and lack of coloration on the bracts of the involucre. The lack of bract appendages also distinguished *Lepidaploa* from the paleotropical subgenus *Ascaricida* (=*Baccharoides* Moench) based on *Vernonia anthelmintica* L. (Cassini 1817a, b). In 1823 Cassini included seven species in the subgenus *Lepidaploa, L. scorpioides* (from *Vernonia scorpioides*), *L. phyllostachya* (same as the earlier *V. arborescens*), *L. aristata, L. albicaulis* (from *V. albicaulis*), *L. lanceolata* (=?*V. longifolia*), *L. canescens* (from *V. canescens*) and *L. buxifolia* in that order. The most notable difference between the 1823 and 1817 listings was the elimination of the two species of *Vernonia* from eastern North America, *V. glauca* and *V. fasciculata.* The latter belong to the *Vernonia* s. str. close to the type, *V. noveboracensis.* Cassini further cited additional species of *Vernonia* mentioned by Kunth (Humboldt et al. 1818) that were "presque indubitables" members of the subgenus *Lepidaploa, V. gracilis, V. tournefortioides* (=*V. scorpioides*), *V. geminata, V. mollis, V. pellita, V. micrantha* and *V. frangulaefolia.* None of the Cassini names or combinations in *Lepidaploa* were valid as of the 1823 publication since *Lepidaploa* was not at that time recognized at the generic level.

A precise typification of the subgenus *Lepidaploa* was not attempted until almost 100 years after the original description. Gleason (1906:165) rather incidentally stated that *Lepidaploa* was based on *V. scorpioides.* To the extent that this can be regarded as a serious lectotypification, this appears to have been an arbitrary selection of the first species listed by Cassini in 1823. The incidental and arbitrary nature of the selection allows the rejection of the unrepresentative species as lectotype. Robinson et al. (1980:428), in a review of subdivisions of the Vernonieae, listed *Lepidaploa* with the lectotype *Vernonia albicaulis,* which is far more representative of the species given by Cassini in 1823. The value of the latter lectotypification has been confirmed in the present series of studies, since *Lepidaploa* can now represent a broader group following its traditionally broader interpretation by such authors as Baker (1873). *Vernonia scorpioides,* which has traditionally represented a narrower concept as a section or series *Scorpioideae,* has now been treated as the type species of a smaller well-defined segregate genus *Cytocymura* (Robinson 1987c).

Shortly after the lectotypification by Robinson et al. (1980), Jones (1980) listed *Lepidaploa* in the synonymy of *Vernonia* with *Vernonia glauca* (L.) Willd. cited as the type. At present, no earlier history for this typification is known. The choice was evidently again an arbitrary selection of the first species listed by Cassini in 1817(b). Such an arbitrary lectotypification would not have to be rejected, but *V. glauca* is an undesirable selection for *Lepidaploa* in view of Cassini's subsequent failure to include the species in the subgenus (1823). The choice is further undesirable because *V. glauca* is an immediate relative of the type species of *Vernonia, V. noveboracensis,* and it usually has shortly appendaged involucral bracts of the type that Cassini (1823) pointedly indicated were lacking in his subgenus *Lepidaploa.* One must conclude that Cassini's (1817b) original inclusion of *V. glauca* in *Lepidaploa* was based on an inadequate understanding of that species. The specimen no. 8428 on the Jussieu herbarium (sheet no. 8428, IDC microedition 6206, fiche 620) that was seen by Cassini seems to have essentially no appendages on the involucral bracts.

The lectotypifications by Gleason (1906) and Jones (1980) share one particularly unwholesome aspect associated with their arbitrary nature. Both attempts were treating *Lepidaploa* only as a synonym of *Vernonia* with no concern for its possible importance as a taxon in its own right. The arbitrary nature of the selections allows for rejection, and the poor choices involved make rejection desirable, even if both had priority.

A major part of the confusion regarding the concept of *Lepidaploa* arises from Cassini's reliance upon the involucral bracts as a character. Some typical *Vernoniae* such as *V. fasciculata* lack appendages on the bracts, while many species now recognized as *Lepidaploa* possess narrowly pointed involucral bracts. Appropriately, Cassini seemed to place little confidence in his 1817 subgenus. The changed listing of species by Cassini in 1823 created a more closely related group with only one species, of those identifiable with modern concepts, lacking seriate-cymes and only two of those species proving, on later examination, to have non-lophate pollen. Unfortunately, Cassini did not accompany his improved grouping with an improved description. Nevertheless, Cassini's confidence in the group had risen sufficiently by 1825 to recognize *Lepidaploa* at the generic level. During the period from 1825 to 1841 a number of authors recognized *Lepidaploa* at the generic level: Cassini (1825), Reichenbach (1828), Bartling (1830), Cassini (1830), and Spach (1841).

DeCandolle (1836) and later major authors did not treat *Lepidaploa* at the generic level. DeCandolle (1836) retained *Lepidaploa* as his section VIII of *Vernonia* containing 195 species including some from Asia and Africa. The type species of *Vernonia* was placed in the section IX. *Ascaricida* (including *Baccharioides*).

Bentham (Bentham & Hooker 1873) broadened the concept of *Lepidaploa* within *Vernonia* to include a series *Paniculatae* which included the type species of *Vernonia,* but he restricted the subgenus *Lepidaploa* geographically to, "Species Americanae ultra 200." The *Lepidaploa* concept of Bentham and his followers such as Baker (1873), Gleason (1922), and Jones (1979b) came to include all American *Vernonia* with unappendaged involucral bracts and a double pappus. As such, the concept included the type of *Vernonia* and fell into the synonymy of the subgenus and section *Vernonia.*

The resurrection of *Lepidaploa* in the present paper is nearly in the sense of Cassini in 1823, though it traces nomenclaturally to the confused concept of 1817. As defined herein, the genus *Lepidaploa* includes 116 species distributed throughout the Neotropical Region, many species occurring in the West Indies, the Andes, and Brazil, and a smaller number occurring in Central America. The genus includes most of the Neotropical species formerly placed in *Vernonia* that have heads in well-developed seriate-cymes as described below. The genus does not include some species with markedly scorpioid seriate-cymes such as *Cyrtocymura scorpioides* and *Eirmocephala brachiata* (Robinson 1987c) or many seriate-cymose members of *Lessingianthus* (Robinson 1988a) and *Mattfeldanthus* (Robinson & King 1979). The distinguishing features such as the sessile heads, reduction in size of inflorescence bracts, styles with well-developed basal nodes, fusion of veins in the corolla lobes, glands on the achenes, lack of glands on the anther appendages, and details of the rhizomatous crests on the pollen are discussed more fully under separate headings.

Inflorescence Form

The inflorescences of the Asteraceae are generally cymose; the great majority of the species, and most Vernonieae, including those in typical *Vernonia,* have a distinctly cymose structure. The inflorescence forms in the tribe have been discussed by many authors (Gleason 1923, Cabrera 1944, Jones 1979b). Some of the inflorescence branches become aligned in a series and may achieve a scorpioid form. The branches are usually marked by heads borne singly or in groups at a series of nodes. In the extreme, each branch appears superficially spicate or racemose in a form that has been referred to by most as a scorpioid cyme. In this series of studies the use of the latter term is restricted to inflorescences such as those of *Cyrtocymura* and *Eirmocephala* which are actually scorpioid, and the more common non-scorpioid forms in the Vernonieae are referred to with the more broadly applicable term seriate-cyme (Figs. 61, 62; Robinson 1987c, 1988a). The extreme forms of seriate-cymose inflorescences in the Vernonieae with heads appearing lateral and sessile are nearly restricted to the few related groups of almost exclusively Neotropical distribution that are treated in the present series of papers on the *Lepidaploa* Complex.

In these inflorescences each branch appears spicate but is actually a series of lateral proliferations. As noted by Gleason (1923) and Cabrera (1944), each head is developmentally terminal and only appears lateral as a result of its displacement by a lateral branch produced at its base. The resulting structure in the Neotropical members of the tribe varies in appearance from a spike to an obvious scorpioid cyme. The most obviously scorpioid forms occur in the more remotely related Neotropical genera with type A pollen, *Cyrtocymura, Eirmocephala* (Robinson 1987c), and *Dipterocypsela,* and in one African species *Vernonia peculiaris* Verdcourt, but the seriate cymes with heads appearing lateral and sessile are otherwise almost completely restricted to the immediate *Lepidaploa* Complex of genera having lophate pollen.

Within the Complex, the seriate-cymes with apparently sessile heads occur in *Lepidaploa* itself, as well as in *Chrysolaena* Robinson (1988b), some of *Lessingianthus* Robinson (1988a), *Mattfeldanthus* Robinson & King (1979), and *Stenocephalum* Sch.Bip. (Robinson 1988a). Variations of the inflorescence with the heads raised on short or long peduncles occur in *Aynia* Robinson (1988c), *Echinocoryne* Robinson (1987b), and many other species of *Lessingianthus.* One of the most distinctive features of *Lepidaploa* appears to be the consistency of the sessile heads. The only distinctly pedunculate heads in the genus are those that are terminal on the branches and a few rare non-terminal pedunculate heads in such species as *V. cleocalderonae* and *V. macahensis,* and specimens such as Wilbur 13260 from Panama illustrated by Keeley (1982). The terminal peduncles really differ from the other heads only in the lack of a subsequent lateral branch, but the presence of a peduncle on a lower head, which is exceedingly rare in *Lepidaploa,* can be interpreted developmentally as a downward displacement of the succeeding lateral branch. The presence of apparent peduncles is comparatively common throughout most of the diversity of the related genus *Lessingianthus.* Thus, while seriate-cymes occur in both *Lepidaploa* and *Lessingianthus,* the "pedunculate" forms are essentially restricted to the latter genus in the pair. The "non-pedunculate" seriate-cyme that is characteristic of *Lepidaploa* and *Mattfeldanthus* is closer to the condition in the sessile-headed but less seriate inflorescences in many other Vernonieae, and it occurs to some extent in all but one genus of the *Lepidaploa* Complex where it appears to be primitive. The "peduncles" in *Lessingianthus* and *Echinocoryne* are rather individually distinctive in the tribe and are considered as derived separately in each of those genera.

As noted by various authors (Baker 1873, Gleason 1923), there is variation in the degree of development of the bracts that are located at the series of nodes in the seriate-cyme. The genera *Cyrtocymura, Dipterocypsela,* and *Eirmocephala* have minute bracts that are scarcely visible under the heads. Members of the more restricted *Lepidaploa* Complex usually have more obvious foliose bracts subtending the heads at each node of the series, but the bracts may vary in size from slightly larger than minute to essentially the size of the vegetative leaves. The bracts of *Mattfeldanthus* and *Stenocephalum* are essentially like vegetative leaves. The bracts of *Chrysolaena* are very small. The bracts in *Lepidaploa* and *Lessingianthus* show contrasting trends in their relative size. Species of *Lessingianthus* with sessile heads subtended by foliose bracts in a seriate-cyme have the bracts similar in size to the vegetative leaves that are below the inflorescence. There is little or no abrupt change in size of foliose elements at the base of the inflorescence. In *Lepidaploa,* the bracts at the base of the inflorescence are almost always at least slightly discontinuous in size from the vegetative leaves immediately below them (Figs. 61, 62), and the inflorescence often has very reduced bracts. In only a few species of *Lepidaploa,* such as the Brazilian *V. obtusifolia,* is there no evident reduction in the size of the foliar structures starting at the base of the inflorescence.

Involucral Bracts

The involucre of *Lepidaploa* is significant for both the ratio of bracts to flowers in the heads and for the differentiation of the bracts.

There has been no systematic study of the ratio of involucral bracts to flowers in the heads of the Vernonieae. Nevertheless, significant differences in the ratios have become evident from counts made during the description of various species and genera. Differences in the ratio are sometimes simply a reflection of the overall number of flowers. In *Stenocephalum* (Robinson 1987a), the higher percentage of bracts is primarily related to the reduced number of flowers, whereas in *Lepidonia* (Robinson & Funk 1987), the nearly equal number of bracts and flowers is related to the comparatively large number of flowers in the heads. In the case of *Echinocoryne* and the type species of *Mattfeldanthus,* the ratio is altered by the extremely high number of involucral bracts in the heads. In *Chrysolaena* the imbalance of the ratio derives from the unusually small number of bracts in the head. Nevertheless, there are also differences in the ratio in some groups that lack extremes in numbers of bracts or flowers. In the type species of *Vernonia* and its immediate relatives, the number of bracts and flowers seems nearly equal, but in *Lepidaploa* and *Lessingianthus* the bracts are usually one and a half to three times as numerous as the flowers.

Many species of *Lepidaploa* have strong differentiation between the outer and inner involucral bracts. The outer bracts are more pointed and are often aristate. The inner bracts are usually blunt with at most a short mucro. A common pattern in the genus is a lower cluster of spreading, slender bracts contrasted with the more erect and appressed, less pointed, inner bracts. Such a pattern occurs in a few species of *Lessingianthus* such as *L. niederleinii,* but the larger heads usually distinguish the members of the latter genus with such involucres from *Lepidaploa.*

Veins of Corolla Lobes

During various studies of the family I have noted that the veins in the corolla lobes of the Vernonieae are more completely fused at the tip than those of many other tribes of the Asteraceae, and in the present study most members of the *Lepidaploa* Complex have been seen to have veins that fuse at the apex more broadly than those in most other species of the Vernonieae. In *Aynia* and *Mattfeldanthus* the fusion is extreme and the lobe tip is filled with a large sclerified shield (Robinson 1988c). Species of *Chrysolaena* have the narrowest veins distally and the weakest fusion of any members of the Complex. *Lepidaploa* and *Lessingianthus* both show a moderate thickening of lobe veins and a further moderate enlargement in the apical fusion that falls far short of the extreme form. Still, the latter is greater than that in most genera of the Vernonieae outside of the Complex such as *Vernonia* s str.

Basal Stylar Node

In *Lepidaploa* the style base characteristically has a large zone of spreading, thick-walled cells that result in a very large disc in dried plants. It is this structure that is here referred to as a basal stylar node. The sclerified disc is sharply angled inward under the base of the style and it leaves a comparatively narrow central area of attachment. Styles of *Lessinginathus, Stenocephalum, Echinocoryne,* and *Chrysolaena* show little or no zone of thick-walled cells at the base and they have no large basal disc. The disc is not sharply angled under the base of the style and the area of attachment is not or scarcely narrower than the style shaft.

There is no functional basis known for the differences in style bases of the members of the *Lepidaploa* Complex, and the changes in style base form must be considered rather rare and essentially random. Nevertheless, style base differences correlate closely with the generic limits in the *Lepidaploa* Complex. This pattern shows the comparative continuity within each genus compared to the broad phyletic gaps between the genera.

Glands on Achenes and Anther Appendages

Short-stalked, capitate glands that produce sesquiterpene lactones are common in the Vernonieae as glandular punctations on the surface of various structures in different genera. *Lepidaploa* often has glands on the achene surface, while *Lessingianthus* never has such glands. In most *Lepidaploa,* the glands occur among the long setulae that cover the achenes, but a few species such as *V. macahensis* from the Rio de Janeiro region, have glanduliferous achenes without setulae.

Glands occur on the anther appendages of various Vernonieae, including three elements among the genera treated in the present series of studies: one of the three species of *Eirmocephala, E. cainarachiensis* (Hieron.) H. Robinson (Robinson 1987c), one specimen of *Lepidaploa* that was identified as possibly *V. helophila,* and six of the seven species of the genus *Chrysolaena.* The remaining related genera, *Aynia, Echinocoryne, Lepidaploa, Lessingianthus, Mattfeldanthus,* and *Stenocephalum,* seem to lack glands except in the one case mentioned above. The various species mentioned in which the glands occur on the appendages, including the species of *Eirmocephala,* are all in groups that also have glands on the achenes.

Pollen

The *Lepidaploa* Complex is characterized by pollen with crests in a lophate pattern, and it includes most of the Neotropical species with lophate pollen that are traditionally placed in the genus *Vernonia* (Figs. 1–54). A lophate pattern occurs also in the phyletically distinct Old World element of the Vernonieae (Figs. 55–58) and ultimately in the related tribe Lactuceae. It has been concluded in this series of studies that the complex and widely occurring lophate form is more primitive than the non-lophate, spinose grains called the *Lychnophora* type by Stix (1960) and Type A by Jones (1979b). Cases of reversion to Type A pollen from lophate forms have been cited in the Old World *Distephanus* Cassini (Robinson & Kahn 1986) and in the Neotropical *Lessingianthus* (Robinson 1988a); other such reversions I presume have occurred many times. Accordingly, the pollen of the *Lepidaploa* Complex is considered to have retained the more primitive pattern in the tribe.

Within the *Lepidaploa* Complex there are further distinctive details of the pollen that can be used in the classification. The variation in structure of the basal columellae under the crests partially correlates with generic concepts, but a SEM is necessary to observe the character. In *Lepidaploa* the columellae show a type that is referred to here as rhizomate or rhizomiform (Figs. 1–51), where the columellar material is weakly attached to the foot layer and is often nearly completely diverted at the base into a horizontal structure (Figs. 6, 15, 16, 25, 30, 33). The rhizomatous crests of this *Lepidaploa* type are known only from the Neotropical *Lepidaploa* Complex in the genera *Lepidaploa, Chrysolaena, Echinocoryne,* and *Stenocephalum* (Robinson 1987a, b, 1988b) and from one species of *Eirmocephala* (Robinson 1987c). The contrasting form, with separate columellae strongly attached to the foot-layer (Figs. 52–56), occurs in diverse elements of the tribe including the Neotropical *Lessingianthus* (Figs. 52, 53), *Aynia,* and *Mattfeldanthus* (Fig. 54) of the *Lepidaploa* Complex, and the African genera such as *Baccharoides* Moench. (Figs. 55, 56). Horizontal structures under the crests in paleotropical Vernonieae such as *Cyanthillium* Blume (Figs. 57, 58) are totally different, being bridges between strongly attached points at the intersections of the crests. Because of the comparatively restricted nature of the rhizomate form, it is regarded as a derived condition in this study.

Within the restricted *Lepidaploa* Complex, a few complications in the pattern of the basal columellar structure are seen, but these are more apparent than real. Firstly, one species of *Mattfeldanthus* has distinct horizontal structures under its pollen crests, but these are intermittent bridges like those of *Cyanthillium.* Secondly, some species of *Lepidaploa* have the rhizomes absent or poorly developed, but these differ from the typical *Lessingianthus* type by the tendency for the columellae under the crests to be narrow and less strongly attached to the foot-layer (Figs. 3, 8, 12, 18, 31, 37–39, 42, 51). The less rhizomate forms in *Lepidaploa* are commonest within the genus in species with Type D pollen.

A taxonomically useful characteristic of the pollen that can be seen with a light microscope is the pattern of the areoles on the surface of the grain. The pollen types that are of significance in the *Lepidaploa* Complex are considered in the following order: Type B, Type C, *Aynia* Type, Type G, and Type D. Of the pollen Types, only B and D seem to characterize related groups, and none characterize a whole genus.

Type B pollen.—The pollen areolation that has been called the *Vernonia argyrophylla*-type by Stix (1960) and Type B by Jones (1979b) is distinguished by colpi that extend from pole to pole with no separate polar areoles and by three equatorial areoles across the intercolpar area in a 1:2:1:2:1 or rarely 1:2:3:2:1 pattern. Type B pollen occurs primarily in *Lessingianthus* subg. *Lessingianthus* (Fig. 52), but grains in some species of *Lepidaploa* also have a third equatorial role in some of their intercolpar regions (Figs. 23, 26, 45, 50). None of the latter has the third areole characteristically in all the intercolpi, and none has strong basal columellae like those of *Lessingianthus.* The intercolpar region in *Lepidaploa* usually differs by having a 1:2:2:1 pattern (Figs. 5, 11, 14, 29, 36, 46) in the C, D, G, and *Aynia* Types.

Type C pollen.—Many species of *Lepidaploa,* including the type species, show pollen grains that have a polar areole. The areole is positioned at the apices of the three colpi. Such grains were called the *Vernonia cognata*-type by Stix (1960) and Type C by Jones (1979b). Type C pollen with rhizomatous crests occurs in *Chrysolaena* (Robinson 1988b) and *Stenocephalum* (Robinson 1987a) of the *Lepidaploa* Complex, and a Type C pollen with non-rhizomatous crests is found in the small subgenus *Oligocephalus* of *Lessingianthus* (Robinson 1988a).

There is a significant variation within the Type C pollens that occur in *Lepidaploa.* The Andean and West Indian elements of the genus are sometimes erratic in the expression of the polar areole. One pole may have the areole while the other end does not. This is often a consistent feature of grains in a species, and the difference probably reflects the relative outward or inward facing positions of the poles in the original pollen tetrads. It would seem a slight loss for neither pole to have an areole, and the Central American *V. tortuosa,* with technically Type G pollen, might have Type C ancestry. Some of the species showing variable poles also have the crests particularly thick on each side of the pores (Figs. 2, 4, 10), a condition reminiscent of Type A grains. The species of *Lepidaploa* with Type C grains that are found in Brazil have characteristically narrower crests (Fig. 17), and they consistently have areoles at both poles.

A number of species with Type C pollen, *Vernonia cleocalderonae* (Figs. 17, 18) from central Brazil, and *V. cotoneaster* (Figs. 12, 18) of a group found in eastern Brazil and northern South America, have basal columellae that are partially non-rhizomatous. Such columellae have been noted elsewhere in *Lepidaploa* only in the members with Type D pollen areolation that is discussed below. In contrast, the West Indian *V. sericea* (Fig. 6), the widely distributed *V. salzmannii* (Figs. 15, 16), and to a lesser extent, *V. canescens* (Fig. 8) of the northern Andes have crests with rhizomiform baculae that peel away from the footlayer comparatively easily.

Aynia Type pollen.—*Vernonia tovarensis* (Figs. 19–24) seems to have a pollen form that is unique in *Lepidaploa* in having the intercolpar areoles nearest the poles actually reaching the poles (Fig. 19). The colpi terminate about half way between the pores and the poles. The pattern of areoles is known from only the one species in *Lepidaploa,* but is the same areolation found in *Aynia* and the comparatively unrelated Central American genus *Harleya* Blake. As in *Aynia,* the crosswalls above and below the pores show a sutural line in the middle, but none of the grains of either *Aynia* or *V. tovarensis* show separation at the median suture of the crosswalls, and it is not possible to say at this time whether they only meet or actually fuse. In spite of the similar areolation, the exine differs from that of *Aynia* by the modification of the basal columellae into a rhizomiform structure of the type found in most of *Lepidaploa.*

Type G pollen.—The majority of species of *Lepidaploa,* especially in Brazil, have Type G pollen that does not have areoles centered at the poles of the grains and does not have crosswalls in the colpi (Figs. 25–33). In these characters the pollen is like Type B of Jones (1979b) or *Vernonia argyrophylla*-type of Stix (1960), and no distinction was made in those earlier studies. More recently the Jones and Stix terms have been applied more narrowly to pollen of the type found in *Lessingianthus* (Robinson 1988a), with three equatorial areoles across the intercolpi and nonrhizomatous columellae. The Type G pollen in *Lepidaploa* usually has intercolpar areoles in a 1:2:2:1 pattern correlated with obviously rhizomiform baculae as seen under the SEM (Figs. 27, 30, 31, 33). The seemingly slight difference has proven one of the more phyletically significant ones in the *Lepidaploa* Complex. The closest approach to the Type B pollen areolation in a species of *Lepidaploa* is in *V. psilostachya* DC. where the colpi reach the poles and there is a variable number of 2 or 3 areoles across the intercolpus in 1 or 2 tiers (Figs. 25–27). Examination shows that even in this species very few of the grains have 3 areoles across all the intercolpi simultaneously. A third intercolpar areole is even less common in other species with Type G pollen.

Type G pollen was earlier distinguished by the author as the *Vernonia geminata*-type (Robinson 1980). Unfortunately, the use of the name *geminata*-type now appears inappropriate as a result of the present study. The Colombian name *Vernonia geminata* H.B.K. was misapplied to a Brazilian species with Type G pollen. The Colombian species is a synonym of *V. canescens* having Type C pollen. The Brazilian species with Type G pollen should have been identified as *V. subsquarrosa.* The present paper adopts the term Type G for pollen that has been previously called the *geminata*-type. The letter is the next that would follow in the series used by Jones for his two studies (1979b, 1981).

Type G pollen is closest to Type C pollen in its structure, and the species involved seem to be interrelated. Type G pollen seems to occur in Brazilian species that are reasonably close in relationship to some others of that area with Type C pollen. Some species of the Andes of Peru and Bolivia such as *V. retrosetosa* and *V. tristis* seem to be possible relatives of Brazilian species. However, the Type G pollen in the central American *V. tortuosa* and the Colombian *V. sclareaefolia* and *V. trilectorum* seems separately derived from more closely related Andean members of *Lepidaploa* having Type C pollen. A brief survey of some andean species shows those with Type G pollen lack resiniferous idioblasts on the achene surface, whereas those with Type C pollen often have such idioblasts.

Type G grains are found outside of *Lepidaploa* in the related genus *Echinocoryne,* and non-rhizomatous grains with similar areolation are seen in the less closely related *Mattfeldanthus.*

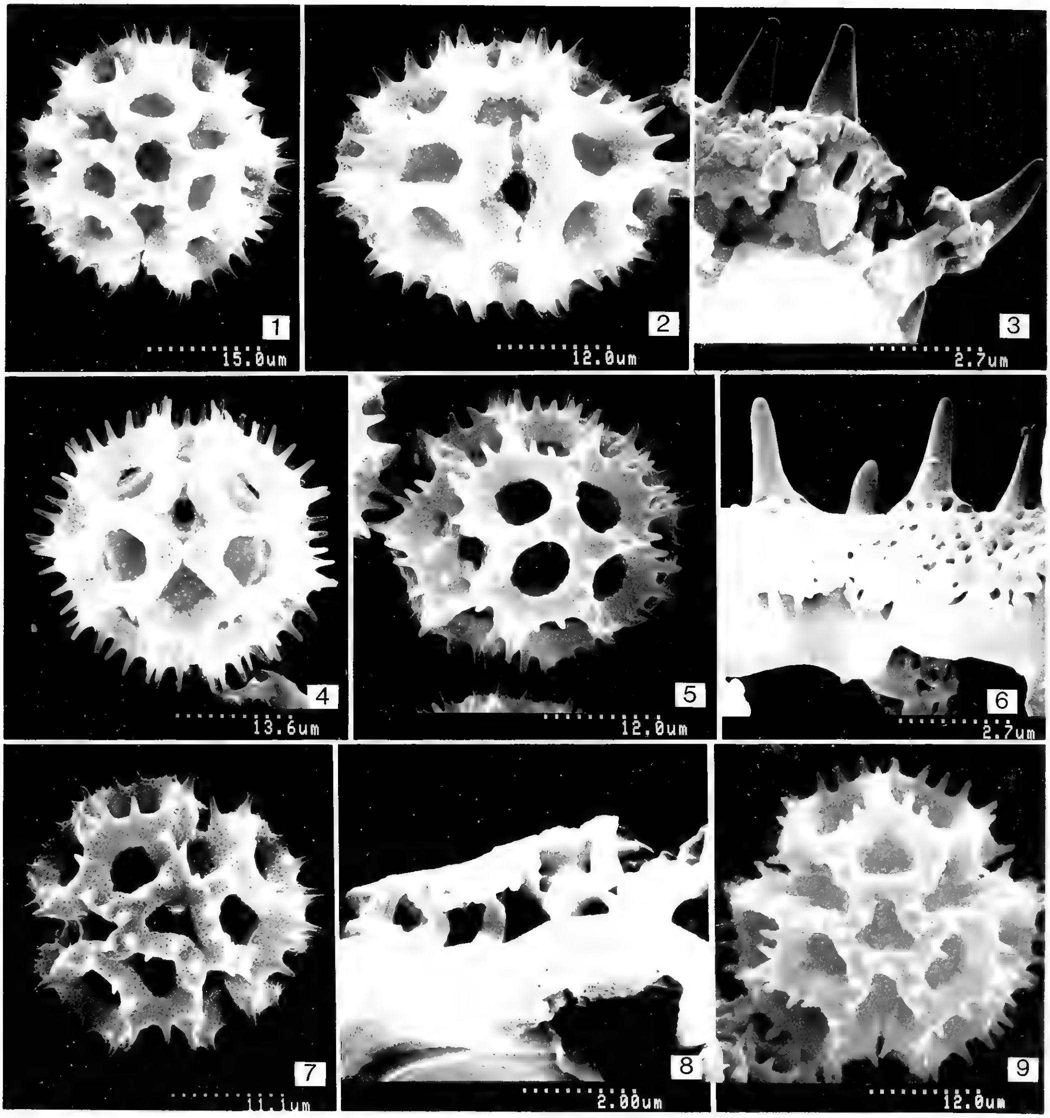
Type D pollen.—A final pollen type within *Lepidaploa* is that referred to by Stix (1960) as the *Vernonia arenaria*-type and by Jones (1979b) as Type D (Figs. 34–51). The intercolpus has a 1:2:2:1 or sometimes a 1:2:1:2:1 areolation pattern and there are no areoles centered on the poles, but the colpus is not continuous. The grains are distinctive by the presence of crosswalls above and below the pore which divide each colpus into three sections (Figs. 35, 40, 41, 44, 49). These are not the partial intrusions into the colpus that are seen in some grains of other pollen types; rather, these crosswalls are complete, unbroken crests. Type D pollen is almost restricted to *Lepidaploa,* but grains with similar crosswalls occur in two species of *Lessingianthus.* Pollen of the two *Lessingianthus* species (Robinson 1988a) differs from that of *Lepidaploa* by the consistency of the 1:2:1:2:1 intercolpar pattern and the strong unconstricted basal columellae. The weak columellae of the Type D pollen in *Lepidaploa* are stronger than those of most members of their genus, but they are not mistakeable for the type found in *Lessingianthus.* The two species of *Lessingianthus* have long-pedunculate heads and they are not particularly like *Lepidaploa* in any feature except the pollen.

The group of species in *Lepidaploa* with Type D pollen is one of the most natural subdivisions in the genus. The distinctive areolation and the trend toward stronger basal columellae in the pollen is correlated in many of the species with a distinctive pubescence of T-shaped hairs on their stems and leaves. The appearance of the pubescence varies from densely sericeous to totally appressed, and it is not matched in other members of *Lepidaploa.*

The essentially non-rhizomatous columellae of the Type D pollen in *Lepidaploa* is interpreted here as a reversion from the rhizomatous condition. There is an irregularity and partial fusion in those columellae and constriction of the bases (Figs. 37–39, 42, 47, 51) not seen in *Lessingianthus.* Only a few other species, such as *V. cotoneaster* and *V. cleocalderonae,* with Type C pollen, have been noted as having similar basal columellae (Figs. 12, 18). In all of these, the columellae show at least some tendency toward the rhizomatous condition, and in a few parts of some grains rhizomiform columellae are present (Figs. 37–39, 42).

Limitations and exclusions.—Although some pollen types evidently reflect related groups within the genus *Lepidaploa,* a subdivision of the genus by pollen alone would be artificial. Only the species with Type D pollen are considered to constitute a phyletic group among themselves. Species with the Type G pollen appear to relate to at least two different elements of the species group having pollen Type C, but these pollen types reflect large groups of species, and they predominate in different geographical areas. Taxonomic subdivisions in the latter group are not expected to coincide completely with the limits of the pollen types. No special status is foreseen for the one Venezuelan species with *Aynia* Type pollen.

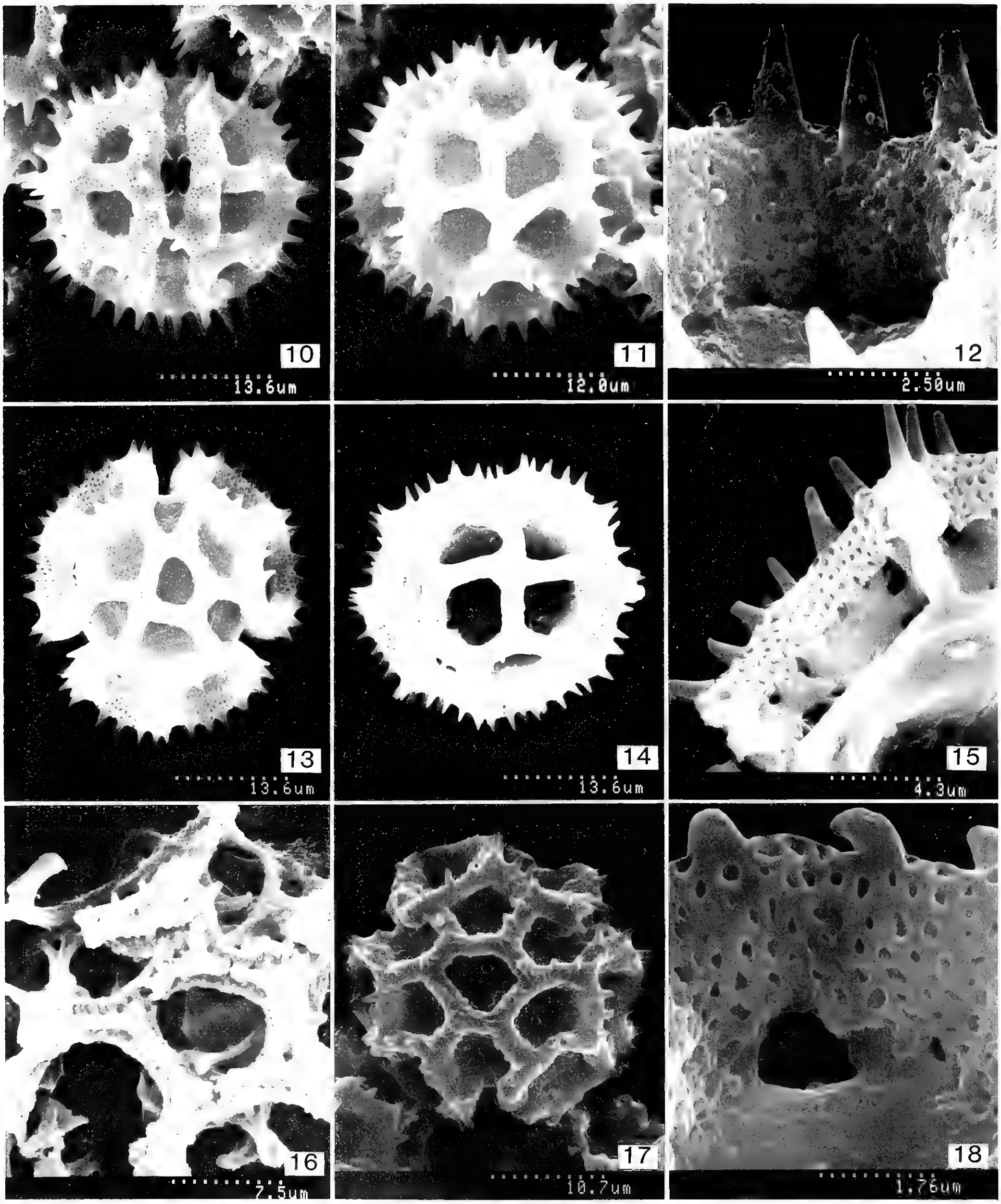
In the following undivided alphabetical list of the species of *Lepidaploa,* the pollen



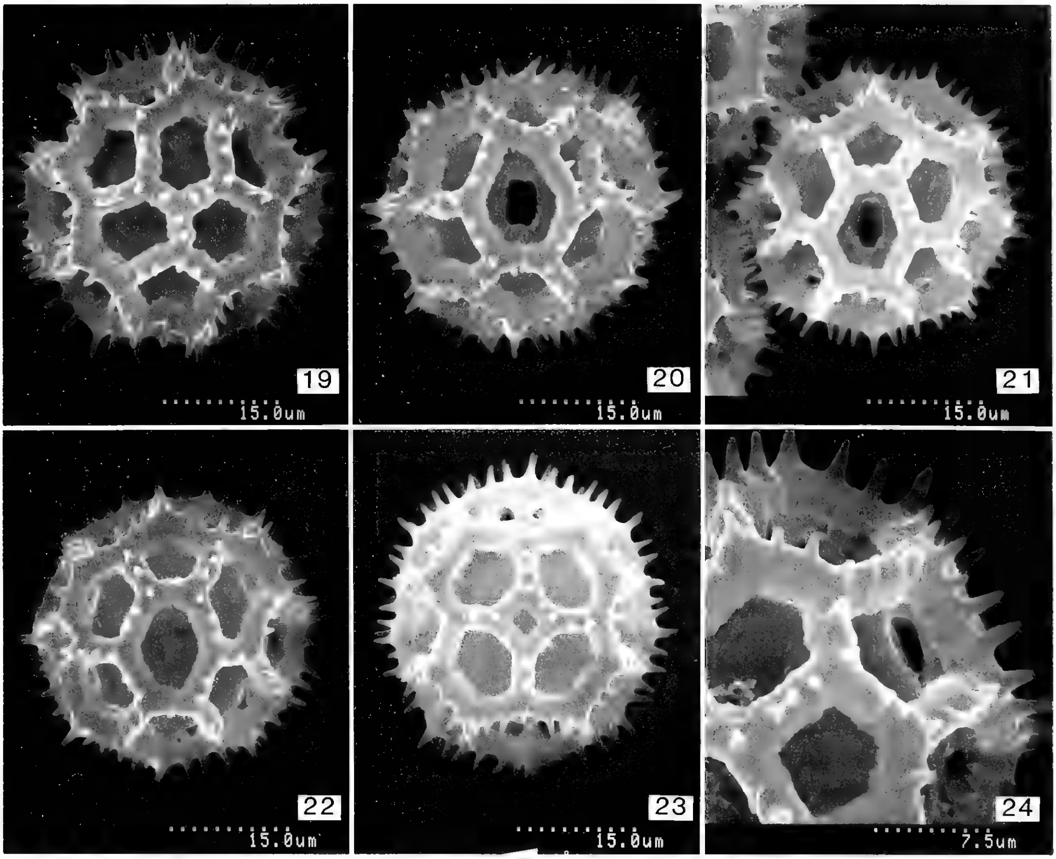
Figs. 1–9. *Lepidaploa,* Type C pollen. 1–3. *L. arborescens* from St. Vincent, Morton 5721. 1. Polar view. 2. Colpar view. 3. Broken grain showing baculae. 4–6. *L. sericea* from Haiti, Leonard 8990. 4. Colpar view. 5. View showing intercolpus. 6. Crest of grain showing rhizomiform baculae broken away from footlayer. 7, 8. *L. canescens* from Ecuador, Hitchcock 20342. 7. Polar view. 8. Broken grain showing baculae. 9. *L. cotoneaster* from Brazil, King & Bishop 8620, polar view.

types are indicated under each of the species as C, D, G, *Aynia* Type, B/G for G Types with a tendency for Type B areolation, and C/G for pollen with polar areoles usually at only one pole.

One Neotropical species examined in this study, *Acilepidopsis echitifolia* (Mart. ex DC.) H. Robinson (1989), synonym *Vernonis ararana* Gardn., of Brazil and Paraguay, has lophate pollen and shows some features that suggest relationship to *Lepidaploa.* However, examination of the pollen (Figs. 59,



Figs. 10–18. *Lepidaploa,* Type C pollen. 10–12. *L. cotoneaster* from Brazil, King & Bishop 8620. 10. Colpar view. 11. Intercolpar view. 12. Detail of crest showing baculae. 13–16. *L. salzmannii* from Peru, Ferreyra 9327 (13, 14); from Brazil, Hatschbach 43889 (15, 16). 13. Polar view. 14. Intercolpar view. 15. Broken grain showing rhizomiform baculae weakly attached to footlayer. 16. Detached exine showing rhizomiform baculae from below. 17, 18. *L. cleocalderonae* from Brazil, Calderon et al. 2689, holotype. 17. Polar view. 18. Detail of crest showing baculae.



Figs. 19–24. *Lepidaploa tovarensis* pollen, from Venezuela, Pittier 12794, isotype. 19. Polar view showing three intercolpar areoles meeting at pole. 20–22. Colpar views showing crosswalls with distinct median sutures. 23. Intercolpar view. 24. Detail of crests showing modified baculae.

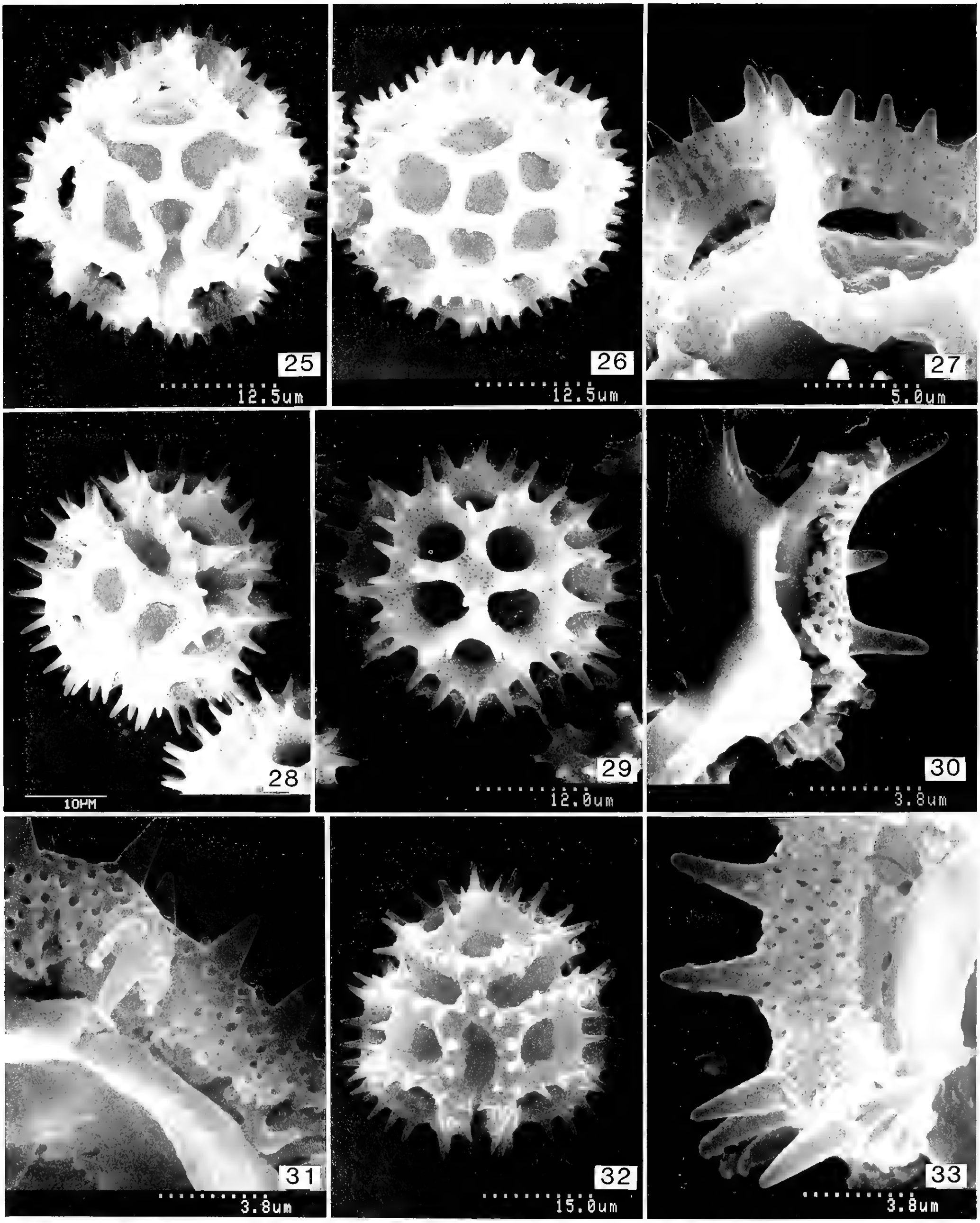
60) shows a type that is called Type E by Jones (1981) in his survey of the Old World members of the tribe. Such pollen is not otherwise known from any *Vernonia sensu lato* native to the Neotropical region. The form of the pollen strongly suggests that the species is actually most closely related to Old World members of the tribe such as the African *Vernonia polysphaera* Baker and the Asian *Acilepis squarrosa* D. Don that have the same type of pollen (Kingham 1976; Jeffrey 1988). Large reddish glands, branched inflorescences, and procumbent bases of the stems help to distinguish the South American *Acilepidopsis* from possible relatives in both hemispheres (Robinson 1989).

Geography

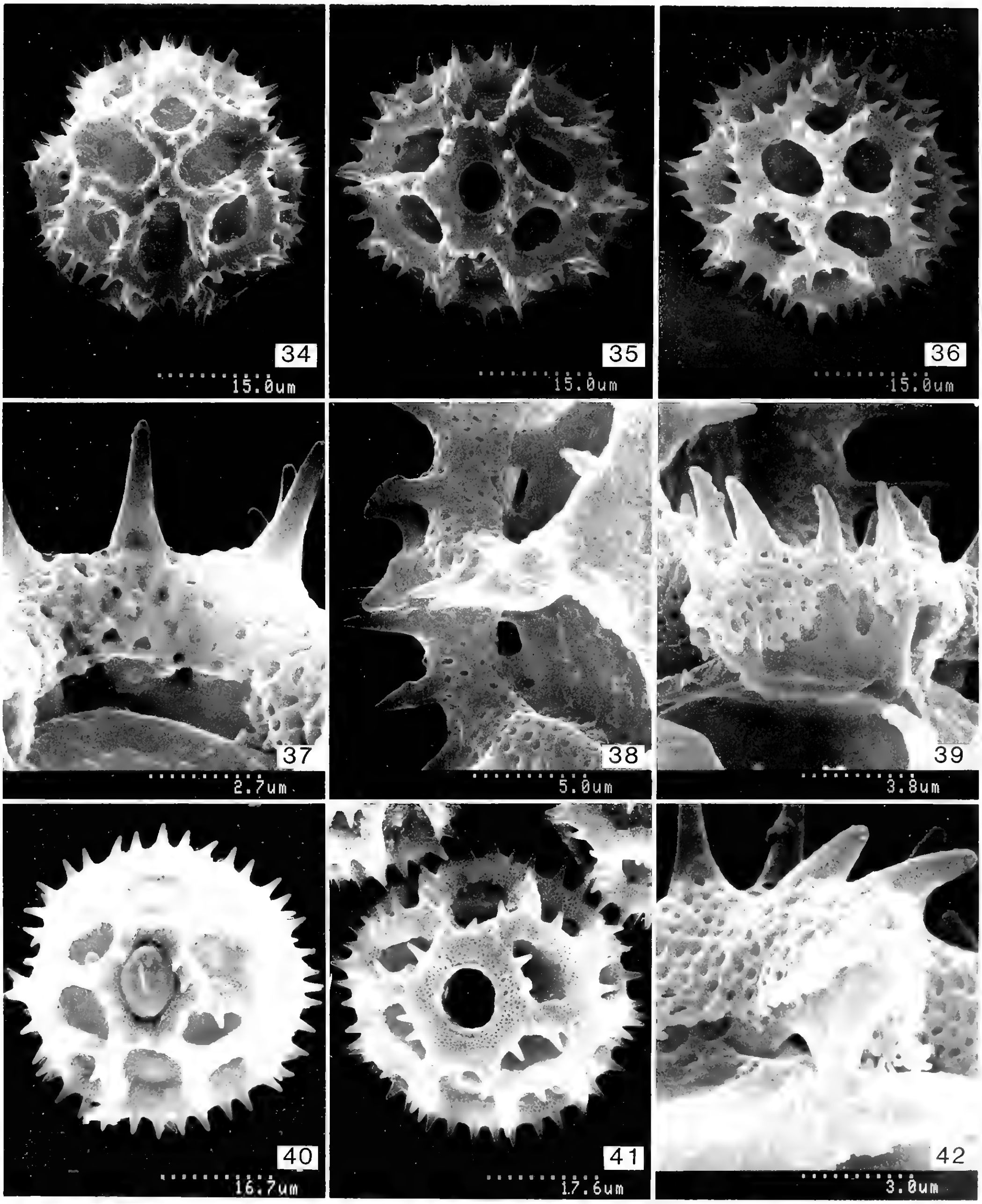
Lepidaploa has the most extensive geographical range of any genus in the related Complex, occurring from Mexico and the West Indies southward through most of montane or savanna areas of South America. In contrast, the other genera are all predominantly or exclusively Brazilian, except the monotypic *Aynia* of Peru.

Chromosome Number

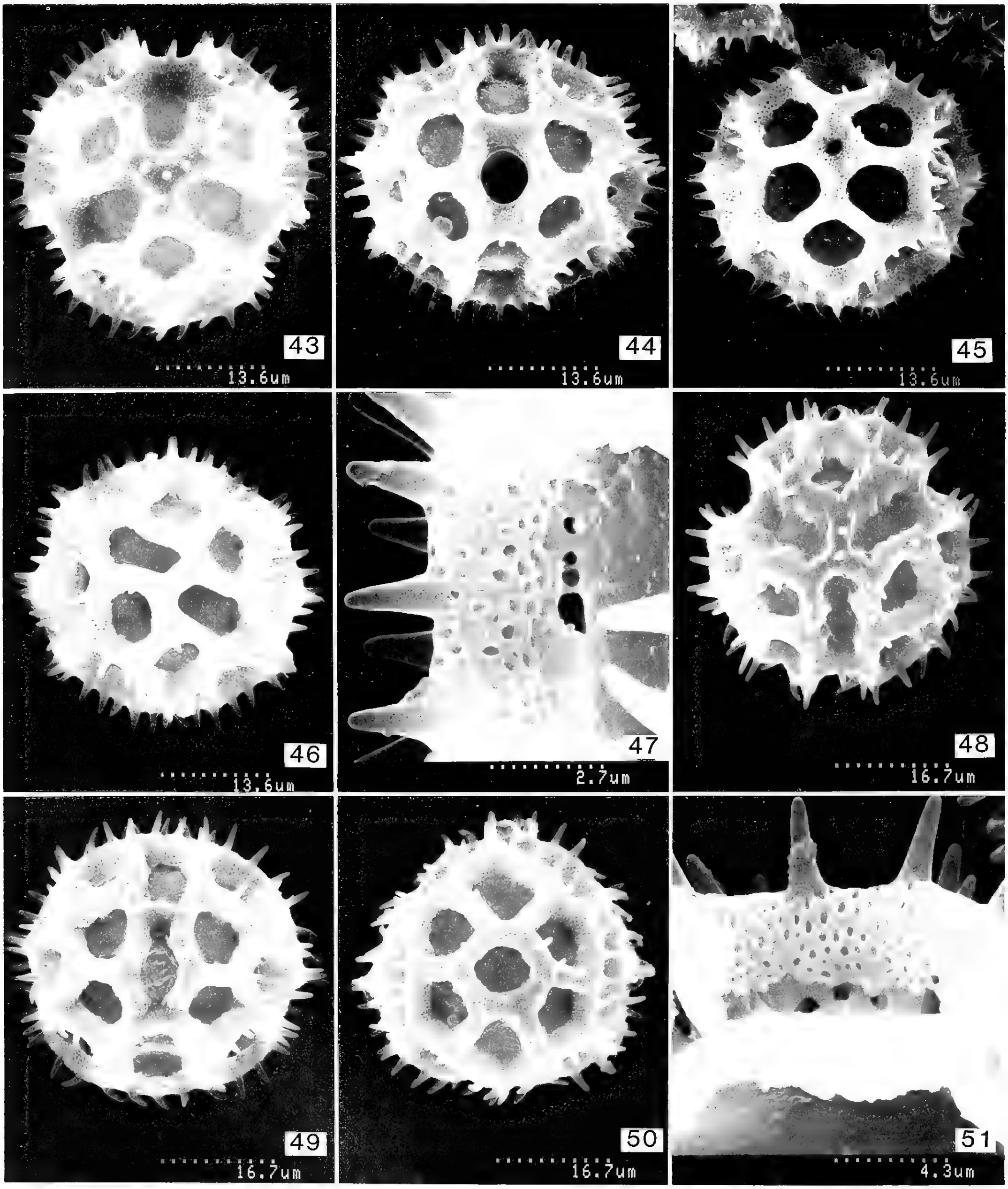
All available counts (Jones 1979a, Keeley 1978) indicate that the *Lepidaploa* Complex has the New World pattern of $n = 17$ chromosomes (Jones 1977). Eleven species of *Lepidaploa* have been counted, including



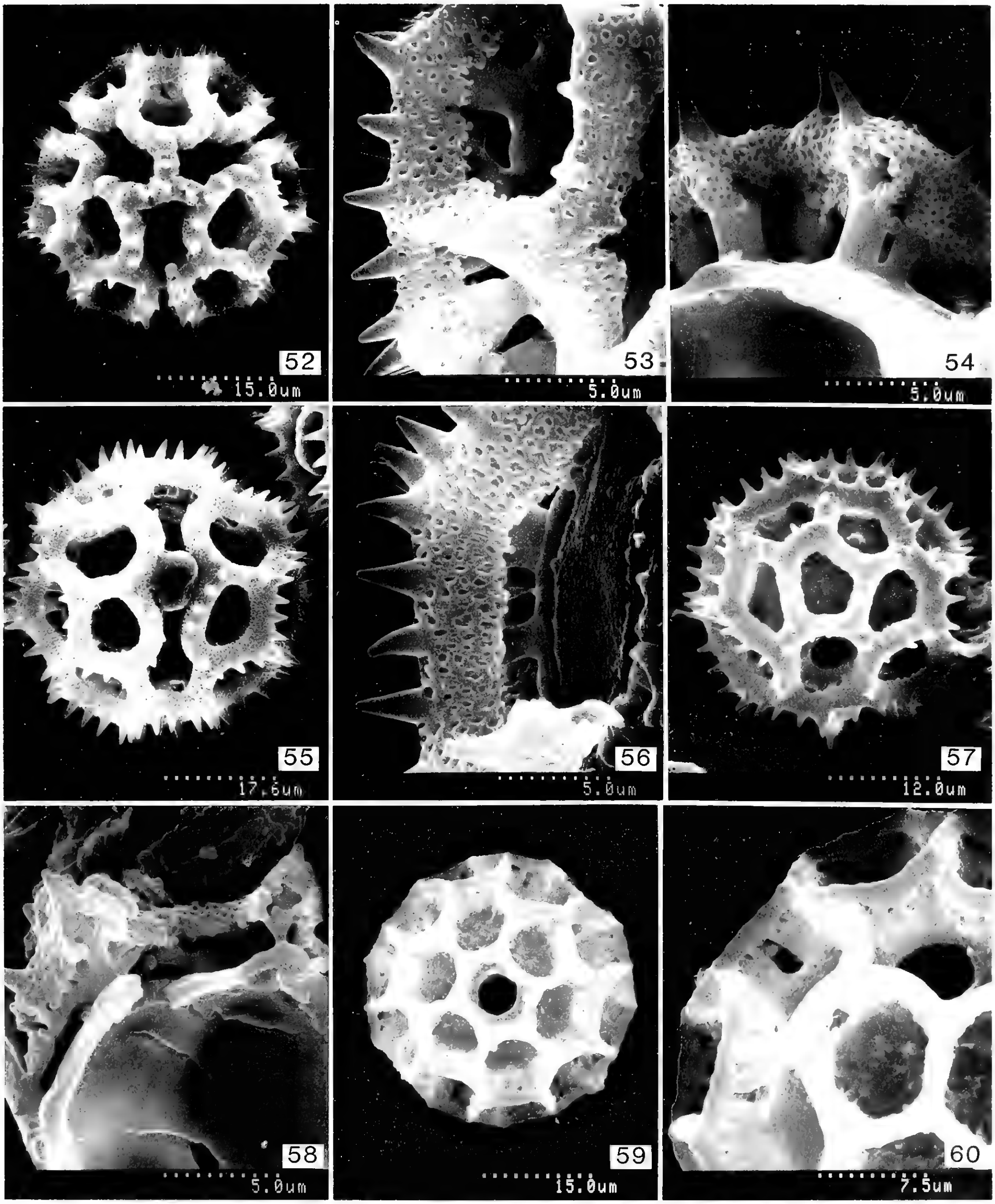
Figs. 25–33. *Lepidaploa,* Type G pollen. 25–27. *L. psilostachya* from Brazil, Riedel & Lund 1745/590. 25. Polar view. 26. Intercolpar view. 27. Detail of crests showing rhizomiform baculae. 28–31. *L. subsquarrosa* from Brazil, Rose 20194 (28–30) and Mimura 491 (31). 28. Polar view. 29. Intercolpar view. 30, 31. Broken grains showing rhizomiform baculae. 32, 33. *L. persericea* from Brazil, Mori et al. 13700. 32. Polar view. 33. Broken grain showing rhizomiform baculae weakly attached to footlayer.



Figs. 34–42. *Lepidaploa,* Type D pollen. 34–39. *L. aurea* from Brazil, Irwin et al. 14595. 34. Polar view. 35. Colpar view showing crosswalls. 36. Intercolpar view. 37–39. Details of crests showing modified baculae. 40–42. *L. tombadorensis* from Brazil, Harley et al. 22906. 40, 41. Colpar views showing crosswalls. 42. Broken grain showing crest with modified baculae.



Figs. 43–51. *Lepidaploa,* Type D pollen. 43–47. *L. chalybaea* from Brazil, Mori & Benton 13094. 43. Polar view. 44. Colpar view showing crosswalls. 45, 46. Intercolpar views showing variation in areole pattern. 47. Detail of crest showing modified baculae and weak attachment to footlayer. 48–51. *L. rufogrisea* from Brazil, Cuatrecasas & Duarte 26641. 48. Polar view. 49. Colpar view showing crosswalls. 50. Intercolpar view. 51. Detail of crest showing modified baculae.



Figs. 52–60. Various lophate pollen types in the Vernonieae. 52, 53. *Lessingianthus rubricaulis* from Colombia, Pennell 10657. 52. Polar view. 53. Detail of crests showing baculae. 54. *Mattfeldanthus nobilis* from Brazil, Hatschbach 50443, broken grain showing baculae. 55, 56. *Baccharoides adoensis* from Rhodesia, Best 336. 55. Colpar view. 56. Detail of crest showing baculae. 57, 58. *Cyanthillium patula* from the Philippines, Steiner 468. 57. View showing pore. 58. Broken grain showing partial rhizomiform bridges under crests. 59, 60. *Acilepidopsis echitifolia* from Paraguay, Pedersen 3269. 59. View showing pore. 60. Detail of crests showing baculae.

one hexaploid, *V. trinitatis.* The base number has also been reported for other genera of the Complex, *Lessingianthus* (Robinson 1988a) and *Chrysolaena* (Robinson 1988b), but the latter genera both show an incidence of tetraploidy that has not yet been reported from *Lepidaploa.*

The known chromosome numbers are given with the pollen type under the species in the taxonomic summary.

Further Distinctions

A number of Brazilian species such as *Vernonia subsquarrosa* have insect galls of a type mentioned in the original description of *V. alvimii* (Robinson 1980). The galls are actually achenes infested with Dipteran larvae so that they grow larger than normal. They are fat and rather fusiform with a much reduced pappus. Such achenes have not been seen in the related genera such as *Lessingianthus.*

None of the species of *Lepidaploa* have the generally larger size of all floral parts that is common in *Lessingianthus.* Only one species belonging to *Lepidaploa, Vernonia eriolepis,* was placed in the *Vernonia* section *Lepidaploa Macrocephalae* of Baker (1873) that included many species now placed in *Lessingianthus. Lepidaploa eriolepis* has some of the smallest floral parts of any species that was included in that section. The difference in size of floral parts in the genera seems to extend to the width of the style shaft and to some extent to size of the pollen. The somewhat larger pollen of *Lessingianthus* may be a factor in the common occurrence of extra intercolpar areoles in that genus.

The difference in average size of floral parts in *Lepidaploa* and *Lessingianthus* is like that which sometimes results from higher chromosome numbers. However, the basic numbers of the two genera both seem to be $n = 17$. Some of the specimens of *Lepidaploa* with larger pollen, approaching that of *Lessingianthus* in size, may have higher ploidy levels as in *V. trinitensis,* but the larger size in *Lessingianthus* seems to be achieved without increase in chromosome number. Future studies should attempt to measure actual DNA content.

Taxonomic Summary

The genus *Lepidaploa* is delimited in the present series of studies in the following manner.

Lepidaploa (Cassini) Cassini

Lepidaploa (Cassini) Cassini *in* G. Cuvier, Dict. Sci. Nat. 36:20. 1825; 60:586. 1830. Rchb., H. G. L., Consp. Regn. Veg. I:99. 1829 [1828]; Bartl., F. G., Ord. Nat. Pl. 136. 1830; Spach, E., Hist. Nat. Vég. 10: 39. 1841.

Vernonia subg. *Lepidaploa* Cassini, Bull. Sci. Soc. Philom. 1817:66. 1817.

Vernonia sect. *Lepidaploa* (Cassini) DC., Prodr. 5:26. 1836.

Annual or perennial herbs or shrubs, erect to spreading, to 1.5(–3.0) m tall; stems, leaves, and involucral bracts sparsely scabrid to sericeous or weakly tomentose, often glandular-punctate. Leaves alternate (opposite in *L. canescens* var. *opposita*), sessile to shortly petiolate. Inflorescence cymose with short or long seriately cymose branches, subcapitular bracts slightly to markedly smaller than nearest vegetative leaves. Heads sessile, broadly campanulate; bracts of involucre 1.3–3.0 times as numerous as florets in the head, unappendaged, in 3–6 series, outer bracts often slender and more spreading with aristate tips, inner bracts persistent, usually more erect and acute. Flowers (8–)10–35 in a head; corollas usually lavender, narrowly funnel-form, throats short but distinct, lobes bearing long hairs, spicules, glands, or with combinations, veins broadly fused at tips of lobes; anther appendages non-glanduliferous (except possibly in *L. helophila*); style base with an expanded node and with sclerified cells below. Achenes prismatic, mostly 8–10-ribbed, usually densely long-setuliferous, often with glands on the surface, with or without resiniferous cells; carpopodia stopper-shaped or turbinate, extending upward among the bases of the lowest setulae, the cells oblong with porose lateral walls; inner pappus of numerous long capillary bristles, about as long as the corolla, outer pappus of distinct shorter scales. Pollen grains 45–50(–60) μm in diameter, lophate with crests rhizomatous or incompletely columellate, columellae narrower at base when present, crest pattern usually with two equatorial intercolpar areoles, sometimes with polar areoles (type C), with crosswalls above and below pores (type D), or with colpi continuous to the poles (type G).

Lectotype: *Vernonia albicaulis* Vahl ex Pers. [=*Lepidaploa glabra* (Willd.) H. Robinson].

The genus *Lepidaploa* can be credited with the following 116 species. The synonymy given below includes basionyms of the accepted species, basonyms of species placed in synonymy, and any subsequent combinations of these names at the species level in *Vernonia.* Synonymies generally follow Keeley (1978) for the West Indies, Aristeguieta (1964) for Venezuela, Jones (1980) for Peru, Cabrera (1944) for Argentina, and have been influenced by Baker (1873) in some of the older names from Brazil.

Lepidaploa acutiangula (Gardn.) H. Robinson, comb. nov.

Vernonia acutiangula Gardner, London J. Bot. 5:225. 1846. Brazil (Maranhão). Pollen C.

Lepidaploa acuminata (Less.) H. Robinson comb. nov.

Vernonia acuminata Less., Linnaea 6:663. 1831. *V. expansa* Gleason, Bull. New York Bot. Gard. 4:186. 1906. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa alvimii (H. Robinson) H. Robinson, comb. nov.

Vernonia alvimii H. Robinson, Phytologia 45:168. 1980. Brazil (Bahia). Pollen G.

Lepidaploa araguensis (Badillo) H. Robinson, comb. nov.

Vernonia araguensis Badillo, Bol. Soc. Venez. Ci. Nat. 10:283. 1946. Venezuela. Pollen C.

Lepidaploa araripensis (Gardn.) H. Robinson, comb. nov.

Vernonia araripensis Gardner, London J. Bot. 5:222. 1846. Brazil (Pará). Pollen C.

Lepidaploa arborescens (L.) H. Robinson, comb. nov.

Conyza arborescens L., Syst. Nat. ed. 10, 2: 1213. 1759. *Vernonia arborescens* (L.) Swartz, Fl. Ind. Occid. 3:1320. 1806. *V. divaricata* Swartz, Fl. Ind. Occid. 3:1319. 1806. *V. divaricata* Less., Linnaea 4:306. 1829. *V. icosantha* DC., Prodr. 5:49. 1836. *V. albicoma* Gleason, Bull. New York Bot. Gard. 4:185. 1906. *V. intonsa* Gleason, Bull. New York Bot. Gard. 4:182. 1906. *V. permollis* Gleason, Bull. New York Bot. Gard. 4:179. 1906. *V. ventosa* Gleason, Bull. New York Bot. Gard. 4:179. 1906. *V. amarantina* Gleason, Bull. Torrey Bot. Club 40:307. 1913. *V. parvuliceps* Ekman, Ark. Bot. 13(15):71. 1914. Antilles, Pollen C, Figs. 1–3; N = 17 (Keeley 1978).

The present concept differs from that of Keeley (1982) by its restriction to Antillean material. Separate specific status is restored for the continental material that was placed in synonymy by Keeley. The continental species is discussed under the name *Lepidaploa canescens.*

Lepidaploa arbuscula (Less.) H. Robinson, comb. nov.

Vernonia arbuscula Less., Linnaea 6:664. 1831. *V. arcuata* Gleason, Bull. Torrey

Bot. Club 33:185. 1906. *V. obcordata* Gleason, Bull. Torrey Bot. Club 33:187. 1906. *V. bahamensis* Griseb., Fl. Brit. W. Ind. 352. 1861. Bahamas. Pollen C; N = 17 (Keeley 1978).

Lepidaploa arenaria (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia arenaria Mart. ex DC., Prodr. 5: 54. 1836. *V. sarmentiana* Gardner, London J. Bot. 5:221. 1846. Brazil (Bahia, Piauhy). Pollen D.

Lepidaploa argyrotricha (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia argyrotricha Sch.Bip. ex Baker in Mart., Fl Bras. 6(2):96. 1873. Brazil (Goiás, Espirito Santo, Minas Gerais, Rio de Janeiro). Pollen C; N = 17 (Keeley 1978).

Lepidaploa aristosquamosa (Britton) H. Robinson, comb. nov.

Vernonia aristosquamosa Britton, Bull. Torrey Bot. Club 18:332. 1891. Bolivia. Pollen G.

Lepidaploa aronifolia (Gleason) H. Robinson, comb. nov.

Vernonia aronifolia Gleason, Bull. Torrey Bot. Club 40:323. 1919. Cuba. Pollen C/G.

Lepidaploa aurea (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia aurea Mart. ex DC., Prodr. 5:58. 1836. Brazil (Bahia, D.F., Goiás, Minas Gerais). Pollen D, Figs. 34–39.

Lepidaploa auyantepuiensis (Aristeg.) H. Robinson, comb. nov.

Vernonia auyantepuiensis Aristeg., Acta Bot. Venez. 2(5–8):362. 1967. Venezuela. Pollen C.

The species seems close to *Lepidaploa ehretiifolia* Benth. but the pubescence of the stems and leaf undersurfaces is coarser and more erect. Also, the pollen is larger (nearly 60 μm in diam.), and there are usually three intercolpar areoles as in Type B pollen. The size of the grains and the coarseness of the hairs may indicate the species is a polyploid.

Lepidaploa barbata (Less.) H. Robinson, comb. nov.

Vernonia barbata Less., Linnaea 4:287. 1829. Brazil (Bahia, Mato Grosso, Minas Gerais). Pollen D.

Lepidaploa bakerana (Britton) H. Robinson, comb. nov.

Vernonia bakerana Britton, Bull. Torrey Bot. Club 18:331. 1891. Bolivia. Pollen C.

Lepidaploa beckii H. Robinson, sp. nov.

Plantae suffrutescentes et interdum subvolubiles 1.4–3.0 m longae laxe ramosae. Caulis brunnei et atrescentes dense sordide velutini. Folia alterna, petiolis 5–10 mm longis dense velutinis; laminae ovato-lanceolatae 15–27 cm longae et 6–11 cm latae base rotundatae ad quintum basilares latissimae margine integrae vel minime remote crenulatae apice breviter anguste acuminatae supra virides in nervis insculptae tenuiter sericeae subtus pallidiores in nervis valde exsculptae perdense sericeae vel sublanatae, nervis secundariis utrinque 14–18. Inflorescentiae dense ramosae in ramis primariis distincte bractiiferae, bracteis foliiformibus plerumque 3–9 cm longis et 1–3 cm latis, bracteis ramulis subnullis. Capitula sessilia in nodis binata vel congesta breviter campanulata 5–6 mm alta; squamae involucri plerumque virides interiores distaliter brunnescentes ca. 40 subimbricatae 3–4-seriatae lanceolatae 1.5–4.0 mm longae et 0.5–1.0 mm latae plerumque extus dense pilosulae et apice subaristatae, interiores sparse minute puberulae apice breviter acutae saepe recurvatae. Flores ca. 30 in capitulo. Corollae albae 4.0–4.5 mm longae extus inferne glabrae distaliter et in marginis lobarum dense spiculiferae, tubis infundibularibus ca. 2 mm longis, faucibus ca. 1 mm longis, lobis oblongo-lanceolatis ca. 2 mm longis et 0.6 mm latis; thecae antherarum ca. 2 mm longae, appendicibus apicalibus ca. 0.5 mm longis glabris; basi stylorum abrupte disciformes. Achaenia ca. 2 mm longae dense sericeo-setuliferae non glandulferae distincte mediocriter idioblastiferae; setae pappi flavae ca. 40 plerumque 3.5–4.0 mm longae superne sensim distincte latiores in sereibus anguste lanceolatae ad 0.8 mm longae. Grana pollinis in diametro ca. 45 μm valde lophata, reticula in typo C. (Fig. 61).

Type.—Bolivia: La Paz: Prov. Nor Yungas, Suapi 16 km hacia Santa Rosa, 1650 m, bosque montañoso, sub-arbusto de 2 m erecto, frutos, en el borde del camino, 25.9.1987, St. G. Beck 13640 (holotype US; isotype LPB).

Paratypes.—Bolivia: La Paz: Prov. Murillo, Suapi 22 km hacia Santa Rosa de Quilo Quilo, 1300 m, restos del monte en el borde del camino, arbusta trepanda alga voluble, frutos en globulos, 25.9.1987, St. G. Beck 13638 (LPB, US); Valley of the Rio Zongo, approx. ½ hour by trail which climbs from the Cahua Hydroelectric Plant on the left bank of the Río Zongo, moist forest with scattered chacos, 16°05′S, 68°03′W, scandent shrub, stems up to 3 m, 23 Apr 1982, J. C. Solomon 7563 (MO; US); Prov. Nor Yungas, 5.5 km below Coroico towards Yolosa (1.4 km above Yolosa), disturbed roadside forest, 1400 m, 16°13′S, 67°44′W, suffrutescent, 1.5 m, corollas white, 16 May 1985, J. C. Solomon 13726 (MO, US), 21.1 km al noroeste del camino entre Yolosa y Caranavi por el camino a Suapi (ca. 2.5 km al oeste de Suapi, cerca del puente sobre el Río Suapi), bosque húmido muy tocado, 16°07′S, 67°47′W, 1200 m, corolas blancas, tallos arqueados hasta 3 m, 27 May 1988, Solomon 18400 (MO, US).

The species is readily distinguished by the large, coarse leaves having rounded, nearly sessile bases and veins impressed in the upper surface. The inflorescence is also distinctive in the branches with many small crowded heads that mostly lack obvious subcapitular bracts. The corollas seem to be unique in having the margins of the lobes densely spiculiferous along their whole length.

Lepidaploa bolivarensis (Badillo) H. Robinson, comb. nov.

Vernonia bolivarensis Badillo, Bol. Soc. Venez, Ci. Nat. 23(103):291. 1963. *Vernonia glandulosa* Badillo, Bol. Soc. Venez. Ci. Nat. 10:283. 1946, not *V. glandulosa* DC., Prodr. 5:22. 1836. Guyana, Venezuela. Pollen C.

Lepidaploa borinquensis (Urban) H. Robinson, comb. nov.

Vernonia borinquensis Urban, Symb. Antill. 3:390. 1903. Puerto Rico. Pollen C/G.

Lepidaploa buchtienii (Gleason) H. Robinson, comb. nov.

Vernonia buchtienii Gleason, Amer. J. Bot. 10:302. 1923. Bolivia. Pollen G.

Lepidaploa canescens (H.B.K.) H. Robinson, comb. nov.

Vernonia canescens H.B.K., Nov. Gen. Sp., folio ed. 4:27. 1818. *V. mollis* H.B.K., Nov. Gen. Sp., folio ed. 4:28. 1818. *V. geminata* H.B.K., Nov. Gen. Sp., folio ed. 4:28. 1818. *V. bullata* Benth. ex Oerst., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1852:67. 1853. *V. arborescens* var. *cuneifolia* Britton, Bull. Torrey Bot. Club 18:311. 1891. *V. sodiroi* Hieron. ex Sodiro, Bot. Jahrb. Syst. 29:1. 1900. *V. volubilis* Hieron., Bot. Jahrb. Syst. 36:460. 1905. *V. hirsutivena* Gleason, Bull. New York Bot. Gard. 4:175. 1906. *V. patuliflora* Rusby, Bull. New York Bot. Gard. 4:376. 1906. *V. purpusii* T. S. Brandegee, Univ. Calif. Publ. Bot.

Fig. 61. Holotype of *Lepidaploa beckii* H. Robinson, Beck 13640 (US).

6:197. 1915. *V. cuneifolia* (Britton) Gleason, Amer. J. Bot. 10:301. 1923, not *V. cuneifolia* Gardner, London J. Bot. 5:215. 1846. *V. pseudomollis* Gleason, Amer. J. Bot. 10:307. 1923. *V. rusbyi* Gleason, Amer. J. Bot. 19:753. 1932, based on *V. arborescens* var. *cuneifolia* Britton. *V. polypleura* Blake, J. Wash. Acad. Sci. 28: 478. 1938. *V. medialis* Standl. & Steyerm., Publ. Field. Mus. Nat. Hist., Bot. Ser. 23:148. 1943. *V. spiritu-sancti* Cuatr., Bot. Jahrb. Syst. 77:58. 1956. *V. unillensis* Cuatr., Bot. Jahrb. Syst. 77:59. 1956. Mexico, Guatemala, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia. Pollen C, Figs. 7, 8.

This species was placed in the synonymy of *Vernonia arborescens* (L.) Swartz by Keeley (1982), but her concept is overly broad. Typical West Indian *Lepidaploa arborescens* and continental *L. canescens* are somewhat similar in aspect, but they are not considered to be close relatives in this study. The continental species has characteristically larger leaves and has smaller, more pubescent involucres. The West Indian *L. arborescens* characteristically has foliose bracts at the immediate bases of the heads, but the continental *L. canescens* essentially lacks such bracts. In the few cases where foliose bracts occur in *L. canescens* (Panama, King 5256, US), they are attached on the opposite side of the stem from the heads. The achene surfaces in *L. canescens* have resiniferous idioblasts, whereas those of *L. arborescens* have glands instead. The synonymy of Keeley is redistributed between the two species.

Lepidaploa canescens var. **opposita** (H. Robinson) H. Robinson, comb. nov.

Vernonia canescens var. *opposita* H. Robinson, Phytologia 49:261. 1981. Colombia.

Lepidaploa carachensis (Badillo) H. Robinson, comb. nov.

Vernonia carachensis Badillo, Ernstia 48: 41. 1988. Venezuela. Pollen C/G.

Lepidaploa chalybaea (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia chalybaea Mart. ex DC., Prodr. 5: 54. 1836. Brazil (Bahia, Ceará). Pollen D, Figs. 43–47.

Lepidaploa chamissonis (Less.) H. Robinson, comb. nov.

Vernonia chamissonis Less., Linnaea 4:304. 1829. *V. parodii* Cabrera, Darwiniana 5: 187. 1941. Brazil (Paraná, Santa Catarina, São Paulo), Argentina (Chaco), Paraguay. Pollen C.

Lepidaploa chrysotricha (Alexander) H. Robinson, comb. nov.

Vernonia chrysotricha Alexander, Lloydia 2:217. 1939. Guyana. Pollen C/G.

Lepidaploa cleocalderonae (H. Robinson) H. Robinson, comb. nov.

Vernonia cleocalderonae H. Robinson, Phytologia 46:108. 1980. Brazil (Amazonas). Pollen C, Figs. 17, 18.

Lepidaploa commutata (Ekman) H. Robinson, comb. nov.

Vernonia commutata Ekman, Ark. Bot. 13(15):77. 1914. Cuba. Pollen C.

Lepidaploa complicata (Wright ex Griseb.) H. Robinson, comb. nov.

Vernonia complicata Wright ex Griseb., Cat. Pl. Cub. 143. 1866. Cuba. Pollen C.

Lepidaploa cordiaefolia (H.B.K.) H. Robinson, comb. nov.

Vernonia cordiaefolia H.B.K., Nov. Gen. Sp., folio ed. 4:29. 1818. Colombia. Pollen C.

Lepidaploa costanensis (Badillo) H. Robinson, comb. nov.

Vernonia costanensis Badillo, Ernstia 23:32. 1984. Venezuela. Pollen C.

Lepidaploa costata (Rusby) H. Robinson, comb. nov.

Vernonia costata Rusby, Mem. Torrey Bot. Club 6:53. 1896. Peru, Bolivia. Pollen G.

Lepidaploa cotoneaster (Willd. ex Spreng.) H. Robinson, comb. nov.

Conyza cotoneaster Willd. ex Spreng., Syst. Veg. 3:509. 1826. *Vernonia cotoneaster* (Willd. ex Spreng.) Less., Linnaea 4:298. 1829. *V. axilliflora* Less., Linnaea 4:297. 1829. *V. debilis* Mart. ex DC., Prodr. 5: 54. 1836. Brazil (Bahia, Minas Gerais). Pollen C, Figs. 9–12.

Lepidaploa coulonioides (H. Robinson) H. Robinson, comb. nov.

Vernonia coulonioides H. Robinson, Phytologia 49:263. 1981. Brazil (Rio de Janeiro). Pollen G.

Lepidaploa crassifolia (Rusby) H. Robinson, comb. nov.

Vernonia crassifolia Rusby, Bull New York Bot. Gard. 8:124. 1912. Bolivia. Pollen G.

Lepidaploa cuiabensis (Baker in Mart.) H. Robinson, comb. nov.

Vernonia cuiabensis Baker in Mart., Fl. Bras. 6(2):37. 1873. Brazil (Mato Grosso). Pollen D.

Lepidaploa danielis (Cuatr.) H. Robinson, comb. nov.

Vernonia danielis Cuatr., Bot. Jahrb. Syst. 77:54. 1956. Colombia. Pollen C.

Lepidaploa decumbens (Gardner) H. Robinson, comb. nov.

Vernonia decumbens Gardner, London J. Bot. 4:115. 1845. Brazil (Espirito Santo, Rio de Janeiro, São Paulo). Pollen G.

The species is close to *Lepidaploa subsquarrosa,* which has been known as *Vernonia geminata* Less., but the stems are stouter and straighter, the leaves are more pointed, and the inflorescence is denser.

Lepidaploa deflexa (Rusby) H. Robinson, comb. nov.

Vernonia deflexa Rusby, Bull. New York Bot. Gard. 4:376. 1907. Bolivia. Pollen G.

Lepidaploa densipaniculata (Rusby) H. Robinson, comb. nov.

Vernonia densipaniculata Rusby, Bull. New York Bot. Gard. 8:126. 1912. Bolivia. Pollen G.

Only the type (Cargadira, Williams 1534, NY) and one recent collection (La Paz, Murillo, below Lago Zongo dam, Solomon 10740, MO, US) have been seen.

Lepidaploa desiliens (Gleason) H. Robinson, comb. nov.

Vernonia desiliens Gleason, Bull. Torrey Bot. Club 40:316. 1913. Cuba. Pollen C.

Lepidaploa edmundoi (Barroso) H. Robinson, comb. nov.

Vernonia edmundoi Barroso, Arq. Jard. Bot. Rio de Janeiro 17:21. 1959. Brazil (Bahia). Pollen D.

Lepidaploa ehretiifolia (Benth.) H. Robinson, comb. nov.

Vernonia ehretiifolia Benth., London J. Bot. 2:39. 1840. *V. schomburgkiana* Sch.Bip., Linnaea 20:509. 1847. Guyana, Venezuela. Pollen C/G.

Lepidaploa ekmanii (Urban) H. Robinson, comb. nov.

Vernonia ekmanii Urban, Ark. Bot. 17(7): 62. 1921. Haiti. Pollen C/G.

Lepidaploa eriolepis (Gardner) H. Robinson, comb. nov.

Vernonia eriolepis Gardner, London J. Bot. 5:224. 1846. *V. riedelii* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):64. 1873. Brazil (Ceará, Mato Grosso, Minas Gerais, Paraná, Santa Catarina, São Paulo). Pollen G.

Lepidaploa ferreyrae (H. Robinson) H. Robinson, comb. nov.

Vernonia ferreyrae H. Robinson, Phytologia 45:158. Feb. 1980. *V. apurimacensis* S. B. Jones, Fieldiana, Bot. N.S. 5:38. Dec 1980. Peru. Pollen C.

Lepidaploa fieldiana (Gleason) H. Robinson, comb. nov.

Vernonia fieldiana Gleason, Bull. Torrey Bot. Club 59:374. 1932. Peru. Pollen G.

Lepidaploa fournetii (H. Robinson & B. Kahn) H. Robinson, comb. nov.

Vernonia fournetii H. Robinson & B. Kahn, Phytologia 58:252. 1985. Bolivia. Pollen G.

Lepidaploa frangulaefolia (H.B.K.) H. Robinson, comb. nov.

Vernonia frangulaefolia H.B.K., Nov. Gen. Sp., folio ed. 4:29. 1818. Colombia. Pollen C.

Lepidaploa fruticosa (L.) H. Robinson, comb. nov.

Conyza fruticosa L., Sp. Pl. ed. 2. 1209. 1763. *Vernonia fruticosa* (L.) Swartz, Fl. Ind. Occid. 3:1323. 1806. *V. buchii* Urban, Repert. Spec. Nov. Regni Veg. 16: 146. 1919. Hispaniola. Pollen C; N = 17 (Keeley 1978).

Lepidaploa glabra (Willd.) H. Robinson, comb. nov.

Conyza glabra Willd., Sp. Pl. 3:1940. 1803, non *Vernonia glabra* Vatke, 1877. *Eupatorium obtusifolium* Willd., Sp. Pl. 3: 1768. 1803, non *Vernonia obtusifolia* Less., 1829. *Vernonia albicaulis* Vahl ex Pers., Syn. Pl. 2(2):404. 1807. *V. longifolia* Pers., Syn. Pl. 2(2):404. 1807. *Lepidaploa lanceolata* Cass., Dict. Sci. Nat. 26:17. 1823, nom. inval., prior to validation of *Lepidaploa* at generic level. *Vernonia punctata* Swartz ex Wikstr., Kongl. Vetensk. Acad. Handl. 1827:72. 1828. *V. emarginata* Wikstr., Kongl. Vetensk. Acad. Handl. 1827:73. 1828. *V. vahliana* Less., Linnaea 4:306. 1829. *Eupatorium secundiflorum* Bertero ex DC., Prodr. 5: 48. 1836. *V. thomae* Benth. ex Oerst, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1852:66. 1853. *V. longifolia* var. *sintenisii* Urban, Symb. Antill. 1:456. 1899. *V. sintenisii* (Urban) Gleason, Bull. New York Bot. Gard. 4:187. 1906. *Vernonia gleasonii* Ekman, Ark. Bot. 13(15): 54. 1914. *V. shaferi* Gleason, Bull. Torrey Bot. Club 46:238. 1919. Puerto Rico, Lesser Antilles. Pollen C; N = 17 (Keeley 1978).

In *Lepidaploa,* the oldest name can be used for this species, even though it (and a second older name) are blocked from use in *Vernonia* by being later homonyms. *Vernonia albicaulis* remains the proper name for the species in *Vernonia.*

Lepidaploa gnaphaliifolia (A. Rich.) H. Robinson, comb. nov.

Vernonia gnaphalifolia A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba, Bot. 2:33. 1850. *V. membranacea* Griseb., Cat. Pl. Cub. 144. 1866. *V. crassinervia* Wright ex Gleason, Bull. New York Bot. Gard. 4: 180. 1906. *V. sublanata* Gleason, Bull. New York Bot. Gard. 4:177. 1906. *V. sublanata* var. *angustata* Gleason, Bull. New York Bot. Gard. 4:177. 1906. *V. angustata* (Gleason) Gleason, Bull. Torrey Bot. Club 40:309. 1913. *V. gnaphaliifolia* var. *platyphylla* Gleason, Bull. Torrey Bot. Club. 46:238. 1919. *V. platyphylla* (Gleason) Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:100. 1929. *V. nervosa* Alain, Contr. Ocas. Mus. Colegio "De la Salle." 18:150. 1960. Cuba. Pollen C.

Lepidaploa gnaphalioides (Sch.Bip. ex Mart.) H. Robinson comb. nov.

Vernonia gnaphalioides Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):78. 1873. Brazil (Minas Gerais, Paraná). Pollen G.

Lepidaploa gracilis (H.B.K.) H. Robinson, comb. nov.

Vernonia gracilis H.B.K., Nov. Gen. Sp., folio ed. 4:27. 1818. *V. moritziana* Sch.Bip., Linnaea 20:511. 1847. Colombia, Venezuela. Pollen C.

The concept follows Badillo (1984).

Lepidaploa grisea (Baker) H. Robinson, comb. nov.

Vernonia grisea Baker in Mart., Fl. Bras. 6(2):61. 1873. Brazil (Amazonas, Ceará, Pará, Piauhy). Pollen D.

The species seems close to *Lepidaploa arenaria* Gardner, but the latter is basically a costal species with more succulent leaves. Vegetatively the species seems close to *L. obtusifolia* of southern Brazil, but the latter belongs to the group with type C pollen. The latter further differs by the rather indistinct cymes in the inflorescence with little or no reduction in the size of the bracts of the inflorescence.

Lepidaploa hagei (H. Robinson) H. Robinson, comb. nov.

Vernonia hagei H. Robinson, Phytologia 45: 176. 1980. Brazil (Bahia). Pollen G.

Lepidaploa harrisii (S. Moore) H. Robinson, comb. nov.

Vernonia harrisii S. Moore, J. Bot. 66:164. 1928. Jamaica. Pollen C.

Lepidaploa helophila (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia helophila Mart. ex DC., Prodr. 5: 50. 1836. *V. subcordata* Gardner, London J. Bot. 5:226. 1846. Brazil (Bahia, Mato Grosso, Minas Gerais, São Paulo). Pollen G.

The distribution and synonymy is taken from Baker (1873), but such a range seems unlikely for a species so poorly represented in collections. A specimen from Bahia (Harley 18497, US) may be this species; it has glands on the anthers with one or two glands on the apical appendages. The material shows no other important characters of the comparatively remotely related genus *Chrysolaena* (Robinson 1988b).

Lepidaploa jenssenii (Ekman ex Urban) H. Robinson, comb. nov.

Vernonia jenssenii Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:98. 1929. Cuba. Pollen C.

Lepidaploa karstenii (Sch.Bip.) H. Robinson, comb. nov.

Vernonia karstenii Sch.Bip., Linnaea 30: 169. 1859. Colombia. Pollen C.

Lepidaploa lehmannii (Hieron.)
H. Robinson, comb. nov.

Vernonia lehmannii Hieron., Bot. Jahrb. Syst. 19:44. 1894. *Vernonia larensis* Badillo, Bol. Soc. Venez. Ci. Nat. 10:285. 1946. Venezuela, Colombia, Ecuador. Pollen C.

Lepidaploa leptoclada (Sch.Bip.)
H. Robinson, comb. nov.

Vernonia leptoclada Sch.Bip., J. Bot. 1:233. 1863. Cuba. Pollen C.

Lepidaploa liesneri (H. Robinson)
H. Robinson, comb. nov.

Vernonia liesneri H. Robinson, Phytologia 49:264. 1981. Venezuela. Pollen C.

Material of this species was the basis for Badillo's (1982) report of the Colombia *Vernonia marguana* Cuatr. from Venezuela. The two species are vegetatively nearly alike and must be closely related. The Colombian species differs by having more robust inflorescences with larger heads bearing more than twice as many flowers (over 20 vs. 8–9) and by bearing more numerous, shorter involucral bracts.

Lepidaploa lilacina (Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia lilacina Mart. ex DC., Prodr. 5: 48. 1836. *V. adamantium* Gardner, London J. Bot. 5:222. 1846. Brazil (Bahia, Minas Gerais). Pollen C.

Lepidaploa luetzelburgii (Mattf.)
H. Robinson, comb. nov.

Vernonia luetzelburgii Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 9:377. 1925. Brazil (Piauhy). Pollen D?

A type photograph shows a species close in habit and pubescence to the more recently described *Lepidaploa pinheiroi* of Bahia, but the leaf tips are rounded and the involucral bracts lack the long apical spines of the latter species.

Lepidaploa macahensis
(Glaziou ex Barroso) H. Robinson,
comb. nov.

Vernonia macahensis Glaziou ex Barroso, Arq. Jard. Bot. Rio de Janeiro 17:21. 1962. Brazil (Espirito Santo, Rio de Janeiro). Pollen C.

I place here also material in herbaria under the name *Vernonia tijucana* Glaziou from Rio de Janeiro. The latter name was never validated by either Glaziou or by Ekman. The lack of validation is in spite of some annotations by Ekman indicating his intention to publish the name. The Barroso publication was the first and only validation for either Glaziou name. Material under the name *V. tijucana* seems to have more entire leaves and more spreading cymose branches compared to typical *Lepidaploa macahensis,* but the differences do not seem worthy of species rank.

Lepidaploa mandonii (Sch.Bip. ex Gleason)
H. Robinson, comb. nov.

Vernonia mandonii Sch.Bip. ex Gleason, Amer. J. Bot. 10:300. 1923. Bolivia. Pollen C.

Lepidaploa mapirensis (Gleason)
H. Robinson, comb. nov.

Vernonia mapirensis Gleason, Amer. J. Bot. 10:307. 1923. Bolivia, Peru. Pollen G.

The species is redelimited to exclude *Lepidaploa trichoclada* that was placed in synonymy by Jones (1980) and exclude the numerous specimens of *L. sordidopapposa* recently annotated by Jones as *Vernonia mapirensis.* The present species, as seen in the type (Buchtien 1533, US) and paratype (Buchtien 2462, US), has leaves similar to *L. canescens,* but the heads are somewhat larger and more densely arranged, the pappus is dirty yellowish, the surfaces of the achenes lack resiniferous idioblasts, and the pollen seems consistently to be type G. One specimen from Paucatambo, Dept. Cuzco, Peru (Vargas 15495, US) seems to be the same species. *Lepidaploa mapirensis* seems closest to *L. tristis,* but the latter is larger, has more erect or retrorse pubescence on the stems, oblong elliptical leaves with the lateral veins widely separated, and heads that are often paired at the nodes.

Lepidaploa mucronifolia (DC.) H. Robinson, comb. nov.

Vernonia mucronifolia DC., Prodr. 5:55. 1836. Brazil (Bahia). Pollen D.

The species seems very similar in aspect to *Lepidaploa obtusifolia* of the Rio de Janeiro area, but the two are apparently not closely related. The present species is a member of the group having Type D pollen and is a more pubescent plant with less obviously striated stems.

Lepidaploa muricata (DC.) H. Robinson, comb. nov.

Vernonia muricata DC., Prodr. 5:55. 1836. Brazil (Minas Gerais, Rio de Janeiro, São Paulo). Pollen G.

Lepidaploa myriocephala (DC.) H. Robinson, comb. nov.

Vernonia myriocephala DC., Prodr. 5:40. 1836. Peru. Pollen C.

The species was placed in the synonymy of *Lepidaploa arborescens* with *L. canescens* by Keeley (1982), but the leaves are less pubescent and the secondary veins are less closely and less regularly arranged.

Lepidaploa nitens (Gardner) H. Robinson, comb. nov.

Vernonia nitens Gardner, London J. Bot. 5: 221. 1846. Brazil (Bahia, Goiás). Pollen D.

Lepidaploa obtusifolia (Less.) H. Robinson, comb. nov.

Vernonia obtusifolia Less., Linnaea 4:308. 1829. Brazil (Rio de Janeiro). Pollen C.

The species superficially resembles some members of the genus from farther north, such as *Lepidaploa grisea* and *L. mucronifolia.* The latter, however, have Type D pollen, and they are not closely related.

Lepidaploa orbicularis (Alain) H. Robinson, comb. nov.

Vernonia orbicularis Alain, Contr. Ocas. Mus. Colegio "De la Salle" 18:15. 1960. *V. leonis* Alain, Contr. Ocas. Mus. Colegio "De la Salle" 18:14. 1960. Cuba. Pollen C.

Lepidaploa pallescens (Gleason) H. Robinson, comb. nov.

Vernonia pallescens Gleason, Bull. New York Bot. Gard. 4:192. 1906. Lesser Antilles. Pollen C.

Lepidaploa pari (Badillo) H. Robinson, comb. nov.

Vernonia pari Badillo, Bol. Soc. Venez. Ci. Nat. 10:284. 1946. Venezuela. Pollen C.

Lepidaploa persericea (H. Robinson) H. Robinson, comb. nov.

Vernonia persericea H. Robinson, Phytologia 44:292. 1979. *V. cognata* var. *lundiana* Baker in Mart., Fl. Bras. 6(2):95. 1873. Brazil (Bahia, Espirito Santo, Minas Gerais, Rio de Janeiro). Pollen G, Figs. 32, 33.

Lepidaploa persicifolia (Desf.) H. Robinson, comb. nov.

Vernonia persicifolia Desf., Cat. Pl. Hort. Par. ed. 3, 400. 1829. *V. acutifolia* Hook., Bot. Mag. 58:t. 3062. 1831. Brazil (Rio de Janeiro). Pollen C.

During much of its taxonomic history, the species has been placed in the synonymy of *Vernonia sericea* L. C. Rich. The latter entity seems to be exclusively West Indian and has no particular resemblance to the present large-leaved species with its large, remote heads.

Lepidaploa pineticola (Gleason) H. Robinson, comb. nov.

Vernonia pineticola Gleason, Bull. New York Bot. Gard. 4:176. 1906. Cuba. Pollen C/G.

Lepidaploa pinheiroi (H. Robinson) H. Robinson, comb. nov.

Vernonia pinheiroi H. Robinson, Phytologia 45:179. 1980. Brazil (Bahia). Pollen D.

Lepidaploa pluvialis (Gleason) H. Robinson, comb. nov.

Vernonia pluvialis Gleason, Bull. Torrey Bot. Club 40:312. 1913. *V. reducta* Gleason, Bull. Torrey Bot. Club 40:313. 1913. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa proctorii (Urbatsch) H. Robinson, comb. nov.

Vernonia proctorii Urbatsch, Syst. Bot. 14: 589. 1989. Puerto Rico. Pollen C/G.

Lepidaploa psilostachya (DC.) H. Robinson, comb. nov.

Vernonia psilostachya DC., Prodr. 5:43. 1836. *V. oxylepis* Sch.Bip. ex Baker in Mart., 6(2):70. 1973. Brazil (Paraná, São Paulo). Pollen B/G, Figs. 25–27.

Lepidaploa purpurata (Gleason) H. Robinson, comb. nov.

Vernonia purpurata Gleason, Bull. Torrey Bot. Club 40:322. 1913. *V. praestans* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26:101. 1921. Cuba. Pollen C/G.

Lepidaploa reflexa (Gardner) H. Robinson, comb. nov.

Vernonia reflexa Gardner, London J. Bot. 5:228. 1846. Brazil (Bahia, Minas Gerais). Pollen D.

Lepidaploa remotiflora (L. C. Rich) H. Robinson, comb. nov.

Vernonia remotiflora L. C. Rich., Actes Soc. Hist. Nat. Paris 1:112. 1792. *V. sessiliflora* Willd. ex Less., Linnaea 4:309. 1829. *V. tricholepis* DC., Prodr. 5:54. 1836. *V. acilepis* Benth. ex Oerst., Vidensk. Meddel. Naturhist. Foren, Kjøbenhavn 1852: 68. 1853. *Vernonia lithospermoides* Baker in Mart., Fl. Bras. 6(2):66. 1873. *V. hirtiflora* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):70. 1873. *V. setososquamosa* Hieron., Bot. Jahrb. Syst. 22:684. 1897. Venezuela, Guyana, Cayenne, Brazil, Paraguay, Bolivia, Argentina. Pollen G.

A type photograph of *Vernonia ovata* Less. shows a plant from Brazil that is possibly related to *Lepidaploa remotiflora,* but it has broadly elliptical leaves and broader heads with recurved rather than straight outer bracts.

Lepidaploa retrosetosa (H. Robinson) H. Robinson, comb. nov.

Vernonia retrosetosa H. Robinson, Phytologia 45:159. 1980. Peru. Pollen G.

Lepidaploa rigida (Swartz) H. Robinson, comb. nov.

Conyza rigida Swartz, Prodr. 113. 1788. *Vernonia rigida* (Swartz) Swartz, Fl. Ind. Occid. 3:1322. 1806. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa rimachii (H. Robinson) H. Robinson, comb. nov.

Vernonia rimachii H. Robinson, Phytologia 49:266. 1981. Peru. Pollen G.

Lepidaploa rufogrisea (St. Hil.)
H. Robinson, comb. nov.

Vernonia rufo-grisea St. Hil., Voy. Distr. Diam. 2:453. 1833. *V. fruticulosa* Mart. ex DC., Prodr. 5:53. 1836. *V. eremophila* Mart. ex DC., Prodr. 5:54. 1836. *V. tricephala* Gardner, London J. Bot. 5:223. 1846. *V. resinosa* Gardner, London J. Bot. 6:419. 1847. *V. saxicola* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):81. 1873. ?*V. oreophila* Malme, Kongl. Svenska Vetenskapsakad Handl. N.S. 32(5):26. 1899. Brazil (Bahia, D.F., Goiás, Mato Grosso, Minas Gerais). Pollen D, Figs. 48–51.

A photograph of the type shows that the older St. Hilaire name applies to the same common species usually known as *Vernonia fruticulosa* Mart. ex DC. The leaves seem to vary in shape from broadly elliptical to linear. A type photograph of *V. oreophila* Malme, of Mato Grosso, seems to represent the same or a closely related species. The leaves of the latter are exclusively ovate and the inflorescences contain very few heads.

Lepidaploa sagraeana (DC.) H. Robinson, comb. nov.

Vernonia sagraeana DC., Prodr. 5:55. 1836. *V. valenzuelana* A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba. Bot. 11:33. 1850. *V. inaequiserrata* Sch.Bip., J. Bot. 1:131. 1863. *V. fallax* Gleason, Bull. Torrey Bot. Club 40:324. 1913. *V. aceratoides* Gleason, Bull. Torrey Bot. Club 40:325. 1913. *V. angusticeps* Ekman, Ark. Bot. 13(15): 14. 1914. *V. linguaefolia* Ekman, Ark. Bot. 13(15):19. 1914. *V. reedii* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26: 97. 1929, not *V. reedii* Daniels, 1907. *V. potrerillona* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26:98. 1929. Cuba. Pollen C/G.

Lepidaploa salzmannii (DC.) H. Robinson, comb. nov.

Vernonia salzmannii DC., Prodr. 5:55. 1836. *V. poeppigiana* DC., Prodr. 5:55. 1836, non *V. poeppigiana* DC., Prodr. 5: 20. 1836. *V. argyropappa* H. Buek., Ind. Gen. Sp. Syn. in DC., Prodr. 2: Praef. v. 1840. *V. miersiana* Gardner, London J. Bot. 4:115. 1845. *V. virens* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):71. 1873. *V. velutina* Hieron., Bot. Jahrb. Syst. 22: 697. 1897. *V. herbertii* Cuatr., Bot. Jahrb. Syst. 77:55. 1956. Central America, Colombia, Peru, Brazil. Pollen C, Figs. 13–16.

Lepidaploa sclareaefolia (Sch.Bip.)
H. Robinson, comb. nov.

Vernonia sclareaefolia Sch.Bip., Linnaea 30: 170. 1859. Colombia. Pollen G.

Lepidaploa segregata (Gleason)
H. Robinson, comb. nov.

Vernonia segregata Gleason, Bull. Torrey Bot. Club 40:327. 1913. Cuba. Pollen C.

Lepidaploa sericea (L. C. Rich.)
H. Robinson, comb. nov.

Vernonia sericea L. C. Rich., Actes Soc. Hist. Nat. Paris 1:112. 1792. *Lepidaploa phyllostachya* Cassini, Dict. Sci. Nat. 26:16. 1823, nom. inval., prior to validation of *Lepidaploa* at generic level. *V. berteriana* DC., Prodr. 5:52. 1836. *Conyza portoricensis* Bertero ex DC., Prodr. 5:52. 1836, nom. nud. *Vernonia racemosa* Delponte, Mem. Reale Acad. Sci. Torino. II, 14: 396. 1854. *V. venusta* Gleason, Bull. New York Bot. Gard. 4:177. 1906. *V. phyllostachya* Gleason, Bull. New York Bot. Gard. 4:181. 1906. *V. angustissima* Wright ex Ekman, Ark. Bot. 13(15):78. 1914. *V. maestralis* Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:99. 1929. Greater Antilles, Virgin Isl. Pollen C, Figs. 4–6; N = 17 (Keeley 1978).

Lepidaploa silvae (H. Robinson)
H. Robinson, comb. nov.

Vernonia silvae H. Robinson, Phytologia 46: 112, 1980. Brazil (Pará). Pollen C.

Lepidaploa solomonii H. Robinson, sp. nov.

Plantae suffrutescentes ad 2 m altae. Caule virides striati sparse minute antrorse strigulosi. Folia alterna, petiolis 1.5–2.5 cm longis; laminae ovato-ellipticae 14–16 cm longae et ad 6.5 cm latae base breviter acutae et minime acuminatae margine integrae vel remote minime crenulatae apice breviter anguste acuminatae supra et subtus subglabrae sparse minute strigulosae supra sparsius. Inflorescentiae supra folia vegetativa laxe ramosae seriate cymosae, bracteae foliiformes distincte minores breviter petiolatae petiolis 3–7 mm longis, laminis lanceolatis 3.0–8.5 cm longis et 0.4–2.4 cm latis in ramulis ultimis subnullis. Capitula sessilia solitaria late campanulata ca. 10 cm alta; squamae involucri in partibus atropurpurascentes ca. 45 subimbricatae 4–5-seriatae graduatae exteriores lanceolatae 2–5 mm longae et 0.8–1.0 mm latae apice subaristatae interiores oblong-lineares ad 8 mm longae apice acutae margine omnino minute fimbriatae extus subglabrae vel perminute puberulae. Flores ca. 30 in capitulo. Corollae ca. 7 mm longae extus plerumque glabrae in partibus apicalibus lobarum breviter spiculiferae, tubis cylindricis 3 mm longis, faucibus late infundibularibus 1.0–1.3 mm longis, lobis linearibus ca. 3 mm longis et 0.6–0.7 mm latis; thecae antherarum ca. 2.5 mm longae, appendicibus apicalibus ca. 0.4 mm longae glabrae; basi stylorum abrupte disciformes. Achaenia ca. 3 mm longa dense sericeo-setulifera non glandulifera et non idioblastifera; setae pappi sordide ca. 30 ca. 6 mm longae subdeciduae superne vix latiores in sereibus exterioribus anguste lanceolatae 1.0–1.5 mm longae. Grana pollinis in diametro ca. 45 μm valde lophata, reticulis in typo G. (Fig. 62).

Type.—Bolivia: La Paz: Prov. Murillo, 44.0 km below Lago Zongo dam, vicinity of Cahua hydroelectric plant, 16°03′S, 68°01′W, 1200 m, moist forest, disturbed, alternating with Chacos and secondary forest, shrub, 2 m, 12–15 Sep 1983, J. C. Solomon 10780 (holotype US; isotype MO).

The species resembles *Lepidaploa sordidopapposa* in the dark involucre and the brownish color of the pappus, but it does not seem closely related. The species is distinctive in the subglabrous aspect of the stems and leaves, the narrowly petiolate vegetative leaves, and the lax, seriate cymes with distinct, foliose bracts.

Lepidaploa sordidopapposa (Hieron.) H. Robinson, comb. nov.

Vernonia sordidopapposa Hieron., Bot. Jahrb. Syst. 22:697. 1897. Bolivia, Ecuador, Peru. Pollen G.

The species is extended to include numerous specimens that have recently been annotated as *Vernonia mapirensis* by Jones for his study of the tribe in Peru (Jones 1980). The present species seems to be characterized by the often crowded heads on shortened inflorescence branches, by the involucre remaining nearly cylindrical when dry, and by the dark pappus. The specimens show a great variation in length of the leaf pubescence and density of involucral pubescence.

Lepidaploa sororia (DC.) H. Robinson, comb. nov.

Vernonia sororia DC., Prodr. 5:40. 1836. *V. coulonii* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):93. 1873. Brazil (Espirito Santo, Rio de Janeiro). Pollen G.

As indicated by Robinson (1987c), the DeCandolle species is not a synonym of *Cyrtocymura scorpioides,* but is an older name for the species that has been known as *Vernonia coulonii.*

Lepidaploa stenophylla (Less.) H. Robinson, comb. nov.

Vernonia stenophylla Less., Linnaea 6:667. 1831. *V. corallophila* Gleason, Bull. Torrey Bot. Club 40:309. 1913. *V. nematophylla* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26:100. 1929. Cuba, Hispaniola. Pollen C.

"Fieldwork supported by the National Science Foundation"

BOLIVIA

COMPOSITAE
Lepidaploa solomonii H.Robinson
Holotype
Dept. La Paz, Prov. Murillo.
44.0 km below Lago Zongo dam, vicinity of Cahua hydroelectric plant.
16°03'S, 68°01'W, elev. 1200 m.
Moist forest, disturbed, alternating with Chacos and secondary forest.

Shrub, 2 m.

12-15 Sept. 1983
J.C. Solomon 10780
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

UNITED STATES
3149580
NATIONAL HERBARIUM

Fig. 62. Holotype of *Lepidaploa solomonii* H. Robinson, Solomon 10780 (US).

Lepidaploa subsquarrosa (DC.) H. Robinson, comb. nov.

Chysocoma paniculata Vell., Fl. Flumin. 327. 1825, non *C. paniculata* [Walter] Gmel. 1792. *Vernonia subsquarrosa* DC., Prodr. 5:41. 1836. *V. albiflora* Gardner, London J. Bot. 6:224. 1847. Brazil (Espirito Santo, Rio de Janeiro, São Paulo). Pollen G, Figs. 28–31.

The species has usually been recognized under the invalid name *Vernonia geminata* Less. Lessing (1829) was not naming a new species but was erroneously identifying Brazilian material as the Colombian *V. geminata* H.B.K. (=*Lepidaploa canescens*). Later attempts (DeCandolle 1836, Baker 1873) to use the name sensu Lessing (exclusively in the atypical sense) were totally invalid. The oldest acceptable name for the species is here raised from synonymy.

Lepidaploa tarijensis (Griseb.) H. Robinson, comb. nov.

Vernonia sericea var. *tarijensis* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24:163. 1879. *V. tarijensis* (Griseb.) Hieron., Bot. Jahrb. Syst. 22:682. 1897. Argentina, Bolivia. Pollen G.

Lepidaploa tenella (D. Nash) H. Robinson, comb. nov.

Vernonia tenella D. Nash, Fieldiana, Bot. 36:74. 1974. Guatemala. Pollen C/G.

Lepidaploa tombadorensis (H. Robinson) H. Robinson, comb. nov.

Vernonia tombadorensis H. Robinson, Phytologia 45:187. 1980. Brazil (Bahia). Pollen D, Figs. 40–42.

Lepidaploa tortuosa (L.) H. Robinson, comb. nov.

Conyza tortuosa L., Sp. Pl. 862. 1753. *C. scandens* Mill., Gard. Dict. ed. 8. *Conyza* no. 11. 1768. *Vernonia schiedeana* Less., Linnaea 6:399. 1831. *V. seemaniana* Steetz, Bot. Voy. Herald 139. 1854. *V. tortuosa* (L.) Blake, Proc. Biol. Soc. Wash. 39:144. 1926. Mexico (Chiapas, Oaxaca, Veracruz), Guatemala, Belize, Honduras, El Salvador, Costa Rica, Panama. Pollen G.

Lepidaploa tovarensis (Gleason) H. Robinson, comb. nov.

Vernonia tovarensis Gleason, Amer. J. Bot. 19:753. 1932. Venezuela. Pollen *Aynia*-type, Figs. 19–24.

Lepidaploa trichoclada (Gleason) H. Robinson, comb. nov.

Vernonia trichoclada Gleason, Bull. Torrey Bot. Club 52:184. 1925. Peru. Pollen G.

This central Peruvian species is resurrected from the synonymy of the Bolivian and southern Peruvian *Lepidaploa mapirensis,* from which it differs in the larger size of the heads, the more erect to retrorse pubescence, and the more oblong leaves with widely separated veins. *Lepidaploa trichoclada* is like the more recently described *L. retrosetosa* of southern Peru in the numerous outer involucral bracts that are as long as the inner bracts. But the latter species has ovate, remotely denticulate leaves with rounded bases and large, foliose bracts in the inflorescence. *Lepidaploa trichoclada* generally resembles the Bolivian *L. tristis,* but the latter has shorter outer involucral bracts and has the heads often paired at the nodes.

Lepidaploa trilectorum (Gleason) H. Robinson, comb. nov.

Vernonia trilectorum Gleason, Bull. Torrey Bot. Club 52:186. 1925. Colombia. Pollen G.

Lepidaploa trinitatis (Ekman) H. Robinson, comb. nov.

Vernonia trinitatis Ekman, Ark. Bot. 13(15): 39. 1914. Trinidad, Venezuela. Pollen C; $N = 51_{II}$ (Keeley 1978).

Lepidaploa tristis (Hieron.)
H. Robinson, comb. nov.

Vernonia tristis Hieron., Bot. Jahrb. Syst. 22:683. 1897. Bolivia. Pollen G.

Lepidaploa uniflora (Miller)
H. Robinson, comb. nov.

Conyza uniflora Miller, Gard. Dict. ed. 8. *Conyza* no. 13. 1768. *Vernonia ctenophora* Gleason, Bull. Torrey Bot. Club 46: 243. 1919. Mexico (Campeche), Guatemala, Belize. Pollen C.

Lepidaploa urbaniana (Ekman ex Urban)
H. Robinson, comb. nov.

Vernonia urbaniana Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:99. 1929. Cuba. Pollen C.

Lepidaploa verticillata
(Proctor ex Adams) H. Robinson,
comb. nov.

Vernonia verticillata Proctor ex Adams, Phytologia 21:409. 1971. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa viminalis (Gleason)
H. Robinson, comb. nov.

Vernonia viminalis Gleason, Bull. New York Bot. Gard. 4:184. 1906. Cuba. Pollen C/G.

Lepidaploa violiceps (H. Robinson)
H. Robinson, comb. nov.

Vernonia violiceps H. Robinson, Phytologia 45:160. 1980. Ecuador. Pollen C.

Lepidaploa virentiformis (Malme)
H. Robinson, comb. nov.

Vernonia virentiformis Malme, Ark. Bot. 24A(8):8. 1932. Bolivia (Beni), Brazil (Mato Grosso). Pollen C.

Lepidaploa wrightii (Sch.Bip.)
H. Robinson, comb. nov.

Vernonia wrightii Sch.Bip., J. Bot. 1:234. 1863. Cuba. Pollen C/G.

Lepidaploa yunquensis (Gleason)
H. Robinson, comb. nov.

Vernonia yunquensis Gleason, Bull. New York Bot. Gard. 4:191. 1906. Cuba.

Acknowledgments

The pollen specimens and photographic prints were prepared by Brian Kahn, Mary Sangrey, and Barbara Eastwood using facilities of the Botany Department Palynological Laboratory and darkroom. The photographs were taken by Suzanne Braden and Brian Kahn of the National Museum of Natural History SEM Laboratory using a Hitachi S-570 scanning electron microscope. Photographs of holotypes were prepared by Victor E. Krantz, Staff Photographer, National Museum of Natural History. Some prints were also prepared by Sherry Pittam and Suzanne Fredericq at the Department of Botany. The editorial efforts of Dr. David Lellinger of the Department of Botany are greatly appreciated.

Literature Cited

Aristeguieta, L. 1964. Compositae. *In* T. Lasser, ed., Flora de Venezuela 10:i–xiii, 1–941, indice 1–16.

Badillo, V. M. 1982. *Vernonia marguana* Cuatr., nueva para Venezuela.—Ernstia 8:7.

———. 1984. Sobre *Vernonia gracilis* HBK. y *V. moritziana* Sch.Bip.—Ernstia 23:12–13.

Baker, J. B. 1873. Compositae. I. Vernoniaceae. *In* C. F. P. Martius, ed., Flora Brasiliensis 6(2):1–180.

Bartling, F. G. 1830. Ordines naturales plantarum. Dieterich, Göttingen, 498 pp.

Bentham, G., & J. D. Hooker. 1873. Compositae. *In* Genera Plantarum 2(1):163–533.

Cabrera, A. L. 1944. Vernonieas Argentinas (Compositae).—Darwiniana 6:265–379.

Cassini, H. 1817a. Aperçu des genres nouveaux formés par M. Henri Cassini dans la famille des Synanthérées. Troisième fascicule.—Bulletin des Sciences de La Société Philomatique de Paris 1817:31–34.

———. 1817b. Aperçu des genres nouveaux formés par M. Henri Cassini dans la famille des Synanthérées. Quatrième fascicule.—Bulletin des Sciences de La Société Philomatique de Paris. 1817:66–70.

———. 1823. Lépidaple, *Lepidaploa.* Pp. 16–24 *in* G. Cuvier, ed., Dictioniare des Sciences Naturelles 26. Levrault Strassbourg. [Reprinted in R. M. King & H. W. Dawson, eds., 1975, Cassini on Compositae, 3 volumes. Oriole Editions, New York.]

———. 1825. Oliganthe, *Oliganthes.* Pp. 18–20 *in* G. Cuvier, ed., Dictioniare des Sciences Naturelles 36. Levrault Strassbourg. [Reprinted in R. M. King & H. W. Dawson, eds., 1975, Cassini on Compositae, 3 volumes. Oriole Editions, New York.]

———. 1830. Zyégée, *Zoegea.* Pp. 560–619 *in* G. Cuvier, ed., Dictioniare des Sciences Naturelles 60. Levrault Strassbourg. [Reprinted in R. M. King & H. W. Dawson, eds., 1975, Cassini on Compositae, 3 volumes. Oriole Editions, New York.]

DeCandolle, A. P. 1836. Prodromus systematis naturalis regni vegetabilis, vol. 5. Treuttel & Würtz, Paris, 706 pp.

Gleason, H. A. 1906. A revision of the North American Vernonieae.—Bulletin New York Botanical Garden 4:144–243.

———. 1922. Vernonieae.—North American Flora 33(1):47–110.

———. 1923. Evolution and geographical distribution of the genus *Vernonia* in North America.—American Journal of Botany 10:187–202.

Humboldt, F. H. A. von, A. J. Bonpland, & C. S. Kunth. 1818. Compositae. *In* Nov. Gen. Sp., folio edition, vol. 4:1–246, pl. 301–412.

Jeffrey, C. 1988. The Vernonieae in East Tropical Africa.—Kew Bulletin 43:195–277.

Jones, S. B. 1977. Vernonieae: Systematic review. Pp. 503–447 *in* V. H. Heywood, J. B. Harborne, & B. L. Turner, eds., The biology and chemistry of the Compositae. Academic Press, London, 1189 pp.

———. 1979a. Chromosome numbers of Vernonieae (Compositae).—Bulletin of the Torrey Botanical Club 106:79–84.

———. 1979b. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the New World.—Rhodora 81:425–447.

———. 1980. The Vernonieae. *In* J. F. Macbride, Flora of Peru.—Fieldiana, Botany n.s. 5:22–73.

———. 1981. Synoptic classification and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the Old World.—Rhodora 83:59–75.

Keeley, S. C. 1978. A revision of the West Indian vernonias (Compositae).—Journal of the Arnold Arboretum 59:360–413.

———. 1982. Morphological variation and species recognition in the Neotropical taxon *Vernonia arborescens* Compositae.—Systematic Botany 7:71–84.

Kingham, D. L. 1976. A study of the pollen morphology of tropical African and certain other Vernonieae (Compositae).—Kew Bulletin 31:9–26.

Lessing, C. F. 1829. De Synanthereis herbarii regii berolinensis dissertatio prima.—Linnaea 4:240–288, 290–356, pl. II.

Reichenbach, H. G. L. 1828. Conspectus regni vegetabilis. Cnobloch, Leipzig, 294 pp.

Robinson, H. 1980. New species of the Vernonieae (Asteraceae). V. Additions to *Vernonia* from Brasil.—Phytologia 45:166–208.

———. 1987a. Studies of the *Lepidaploa* complex (Vernonieae: Asteraceae). I. The genus *Stenocephalum* Sch. Bip.—Proceedings of the Biological Society of Washington 100:578–583.

———. 1987b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). II. A new genus, *Echinocoryne.*—Proceedings of the Biological Society of Washington 100:584–589.

———. 1987c. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). III. Two new genera, *Cyrtocymura* and *Eirmocephala.*—Proceedings of the Biological Society of Washington 100: 844–855.

———. 1988a. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). IV. The new genus, *Lessingianthus.*—Proceedings of the Biological Society of Washington 101:929–951.

———. 1988b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). V. The new genus, *Chrysolaena.*—Proceedings of the Biological Society of Washington 101:952–958.

———. 1988c. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). VI. A new genus, *Aynia.*—Proceedings of the Biological Society of Washington 101:959–965.

———. 1989. *Acilepidopsis,* a new genus of Vernonieae from South America (Asteraceae).—Phytologia 67:289–292.

———, F. Bohlman, & R. M. King. 1980. Chemosystematic notes on the Asteraceae. III. Natural subdivision of the Vernonieae.—Phytologia 46: 421–436.

———, & V. A. Funk. 1987. A phylogenetic analysis of *Leiboldia, Lepidonia,* and a new genus *Stramentopappus* (Vernonieae: Asteraceae).—Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 108:213–228.

———, & B. Kahn. 1986. Trinervate leaves, yellow flowers, tailed anthers, and pollen variation in *Distephanus* Cassini (Vernonieae: Asteraceae).—Proceedings of the Biological Society of Washington 99:493–501.

———, & R. M. King. 1979. *Mattfeldanthus mutisioides* gen. et spec. nov. (Asteraceae: Vernonieae) from Bahia, Brazil.—Willdenowia 9:9–12.

Spach, E. 1841. Histoire naturelle des végétaux, vol. 10. Phanaérogames. Roret, Paris, 572 pp.

Stix, E. 1960. Pollenmorphologische untersuchungen an Compositen.—Grana Palynologica 2(2):41–104, pl. 1–21.

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 19 December 1989 in Vol. 46, Part 4 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

2683 *Gryphaea pitcheri* Morton, 1834 (currently *Texigryphaea pitcheri*; Mollusca, Bivalvia): proposed conservation.

2554 *Myriochele* Malmgren, 1867 and *Myriochele oculata* Zaks, 1923 (Annelida, Polychaeta): proposed conservation.

2637 *Buthus vittatus* (currently *Centruroides vittatus*; Arachnida, Scorpionida): proposed recognition of Wood (1863) as author of the specific name and designation of a neotype, and *Centrurus hentzi* (currently *Centruroides hentzi*) Banks, 1904: proposed conservation of the specific name.

2711 *Shoemakerella* Pirlot, 1936 (Crustacea, Amphipoda): proposed designation of *Lysianax cubensis* Stebbing, 1897 as the type species.

2685 *Corisa verticalis* Fieber, 1851 (currently *Trichocorixa verticalis*; Insecta, Heteroptera): proposed conservation of the specific name.

2678 *Curculio viridicollis* Fabricius, 1792 (currently *Phyllobius viridicollis*; Insecta, Coleoptera): proposed conservation of the specific name, and *Rhyncolus* Germar, 1817: proposed designation of *Curculio ater* Linnaeus, 1758 as the type species.

2676 *Ochthebius* Leach, 1815 (Insecta, Coleoptera): proposed conservation of *Elophorus marinus* Paykull, 1798 as the type species.

2702 *Culex stigmatosoma* Dyar, 1907 and *C. thriambus* Dyar, 1921 (Insecta, Diptera): proposed conservation of the specific names by the suppression of *C. peus* Speiser, 1904.

2694 *Exoprosopa* Macquardt, 1840 (Insecta, Diptera): proposed confirmation of *Anthrax pandora* Fabricius, 1805 as the type species.

2719 *Musca heraclei* Linnaeus, 1758 (currently *Euleia heraclei*; Insecta, Diptera): proposed conservation of *heraclei* as the correct spelling of the specific name.

2688 *Callionymus pusillus* Delaroche, 1809 (Osteichthyes, Perciformes): proposed conservation of the specific name.

1173 *Muraena* Linnaeus, 1758 (Osteichthyes, Anguilliformes): proposed confirmation of *Muraena helena* Linnaeus, 1758 as the type species, so conserving *Anguilla* Shaw, 1803.

2684 *Haplocanthosaurus* Hatcher, 1903 (Reptilia, Saurischia): proposed conservation.

2691 *Atheris* Cope, 1862 (Reptilia, Serpentes): proposed conservation, and proposed confirmation of *Vipera chlorechis* Pel, [1851] as the valid name of the type species.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with 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 Stop 108, Smithsonian Institution, Washington, D.C. 20560.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed in order of receipt by a board of Associate Editors and appropriate referees.

Proofs.—First proofs are submitted to authors for correction and approval. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, changes at proof stages, and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

Presentation.—Manuscripts should be typed **double-spaced throughout** (including tables, legends, and footnotes) on one side of 8½ × 11 inch sheets, with at least one inch of margin all around. Submit three copies complete with tables, figure captions, and figures (plus originals of the illustrations), and retain an author's copy. Pages must be numbered consecutively. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s') Address(es), Appendix, Figure Legends, Figures (each numbered and identified), Tables (**double-spaced throughout,** each table numbered with an Arabic numeral and with heading provided).

Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is required for descriptions and diagnoses. Literature citations in the text should be in abbreviated style (author, date, page), except in botanical synonymies, with unabbreviated citations of journals and books in the Literature Cited sections. Direct quotations in the text must be accompanied by author, date, **and pagination.** The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate figure and table placement in pencil in the margin of the manuscript. Plan illustrations in proportions that will efficiently use space on the type bed of the Proceedings. **Original illustrations should not exceed 15 × 24 inches.** Figures requiring solid black backgrounds should be indicated as such when the manuscript is submitted, but should not be masked.

CONTENTS

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 103 NUMBER 3
25 SEPTEMBER 1990
ISSN 0006-324X

PROCEEDINGS

Editor: C. Brian Robbins

Associate Editors

Classical Languages: George C. Steyskal
Plants: David B. Lellinger
Insects: Wayne N. Mathis
Invertebrates: Stephen D. Cairns
Frank D. Ferrari
Rafael Lemaitre
Vertebrates: G. David Johnson

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

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

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

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

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 501–508

COMMENTS ON THE NOMENCLATURE OF SOME NEOTROPICAL BATS (MAMMALIA: CHIROPTERA)

Alfred L. Gardner and Carolyn S. Ferrell

Abstract.—We examine four nomenclatural problems concerning Neotropical bats and conclude that *Platyrrhinus* has priority over *Vampyrops*; *Anthorhina* is a junior objective synonym of *Tonatia*; and Cabrera, as first reviser, selected the spelling *Molossus barnesi* over *M. burnesi.* We recommend that Wied-Neuwied, not Oken, be considered the author of *Diclidurus albus,* although the code of zoological nomenclature does not directly address this particular situation.

We resolve four nomenclatural problems concerning Neotropical bats that arose during the course of research on Latin American mammals. The first problem concerns use of *Platyrrhinus* Saussure, 1860, versus *Vampyrops* Peters, 1865a, for a genus of relatively common fruit-eating bats (Phyllostomidae: Stenodermatinae). Next, we find that the name *Anthorhina* Lydekker, *in* Flower & Lydekker, 1891, (Phyllostomidae: Phyllostominae) has been misapplied. Third, confusion still exists over which spelling, *Molossus burnesi* or *M. barnesi* Thomas, 1905, (Molossidae) is correct according to the International Code of Zoological Nomenclature (ICZN 1985). Last, we examine the issue of authorship raised by Carter & Dolan (1978) concerning the name *Diclidurus albus.*

Platyrrhinus versus *Vampyrops*

Platyrrhinus was proposed by Saussure (1860:429) to distinguish as a group the three taxa Gervais (1856) included in his *Artibaeus* [sic] from true *Artibeus* Leach, 1821; therefore, *Platyrrhinus* Saussure is an exact equivalent of *Artibaeus* Gervais (unjustified emendation of *Artibeus* Leach). The three species of *Platyrrhinus* (Saussure, 1860) are: *P. lineatus* (Geoffroy St.-Hilaire, 1810); *P. undatus* (Gervais, 1856), = *Stenoderma rufum* Desmarest, 1820; and *P. jamaicensis* (Gervais, 1856), = *Ariteus flavescens* (Gray, 1831), not *Artibeus jamaicensis* Leach, 1821. Saussure (1860) said the most common species is *P. lineatus*; he did not select a type species for *Platyrrhinus.*

The first use of *Vampyrops* was in a prospectus of the Chiroptera by Peters (1865a: 257) as a subgenus of *Stenoderma.* Peters (1865a) listed *Platyrhinus* [sic] Saussure and *Artibeus* Gervais as the only synonyms of *Vampyrops.* These names and their respective authors constitute an indication, in the sense of Article 12 of the International Code of Zoological Nomenclature (ICZN 1985), validating *Vampyrops* from Peters (1865a), and not Peters (1865b) as usually cited. *Artibaeus* Gervais, 1856, and *Platyrrhinus* Saussure, 1860, are identical in content. *Artibaeus* Gervais is an unjustified emendation of *Artibeus* Leach, 1821, first used by Agassiz (1847); therefore, it is not an available name for this group. *Vampyrops* Peters (1865a) should be considered a new name for *Platyrrhinus* Saussure, 1860.

Peters (1865b) commented that *Platyrhinus,* which here and earlier (1860:754, 1865a:257) he spelled with one "r," had already been used in 1798 for a coleopteran. Obviously he considered the double-r spelling of *Platyrrhinus* Saussure to be equivalent to *Platyrhinus* Schellenberg, 1798, a genus of anthribid beetles. In this later paper, Peters (1865b:356, footnote) used the name *Platyrhinus* Saussure in the synonymies of *Artibeus* Leach, *Phyllops,* and *Vampyrops.* Listing *Platyrhinus* as a synonym of *Artibeus* implies a misinterpretation of Saussures' intent, because Saussure used *Platyrrhinus* to distinguish the three taxa he clearly excluded from *Artibeus.*

When Peters (1865b:356) proposed the name *Phyllops,* he listed *A. jamaicensis* Gervais under *Ph*[*yllops*]. *albomaculatus* Gundlach and *A. undatus* Gervais under *Ph*[*yllops*]. *personatus* Natterer [Wagner]. On the same page Peters listed "*Ph*[*yllostoma*]. *lineatum* Geoffroy, Gervais, and *V*[*ampyrops*]. *vittatus* Ptrs.," as the only species under *Vampyrops.* Thus he restricted *Vampyrops* to only one of the species Saussure (1860) included in *Platyrrhinus.* Peters (1865b) did not indicate a type species for *Vampyrops.*

Dobson (1878) listed *Platyrrhinus* Saussure as a synonym under both *Artibeus* Leach and *Vampyrops* Peters, but inexplicably not under *Stenoderma* Geoffroy St.-Hilaire, in the synonymy of which he included *A. jamaicensis* Gervais and *A. undatus* Gervais.

Thomas (1900:269) designated *Phyllostoma lineatum* Geoffroy St.-Hilaire as the type species of *Vampyrops* Peters (1865b). Obviously, *Phyllostoma lineatum* Geoffroy St.-Hilaire is the type species of *Vampyrops* Peters (1865a:257), which is the earliest available date of its usage. Because *Vampyrops* Peters (1865a) must be considered a new or replacement name for *Platyrrhinus* Saussure, 1860, *Phyllostoma lineatum* Geoffroy St.-Hilaire is the type species of *Platyrrhinus* as well. Palmer (1904:545) also identified the type species of *Platyrrhinus* Saussure as *Phyllostoma lineatum* Geoffroy St.-Hilaire, and he too believed the name to be preoccupied by *Platyrhinus* Clairville [Schellenberg], 1798.

As eloquently stated by de la Torre & Starrett (1959), *Vampyrops* had enjoyed universal usage in this century until Hershkovitz (1958:613) noted in a list of mammalian genera that *Platyrrhinus* antedated *Vampyrops.* The basic thesis of de la Torre & Starrett's report (1959) is that Fabricius' (1801:408) spelling, *Platyrrhinus,* was an unjustified emendation of *Platyrhinus* Clairville [Schellenberg], 1798, and invalidated any subsequent name of the same spelling because of homonymy. If this were true, *Vampyrops* would be the earliest available name for this genus of bats.

Hall & Kelson (1959:131) listed *Vampyrops* as a junior synonym of *Platyrrhinus* without comment. Hall (1981:144) continued to use *Platyrrhinus* in place of *Vampyrops* and expressed his opinion that *Platyrrhinus* Fabricius, 1801, was merely an incorrect subsequent spelling of *Platyrhinus* Clairville [Schellenberg], 1798, and had no nomenclatural status and, therefore, could not invalidate *Platyrrhinus* Saussure.

We examined Fabricius (1801) and found the double-r spelling of *Platyrhinus* appears only in synonymy (p. 408) and is simply an incorrect subsequent spelling, not an emendation as claimed by de la Torre & Starrett (1959). Then, with the assistance of specialists much more familiar with anthribid beetles and the older entomological literature, we examined the literature up to 1860. We found that *Platyrhinus* as well as Platyrhinidae were commonly spelled with either one or two r's, sometimes with both spellings in the same publication. However, each instance of the double-r spelling was clearly another incorrect subsequent spelling of *Platyrhinus* Schellenberg, not an emendation. We have not carefully examined the post-1860 entomological literature, because any emendation after that date would be invalidated by *Platyrrhinus* Saussure. Our conclusion is that *Platyrrhinus* Saussure, 1860, as used by Hall (1981), Hall & Kelson (1959), and Hershkovitz (1958), is the earliest available name for the genus of bats often referred to under the name of its junior objective synonym *Vampyrops* Peters, 1865a.

There has been confusion over the identity of the author of the anthribid beetle genus *Platyrhinus.* The work in which the name appears was published simultaneously in French and German. The text is unusual because its German original form, appears on left-facing pages and the translated French form appears first on right-facing pages of each leaf. Schellenberg is the author of the original version; the French translation is by Clairville. Clairville has been credited by a number of authors (e.g., de la Torre & Starrett 1959, Gutfleisch 1859, Hall 1981, Palmer 1904) with the name *Platyrhinus* either because it appears in the French translation ahead (p. 112) of its appearance in the original German (p. 113), or because it was presumed to be the original text as the French translation appears before the German version.

Status of *Anthorhina* Lydekker, 1891

Anthorhina Lydekker, *in* Flower & Lydekker, 1891, is a replacement name for *Tylostoma* Gervais, 1856, which is preoccupied by *Tylostoma* Sharpe, 1849, a genus of gastropods. When proposed by Gervais (1856:49), *Tylostoma* contained two species: *Tylostoma bidens* (=*Vampyrus bidens* Spix) and *Tylostoma crenulatum* (=*Phyllostoma crenulatum* Geoffroy St.-Hilaire). He did not indicate a type species. Palmer (1904:698), while saying *Tylostoma* Gervais was preoccupied by *Tylostoma* Sharpe, 1849, gave "*Phyllostoma bidens* Spix" as the type species.

We examined the content of *Tylostoma* Gervais because we knew that *Anthorhina* Lydekker, *in* Flower & Lydekker, 1891, was a replacement name and that most authors (e.g., Hall 1981, Hall & Kelson 1959, and Miller 1907) considered *Phyllostoma crenulatum* Geoffroy St.-Hilaire to be the type species of *Anthorhina.* However, Palmer (1904) had already in effect designated *Phyllostoma bidens* Spix as the type species of *Tylostoma* Gervais, and (p. 108) the type species of *Anthorhina* (which he consistently misspelled as *Anthorina*). Furthermore, we knew that *Phyllostoma bidens* Spix (=*Vampyrus bidens* Spix, 1823) was the type species of *Tonatia* Gray, 1827, and that *Phyllostoma bidens* could not be the type species of both *Anthorhina* and *Tonatia* unless the genera were synonyms.

In his description of *Tylostoma,* Gervais gave the combined number of premolars and molars as five above and below (2/2 premolars, 3/3 molars). Peters (1856:304) suggested that an examination of Gervais' specimen of "*V*[*ampyrus*]. (*Tylostoma*) *bidens* Spix" might show another premolar in the lower tooth row. Tomes (1861:107) also gave the premolars as two above and below for *Tylostoma,* cited *Vampyrus bidens* Spix as an example, and listed *Phyllostoma childreni* Gray, 1838, in the synonymy. Peters (1865c:514) listed *Phyllostoma childreni* Gray and *Tylostoma bidens* Gervais under *Tylostoma,* saying that, although he did not know these species from personal observation, they could not be identical to *Vampyrus bidens* Spix as claimed by Gervais (1856) and Tomes (1861). The reason was he had examined Spix's specimen and it had six lower cheek teeth on each side. Based on its dental formula, Peters (1865c:509) cited *Vampyrus bidens* Spix under the genus *Lophostoma* (=*Tonatia* Gray, 1827). Gray (1866:114) included *Phyllostoma childreni* under *Tylostoma* as *T. childreni* and gave the premolar count as two above and below.

After visiting the Leiden and British Museums, Peters (1866:674) said the type of *Phyllostoma childreni* Gray had three lower premolars and was the same as *Lophostoma bidens* (Spix). Later, Peters (1869) also changed his opinion about *Tylostoma bidens* Gervais when he was able to examine Gervais' specimen in the Paris Museum. Peters (1869:396) confirmed that it too was the same species as *Vampyrus bidens* Spix with three lower premolars on each side, not two as described by Gervais. Therefore Gervais' identification of his specimen with *Vampyrus bidens* Spix was correct, but the tooth count was wrong. However, as Peters (1869) confirmed, *Phyllostoma crenulatum* Geoffroy St.-Hilaire, had only two lower premolars and did fit the criteria Gervais (1856:49) established for *Tylostoma.*

Subsequently (e.g., Dobson 1878), *Tylostoma* Gervais was used in the restricted sense exclusively for *Phyllostoma crenulatum* Geoffroy St.-Hilaire, or its synonyms. This also is true of the replacement name *Anthorhina* Lydekker, *in* Flower & Lydekker, after 1891. Simpson (1945) treated *Anthorhina* and *Mimon* as congeneric; as did Handley (1960) who said, "the nominal genera *Anthorhina* and *Mimon* are not distinguishable even as subgenera." However, Husson (1962, 1978) argued for the continued use of *Anthorhina* at the generic level. Other authors (Cabrera 1958, Gardner & Patton 1972, Goodwin & Greenhall 1961, Hill 1964) have used *Anthorhina* as a subgenus of *Mimon.* Although usage following Dobson (1878) clearly was restricted (see ICZN 1985:Article 69b) to the taxon originally described as *Phyllostoma crenulatum* or its synonyms, that usage was invalidated by Palmer (1904) when he designated *Phyllostoma bidens* as the type species of *Tylostoma.*

Our conclusion, in accordance with Article 69a (ICZN 1985), is that *Tylostoma* Gervais, 1856, with type species *Tylostoma bidens* (Spix, 1823) by subsequent designation (Palmer 1904), is a junior objective synonym of *Tonatia* Gray, 1827, because they have the same type species. Therefore, the replacement name *Anthorhina* Lydekker, *in* Flower & Lydekker, 1891, also is a junior synonym of *Tonatia.* Regardless of whether or not the taxa previously called *Anthorhina crenulatum* (Geoffroy St.-Hilaire, 1803) and *Mimon koepckeae* Gardner & Patton, 1972, are considered distinct from the genus *Mimon* at either the generic or subgeneric level, the name *Anthorhina* cannot be used for them. If these taxa are considered distinct genera or subgenera, there is no name available for them. Incidentally, most authors date *Phyllostoma crenulatum* from Geoffroy St.-Hilaire, 1810; however, the correct citation is *Phyllostoma crenulatum* Geoffroy St.-Hilaire, 1803.

Molossus burnesi versus *M. barnesi*

In the original description (Thomas 1905), the spelling *M. burnesi* in the heading of the account was a typesetter's error. Thomas (1905:585) used the spelling *M. barnesi* in the text and said the specimen was presented by W. Barnes. Cabrera (1958:129) used the spelling *Molossus barnesi,* listed both *M. burnesi* and *M. barnesi* in its synonymy, and said that *M. burnesi* was a typographical error. Husson (1962:259), citing Article 32b of the International Code of Zoological Nomenclature (ICZN 1961), claimed that Miller (1913), as first reviser, had fixed the spelling as *M. burnesi,* and that Cabrera's (1958) action was invalid. Carter & Dolan (1978:96) cited Article 32a(ii) and Article 32c (ICZN 1961) in their claim that, because there was internal evidence showing *M. burnesi* to be an error, the name was an incorrect original spelling, had no status, and should be corrected. They corrected the spelling to *M. barnesi.*

Actually Carter & Dolan (1978) and Husson (1962) were both correct as far as the Code is concerned. The original description of *M. barnesi* contained two original spellings of the name as well as internal evidence that the first spelling (*M. burnesi*) was incorrect. Therefore, the first reviser could either select one of the original spellings or cite internal evidence that the first spelling was an error and make the correction. Carter & Dolan (1978) and Husson (1962), however, apparently misunderstood the meaning of the term "reviser" as intended by the Code (ICZN 1961, 1985). To revise a nomenclatural problem involving two or more original spellings, the reviser must show awareness of the different names or spellings and make a selection from among them. Miller (1913) revised the content of the genus *Molossus,* but did not revise the species *M. barnesi.* Cabrera (1958), as the first reviser, selected the spelling *M. barnesi* and put *M. burnesi* in synonymy. Although valid, the action by Carter & Dolan (1978) was unnecessary.

Authorship of *Diclidurus albus*

When Wied-Neuwied (1820:column 1629) described *Diclidurus* in Oken's Isis, he intended to apply the name *D. freyreisii* (in honor of the collector) to the only known species. Oken (*in* Wied-Neuwied 1820:column 1630, footnote) as editor, substituted *D. albus* for *D. freyreisii* saying that while his majesty [Wied-Neuwied] thought to name the species *D. freyreisii,* we have avoided that because science does not need honors. In other words, he did not believe in patronymics and considered *albus* descriptive of a white bat. Carter & Dolan (1978), although following tradition in assigning authorship of *D. albus* to Wied-Neuwied, suggested that Oken should be credited with authorship. Both Schinz (1821) and Wied-Neuwied (1826) attributed the name to Oken. The suspicion (Carter & Dolan 1978:23) that Wied-Neuwied was unaware of Oken's publication of the account in which the description of *D. albus* appears is unfounded. No one questions attributing authorship of *Diclidurus* to Wied-Neuwied. Clearly Wied-Neuwied prepared the report and Oken made the changes without informing him. Does that make Oken the author of *D. albus*?

This peculiar situation does not appear to be addressed by Article 50 or any other provision of the Code (ICZN 1985). Article 50 states, "The author of a name is the person who first publishes it in a way that satisfies the criteria of availability. . . . If it is clear from the contents of the publication that only one of joint authors, or some other person, is alone responsible both for the name and for satisfying the criteria of availability other than publication, then that person is the author of the name." Wied-Neuwied is alone responsible for satisfying the criteria of availability, but he did not provide the name. Oken clearly is responsible for the name, but he did not satisfy the criteria of availability.

One approach simply is to state the obvious. In the sense of the Code, a name must have an author(s). It follows that if two people are involved and one cannot be the author, then the other must be the author. The name was changed by Oken; however, because Oken did not otherwise satisfy the criteria of availability, he cannot be the author. Therefore, Wied-Neuwied is the author by default.

Another approach is to claim that Oken's substitution of *D. albus* constitutes an unjustified emendation of *D. freyreisii,* the name Wied-Neuwied intended. The major problem with this approach is that *D. freyreisii* was not an established name by 1820. Wied-Neuwied (1826:247) seemed resigned to the name *D. albus* saying that he would have continued using *D. freyreisii* (as he did in 1821) if the legend under the figure (Wied-Neuwied 1820) had not been dropped. Apparently, the legend contained the name *D. freyreisii.* Whichever argument is invoked, we recommend continuing the tradition to attribute authorship of *D. albus* to Wied-Neuwied and consider Oken's action as an example of an editor having gone beyond proper editorial limits.

Acknowledgments

We are extremely grateful to the following persons in the Department of Entomology, National Museum of Natural History, for their assistance with the nomenclatural issues addressed herein: C. W. Sabrosky for patient instruction on interpreting the Code, F. C. Thompson for his insight concerning nomenclatural problems, and G. C. Steyskal for allowing us to draw on his wealth of knowledge of languages and assisting us with some of the older literature. B. Valentine, Ohio State University, was especially helpful during our review of the status of *Platyrrhinus* Saussure. We are grateful to him for checking references not immediately available to us and for sharing his knowledge of the older entomological literature.

Literature Cited

Agassiz, L. 1847. Nomenclator zoologicus, continens nomina systematica generum animalium tam viventium quam fossilium, secundum ordinem alphabeticum deposita, adjectis auctoribus, libris in quibus reperiuntur, anno editionis, etymologia et familiis, ad quas pertinent, in variis classibus. Fasciculus XII. Continens indicem universalem. Jent et Gassmann, Soloduri, viii + 393 pp. [Dated 1846 on inner title page (title differs from that given above), but 1847 on cover.]

Cabrera, A. 1958. Catálogo de los mamíferos de America del Sur.—Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoológicas 4(1):iv + 308 pp.

Carter, D. C., & P. G. Dolan. 1978. Catalog of type specimens of Neotropical bats in selected European museums.—Special Publications, The Museum, Texas Tech University 15:1–136.

de la Torre, L., & A. Starrett. 1959. Name changes and nomenclatural stability.—Natural History Miscellanea 167:1–4.

Desmarest, A. G. 1820. Mammalogie ou description des espèces de mammifères. Premier partie, contenant les ordres de bimans, des quadrumanes et des carnassiers. Pp. viii + 1–276 *in* Encylopédie Méthodique . . . , 196 vols. Veuve Agasse, Paris.

Dobson, G. E. 1878. Catalogue of the chiroptera in the collection of the British Museum. British Museum (Natural History), London, xlii + 567 pp., 29 pls.

Fabricius, J. C. 1801. Systema eleutheratorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus.—Bibliopolii Academici Novi, Kiliae, 2:1–687.

Flower, W. H., & R. Lydekker. 1891. An introduction to the study of mammals living and extinct. Adam and Charles Black, London, xvi + 763 pp.

Gardner, A. L., & J. L. Patton. 1972. New species of *Philander* (Marsupialia: Didelphidae) and *Mimon* (Chiroptera: Phyllostomidae) from Peru.—Occasional Papers of the Museum of Zoology, Louisiana State University 43:1–12.

Gervais, P. 1856. Deuxième mémoire. Documents zoologiques pour servir à la monographie des chéiroptères Sud-Américains. Pp. 25–88 *in* P. Gervais, ed., Mammifères. *In* Animaux nouveau ou rares recueillis pendant l'expédition dan les parties centrales de l'Amérique du Sud, de Río de Janeiro a Lima, et de Lima au Para; exécutée par ordre du gouvernement Français pendant les années 1843 à 1847, sous la direction du comte Francis de Castelnau. (F. de Castelnau, ed.). P. Bertrand, Paris, 1855, 1(2):1–116, 20 pls. [See Sherborn & Woodward, 1901, for date of publication.]

Geoffroy St.-Hilaire, E. 1803. Catalogue des mammifères du Muséum National d'Histoire Naturelle. Paris, 272 pp.

———. 1810. Sur les phyllostomes et les mégadermes, deux genres de la famille des chauve-souris.—Annales du Muséum d'Histoire Naturelle, Paris 15:157–198, pls. 9–12.

Goodwin, G. G., & A. M. Greenhall. 1961. A review of the bats of Trinidad and Tobago.—Bulletin of the American Museum of Natural History 122:187–302, pls. 7–46.

Gray, J. E. 1827. A synopsis of the species of the class Mammalia. Pp. 1–392 *in* The animal kingdom arranged in conformity with its organization, by the Baron Cuvier, . . . with additional descriptions of all the species hitherto named, and of many not before noticed, by Edward Griffith . . . and others. Geo. B. Whittaker, London, vol. 5.

———. 1831. Descriptions of some new genera and species of bats.—The Zoological Miscellany, Part 1, pp. 37–38.

———. 1838. A revision of the genera of bats (Vespertilionidae), and the description of some new genera and species.—Magazine of Zoology and Botany 2:483–505.

———. 1866. Revision of the genera of *Phyllostomidae,* or leaf-nosed bats.—Proceedings of the Zoological Society of London 1866:111–118.

Gutfleisch, V. 1859. Die Käfer Deutschlands. John. Phil. Diehl, Darmstadt, xvi + 661 pp.

Hall, E. R. 1981. The mammals of North America. Second edition. John Wiley & Sons, New York, 1:xviii + 600 + 90 pp.

———, & K. R. Kelson. 1959. The mammals of North America. Ronald Press Co., New York, xxx + 546 + 79 pp.

Handley, C. O., Jr. 1960. Descriptions of new bats from Panama.—Proceedings of the United States National Museum 112:459–479.

Hershkovitz, P. 1958. A geographical classification of Neotropical mammals.—Fieldiana: Zoology 36:581–620.

Hill, J. E. 1964. Notes on bats from British Guiana, with the description of a new genus and species of *Phyllostomidae.*—Mammalia 28:553–572.

Husson, A. M. 1962. The bats of Suriname.—Zoologische Verhandelingen, Rijksmuseum van Natuurlijke Historie, Leiden, 58:1–282, 30 pls.

———. 1978. The mammals of Suriname. E. J. Brill, Leiden, xxxiv + 569 pp., 160 pls.

ICZN. 1961. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology. International Trust for Zoological Nomenclature, London, xviii + 176 pp.

———. 1985. International Code of Zoological Nomenclature adopted by the XX General Assembly of the International Union of Biological Sciences.—International Trust for Zoological Nomenclature, London, xx + 338 pp.

Leach, W. E. 1821. The characters of seven genera of bats with foliaceous appendages to the nose.—Transactions of the Linnean Society of London 13:73–82, pl. 7.

Miller, G. S., Jr. 1907. The families and genera of bats.—Bulletin of the United States National Museum 57:xvii + 282 pp., 14 pls.

———. 1913. Notes on the bats of the genus Molossus.—Proceedings of the United States National Museum 46:85–92.

Palmer, T. S. 1904. Index generum mammalium.—North American Fauna 23:1–984.

Peters, W. 1856. Über die Chiropterengattungen *Mormops* und *Phyllostomata.*—Abhandlungen der Königlichen Preussische Akademie der Wissenschaften zu Berlin 1857:287–310, 2 pls.

———. 1860. Eine neue Gattung von Flederthieren, *Chiroderma villosum,* aus Brasilien vor.—Monatsberichte der Königlichen Preusschen Akademie der Wissenschaften zu Berlin 1861:747–755.

———. 1865a. Abbildungen zu einer Monographie der Chiropteren vor und gab eine Übersicht der von ihm befolgten systematischen Ordnung der bicher gehörigen Gattungen.—Monatsberichte der Königlichen Preusschen Akademie der Wissenschaften zu Berlin 1866:256–258.

———. 1865b. Über Flederthiere (*Vespertilio soricinus* Pallas, *Choeronycteris* Lichtenst., *Rhinophylla pumilio* nov. sp., *Artibeus fallax* nov. sp., *A. concolor* nov. sp., *Dermanura quadrivittatum* nov. sp., *Nycteris grandis* n. sp.).—Monatsberichte der Königlichen Preusschen Akademie der Wissenschaften zu Berlin 1866:351–359.

———. 1865c. Über die zu den *Vampyri* gehörigen Flederthiere und über die natürliche Stellung der Gattung *Antrozous.*—Monatsberichte der Königlichen Preusschen Akademie der Wissenschaften zu Berlin 1866:503–524.

———. 1866. Fernere Mittheilungen zur Kenntniss der Flederthiere, namentlich über Arten des Leidener und Britischen Museums.—Monatsberichte der Königlichen Preusschen Akademie der Wissenschaften zu Berlin 1867:672–681.

———. 1869. Über neue oder weniger bekannte Flederthiere, besonders des Pariser Museums.—Monatsberichte der Königlichen Preusschen Akademie der Wissenschaften zu Berlin 1869: 391–406.

Saussure, H. de. 1860. Note sur quelques mammifères du Mexique.—Revue et Magasin de Zoologie, Serie 2 12:1–11, 53–57, 97–110, 241–254, 281–293, 377–383, 425–431, 479–494, 4 pls. [Also printed as an independently-paginated, 82-page separate.]

Schellenberg, J. R. 1798. Helvetische Entomologie; oder Verzeichness der Schweizerischen Insekten nach einer methode geordnet. Orell, Füssli und Compagnie, Zürich, 1:1–149 + 4 unnumbered, 16 pls. [Translated by J. P. de Clairville, 1798. Entomologie Helvetique ou catalogue des insects de la Suisse rangées d'après une nouvelle methode.]

Schinz, H. 1821. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Säugethiere und Vógel. J. G. Cotta'schen Buchhandlung, Stuttgart und Tübingen, 1:xxxviii + 894 pp.

Sharpe, D. 1849. On *Tylostoma,* a proposed genus of gasteropodous mollusks.—The Quarterly Journal of the Geological Society of London 5: 376–380, pl. 9.

Sherborn, C. D., & B. B. Woodward. 1901. Dates of publication of the zoological and botanical portions of some French voyages.—Part II. Ferret and Galinier's 'Voyage en Abyssinie'; Lefebvre's 'Voyage en Abyssinie'; 'Exploration scientifique de l'Algérie'; Castelnau's 'Amérique du Sud'; Dumont d'Urville's 'Voyage de l'Astrolabe'; Laplace's 'Voyage sur la Favorite'; Jacquemont's 'Voyage dans l'Inde'; Tréhouart's 'Commission scientifique d'Islande'; Cailliaud, 'Voyage à Méroé'; 'Expédition scientifique de Morée'; Fabre, 'Commision scientifique du Nord'; du Petit-Thouars, 'Voyage de la Vénus'; and on the dates of the 'Faune Française'.—Annals and Magazine of Natural History Ser. 7, 8:161–164, 333–336, 491–494.

Simpson, G. G. 1945. The principles of classification and a classification of mammals.—Bulletin of the American Museum of Natural History 85: xvi + 1–350.

Spix, J. B. von. 1823. Simiarum et vespertilionum Brasiliensium species novae, ou, Histoire naturelle des espèces nouvelles de singes et de chauves-souris observées et recueilles pendant le voyage dans l'intérieur du Brésil exécuté par ordre de S. M. le Roi de Bavière dan les années 1817, 1818, 1819, 1820. Francisci Seraphici Hübschmanni, Monachii, vii + 72 pp., 38 pls.

Thomas, O. 1900. Descriptions of new Neotropical mammals.—Annals and Magazine of Natural History Ser. 7, 5:269–274.

———. 1905. New Neotropical *Molossus, Conepatus, Nectomys, Proechimys,* and *Agouti,* with a note on the genus *Mesomys.*—Annals and Magazine of Natural History Ser. 8, 15:584–591.

Tomes, R. F. 1861. Observations on the genus Vampyrus, and its allies.—Proceedings of the Zoological Society of London 1861:102–109, 1 pl.

Wied-Neuwied, M. P. zu. 1820. Diclidurus, Klappenschwanz. Ein neues genus der Chiropteren aus Brasilien.—Isis von Oken, 1819 4–5:columns 1629–1630.

———. 1821. Reise nach Brasilien in de Jahren 1815 bis 1817. H. L. Brönner, Frankfurt am Mein, 2: v–xvii + 345 pp., pls. 15–22, i–viii.

———. 1826. Bëitrage sur Naturgeschicte von Brasilien. Verzeichniss der Amphibien, Säugthiere und Vögel, welche auf einer Reise zwischen dem 13ten und dem 23sten Grade südlicher Breite im östlichen Brasilien beobachtet wurden. II. Abtheilung. Mammalia. Säugthiere. Gr. H. S. priv. Landes-Industrie-Comptoirs, Wiemar, 2: 1–622, 5 pls.

(ALG) Biological Survey Field Station, National Ecology Research Center, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560; (CSF) James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota 55455.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 509–515

REDESCRIPTION OF *POLYIPNUS FRASERI* FOWLER, 1934 (TELEOSTEI: STOMIIFORMES: STERNOPTYCHIDAE), WITH REMARKS ON PAEDOMORPHOSIS

Antony S. Harold

Abstract.—The sternoptychid *Polyipnus fraseri* Fowler, 1934 was described from a single specimen from the Philippine Islands. In recent revisions the species has been synonymized; authors have treated the unusual morphology displayed by Fowler's specimen as an abnormality. Comparison of the holotype with new material from the Philippine Sea reveals that *P. fraseri* is not aberrant and should be recognized as a valid species. Furthermore, this species possesses a unique posterior preopercular spine. The redescription includes a discussion of the characters that have led to systematic confusion. Examination of ontogenetic trajectories of supra-anal photophore addition for all 22 nominal species of *Polyipnus* shows that the juvenile-like features of adult *P. fraseri* are probably a result of some paedomorphic process, but the paucity of material precludes further analysis.

The peculiar species *Polyipnus fraseri* Fowler, 1934 became known, like many deep ocean forms, through the expeditions of R/V *Albatross.* A single specimen was taken in the waters around the Philippines at a maximum depth of just over 1000 m. In his revision of the hatchetfishes, Schultz (1961) provided additional description of Fowler's specimen, and included an improved illustration. The next published work on the group was Baird (1971) in which *P. fraseri* was synonymized with *P. tridentifer* McCulloch, 1914, without comment. Borodulina (1979) placed *P. fraseri* in the synonymy of *P. spinosus* Günther, 1887. Yamamoto (1982) reported a specimen from the Philippine Sea (Kyushu-Palau Ridge) which was ascribed to *P. fraseri,* but the author thought it might represent a "larval form of one of the other species."

Borodulina (1979) did not state whether she had seen the holotype of *P. fraseri* (or any other material) but did comment on some of the unusual characteristics shown by published drawings. In her opinion some of the features could be explained by "retention of juvenile features," but she continued . . . "this is contradicted by the large size of the specimen" (Borodulina 1979:8). The latter statement is confusing because it was the large size of the specimen that suggested that juvenile features had been retained.

I believe that Borodulina was essentially correct in recognizing that paedomorphic features are apparent in *P. fraseri.* In this paper I compare ontogenetic trajectories (sensu Alberch et al. 1979) for all nominal species of *Polyipnus* (material listed in Appendix) to develop a heterochronic explanation of the problematical photophore features of *P. fraseri.* The solving of such a problem requires a phylogenetic framework (Fink 1982) but an explicit statement of interspecific relationships for *Polyipnus* is not yet available. However, for the present purpose it is sufficient to accept the monophyly of the genus *Polyipnus* (Weitzman 1974) and the *P. spinosus* complex, including *P. fraseri* (Harold 1989).

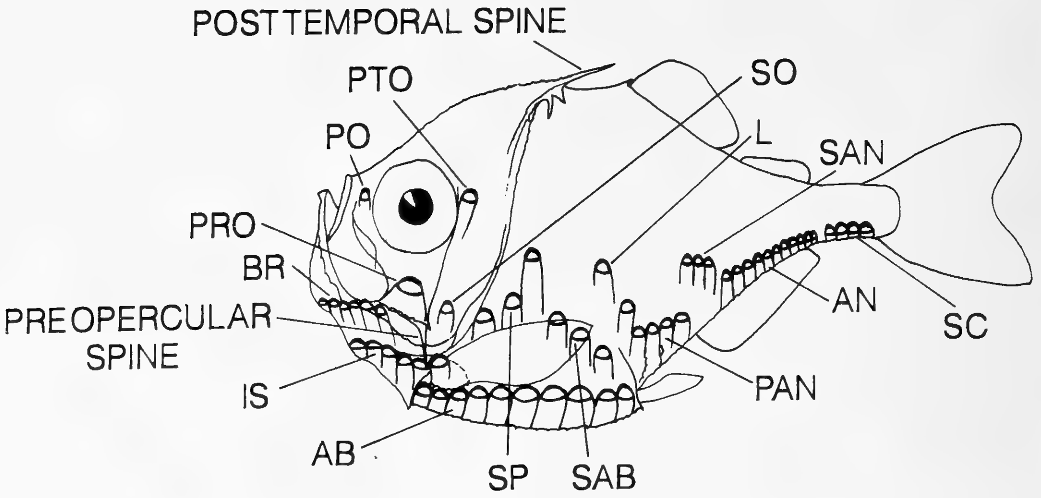


Fig. 1. Locations of spines and photophore clusters in *Polyipnus* species. Abbreviations defined in Methods section. Redrawn from Schultz (1961).

Methods

Measurements and meristics were made following Hubbs & Lagler (1958). Fin-ray counts are the totals, including rudimentary and unbranched elements. All body lengths are SL. Terminology and abbreviations of photophore clusters, which follows Ahlstrom et al. (1984), is illustrated in Fig. 1 and briefly defined here: AB, abdominal; AN, anal; BR, branchiostegal; IS, isthmus; L, lateral; PAN, preanal; PO, preorbital; PRO, preopercular; PTO, postorbital; SAB, supra-abdominal; SAN, supra-anal; SC, subcaudal; SO, subopercular; SP, suprapectoral. Individual photophores of a cluster are referred to by number, counting from the anterior. Institutional abbreviations follow Leviton et al. (1985).

Systematic Section

Polyipnus fraseri Fowler, 1934
Fig. 2

Polyipnus fraseri Fowler, 1934:257–258.—Schultz, 1961:642.—Schultz, 1964:267.—Yamamoto, 1982:327.—Fujii, 1984:47.—Harold, 1989:874–875.

Polyipnus tridentifer.—Baird, 1971:86 (incorrect spelling and year: "*Polyipnus frazeri* Fowler, 1933").

Polyipnus spinosis [sic].—Borodulina, 1979: 7–8 (incorrect spelling of *Polyipnus spinosus*).

Diagnosis.—A member of the genus *Polyipnus* Günther, 1887 with four anal and no supra-anal photophores, and a unique posterior preopercular spine. Eye relatively large, orbit length about one quarter of standard length. Two pigment bars extending down flank from dorsum.

Description of holotype.—Body deep, compressed, anterior body profile round (Fig. 2). Caudal peduncle extremely narrow. Head relatively large. Ventral margin of dentary, and frontal ridges smooth, the latter terminating posteriorly in a spine above center of eye. Parietal ridge reduced, smooth. Posttemporal dorsal arm smooth, posterolateral keel of ventral arm deeply serrated. Dorsal and ventral arms joined by broad web-like ossification, producing extensive armored shield between occiput and dorsal fin origin. Three prominent posttemporal spines: dorsal element longest, reaching beyond dorsal fin origin, ventral and median spines about half length of dorsal spine.

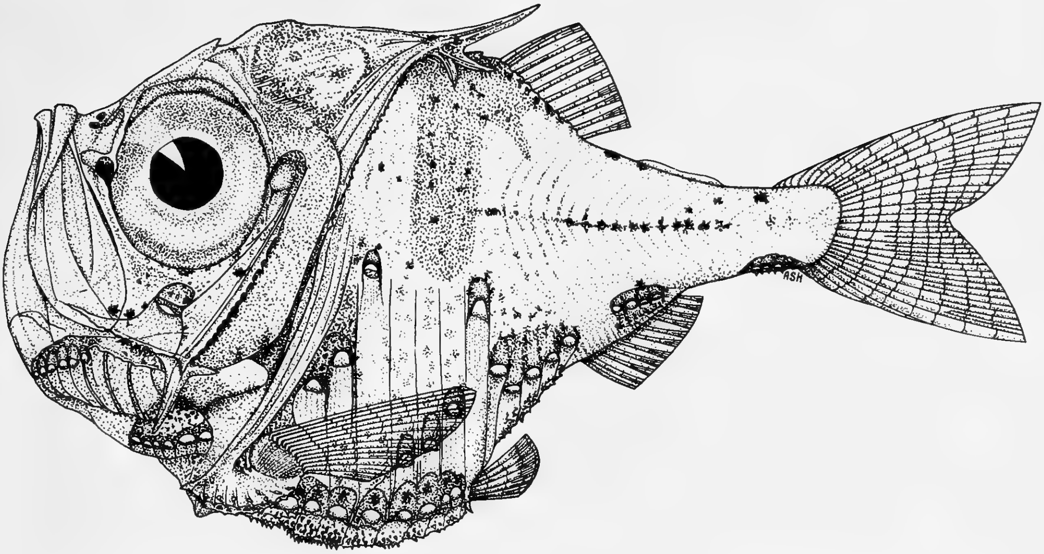


Fig. 2. *Polyipnus fraseri* Fowler, 1934, holotype, 40.4 mm, USNM 92324. Jaws and fin rays reconstructed, after Schultz (1961).

Ventral spine curving slightly towards anterior, median spine curved dorsally. Pectoral shield with many short spines over entire surface and a group of about six spines present on lateral knob adjacent to pectoral fin radials. Preopercular keels on dorsal and anterolateral limbs deeply serrate. Two preopercular spines: ventral spine long, about half orbit length, and narrow; posterior spine about one third length of ventral spine, and directed posteriorly. Dorsal preopercular spine absent. Dorsal blade not visible externally. Adipose fin present. Finray counts: dorsal (10), anal (11), pectoral (14), pelvic (7). Gill rakers 7 + 13. Morphometrics (percent of standard length): head length 38.0; orbit length 23.0; body depth 65.8; caudal peduncle depth 11.3; caudal peduncle length 22.2; dorsal fin length 15.3; anal fin length 16.6; preanal length 70.5; predorsal length 58.7; preventral length 67.1; postdorsal length 48.8; postanal length 38.1; length of SC photophore cluster 5.3; distance between AN and SC photophore clusters 11.9.

Photophore counts typical of *Polyipnus* species except for AN and SAN series (given below): IS (6); BR (6); PO (1); PTO (1); PRO (1); SO (1); SP (3), stepped dorsally from anterior to posterior, second very slightly above first with third elevated to level of anal fin insertion; SAB (3), stepped dorsally in approximately equal increments from anterior to posterior; AB (10), each photophore scale covered with minute denticles, photophores #1 and #2 small, located under pectoral shield proximal to medial axis, #3 to #10 follow arc of abdominal keel; L (1), at level slightly below SP #3; PAN (5), first well above second, #2 to #5 in line parallel with ventral body margin; SAN (0); AN (4) and SC (4), relatively small, scales denticulate.

Dark dorsomedian pigment present, extending from occiput to mid-point of dorsal fin. Ventral margin of dorsomedian pigment extending down flank as two distinct bars. Anterior bar broad, terminating bluntly at level of photophore SP #3. Posterior bar shorter, tapered, arising at posterodorsal base of anterior pigment bar and extending posteroventrally. Isolated melanophores located on preopercle, dorsal fin base, caudal peduncle and posterior midline.

Distribution.—Philippine Islands and Philippine Sea, to a maximum depth of about 1000 m. Using bathymetric criteria this species should be considered mesopelagic although, like other species of *Polyipnus,* it appears to occur in areas of abrupt sea floor topography (i.e., continental slope and rises), and may be benthopelagic.

Holotype.—PHILIPPINE ISLANDS: Buton Strait, R/V *Albatross* Sta. 5476, 12°56′24″N latitude, 124°25′24″E longitude, open-net tow to 1032 meters, USNM 92324 (40.4 mm SL).

The following non-type specimen was also examined:

PHILIPPINE SEA: Kyushu-Palau Ridge, 26°46.01′N latitude, 135°19.00′E longitude, 322–340 meters, BSKU 29353 (32.4 mm SL).

Remarks.—The examination of new material has contributed to the recognition of *Polyipnus fraseri* as a distinct species that can be distinguished from all congeners by the absence of the supra-anal photophore cluster, and the presence of four anal photophores and a unique posterior preopercular spine. Although it has not been possible to examine the gonads of *P. fraseri*, the specimens possess highly denticulate ventral photophore scales as do adults of other species belonging to the *P. spinosus* complex. Usually only juveniles (up to about 15 mm SL) have as few as 4 anal photophores (see Fig. 3 in which all nominal species of *Polyipnus* are represented). Additions of photophores are usually made at body sizes up to 30 mm SL (lowest AN count in other species at that standard length is 7). Rate of addition is probably quite low in *P. oluolus* Baird, 1971 as well (Fig. 3: 6 AN photophores at 26.9 mm SL, only known specimen). The largest individual of another species with no SAN photophores is 16.9 mm SL (*P. ruggeri* Baird, 1971). With so much interspecific and ontogenetic variation in photophore number, and only one specimen known, Baird (1971) and Borodulina (1979) believed they were taking a conservative approach in synonymizing *P. fraseri.*

Relative size of various elements of the skull are also atypical and seem to be correlated with enlargement of the eye. As percentages of standard length, *P. fraseri* has an orbital length of 18.0 to 23.0, 13.6 to 19.0 in other species at SL less than 25 mm, and 10.8 to 17.2 in other species at SL greater than 25 mm.

Polyipnus fraseri is a member of the *P. spinosus* complex, a monophyletic group of Indo-Pacific species with denticulate abdominal keel scales and a multispinose posttemporal. Arrangement and shape of posttemporal spines in *P. fraseri* is most similar to that of *P. spinifer, P. spinosus* and *P. stereope,* all of which have large dorsal and prominent, but much shorter, basal spines.

Discussion

The specialized Type Alpha photophores of sternoptychids develop and increase in numbers by budding anteriorly from a common gland (Weitzman, in Ahlstrom et al. 1984:195), a mechanism which is thought to be a synapomorphy of the ten genera in the family, as Weitzman (1974) defined it. In general, development of gonostomatids and sternoptychids is protracted and photophores do not reach their full complement until comparatively late in life. Among the more unusual features of *P. fraseri* are the absence of supra-anal photophores and the presence of only four anal photophores. In adults of the other 21 species in the genus there are typically three supra-anal photophores (one per myomere), located between the preanal and anal clusters, and six or more photophores in the anal cluster. Since these two clusters of luminescent organs are the last to appear ontogenetically in this genus, it is reasonable to conclude that their

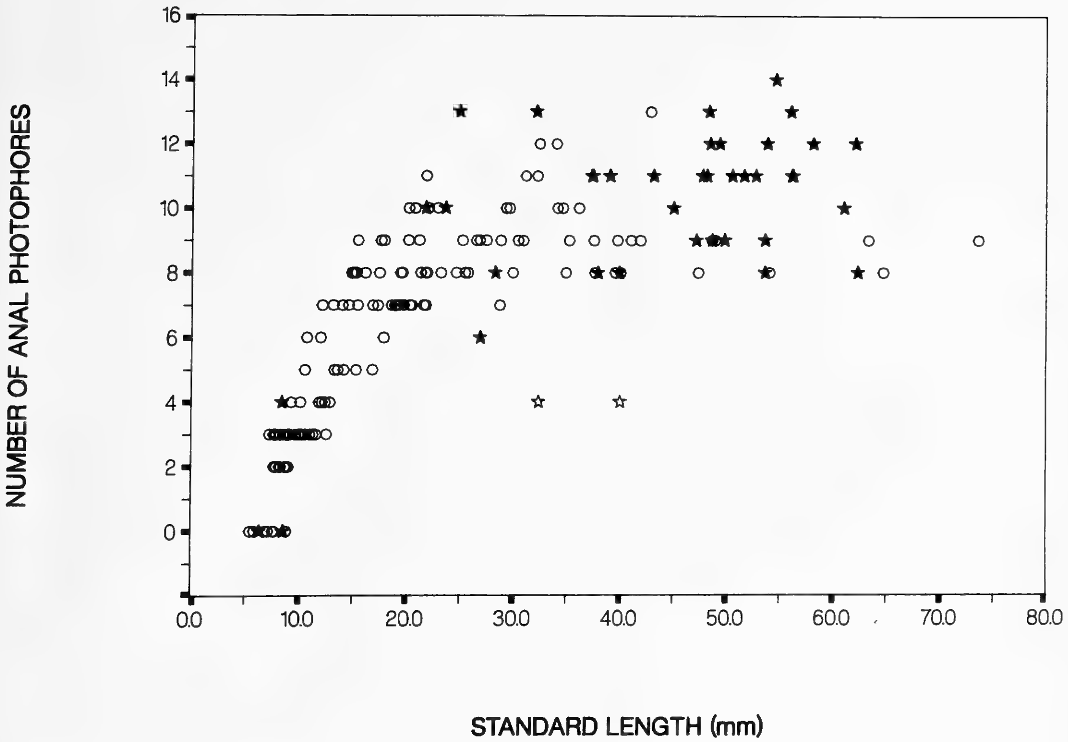


Fig. 3. Number of anal photophores plotted against standard length for 22 *Polyipnus* species. All stars = *P. spinosus* complex; open stars = *P. fraseri*; circles = *P. asteroides* and *P. laternatus* complexes combined (i.e., all other species).

absence or reduced numbers in *P. fraseri* is a result of some process producing paedomorphic development.

The occurrence of species exhibiting paedomorphosis has been noted for a diverse assemblage of fishes (Fink 1981, Weitzman & Vari 1988), including the deep-sea families Gonostomatidae (Ahlstrom et al. 1984), Stomiidae (Fink 1985), and Sternoptychidae (Weitzman 1974). The existence of species or higher taxa with juvenile-like features in adults can be a source of difficulty in systematics. It is now generally accepted that much of observed morphological diversity, including otherwise perplexing morphologies, may result through heterochronic alteration of developmental programs. A framework for interpretation of such cases has been emerging over the past decade (see Alberch et al. 1979, Fink 1982, Kluge 1988). Figure 3, which compares relative growth of structures among related taxa, can be interpreted as a set of ontogenetic trajectories. Due to unavailability of a growth series of *P. fraseri* it is not possible to compare slopes with other species or to plot sizes at which various events take place. It is clear, however, that rate of photophore addition to the anal cluster is probably lower than in other species. In a form that reaches a body size comparable to possible sister taxa and *Polyipnus* outgroups (*P. asteroides* Schultz, 1938 and *P. laternatus* Garman, 1899 complexes), such development is considered neotenic. Alternatively, the presence of four anal photophores could be the result of late onset of growth with the rate of addition the same as in other species (i.e., postdisplacement). The supra-anal photophore cluster is absent in the two known specimens but the possibility remains that *P. fraseri* reaches a much larger body size and has unusually protracted development of AN and SAN photophores. In either case, when compared with all known possible immediate outgroups, it appears probable that some process has affected the general ontogenetic program of photophore development. Without material representing the entire size range of *P. fraseri* it is not possible to comment on rate of appearance of the other groups of luminescent organs, or to say which of the possible heterochronic explanations is the more likely. Since *P. fraseri* is a member of the *P. spinosus* complex, then the distribution of ontogenetic photophore characters (absence of SAN, low AN number) is such that their states in *P. fraseri* are most parsimoniously interpreted through outgroup comparison as apomorphic.

Qualitatively, the body shape (e.g., large orbit; narrow caudal peduncle) of *P. fraseri* is very similar to juveniles of other species of the *P. spinosus* complex and the outgroups. The possibility remains that the known specimens of *P. fraseri* are juveniles of a large species. However, this explanation requires very early development of photophore-scale denticles relative to the appearance of typically adult photophore features.

Acknowledgments

I'm grateful to A. P. Andriashev, K. E. Hartel, S. L. Jewett, K. Kawaguchi, H. Kishimoto, K. Matsuura, M. McGrouther, N. R. Merrett, J. Nielsen, O. Okamura, N. V. Parin, J. R. Paxton, S. J. Raredon, C. B. Renaud, H. J. Walker, S. H. Weitzman, and J. Williams who provided study material. I thank H. Griffith, G. D. Johnson, R. D. Mooi, R. J. Mooi, and S. H. Weitzman whose comments led to an improved manuscript. This research was supported by NSERC (Natural Sciences and Engineering Research Council of Canada) grant #330068 to R. L. Haedrich.

Literature Cited

Ahlstrom, E. H., W. J. Richards, & S. H. Weitzman. 1984. Families Gonostomatidae, Sternoptychidae, and associated stomiiform groups: development and relationships. Pp. 184–198 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds., Ontogeny and systematics of fishes. Special Publication Number 1, American Society of Ichthyologists and Herpetologists, 760 pp.

Alberch, P., S. J. Gould, G. F. Oster, & D. B. Wake. 1979. Size and shape in ontogeny and phylogeny.—Paleobiology 5(3):296–317.

Baird, R. C. 1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (family Sternoptychidae).—Bulletin of the Museum of Comparative Zoology, Harvard University 142(1):1–128.

Borodulina, O. D. 1979. Composition of the "*Polyipnus spinosus* complex" (Sternoptychidae, Osteichthyes) with a description of 3 new species of the group.—Journal of Ichthyology 19(2):1–10.

Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes.—Journal of Morphology 167:167–184.

———. 1982. The conceptual relationship between ontogeny and phylogeny.—Paleobiology 8(3): 254–264.

———. 1985. Phylogenetic relationships of the stomiid fishes (Teleostei: Stomiiformes). Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 171, 127 pp.

Fowler, H. G. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas.—Academy of Natural Sciences of Philadelphia, Proceedings 85:233–437.

Fujii, E. 1984. Family Sternoptychidae. Pp. 47–48, pl. 49L *in* H. Masuda, K. Amaoka, C. Araga, T. Uyeno, and T. Yoshino, eds., Fishes of the Japanese Archipelago. Tokai University Press, Tokyo, 433 pp., 370 pl.

Harold, A. S. 1989. A new species of *Polyipnus* (Stomiiformes: Sternoptychidae) from the Coral Sea, with a revised key to the species of the *P. spinosus* complex.—Copeia 1989(4):871–876.

Hubbs, C. L., & K. F. Lagler. 1958. Fishes of the Great Lakes region. The University of Michigan Press, Ann Arbor, 213 pp.

Kluge, A. G. 1988. The characterization of ontogeny. Pp. 57–81 *in* C. J. Humphries, ed., Ontogeny and systematics. Columbia University Press, New York, 236 pp.

Leviton, A. E., R. H. Gibbs, Jr., H. Heal, & C. E. Dawson. 1985. Standards in ichthyology and herpetology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985(3):802–832.

Schultz, L. P. 1961. Revision of the marine silver hatchetfishes (family Sternoptychidae).—Proceedings of the United States National Museum 112(3449):587–649.

———. 1964. Family Sternoptychidae. Pp. 241–273 *in* H. B. Bigelow et al., eds., Fishes of the Western North Atlantic, Part 4, Isospondyli. Sears Foundation for Marine Research Memoir No. 1, 599 pp.

Weitzman, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families.—Bulletin of the American Museum of Natural History 53(3):327–478.

———, & R. P. Vari. 1988. Miniaturization in South American freshwater fishes: an overview and discussion.—Proceedings of the Biological Society of Washington 101:444–465.

Yamamoto, E. 1982. Sternoptychidae. P. 327 *in* O. Okamura, K. Amaoko, and F. Mitani, eds., Fishes of the Kyushu-Palau Ridge and Tosa Bay. Japan Fisheries Resource Conservation Association, Tokyo, 435 pp.

Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada, A1B 3X9.

Appendix

Comparative material examined.–P. aquavitus Baird, 1971: USNM 298928, 1 (17.5 mm), USNM 298927, 1 (15.4 mm), USNM 298925, 10 (10.6–17.9 mm), AMS I.19761-029, 10 (10.2–34.1 mm), AMS I.16492-008, 3 (12.0–14.9 mm), AMS I.20310-017, 3 (17.6–20.7 mm), AMS I.19762-002, 3 (21.2–34.6 mm), AMS I.20316-005, 3 (20.2–36.1 mm); *P. asteroides* Schultz, 1938: MCZ 66695, 1 (41.9 mm), MCZ 66696, 1 (30.9 mm); *P. elongatus* Borodulina, 1979: AMS I.21975-007, 2 (54.6–65.0 mm); *P. indicus* Schultz, 1961: personal collection, uncatalogued, 3 (53.6–62.3 mm); *P. inermis* Borodulina, 1981: personal collection, uncatalogued, 3 (48.6–49.8 mm); *P. kiwiensis* Baird, 1971: AMS I.15984-002, 1 (48.6 mm), AMS I.24496-001, 1 (73.6 mm); *P. laternatus* Schultz, 1938: USNM 298924, 3 (32.4–42.8 mm), MCZ 40575, 1 (31.1 mm); *P. matsubarai* Schultz, 1961: ORIT 2572–2578, 2580, 2582, 2585, 2587, 11 (18.6–41.0 mm), NMC 79-0009, 1 (97.4 mm); *P. meteori* Kotthaus, 1967: MCZ 64694, 1 (17.9 mm), ZMUC P206931, 1 (37.6 mm), ZMUC P206928, 1 (54.0 mm), ZMUC P206929, 2 (12.2–21.3 mm), SIO 61-541-10, 1 (28.7 mm), USNM 256965, 1 (20.3 mm); *P. nuttingi* Gilbert, 1905: BPBM 24892, 3 (28.3–39.9 mm), BPBM 23779, 1 (47.1 mm); *P. oluolus* Baird, 1971: holotype, USNM 204390, 1 (26.9 mm); *P. omphus* Baird, 1971: USNM 256967, 1 (32.2 mm); *P. parini* Borodulina, 1979: holotype, ZIL 43997, 1 (61.0 mm), illustration (Borodulina, 1979: Fig. 3) and x-radiograph; *P. polli* Schultz, 1961: MCZ 80400, 27 (9.7–34.9 mm); *P. polli*?: MCZ 80401, 13 (5.9–11.0 mm); *P. ruggeri*: USNM 298920, 1 (16.9 mm), USNM 298920, 2 (8.9–12.6), ZMUC P202814, 1 (24.6 mm), ZMUC P206958, 1 (21.6 mm), ZMUC P206956, 1 (63.3 mm), AMS I.27166-004, 1 (64.7 mm), AMS I.20312-007, 1 (21.3 mm), AMS I.20066-014, 1 (48.9 mm), AMS I.21372-006, 1 (25.5 mm); *P. spinifer* Borodulina, 1979: USNM 289176, 3 (21.7–24.9 mm), ORIT 2552, 2555, 2556, 3 (48.1–50.5 mm), AMS I.22808-028, 6 (32.1–51.6 mm), AMS I.22817-014, 6 (50.5–56.2 mm); *P. spinosus* Günther, 1887: holotype, BMNH 1987.12.7.159, 1 (45.0 mm); *P. stereope* Jordan and Starks, 1904: ORIT 2519, 1 (47.7 mm); *P. tridentifer* McCulloch, 1914: AMS I.18711-014, 3 (48.4–62.1 mm); *P. triphanos* Schultz, 1938: ZMUC P206963, 2 (26.5–30.4 mm), AMS I.24338-001, 1 (47.3 mm); *P. unispinus* Schultz, 1938: *Polyipnus* sp. (*P. spinosus* complex): USNM 298929, 1 (6.4 mm), AMS I.27171-007, 1 (8.6 mm), AMS I.27166-003, 1 (8.4 mm); *Polyipnus* sp.: MCZ uncatalogued, field no. RHB 2056, 14 (5.5–10.3 mm), USNM 298929, 1 (9.3 mm), USNM 298926, 1 (7.3 mm), MCZ 80402, 1 (9.2 mm).

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 516–524

A NEW, UNUSUALLY SEXUALLY DIMORPHIC SPECIES OF *BRYCONAMERICUS* (PISCES: OSTARIOPHYSI: CHARACIDAE) FROM THE PERUVIAN AMAZON

Richard P. Vari and Darrell J. Siebert

Abstract.—*Bryconamericus pectinatus,* a new species of characid fish, is described from the Río Manú basin in southeastern Peru. Males of the species are characterized by unique elaborations of the distal portions of the anterior branched rays of the anal fin. They are also distinctive in the expansion of the anterior basal pterygiophores of the anal fin, and in the presence of lobulate bodies, evidently consisting of glandular tissue, along the base of the anterior portion of that fin.

Resumen.—*Bryconamericus pectinatus* es una nueva especie de los carácidos que proviene de la cuenca del río Manú, al sureste del Perú. Los machos de esta especie se caracterizan por la singular elaboración de una porción distal de los radios anteriores no ramificados de la aleta anal. Se los puede distinguir por el ensanchamiento de los pterygióphoros de la aleta anal y en la presencia de cuerpos lobulados que evidentemente consta de un tejido glandular a lo largo de la base de la parte anterior de esta aleta.

As presently defined, the characid genus *Bryconamericus* Eigenmann (*in* Eigenmann et al. 1907) consists of some three dozen relatively small-sized species (Géry 1977: 386). Species of *Bryconamericus* occur in a variety of freshwater ecosystems at lower altitudes across a broad expanse of South and Central America to both sides of the Andean cordilleras. The genus is most diverse, however, in the Atlantic drainages of the continent, in particular through the vast reaches of the Amazon basin. In their compendium of the freshwater fishes of Peru, Ortega & Vari (1986:7) listed ten species of *Bryconamericus* as occurring in the myriad river systems that drain the part of the country to the east of the Andean Cordilleras. Those authors, following Böhlke et al. (1978), noted, however, that the entire neotropical freshwater fish fauna is still poorly understood, and that their tentative listing of the species known from Peru would undoubtedly undergo numerous modifications in the future. In the course of studying a collection of fishes from Río Manú system of the Río Madre de Dios basin in southeastern Peru, we discovered an undescribed species assignable to *Bryconamericus* that differs from the other members of the genus in several striking features. The most noteworthy of these are the unusual modifications of the anterior anal-fin rays and associated basal pterygiophores in adult males. Males are also characterized by a series of lobulate, evidently glandular, bodies along the lateral surfaces of the anterior anal-fin rays.

Methods.—All measurements are given as proportions 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 in the Weberian apparatus and considers the fused PU_1+U_1 as a single element. In the counts of elements in the median and pelvic fins, lower-case Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. For meristic values the range for each value for the holotype and measured paratypes is presented first, with the value for the holotype indicated in brackets.

The following abbreviations are used for institutions: CM—Carnegie Museum, Pittsburgh; FMNH—Field Museum of Natural History, Chicago; MHN-USM—Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; and USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Bryconamericus pectinatus, new species
Figs. 1–5, Table 1

Holotype.—MHN-USM 2057, 27.3 mm SL, female. Peru, Departamento Madre de Dios, Provincia Manú, Parque Nacional de Manú, second large quebrada along Trail 1 leading to the east from Pakitza, tributary of Río Manú (approx. 11°50′S, 71°21′W); H. Ortega, D. Siebert, M. Rauchenberger, I. Samanez, G. Contreras, and J. Cánepa; 13 Sep 1988.

Paratypes.—15 specimens collected with holotype, MHN-USM 2058, 7 specimens; USNM 303442, 8 specimens including 3 males, 17.0–23.6 mm SL (1 specimen cleared and counterstained for cartilage and bone). Ten specimens collected downstream of holotype locality by same collectors, 17 Sep 1988; MHN-USM 2059, 5 specimens including 2 males; USNM 303441, 5 specimens, 19.8–34.8 mm SL (1 specimen cleared and counterstained for cartilage and bone).

Diagnosis.—The combination of a single row of teeth on the dentary, two rows of teeth on the premaxilla with four teeth in the inner series that are larger than those of the outer row, the limited number of teeth along the anterior margin of the maxilla, the simple curve to the border of the upper jaw, the lack of scales on the caudal fin, the large third infraorbital contacting the preopercle along its posterior and ventral margins, setiform gill-rakers, the complete laterosensory canal system on the body, and the absence of a glandular pouch on the caudal fin in males serve to assign the species to *Bryconamericus.* Within the genus, *B. pectinatus* can be distinguished by autapomorphic modifications of the anterior rays of the anal fin and of the associated basal pterygiophores, and by the presence of lobulate, evidently glandular, bodies along the anterior anal-fin rays (see "Description" below). The species is also distinctive within the genus on the basis of the combination of a relatively low number of anal-fin rays, a robust body that is relatively deep in adults, the possession of 32 or more lateral-line scales to the hypural joint, the absence of dark pigmentation on the tips of the caudal-fin lobes, and the presence of 5 or 6 moderately sized teeth on the maxilla.

Description.—Body robust, slightly more compressed in smaller individuals (Figs. 1, 2). Dorsal profile of head nearly vertical along upper lip, distinctly convex from margin of upper lip to vertical line through posterior nostril, slightly convex from that line to rear of head. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin, more convex in larger, deeper bodied specimens; straight and posteroventrally slanted at base of dorsal fin, gently convex from base of last dorsal-fin ray to caudal peduncle, convexity more pronounced in larger individuals. Ventral profile of head notably convex anteriorly, less so posteriorly. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle; convexity more pronounced in larger specimens. Greatest body depth located slightly anterior of origin of dorsal fin. Caudal peduncle somewhat laterally compressed, deeper in adult males (0.146–0.164

of SL) than adult females (0.121–0.139 of SL). No sexual dimorphism obvious in other examined morphometric features.

Head relatively large, overall profile rounded anteriorly. Jaws equal, mouth terminal; lips fleshy with brown tips of teeth in outer row on premaxilla visible when mouth closed; ventral margin of upper jaw concave, main axis of maxilla aligned posteroventrally, posterior tip of maxilla extending below orbit, reaching posteriorly nearly to vertical line through center of eye. Nostrils on each side of head very close to each other; opening of anterior nares vertically ovoid; opening of posterior nares crescent-shaped; thin flap of skin extending laterally from strip of tissue separating two nares. Orbital rim free, no adipose eyelid present.

Six well-ossified infraorbitals present, each bearing laterosensory canal segment. Third infraorbital very large, ventral and posterior margins contacting lateral surface of preopercle. Fourth infraorbital without posterior branch of laterosensory canal. Laterosensory canal segment in sixth infraorbital (dermosphenotic) consisting of a single tube. No supraorbital present.

Lower jaw with single series of 11 to 13 teeth. First three teeth largest, fourth tooth somewhat smaller, fifth tooth through end of dentary series distinctly smaller than fourth, gradually diminishing in size posteriorly. First five teeth typically tricuspidate with central cusp distinctly larger. Second tooth often with additional very small cusp on lateral margin. Fourth tooth either tricuspidate or bicuspid, sometimes with two conditions in a single specimen; when bicuspid posterior cusp large, posterior margin straight, not recurved. Sixth tooth bicuspid; remaining teeth on lower jaw unicuspid.

Two rows of teeth on premaxilla; teeth of inner row larger. Six teeth in outer row, orientation of main axis of teeth alternating slightly anteriorly and posteriorly, resulting in a wavy margin of tooth edges when examined in ventral view. Outer row teeth bicuspid, with medial cusp much larger. Four teeth in inner row of premaxilla; with three to five cusps, middle cusp distinctly larger. Maxilla with five or six small tricuspidate teeth along upper half of exposed anterior margin; dorsal tooth on maxilla situated proximate to lateral tooth of inner row of premaxilla.

Dorsal-fin rays ii,8 or ii,9 [ii,9]. Margin of dorsal fin rounded, second unbranched and first branched rays subequal; depressed fin not reaching anterior margin of adipose fin in smaller specimens, overlapping anterior of fin in largest specimens examined. Adipose fin moderately developed in all specimens. Pectoral-fin rays 10 to 12 [11]. Margin of pectoral fin rounded; tip of fin extends nearly to vertical line through insertion of pelvic fin in smaller specimens, just slightly short of that line in largest specimens examined. Pelvic-fin rays 6 to 8 [7]. Margin of pelvic fin rounded; reaches beyond vertical line through origin of anal fin in smaller specimens, barely reaches or just short of that line in larger individuals. Caudal fin forked, lobes rounded; 7 or 8 procurrent rays both dorsally and ventrally. Anal-fin rays vi,12 to 14 (counts taken from radiographs; two or three anterior unbranched rays not apparent in specimens that have not been cleared and stained or radiographed).

Anal fin with pronounced sexual dimorphism in adults (sex verified by dissection). First branched anal-fin ray in females longest, remaining branched rays becoming progressively shorter posteriorly. Margin of anal fin in females somewhat emarginate (see Fig. 1).

Males with posterior unbranched and anterior branched anal-fin rays distinctively modified, longest rays proportionally shorter than in females (compare Figs. 1 and 2). Unbranched anal-fin rays of males, in particular last unbranched ray, but also rays hidden by body tissue and scales, thickened basally (Fig. 4). First branched ray with

Fig. 1. *Bryconamericus pectinatus,* new species, holotype, MHN-USM 2057, 27.3 mm SL, female. Peru, Departamento Madre de Dios, Provincia Manú, Parque Nacional de Manú.

distal portion significantly expanded anteroposteriorly, division of distal ray segments highly asymmetrical, with progressive subdivision of posterior, but not anterior half of each branched ray segment (Fig. 3). This condition contrasts with typical progressive distal subdivision of both anterior and posterior branches of anal-fin ray in females of the species and other characiforms (compare Fig. 3 with figs. 38 to 43 in Weitzman & Fink 1985). Distal portions of second through fourth branched anal-fin rays also somewhat expanded anteroposteriorly; degree of distal expansion progressively decreasing posteriorly along fin, never as pronounced as in first branched ray (Fig. 3). Form of posterior anal-fin rays comparable to those in females of species.

Proximal portions of enlarged anal-fin rays and ventral sections of associated basal pterygiophores of males thickened relative

Fig. 2. *Bryconamericus pectinatus,* new species, paratype, USNM 303441, 34.8 mm SL, male. Peru, Departamento Madre de Dios, Provincia Manú, Parque Nacional de Manú.

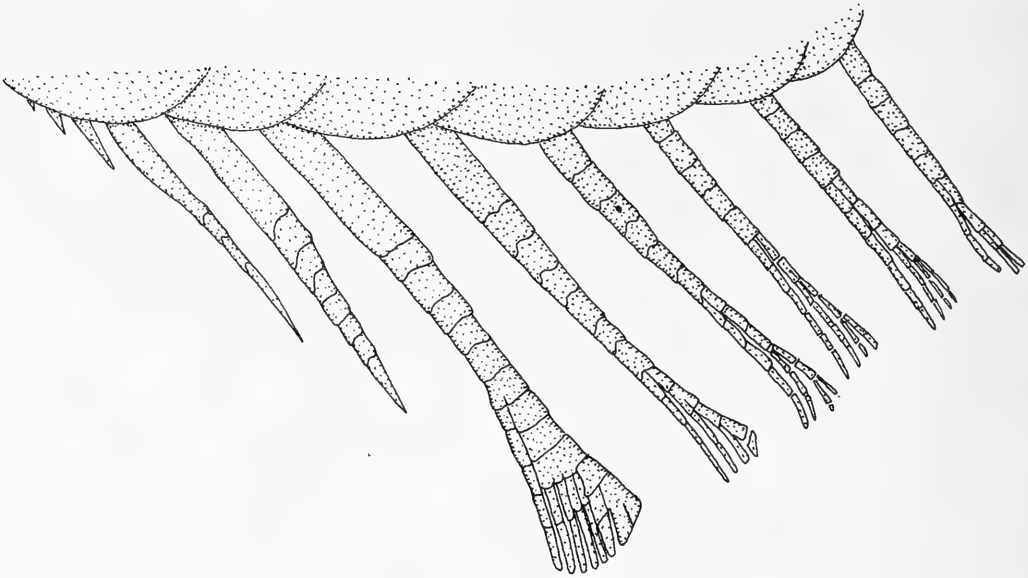


Fig. 3. *Bryconamericus pectinatus,* male paratype, USNM 303441; 32.0 mm SL; anterior rays of anal fin and associated basal sheath of scales; anterior to left.

to condition in females (compare within Fig. 4), and in comparison to typical morphology of these elements in other characids. First and second basal pterygiophores in males more closely associated with hemal spines of proximate vertebrae than in females (Fig. 4). Large males with mass of lobulate material extending ventrally from under scales across lateral surface of anal-fin membranes (Fig. 5). Lobulate bodies across membranes of anal fin extend nearly to end of exposed unbranched fin-rays; only reaching about one half distance to tip of anterior branched fin rays. Such lobulate bodies on anal fin not known elsewhere in *Bryconamericus* or among other characids. Lobulate bodies appear to be glandular, but limited available material prevents histological confirmation of this supposition.

Scales cycloid, thin. Caudal fin not scaled. Anal fin with 1 or 2 series of scales overlapping bases of fin rays along anterior two thirds of fin. One series of scales overlapping proximal portions of unbranched rays, 2 series over bases of anterior 4 or 5 branched rays. Pored lateral-line scales extend from supracleithrum to hypural joint 32 to 36 [33]; all scales of lateral line pored, canals in lateral-line scales straight; 3 series of scales extend beyond hypural joint onto caudal-fin base; 6 to 6½ [6½] scales in transverse series from origin of dorsal fin to lateral line; 5 to 6 [6] scales in transverse series from lateral line to origin of anal fin.

Total vertebrae 35 (2), 36 (5), 37 (4).

Color in alcohol.—Overall coloration of specimens fixed in formalin and preserved in alcohol light tan. No guanine remaining on scales. Scattered small chromatophores on lower lip, snout, dorsal portion of head, area posterior and ventral to orbit, and on dorsal half of opercle. Pigmentation most intense on dorsal portion of head, most notably in smaller specimens. Distinct, vertically elongate, patch of deep-lying chromatophores forming humeral spot. Humeral spot separated anteriorly from pigmented portion of opercle by region with few or no dark chromatophores. Diffuse mid-lateral stripe of small dark chromatophores extending posteriorly from slightly behind humeral spot to rear of caudal peduncle. Stripe more obvious posteriorly at all body sizes, overall intensity greater in larger individuals. Portion of stripe on caudal peduncle most heavily pigmented. Margins of scale pockets on dorsal portion of body outlined by series of small dark chromatophores, intensity greater in adult specimens.

Dorsal-fin rays outlined by series of small dark chromatophores, pigmentation most intense in large males. Membranes of dorsal-fin rays dusky. Middle and most ventral rays of caudal fin dusky. Hyaline region on fin separates dusky dorsal caudal-fin rays from pigmented middle rays. Similar unpigmented patch on basal portion of middle rays of lower lobe of caudal fin. Anal fin hyaline in smaller specimens, with small chromatophores giving distal portions of rays dusky appearance in larger individuals. Paired fins hyaline in specimens of all sizes.

Distribution.—Known only from the type locality, the upper Río Manú of southeast Peru.

Etymology.—The species name, *pectinatus,* from the Latin for rake or comb, refers to the stiffened, subdivided, comb-like anterior rays of the anal fins in the males of the species.

Ecology.—The specimens were collected in a small, moderately flowing, rainforest stream with a rock and mud bottom.

Remarks.—*Bryconamericus pectinatus* demonstrates a number of striking features not encountered elsewhere in the genus, most notably the modifications of the anterior anal-fin rays and associated basal pterygiophores in males. We are consequently confronted with a choice of expanding the definition of *Bryconamericus* to include this very distinctive species or proposing a new monotypic genus for the species. Many authors publishing on characiforms have segregated equally distinctive species in monotypic genera rather than expand the definition of previous genera to accommodate the features of newly discovered species.

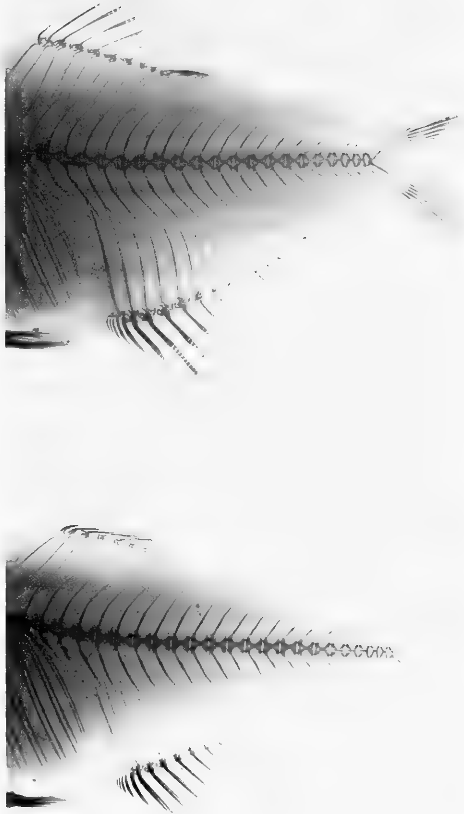


Fig. 4. Positives of radiographic plates of anal-fin regions of *Bryconamericus pectinatus*; top, male, USNM 303441, 34.8 mm SL; bottom, female, USNM 303441, 28.6 mm SL. Anterior to left.

Fink (1976), for example, decided to describe a new genus, *Eretmobrycon,* for *E. bayano,* a *Bryconamericus*-like species from Panama characterized by specializations of the caudal and pelvic fins. In his opinion (1976:340) it "seems best to recognize the unique specilizations of *E. bayano* and place it in a monotypic genus."

The choice between these alternatives, the expansion of the definition of a previous genus, and the proposal of a new genus, is

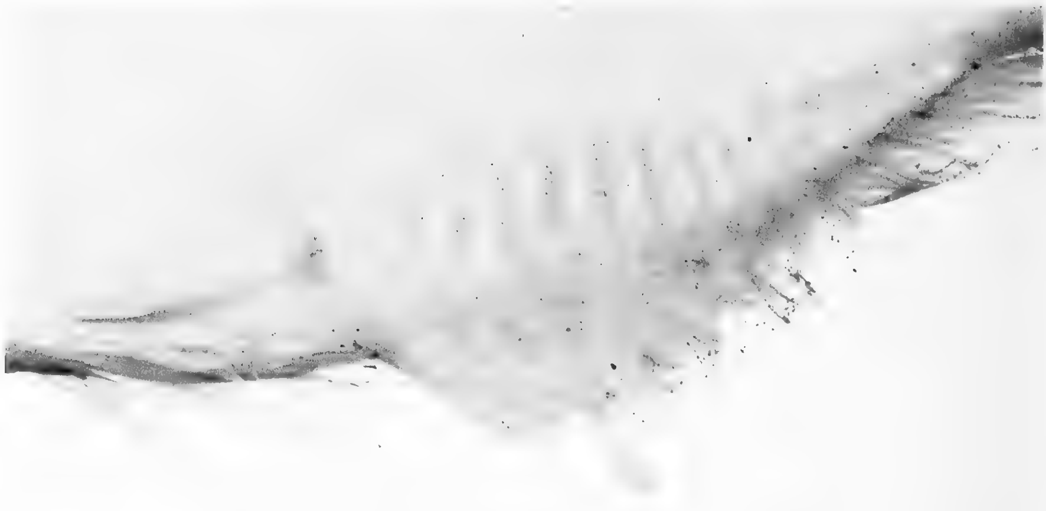


Fig. 5. *Bryconamericus pectinatus,* male, USNM 303441; 34.8 mm SL. Close-up of anal fin showing lobulate, possibly glandular tissue extending lateral to anterior fin-rays. Anterior to left.

somewhat arbitrary given the general lack of information on relationships between *Bryconamericus* and its possible close relatives. The primary basis for our placement of the new species within the *Bryconamericus* is its possession of the combination of characters that are presently considered diagnostic for the genus (see Diagnosis). The distinctive features of *Bryconamericus pectinatus,* in turn, are autapomorphies for the species, with no bearing at present on the question of its phyletic associations. We must admit, however, that we have little confidence that *Bryconamericus* in this broad sense represents a natural (monophyletic) component of the Characidae, or that the closest relatives of *B. pectinatus* consequently occur within that genus. Problems with the naturalness of *Bryconamericus* have been long recognized, even by Eigenmann who first proposed the genus in 1907. Eigenmann subsequently commented (1927: 358) "There are three or four recognizable groups in the genus *Bryconamericus* and these may have been independently derived from various species of Astyanax and Hemibrycon." Questions concerning the naturalness of many New World characiform taxa and problems with the utility of many commonly used diagnostic features within the order, including those pertinent to *Bryconamericus,* also have been noted more recently by Fink (1976), Vari & Géry (1980), Weitzman & Fink (1983), and others. Given these general problems and the specific questions concerning the monophyly of *Bryconamericus* cited by Eigenmann, there is little likelihood that the inclusion of *B. pectinatus* in the genus will disrupt a natural assemblage. In light of this situation the provisional inclusion of *B. pectinatus* within *Bryconamericus* is, in our view, preferable to the creation of a new monotypic genus.

One other genus in the Characidae, *Carlastyanax* Géry (1972) demonstrates certain similarities with *Bryconamericus pectinatus* which raises the question of a possible close relationship between these two taxa. The type species of *Carlastyanax, Astyanax aurocaudatus* Eigenmann (1913:26), was collected in the upper Río Cauca, a tributary of the Río Magdalena of northwestern Colombia, which drains into the Caribbean Sea.

Table 1.—Morphometrics of *Bryconamericus pectinatus,* new species. Standard length is expressed in mm; measurements 1 to 11 are proportions of standard length; 12 to 16 are proportions of head length. Values for paratypes represent ranges of measured specimens.

	Holotype	Paratypes
Standard length	27.3	17.0–34.8
1. Greatest body depth	0.395	0.328–0.420
2. Snout to dorsal-fin origin	0.623	0.561–0.631
3. Snout to pectoral-fin insertion	0.296	0.269–0.288
4. Snout to pelvic-fin insertion	0.532	0.484–0.537
5. Snout to anal-fin origin	0.691	0.636–0.689
6. Origin of dorsal fin to hypural fin	0.454	0.430–0.482
7. Length of longest dorsal-fin ray	0.234	0.220–0.244
8. Pectoral-fin length	0.227	0.206–0.237
9. Pelvic-fin legnth	0.150	0.136–0.169
10. Caudal-peduncle depth	0.139	0.121–0.164
11. Head length	0.308	0.295–0.311
12. Snout length	0.223	0.210–0.260
13. Orbital diameter	0.329	0.291–0.350
14. Postorbital length	0.447	0.440–0.500
15. Upper jaw length	0.450	0.435–0.456
16. Interorbital width	0.329	0.320–0.350

Eigenmann (1927:322) subsequently noted that the species "ought probably to be distinguished generically," but did not propose a new genus for the species. Géry (1972:16–21), however, following on that suggestion, proposed *Carlastyanax* for *Astyanax aurocaudatus. Carlastyanax aurocaudatus* and *Bryconamericus pectinatus* are similar in their blunt, massive heads, heavy bodies, and in the presence of two series of scales along the base of the anal fin. These features are, however, hardly unique to these species within the Characidae. Géry (1972:18) also notes that the anterior rays of the anal fin in *Carlastyanax aurocaudatus* are sexually dimorphic, with those in males being thickened, another possible similarity with *Bryconamericus pectinatus.*

Examination of the holotype of *Astyanax aurocaudatus* (FMNH 56882, formerly CM 5162) and part of the paratype series of the species (FMNH 56883, formerly CM 5163a-d) has shown that those specimens and *Bryconamericus pectinatus* differ in numerous details. The basally expanded anterior anal-fin rays in the holotype of *Astyanax aurocaudatus* show none of the asymmetrical distal branching and anteroposterior expansion characteristic of *Bryconamericus pectinatus.* Neither does *Astyanax aurocaudatus* show any indication of the modifications of the anterior basal pterygiophores, or possess the lobulate, possibly glandular, bodies found along the basal portion of the anal-fin membranes in males of *Bryconamericus pectinatus.*

Géry (1972) listed a number of diagnostic features for *Carlastyanax.* Notable differences between that genus and *Bryconamericus pectinatus* include the degree of development of the third infraorbital (small in *aurocaudatus,* very well developed in *pectinatus*), morphology of the third dentary tooth (posterior cusp greatly recurved in *aurocaudatus,* tricuspid or non-recurved bicuspid in *pectinatus*), and form of the anterior nostril (tubular in *aurocaudatus,* a simple opening in *pectinatus*). Admittedly, neither these differences, nor others we could detail would serve to refute a hypothesis that these two species are closely related. Alternatively we have been unable to identify any derived feature indicative of a close relationship between the two taxa. In the absence of such information we prefer to take a conservative course of action and assign *pectinatus* to *Bryconamericus.*

Acknowledgments

The material of *Bryconamericus pectinatus* was collected during a survey funded by the BIOLAT program of the National Museum of Natural History, Smithsonian Institution. The ichthyological collecting program was a collaborative effort between USNM and MHN-USM. The assistance of Prof. Hernán Ortega and his colleagues (MHN-USM) in all facets of the project is greatly appreciated. Dr. Barry Chernoff and Ms. Mary Anne Rogers (FMNH) arranged for the loan of the holotype and part of the paratype series of *Astyanax aurocaudatus.* Figures 1, 2, 4, 5 were prepared by Mr. Theophilus B. Griswold. The Spanish "Resumen" was translated by Dr. Ramiro Barriga of the Escuela Politécnica Nacional, Quito, Ecuador. This paper was improved by the suggestions of Dr. Stanley H. Weitzman (USNM), Dr. Wayne C. Starnes (USNM), Dr. Scott A. Schaefer (Academy of Natural Sciences of Philadelphia), Dr. Thomas A. Munroe (National Marine Fisheries Service, Systematics Laboratory), and two anonymous reviewers. We thank all of the above for their assistance and interest. Research associated with this study was supported in part by the Neotropical Lowland Research Program of the International Environmental Sciences Program of the Smithsonian Institution. This is contribution no. 1, Biological Diversity in Latin America (BIOLAT) Project, Smithsonian Institution.

Literature Cited

Böhlke, J., S. H. Weitzman, & N. A. Menezes. 1978. Estado atual da sistemática dos peixes de água doce da América do Sul.—Acta Amazonica 8(4): 53–62.

Eigenmann, C. H. 1913. Some results from an ichthyological reconnaissance of Colombia, South America. Part II.—Indiana University Studies 18:1–30.

———. 1927. The American Characidae.—Memoirs of the Museum of Comparative Zoology 43(4): 311–428.

———, W. L. McAtee, & D. P. Ward. 1907. On further collections of fishes from Paraguay.—Annals of the Carnegie Museum 4(2):110–157.

Fink, W. L. 1976. A new genus and species of characid fish from the Bayano River basin, Panamá (Pisces: Cypriniformes).—Proceedings of the Biological Society of Washington 88(30):331–344.

Géry, J. 1972. Contribution à l'étude des poissons characoïdes de l'équateur.—Acta Humboldtiana, Series Geologica, Palaentologica et Biologica 2:1–110.

———. 1977. Characoids of the world. T.F.H. Publications, Neptune City, New Jersey, 672 pp.

Ortega, H. & R. P. Vari. 1986. Annotated checklist of the freshwater fishes of Peru.—Smithsonian Contributions to Zoology 437:1–25.

Vari, R. P., & J. Géry. 1980. *Cheirodon ortegai,* a new markedly sexually dimorphic cheirodontine (Pisces: Characoidei) from the Rio Ucayali of Peru.—Proceedings of the Biological Society of Washington 93(1):75–92.

Weitzman, S. H., & W. L. Fink. 1983. Relationships of the Neon Tetras, a group of South American freshwater fishes (Teleostei, Characidae), with comments on the phylogeny of New World Characiforms.—Bulletin of the Museum of Comparative Zoology 150(6):339–395.

———, & S. V. Fink. 1985. Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae).—Smithsonian Contributions to Zoology 421:1–121.

Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Present address of Siebert: Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD, England.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 525–542

MOOJENICHTHYS MIRANDA-RIBEIRO (PISCES: OSTARIOPHYSI: CHARACIDAE), A PHYLOGENETIC REAPPRAISAL AND REDESCRIPTION

Ricardo M. C. Castro and Richard P. Vari

Abstract.—The Neotropical characiform characid genus *Moojenichthys* Miranda-Ribeiro is hypothesized to form a monophyletic lineage with *Triportheus* Cope on the basis of shared derived features of the pectoral girdle and perhaps of the first infraorbital. Autapomorphies for *Moojenichthys* are discussed. *Moojenichthys myersi* Miranda-Ribeiro, the only member of the genus, is redescribed. This species is apparently endemic to the Rio do Braço system of the state of Bahia, Brazil.

Resumo.—Uma hipótese de relações filogenéticas reunindo em um só grupo monofilético os gêneros neotropicais *Moojenichthys* e *Triportheus,* ambos pertencentes à família Characidae e à ordem Characiformes, é formulada com base na posse em comum de caracteres derivados na cintura escapular e, possivelmente, primeiro infra-orbital. *Moojenichthys myersi* Miranda-Ribeiro, o único membro do gênero, é redescrito. Esta espécie é, aparentemente, endêmica da bacia do Rio do Braço, no estado da Bahia, Brasil, e consiste na única ocorrência de um representante da linhagem evolutiva *Triportheus-Moojenichthys* nos rios costeiros do leste do Brasil, excluindo o rio São Francisco.

Miranda-Ribeiro (1956:546) proposed the characid genus *Moojenichthys* for a single species, *M. myersi,* first described in that publication on the basis of two specimens collected in the Rio do Braço, near Ilhéus in the state of Bahia of eastern Brazil. *Moojenichthys myersi* has a number of external anatomical features unusual within the Characiformes. Perhaps the most striking of these are its elongate, laterally flattened body, and the pronounced, laterally compressed mid-ventral keel. Although the thoracic keel is not obvious in specimens of *Moojenichthys* under 15 mm SL, mid- to large-sized individuals of the genus have a distinct mid-ventral ridge extending from the isthmus posteriorly to the origin of the pelvic fin.

In his original description of *Moojenichthys* Miranda-Ribeiro stated that the genus was "related" to *Triportheus* Cope (1872) and *Clupeacharax* Pearson (1924) both of which also have elongate, laterally compressed bodies characterized by varyingly developed mid-ventral keels. Miranda-Ribeiro did not explicitly state which characters lead him to propose that these species are "related," presumably closely. It seems reasonable, nonetheless, to assume that the overall similarities in body shapes, particularly the presence of mid-ventral keels, contributed significantly to this hypothesis.

Despite the distinctive external morphology of *Moojenichthys myersi,* subsequent references to the genus and species are extremely limited. Géry (1972:55), in his key to New World characiforms, commented that *Triportheus* and *Moojenichthys* are probably derived from *Brycon* Müller and Troschel, and on the next page proposed that *Clupeacharax* is close to *Triportheus* (1972:56). More recently, Géry (1977: 346) again emphasized the similarities between *Moojenichthys* and *Triportheus,* noting, however, that the reported dentition of *M. myersi* is more reminiscent of the subfamily "Tetragonopterinae" of the family Characidae. In that publication Géry did not comment on Miranda-Ribeiro's proposal of a possible relationship between *Moojenichthys* and *Clupeacharax,* but rather segregates *Clupeacharax* in the monotypic subfamily Clupeacharacinae. Castro (1981:138), in turn, cited some external similarities between *Clupeacharax* and *Engraulisoma* Castro.

Other than for the original description by Miranda-Ribeiro (1956) and Géry's brief comments (1972, 1977), we know of no published citations of *Moojenichthys.* Similarly, the primary ichthyological literature apparently does not include records of the subsequent capture of the species. This is not surprising given that *M. myersi* is apparently endemic to the Rio do Braço system, a poorly sampled river basin that drains into the Atlantic Ocean slightly north of the city of Ilhéus in the state of Bahia, Brazil.

Recent collecting efforts in the coastal rivers of Bahia associated with our revisionary studies of the characiform families Curimatidae and Prochilodontidae, have resulted in the capture of a large series of *Moojenichthys myersi* with a much greater range of standard lengths than available to Miranda-Ribeiro. This additional material allows us to provide a detailed redescription of the genus and species. Those specimens also permit anatomical studies to evaluate previous suggestions about the relationships of *Moojenichthys.*

Methods.—All measurements are given as proportions of standard length (SL) except for subunits of the head which are presented as proportions of head length (HL). Lateral-line scale counts include all pored scales along that series, including the scales posterior of the hypural joint. Vertebral counts were taken from radiographs, and specimens cleared and counterstained for bone and cartilage. The vertebral count includes the four vertebrae incorporated in the Weberian apparatus, and considers the fused PU_1+U_1 as a single element. In counts of median and pelvic fins, lower-case Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The range for each meristic value of all measured specimens is presented first, with the value for the holotype indicated in square brackets. Measurements were made following the methods outlined in Fink & Weitzman (1974:1–2).

The following institutional abbreviations are used: ANSP—Academy of Natural Sciences of Philadelphia; MNRJ—Museu Nacional, Rio de Janeiro; MZUSP—Museu de Zoologia, Universidad de São Paulo; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and FFCLRP-USP—Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo.

Phylogenetic Analysis

As noted in the introductory comments, Miranda-Ribeiro (1956:546) considered *Moojenichthys, Triportheus,* and *Clupeacharax* to be related, albeit without specifically stating the basis for his opinion. A number of questions exist about the phylogenetic associations of these taxa, and at least in the case of *Triportheus* the species-level classification of the genus remains unsettled.

Moojenichthys myersi has been collected only in the Rio do Braço system of eastern Brazil. *Clupeacharax* includes a single species, *C. anchoveoides,* a poorly known fish reported from scattered sites ranging from Argentina (Miquelarena & Casciotta 1982:333), through Bolivia (Pearson 1924: 47) and Peru (Ortega & Vari 1986:8), to Ecuador (Stewart et al. 1987:26). *Triportheus,* a much more speciose genus well represented in museum collections, is found on both sides of the Andean Cordilleras across much of lowland South America. Miranda-Ribeiro (1941), who applied *Chalcinus* Cuvier & Valenciennes (1849) to the members of *Triportheus,* recognized eleven species including *Chalcinus culter* Cope which Fowler (1907) segregated in the genus *Coscinoxyron.* Myers (1940:170) pointed out that *Chalcinus* was already occupied in the Hymenoptera, and that *Triportheus* was the next available name for the members of the genus. Schultz (1944:273) and Weitzman (1960:239) agreed that Miranda-Ribeiro's revisionary effort was unsatisfactory, a view that we share. Géry (1977:343, 654) in his key to the members of *Triportheus,* recognized only nine of the nominal species as valid, and tentatively retained *culter* in *Triportheus.* This uncertainty concerning the recognizable species of *Triportheus* complicates a determination of whether the genus is monophyletic. Those questions are beyond the scope of this study. We will, rather, attempt to determine the phyletic relationships of *Moojenichthys,* and critically evaluate suggestions that the genus is related to *Triportheus* and *Clupeacharax.*

Mid-ventral keel.—One of the most obvious features of *Moojenichthys* is the distinct mid-ventral keel that extends posteriorly from the isthmus to between the origins of the pelvic fins. Whereas the posterior portion of this keel is formed by fleshy tissue, the anterior portion is underlain by asymmetrically expanded coracoid bones. The somewhat irregular anterior margins of the coracoids are relatively short where they meet the anteroventral margins of the cleithra (Fig. 1B). The dorsal margin of the coracoids in *Moojenichthys* gradually rises posteriorly to the region where it articulates with the scapula and mesocoracoid. As a consequence, the overall proportions of the plate-like ventral portion of the coracoid are distinctly asymmetrical in lateral view, with the posterior margin of the coracoid notably deeper than the anterior border of the bone. Such asymmetrically expanded coracoids are relatively unusual within characiforms. A horizontally rectangular, moderately-sized coracoid with an overall horizontally rectangular form is found in the vast majority of characiforms of all families (e.g., Characidae (*Brycon,* Fig. 1A); Prochilodontidae, see Roberts 1973:fig. 24; Hemiodontidae, see Roberts 1974:figs. 16, 53; Lebiasinidae, see Weitzman 1964:fig 10; Parodontidae, see Roberts 1974:fig. 76; and Erythrinidae, see Starks 1930:fig. 8). Indeed, only the characiform families Characidae and Gasteropelecidae include taxa in which the coracoids are dramatically expanded to form distinct thoracic keels. Within the Characidae enlarged coracoids are absent among Old World members of the family, and the vast majority of Neotropical characids similarly lack significant expansions of these bones (e.g., *Acestrorhynchus,* see Roberts 1969:fig. 52; and *Brycon* (Fig. 1A), see also Weitzman 1962:figs. 18, 19). As noted in the introductory section, the species of *Triportheus* are also characterized by a distinct thoracic keel. The coracoids in *Triportheus* are similar to those of *Moojenichthys* in being asymmetrically and vertically expanded in lateral view. In *Triportheus,* however, the dorsal margin of the plate-like ventral portion of the ossification is more steeply angled, and the posterior margin of the bone much more extensive vertically than that in *Moojenichthys* (Fig. 1C). This gives the profile of the bone a near equilateral triangular appearance. Given that most characids and non-characid characiforms lack enlarged coracoids, the common occurrence of expanded coracoids found in *Moojenichthys* and *Triportheus* is reasonably hypothesized as a derived character which, in turn, would be congruent with the hypothesis that the two genera are sister taxa.

Expanded coracoids associated with a thoracic keel are, however, not unique to *Moojenichthys* and *Triportheus* among characiforms. As noted in the introductory discussion, an enlargement of that element

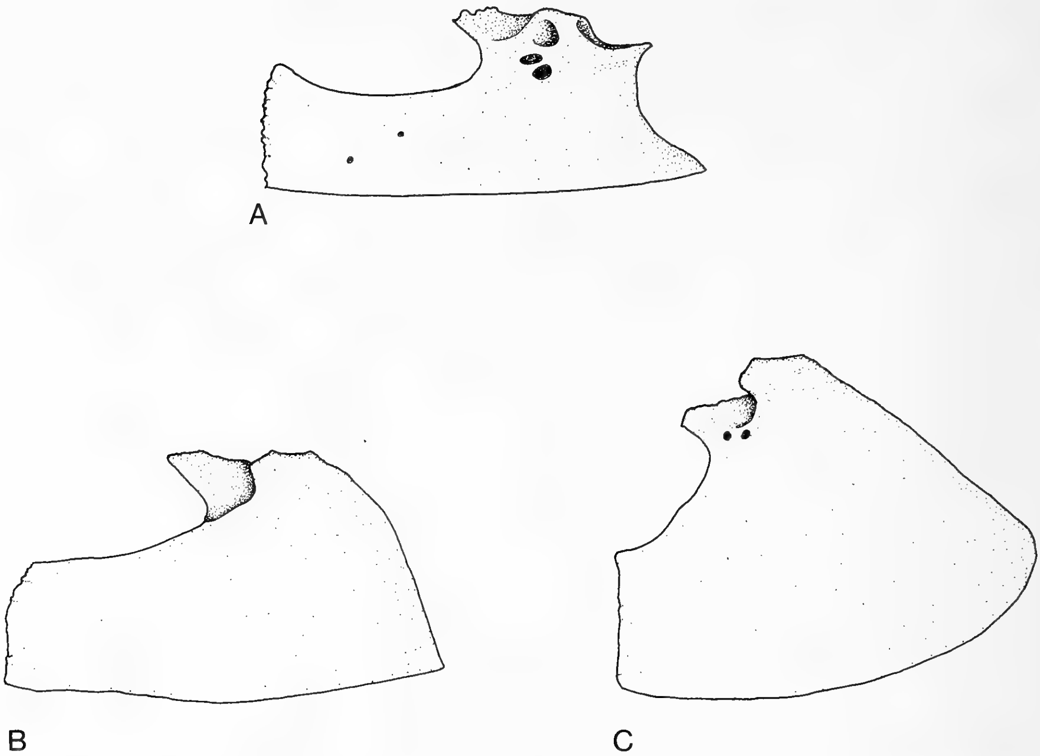


Fig. 1. Coracoids of A) *Brycon falcatus,* USNM 226161, 75.1 mm SL; B) *Moojenichthys myersi,* USNM 304497, 84.8 mm SL; and C) *Triportheus angulatus,* USNM 270343, 76.6 mm SL; right side, medial view, anterior to left.

also occurs in *Clupeacharax* and may have lead Miranda-Ribeiro to suggest that the genus was related to *Moojenichthys.* Starks (1930:22–23, fig. 9) described and figured the expanded coracoid of *Rhaphiodon* Agassiz, a genus of large predatory Neotropical characiforms. Weitzman (1960:239) noted that a keeled thorax and expanded coracoids, although unusual among characiforms (his "characids"), also occur in *Piabucus* Oken, *Pseudocorynopoma* Perugia, *Rhaphiodon,* and the genera *Carnegiella* Eigenmann, *Gasteropelecus* Pallas, and *Thoracocharax* Fowler, the last three of which together constitute the Gasteropelecidae (sensu Greenwood et al. 1966:395). Expanded coracoids also are found in *Cynodon* Spix, *Hydrolycus* Müller and Troschel and *Gnathocharax* Fowler. All of the above cited taxa appear to be surface feeders which, with the exception of the Gasteropelecidae, also have moderately to distinctly elongate bodies.

The occurrence of expanded coracoids in a number of characid taxa other than *Moojenichthys* and *Triportheus* brings, into question the appropriateness of using that feature to propose a close relationship for those genera. Weitzman suggested (1954: 230–231) that the specialized expansions of the coracoids probably arose several times within the Characiformes. The present poor understanding of phylogenetic relationships within the Characiformes in general, and the Characidae in particular, restricts the degree to which we are able to critically evaluate that suggestion in all instances. Nonetheless, subsequent research by various researchers has yielded data that support Weitzman's suggestion, and which indicates that the occurrence of expanded coracoids in characids other than *Moojenichthys* and *Triportheus* is homoplastic relative to that feature in those genera.

Vari (1977:4–6) discussed a series of distinctive derived features of the posterior chamber of the gas-bladder and of the anterior proximal pterygiophores of the anal fin that unite *Piabucus* with *Iguanodectes* Cuvier. In *Iguanodectes* the pre-pelvic region is transversely rounded. *Pseudocorynopoma* is a member of the subfamily Glandulocaudinae, a taxon which Weitzman et al. (1985:112–113) noted may not represent a monophyletic assemblage. Nonetheless those authors tentatively suggested that *Pseudocorynopoma* may be part of a monophyletic subset of genera within the Glandulocaudinae. Other species in the subfamily lack keeled thoracic regions. Howes (1976) united *Rhaphiodon, Cynodon,* and *Hydrolycus* as a tribe, the Cynodontini, and hypothesized on the basis of a variety of characters that the lineage consisting of these three genera was most closely related to various genera of the characid tribe Characini. The Characini, in turn, consists of species in which the coracoids are not dramatically enlarged.

Thus the available evidence indicates that the characid taxa with keeled thoracic regions cited in the previous paragraph are each in turn most closely related to species or species groups without that derived modification. The species with expanded coracoids cited in the immediately preceding section also lack the derived features of the infraorbital series and lateral ethmoid common to *Moojenichthys* and *Triportheus* (see discussions in following sections). Consequently it is most parsimonious to assume that the pre-pelvic keels of *Piabucus, Pseudocorynopoma, Rhaphiodon, Cynodon,* and *Hydrolycus* are homoplastic relative to the expanded coracoids in *Moojenichthys* and *Triportheus.*

Information concerning the phylogenetic relationships of the Gasteropelecidae, *Clupeacharax,* and *Gnathocharax* is somewhat more equivocal. The three genera of the Gasteropelecidae constitute a highly derived lineage presumably derived from some component of what is now recognized as the Characidae (Weitzman 1954:243). Although the closest relatives of the Gasteropelecidae remain to be elucidated, we agree with Weitzman (1954) that the overall characters of gasteropelecids differ dramatically from those of *Triportheus* and that gasteropelecids are apparently evolved from a different subunit within the Characiformes. Although a resolution of the phylogenetic associations of gasteropelecids would require an analysis that extends far beyond the scope of this paper, one feature of the Gasteropelecidae is noteworthy relative to this question. Weitzman & Fink (1983:391) noted that the supraorbital bone is absent in all the "tetragonopterine" characids they examined. The supraorbital is widely distributed among characiforms, and also among the members of the Characidae both in the New World and Africa. The absence of that ossification is thus hypothesized to be a derived condition within the Characidae. The supraorbital is absent in the Gasteropelecidae (see Weitzman 1954:7), and the common absence of the supraorbital in "tetragonopterines" and gasteropelecids may be a derived feature indicative of common ancestry of those taxa. Both *Triportheus* and *Moojenichthys,* in contrast, retain a supraorbital.

The relationships of *Gnathocharax,* a monotypic genus of the Amazon basin with an expanded coracoid, are still unresolved. *Gnathocharax* lacks the distinct anterior process of the lateral ethmoid common to *Moojenichthys, Triportheus, Brycon,* and various other characids (see discussion under "Autapomorphies of *Moojenichthys*"). *Gnathocharax* also does not have the distinctive modification of the first infraorbital found in *Moojenichthys, Triportheus,* and at least some species of *Brycon.* Finally, *Gnathocharax* lacks a supraorbital and is characterized by conical dentition typical of the characid tribe Characini and groups probably aligned with that tribe (see also discussions concerning the monophyly of the Characini by Menezes (in Sazima 1983), Vari (1986), and Weitzman & Vari (1987)). The cumulative data is congruent with the hypothesis that the coracoid expansion in *Gnathocharax* is homoplastic relative to that in *Moojenichthys* and *Triportheus.*

The phylogenetic relationships of *Clupeacharax,* the last characid genus in our list of genera with expanded coracoids are uncertain. Castro (1981:138) noted a series of similarities between *Clupeacharax* and *Engraulisoma* which has non-expanded coracoids. Ongoing studies by one of us (RMCC) are aimed at analyzing the significance of these similarities between *Clupeacharax* and *Engraulisoma.* In the interim nonetheless, several features of *Clupeacharax* bring into question the hypothesis of a close relationship between that genus and *Moojenichthys* as first proposed by Miranda-Ribeiro (1956). *Clupeacharax* lacks the derived form of the first infraorbital common to *Moojenichthys, Triportheus* and some species of *Brycon* (see discussion under "Infraorbitals"). Furthermore, *Clupeacharax* lacks the anterior process of the lateral ethmoid common to *Triportheus, Moojenichthys, Brycon,* and various other characids (see discussion under "Autapomorphies of *Moojenichthys*"). Thus even in the absence of a detailed analysis of the relationships of *Clupeacharax* it is more parsimonious to hypothesize that the enlargement of the coracoids in that genus are homoplastic with respect to those in *Moojenichthys* and *Triportheus.*

In summary, the presence of expanded coracoids in gasteropelecids and various characids besides *Moojenichthys* and *Triportheus,* thus appears to have arisen independently of that feature in those genera. The possession of asymmetrically vertically enlarged coracoids is consequently proposed as a synapomorphy for *Moojenichthys* and *Triportheus.*

In our introductory discussion we note that Géry (1977:346) commented that the dentition of *Moojenichthys* is "approaching [that of] the Tetragonopterinae." The presence of a supraorbital in *Moojenichthys myersi* argues, however, against a close phylogenetic alignment of *Moojenichthys* with tetragonopterines in which that ossification is apparently absent (Weitzman & Fink 1983:391).

Infraorbitals.—A second possible synapomorphy for *Triportheus* and *Moojenichthys* is found in the infraorbital series. *Moojenichthys* and *Triportheus* have the series of ossifications surrounding the orbit typical for characiforms, six infraorbitals, a supraorbital, and an antorbital. The most notable feature in these series of ossifications in *Moojenichthys* and *Triportheus* involves the form of the first infraorbital and its association with the second infraorbital. The posteroventral portion of the first infraorbital in both *Moojenichthys* and *Triportheus* extends distinctly ventral of the anteroventral portion of the second infraorbital thereby significantly reducing the degree to which the latter element enters into the outer margin of the infraorbital series (Fig. 2). This association of the two anteriormost infraorbital elements differs from the morphology of these bones in *Clupeacharax, Rhaphiodon, Piabucus, Pseudocorynopoma, Carnegiella, Gasteropelecus, Thoracocharax, Cynodon, Hydrolycus, Gnathocharax,* the other characid genera known to have expanded coracoids. In those other taxa the first and second infraorbitals meet along a straight anteroventrally to posteroventrally aligned juncture without any invasion by the first infraorbital of the area primitively occupied by the anteroventral portion of the second infraorbital.

Although the derived form of the first and second infraorbitals in *Moojenichthys* and *Triportheus* serves to distinguish those taxa

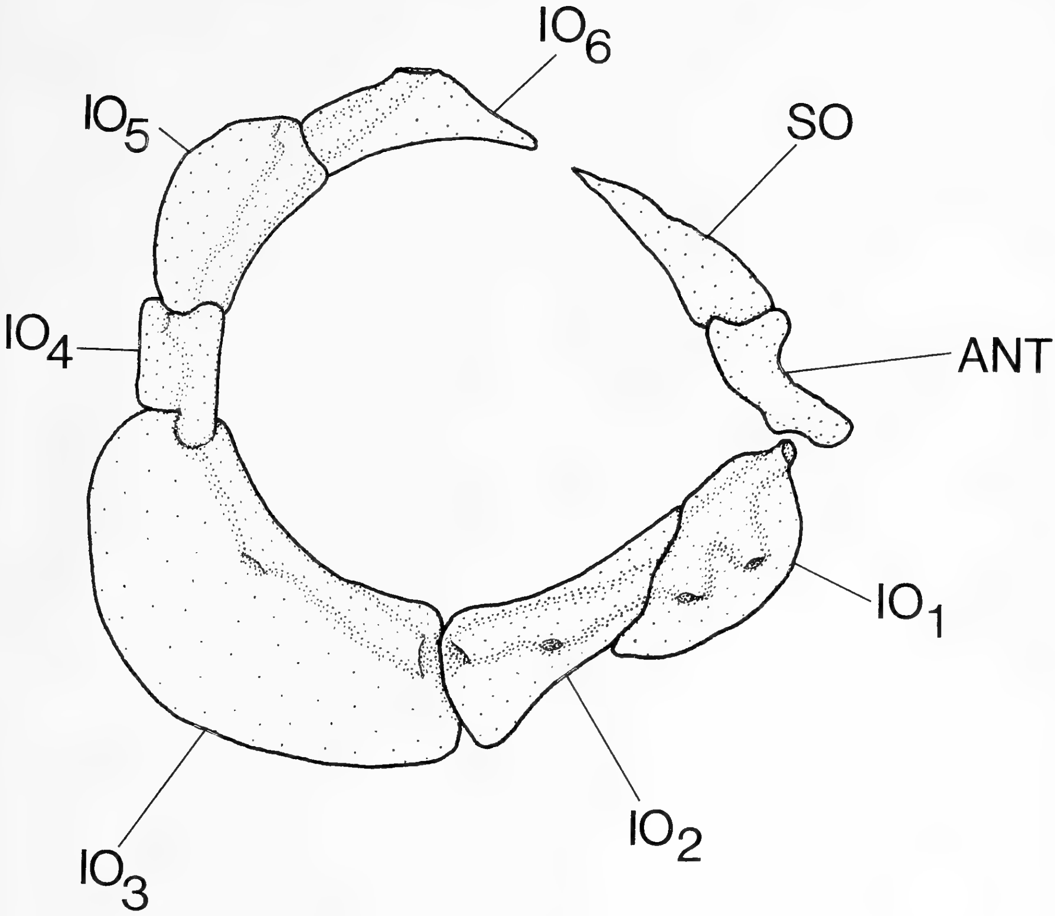


Fig. 2. Infraorbitals and supraorbital of *Moojenichthys myersi,* USNM 304497, 84.8 mm SL, right side, anterior to right. Abbreviations: ANT—antorbital; IO—infraorbitals (1 to 6); SO—supraorbital.

from other characids with expanded coracoids, we should note that the occurrence of such modifications of the infraorbitals extends beyond *Moojenichthys* and *Triportheus.* Howes (1982:5) illustrated a morphology of the first and second infraorbitals in *Brycon acuminatus* (Eigenmann & Norris) apparently comparable to that in *Moojenichthys* and *Triportheus.* At least some other species of *Brycon,* in contrast, have more generalized associations between the first two infraorbitals (e.g., *B. meeki,* see Weitzman 1962:fig. 8).

Brycon has been suggested to be a likely close relative to *Triportheus* by both Regan (1911:18) and Weitzman (1960:243). In his overview of the former genus Howes (1982: 1) questioned whether *Brycon* is monophyletic, but utilized the traditional concept of the genus until future phylogenetic and revisionary studies can be undertaken. In the absence of such phylogenetic data Howes excluded *Triportheus* from *Brycon* on the basis of the presence of the mid-ventral keel in the latter genus; noting that *Triportheus* shares, however, all the other diagnostic characters of *Brycon.* The various similarities between *Triportheus* and *Brycon* noted by Regan, Weitzman, and Howes, and the derived features of the infraorbitals cited above for *Moojenichthys, Triportheus,* and at least some species of *Brycon,* raise the question of whether the lineage formed by *Triportheus* and *Moojenichthys* may be most closely related to some subunit of *Brycon.* Resolution of that question must await further revisionary and phylogenetic studies of both *Triportheus* and *Brycon.*

Autapomorphies of Moojenichthys myersi.—Within the lineage formed by *Moojenichthys, Triportheus,* and possibly *Brycon* or some subunit of the latter genus (see immediately preceding discussion), one of the more notable derived features for *Moojenichthys myersi* (hereafter referred to as *Moojenichthys*) is the absence of the single symphysial tooth posterior to the main row of dentition on each dentary. Such symphysial teeth are common to all members of *Triportheus* and *Brycon,* and also occur in *Chalceus* Cuvier. *Chalceus* shares all the defining characters of *Brycon,* but is excluded from *Brycon* because it possesses a supramaxilla (Howes 1982:1–2). An inner row of teeth on the dentary developed to varying degrees also occur in various characiforms in both the New World (e.g., Lebiasinidae, Weitzman 1964:143) and Africa (e.g., diverse genera in the Characidae, see Poll 1957:95, and Distichodontidae, Vari 1979:275–277). This broad phyletic distribution of symphysial teeth both in groups proximate to *Moojenichthys* and other more distantly related characiforms, makes it most parsimonious to hypothesize that the absence of the symphysial dentary teeth in *Moojenichthys* is a derived loss.

The ventrally recurved form of the maxillary dentition and the large number of teeth along the anterior margin of the maxilla distinguish *Moojenichthys* (Fig. 3) from all examined species of *Triportheus.* The ventrally recurved maxillary teeth in *Moojenichthys* are unique within the assemblage formed by that genus, *Triportheus,* and possibly *Brycon,* and are hypothesized to be an autapomorphy for *Moojenichthys.* In contrast, the large number of teeth (14 to 20) along the anterior margin of the maxilla in *Moojenichthys* is more difficult to evaluate. On the one hand that dentition does serve to readily separate *Moojenichthys* from *Triportheus* which has only 2 to 4 teeth in that series. Alternatively the species of *Brycon* have 10 to 30 teeth along the maxilla (Howes 1982:46), with most species overlapping the range in tooth number of *Moojenichthys* to some degree. This common occurrence of large numbers of maxillary teeth in *Moojenichthys* and *Brycon* raises the possibility that the relatively few maxillary teeth in *Triportheus* may be synapomorphic for the members of that genus, and that the high number of maxillary teeth in *Moojenichthys* is primitive.

A final noteworthy autapomorphy for *Moojenichthys* involves the anterior portion of the lateral ethmoids. In *Moojenichthys, Brycon* and *Triportheus* the anterior surface of the lateral ethmoid bears a distinct process that extends anteriorly and medially to contact the posterodorsal surface of the vomer (see Weitzman 1962:fig. 3 for an illustration of the condition in *Brycon meeki*). In *Moojenichthys* the anterior process of the lateral ethmoid is developed into an elongate anteriorly-tapering process (Fig. 4) that is significantly longer than comparable processes in *Triportheus* and *Brycon.* Anteriorly this elongate anterior process of the lateral ethmoid in *Moojenichthys* contacts a distinct lateral process situated on the dorsal surface of the vomer. The space between the anterior processes of the paired lateral ethmoids and dorsal of the vomer and parasphenoid is, in turn, filled by a large cartilage mass comparable to that in *Brycon, Triportheus,* and many other characids. Although the presence of the anterior process of the lateral ethmoid is not unique to *Moojenichthys,* the degree of the anterior elongation of the structure is not equalled in other examined characiforms and this modification is thus considered autapomorphic for the genus.

The relationship of the anterior process

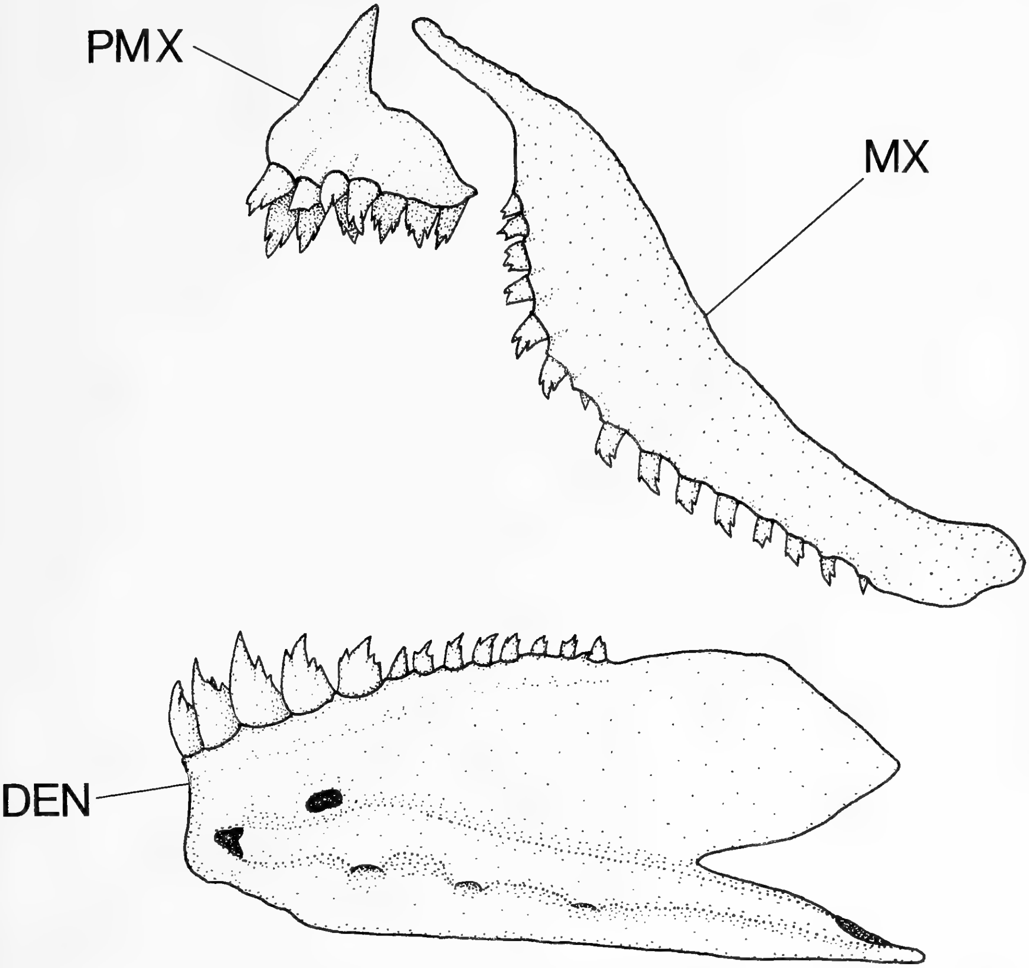


Fig. 3. Upper and lower jaws of *Moojenichthys myersi,* USNM 304497, 84.8 mm SL; left side, anterior to left; individual bones separated from positions in life. Abbreviations: DEN—dentary; MX—maxilla; PMX—premaxilla.

of the lateral ethmoid to the parasphenoid, vomer, and associated median cartilage in *Moojenichthys* is also distinctive. When present, the anterior process of the lateral ethmoid in characids usually extends directly along the lateral margin of the parasphenoid and vomer (e.g., *Brycon meeki,* see Weitzman 1962:fig. 3). *Moojenichthys,* in contrast, has a distinct vertical gap between the ventral margin of the anterior process of the lateral ethmoid and the dorsal surface of the vomer. This results in a broad lateral exposure of the median cartilage mass (Fig. 4). This relationship of the lateral ethmoid and proximate bones and cartilages is unknown in *Triportheus, Brycon* and other examined characiforms, and is consequently hypothesized to represent an additional autapomorphy for *Moojenichthys.*

Moojenichthys Miranda-Ribeiro

Moojenichthys Miranda-Ribeiro 1956:546 [type *Moojenichthys myersi* Miranda-Ribeiro, by original designation].—Géry 1972:55 [possible derivation from *Brycon*].—Géry 1977:346 [similarities with *Triportheus* noted; dentition compared with that of "Tetragonopterinae"].

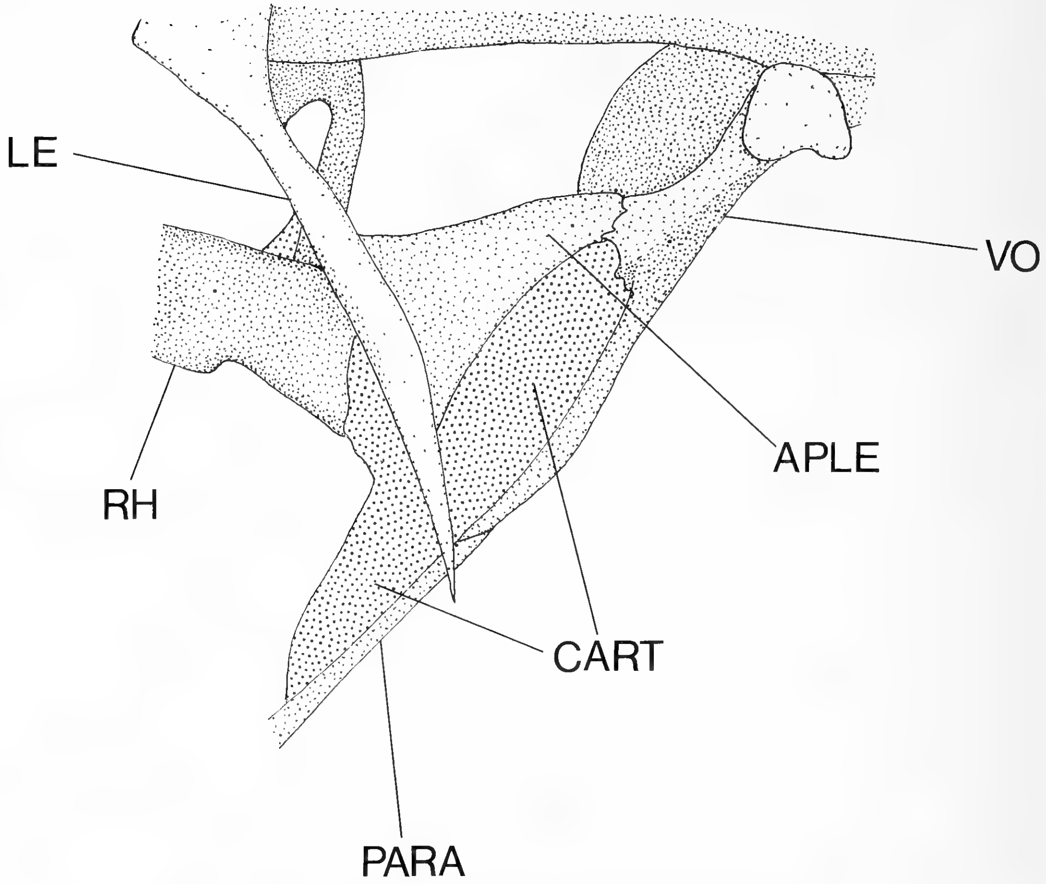


Fig. 4. Anterior portion of the neurocranium of *Moojenichthys myersi,* USNM 304497, 84.8 mm SL; right side, lateral view, anterior to right. Abbreviations: APLE—anterior process of lateral ethmoid; CART—cartilage; LE—main body of lateral ethmoid; PARA—parasphenoid; RH—rhinosphenoid; VO—vomer.

Diagnosis.—Within the clade formed by *Moojenichthys* and *Triportheus* only the former genus lacks the paired symphysial teeth posterior to the main row of dentary dentition. *Moojenichthys* also differs from *Triportheus* in the numerous ventrally recurved teeth along the anterior margin of the maxilla, and in the derived degree of development and position of the anterior process of the lateral ethmoid. *Moojenichthys* can also be distinguished from *Triportheus* on the basis of its possession of two rather than three rows of teeth on the premaxilla, and in having numerous teeth along much of the anterior margin of the maxilla rather than several teeth limited to the dorsal portions of the maxilla.

Remarks.—The derived features described above are congruent with the hypothesis that *Moojenichthys* forms a monophyletic lineage with *Triportheus,* or with *Triportheus* and a subunit of *Brycon.* This conclusion raises the question of whether it is appropriate to continue to recognize a monotypic *Moojenichthys,* or whether that genus should be synonymized into *Triportheus.*

Moojenichthys is characterized by a series of autapomorphic features. Within the Characiformes such phenetically distinct taxa have been traditionally segregated into monotypic genera. We reject the criterion of phenetic distinctness as an a priori basis for the continued recognition of *Moojenichthys,* but nonetheless suggest that it is premature to synonymize *Moojenichthys* into *Triportheus.* Our decision is a consequence of the present poor knowledge of the phylogenetic relationships within *Triportheus.* Until such time as we have a rigorous hypothesis of the relationships within *Triportheus* it is impossible to hypothesize whether *Moojenichthys* is the sister-group to that genus, and thus could be preserved, or simply represents a subunit of *Triportheus.* In the latter case the continued recognition of *Moojenichthys* would result in a paraphyletic *Triportheus.* That problem could be resolved in one of several ways depending on the topology of the phylogenetic tree for the clade consisting of *Moojenichthys* plus *Triportheus. Moojenichthys* could be synonymized into *Triportheus* along with *Coscinoxyron,* a genus not presently recognized by most authors. Alternatively the topology of the phylogenetic tree might be such that it would be possible to continue to recognize *Moojenichthys* either by expanding the definition of the genus, or by recognizing one or more other genera in the clade in addition to *Triportheus* and perhaps *Coscinoxyron.* Given these diverse possibilities, we continue to use *Moojenichthys* in this study.

Moojenichthys myersi Miranda-Ribeiro
Figs. 1–7, Table 1

Moojenichthys myersi Miranda-Ribeiro, 1956:546–547, fig., type locality: "Braço River, Ilhéos [=Ilhéus], state of Bahia, Brazil.—Géry, 1977:346 [citation; possible relationships].

Diagnosis.—See "Diagnosis" of *Moojenichthys* above.

Description.—Morphometrics of holotype, paratype and larger examined non-type specimens presented in Table 1. Body elongate, distinctly compressed laterally in all specimens greater than 25 mm SL, somewhat less so in smaller individuals. Greatest body depth located slightly anterior to vertical line through origin of pelvic fin, approximately equal to one-half length of longest pelvic-fin ray in specimens over 50 mm SL; body not as deep and mid-ventral keel less developed in smaller examined specimens. Dorsal profile of head slightly convex from margin of lip to vertical line through posterior nostril, nearly straight from that line to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin, posteroventrally slanted and somewhat convex along base of dorsal fin; straight from posterior termination of dorsal fin to adipose fin, and moderately concave along caudal peduncle. Dorsal portion of body obtusely keeled transversely anterior to dorsal fin; transversely rounded posterior to fin. Ventral profile of head distinctly convex over lip, straight along anteroventral margin of jaw, and distinctly convex ventral to joint with quadrate. Ventral profile of body irregular, distinctly convex overall; very slightly convex from isthmus nearly to vertical line through origin of pectoral fin; convexity greater from that line to origin of pelvic fin; straight to slightly concave from origin of pelvic fin to anterior termination of anal fin; straight and posterodorsally slanted along base of anal fin; slightly concave along dorsal peduncle. Distinct mid-ventral keel extending from isthmus to between origins of pelvic fins; keel less developed in specimens under 20 mm SL; increasingly obvious in individuals over 30 mm SL, most developed in specimens of over 50 mm SL. Scales along margin of keel flat, not folded over edge of keel.

Head obtusely pointed in profile; mouth terminal, lower jaw longer than upper, with dentigerous portion of maxilla distinctly angled posteroventrally. Maxilla extending posteriorly under orbit to vertical line through anterior margin of pupil. Nostrils of each side close together; anterior opening

Table 1.—Morphometrics of *Moojenichthys myersi.* Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 18 are percentages of head length. Dashes indicate measurement that could not be taken due to damage to holotype. Range includes values for 24 specimens (holotype, MNRJ 4127; paratype MNRJ 4128; and 22 of the larger non-type specimens out of USNM 304497, MZUSP 40227, MNRJ 11605, and ANSP 164288), with the exception of length of the longest dorsal-fin ray which is based on 23 specimens, and length of the longest pectoral-fin ray which is based on 22 specimens.

	Holotype	Paratype	Range	Mean
Standard length	96.6	85.8	27.0–96.6	69.1
1. Greatest body depth	25.7	25.5	22.2–28.7	27.0
2. Snout to dorsal-fin origin	65.2	62.0	60.7–65.4	62.8
3. Length of base of dorsal fin	8.2	7.5	7.1–8.7	7.8
4. Posterior terminus of dorsal fin to adipose fin	18.0	17.8	16.4–19.8	18.0
5. Posterior terminus of dorsal fin to caudal-fin base	28.9	29.6	27.9–32.4	29.8
6. Snout to origin of pelvic fin	49.6	50.5	46.7–51.3	49.2
7. Snout to origin of anal fin	68.7	67.6	62.2–68.7	65.3
8. Length of base of anal fin	31.5	28.3	28.1–32.1	30.4
9. Length of caudal peduncle	8.7	9.8	8.0–10.6	9.2
10. Length of longest dorsal-fin ray	16.8	15.3	15.3–18.6	16.8
11. Length of longest pectoral-fin ray	—	32.1	24.4–32.1	30.1
12. Length of longest pelvic-fin ray	14.7	13.6	11.1–15.0	13.5
13. Least depth of caudal peduncle	7.6	7.0	6.3–8.7	7.9
14. Head length	24.1	24.2	23.7–29.0	24.6
15. Snout length	23.6	22.6	20.0–27.0	23.5
16. Orbital diameter	36.1	36.5	31.7–38.9	36.3
17. Postorbital head length	38.2	36.5	29.3–41.8	38.1
18. Interorbital width	24.0	24.0	19.1–27.6	24.5

circular, posterior kidney-shaped. Eye relatively large, without adipose eyelid. Median fronto-parietal fontanel well developed; completely separating parietals; frontals in contact only anteromedially and at epiphyseal bar. Fontanel becoming progressively wider posteriorly, extending onto dorsomedial surface of supraoccipital.

Infraorbital series complete (Fig. 2), all infraorbitals with laterosensory canal segments. Sixth infraorbital (dermosphenotic) with single tubular laterosensory canal segment. First infraorbital expanded anteroventrally, with distinctly convex anterior margin, anterior portion extends over lateral surface of maxilla; laterosensory canal segment with three sections in larger specimens. Supraorbital and antorbital present.

Four branchiostegal rays, first three attached to anterior ceratohyal, fourth to posterior ceratohyal. Gill-rakers relatively elongate, 17 or 18+1+40 to 42 rakers on outermost gill-arch (in 2 larger cleared and counterstained specimens).

Lower jaw with one row of 12 to 14 teeth on each side on each dentary (Fig. 3); number of teeth greater in largest specimens; inner row consisting of single symphysial tooth absent. Anterior 5 teeth on dentary notably larger than remainder, with 5 cusps, medial cusp distinctly largest. Remaining teeth usually tricuspidate, rarely unicuspidate, with largest cusp recurved somewhat posteriorly. Teeth on premaxilla in two rows; teeth of inner row larger (Fig. 3). Four tricuspidate teeth of approximately equal size in outer row. Six teeth in inner row on premaxilla; 2 medial teeth largest, subequal; remaining teeth gradually becoming smaller laterally; medial tooth tricuspidate, remaining teeth in row with 5 cusps. Lateral tooth of inner row of premaxilla approximates dorsal tooth on maxilla. Anterior margin of maxilla distinctly convex, with single row

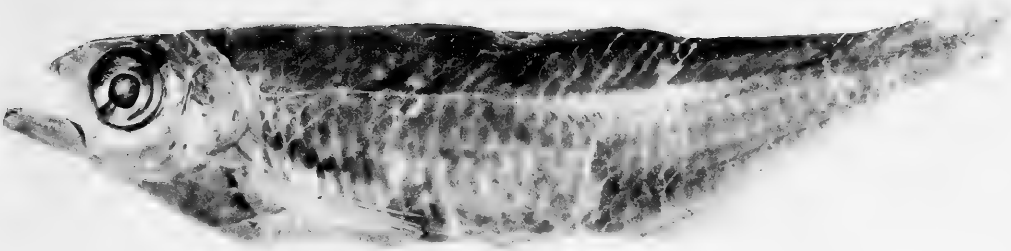


Fig. 5. *Moojenichthys myersi,* Brazil, Bahia, "Braço river" [=Rio do Braço], Ilhéos [=Ilhéus]; MNRJ 4127, holotype, 96.6 mm SL.

of teeth (Fig. 3). Teeth on maxilla distinctly smaller than smallest tooth on premaxilla; typically unicuspidate in specimens of approximately 27 mm SL, bicuspidate or usually tricuspidate in specimens of about 40 mm SL and greater. Smaller specimens with 2 to 9 teeth limited to upper one-quarter to one-half of anterior margin of maxilla; larger specimens with 14 to 20 teeth arranged along nearly entire anterior margin of maxilla. Largest cusp of teeth on maxilla recurved ventrally.

Scales cycloid, thin, relatively large. Lateral line distinctly decurved ventrally, completely pored from supracleithrum to base of middle rays of caudal fin. Forty to 43 [42] scales in lateral line (70% of specimens with 42 scales); 6 or 7 [7] scales in transverse series from origin of dorsal fin to lateral line; 3 or 4 [3] scales in transverse series from origin of pelvic fin to lateral line (4 scales present in only 1 specimen); 3 or 4 [3] scales in transverse series from origin of anal fin to lateral line; 17 to 21 [20] scales along mid-dorsal line between tip of supraoccipital process and origin of dorsal fin (60% of specimens with 19 or 20 scales); 9 or 11 [11] scales along mid-dorsal line between posterior termination of dorsal fin and adipose fin (91% of specimens with 10 or 11 scales); 13 to 15 [13] horizontal scale rows around caudal peduncle (86% of specimens with 14 or 15 scales).

Dorsal-fin rays ii,8 or 9 or iii,9 [ii,9] (ii,9 most common); anal-fin rays iv,31 to 35, or v,33 [iv,33] (iv,33 most common); pectoral-fin rays i,9 to 12 followed by 0 to ii unbranched rays [i,10,i] (i,10,i most common); pelvic-fin rays i,6 [i,6]; principal caudal-fin rays 10/9 [10/9].

Dorsal fin profile obtusely acute, posterior unbranched and first branched ray subequal; posterior unbranched ray typically slightly longer. Dorsal fin situated on posterior half of body; origin of fin located slightly posterior of vertical line through anterior terminus of anal fin, closer to base of caudal fin than to tip of snout. Longest dimension of adipose fin approximately equal to horizontal width of pupil; origin of adipose fin slightly anterior of vertical line through posterior terminus of anal fin. Pectoral fin large, profile distinctly acute; when fin depressed, tip extends to vertical line approximately two-thirds distance along pelvic fin. Pelvic fin profile obtusely acute, origin of fin at posterior margin of mid-ventral keel, tip of depressed fin extending posteriorly slightly beyond anus, but falling short of anterior terminus of anal fin. Axillary pelvic scale present, its length about one-third that of longest pelvic-fin ray. Cleared and counterstained 84.8 mm SL male with 6 to 15 basally directed bony hooks along posterior margins of first 5 branched pelvic-fin rays. Ventral margin of anal fin somewhat rounded anteriorly, with last unbranched and first branched rays

Fig. 6. *Moojenichthys myersi,* Brazil, Bahia, Rio do Braço, 2 km SW of town of Rio do Braço, on Fazenda Luzia, USNM 304496, 33.4 mm SL.

longest, subequal, following 10 to 12 branched rays rapidly decreasing in length, remaining anal-fin rays slowly decreasing in length. Males with 1 to 8 basally-directed bony hooks along posterior margins of distal sections of 7 to 14 longest anal-fin rays. Caudal fin forked, lobes obtusely pointed.

Total vertebrae 39 (2), 40 (20), 41 (2) [40].

Color in life.—Descriptions based on color transparencies of a series of recently preserved specimens captured in August 1988 and February 1989. Overall coloration of specimens ranging from 15.9 to 33.4 mm SL clear to yellowish. Iris, lower jaw, infraorbital region, opercle, and peritoneum silvery. Tip of lower jaw, snout, dorsal portions of body and basal portions of caudal fin light yellow. Traces of yellow pigmentation apparent on dorsal, adipose, and anal fins. Other fins hyaline. Mid-lateral dark stripe on body quite obvious, but somewhat masked anteriorly by guanine. Dark stripe above anal fin, and dark pigmentation on all fins clearly visible.

Specimens above approximately 50 mm SL bright silver overall, somewhat darker along dorsal portions of head and body. Dense guanine on scales completely masking both dark stripes along mid-lateral surface of body, and those on ventrolateral surface of body above anal fin. Dark pigmentation on fins as in preserved specimens.

Coloration in preservative.—Overall ground color of specimens fixed in formalin and lacking guanine on scales yellowish brown. Dense fields of small, dark chromatophores on upper lip, snout, and dorsal surface of head (Figs. 5–7). Very intense, horizontally elongate stripe of dark pigmentation along dorsal portion of lower lip; less intense dark pigmentation ventral to this on lower jaw. Scattered small dark chromatophores on lateral surface of head anterior to orbit and on opercle; pigmentation more obvious in specimens totally lacking guanine on head.

Body with mid-lateral stripe of small, dark chromatophores extending from supracleithrum posteriorly to caudal peduncle; stripe gradually expanding vertically posteriorly; broadened into distinctly wider diffuse dark spot on lateral surface of caudal peduncle. Body dorsal of dark mid-lateral stripe with margins of scales outlined by dark chromatophores; pattern most obvious in medium sized specimens, somewhat obscured by overall dusky appearance of dorsal portions of body in larger specimens. Stripe of dark chromatophores extending posterodorsally along ventrolateral portion of body from slightly anterior of vertical through anterior terminus of fin posteriorly to posterior terminus of fin. Stripe wider and distinctly separated from base of anal fin anteriorly, becoming gradually narrower and approaching base of anal-fin rays posteriorly.

Fig. 7. *Moojenichthys myersi,* Brazil, Bahia, Rio do Braço, 2 km SW of town of Rio do Braço, on Fazenda Luzia, MZUSP 40227, 81.6 mm SL.

Dorsal fin with dense field of dark chromatophores along distal portions of rays and membranes. Margins of adipose fin in larger specimens outlined by scattered dark chromatophores. Anterior rays of pectoral and pelvic fins outlined by series of small dark chromatophores. Anterior margin and distal portions of anal fin dusky, most rays outlined distally by dark chromatophores. Caudal fin dusky in specimens of all sizes, rays outlined by series of small dark chromatophores.

Common names.—Brazil, Bahia, Ilhéus: "Mossarupè," "Piaba-faca," and "Canivete" (Miranda-Ribeiro, 1956:547). During the 1988 and 1989 expeditions the only name used by local fishermen was "Piaba-faca."

Ecology.—Specimens collected during the 1988 and 1989 expeditions were collected in black waters containing limited suspended material. The area surrounding the river was originally a portion of the Atlantic Coastal Forest, but much of the understory vegetation has been replaced by cocoa trees. In the areas sampled for fishes the Rio do Braço was between 10 and 25 m wide, ranged from 1.5 to 3 m deep, and had mats of floating vegetation along its margins. The bottom was sandy-mud with scattered boulders.

Other fishes captured with *Moojenichthys myersi* and the families to which they are presently assigned were *Steindachnerina elegans* (Curimatidae); *Nematocharax venustus, Oligoscarcus macrolepis, Astyanax* sp., *Characidium* sp. (Characidae); *Hoplias* sp. (Erythrinidae); *Rhamdia* sp. (Pimelodidae); *Poecilia* sp. (Poeciliidae); *Astronotus ocellatus* and *Geophagus brasiliensis* (Cichlidae). The *Astronotus ocellatus* record represents an introduction.

Diet.—Examination of the stomach contents of the three cleared and counterstained specimens shows that the species eats mosquito larvae and other aquatic invertebrates.

Distribution.—Known only from the Rio do Braço in the state of Bahia, Brazil. The original description of *Moojenichthys myersi* states that the type material was collected in the "Braço river, Ilhéos." In actuality the mouth of the "Braço river" [=Rio do Braço] is located approximately 7 km along the coast north of the city of Ilhéus ("Ilhéos" of Miranda-Ribeiro). Limited ichthyological collecting has taken place in the Bahian coastal drainages near the Rio do Braço. Thus the lack of records of *Moojenichthys myersi* from other neighboring river systems may be a consequence of poor sampling.

Material examined.—Brazil. Bahia: "Braço river," Ilhéos [=Ilhéus], MNRJ

4127, 1 specimen, holotype, 96.6 mm SL; same locality, MNRJ 4128, 1 specimen, paratype, 85.8 mm SL; Ilhéus, Fazenda Pirataquicê, MNRJ 5572, 1 specimen, 78.2 mm SL (locality not found in examined gazetteers or maps); Rio do Braço, 2 km SW of town of Rio do Braço (approx. 14°39′S, 39°16′W), on Fazenda Luzia, USNM 304497, 9 specimens, 20.5–84.8 mm SL (1 specimen, 84.8 mm SL, cleared and counterstained); USNM 304496, 15 specimens, 17.8–33.4 mm SL (1 specimen, 27.0 mm SL, cleared and counterstained); MZUSP 40226, 15 specimens, 15.9–30.5 mm SL; MZUSP 40227, 9 specimens, 19.6–84.1 mm SL (1 specimen, 56.0 mm SL, cleared and counterstained); ANSP 164287, 3 specimens, 17.4–26.5 mm SL; ANSP 164288, 2 specimens, 63.4–76.0 mm SL; MNRJ 11604, 3 specimens, 20.1–24.4 mm SL; MNRJ 11605, 2 specimens, 63.4–74.9 mm SL.

Comparative cleared and stained material examined.—Brycon falcatus, USNM 226161, 2 specimens. *Carnegiella strigata,* USNM 225245, 5 specimens. *Clupeacharax anchoveoides,* USNM 302245, 1 specimen. *Cynodon gibbus,* USNM 270338, 2 specimens. *Engraulisoma taeniatum,* USNM 302225, 1 specimen. *Gasteropelecus sternicla,* USNM 226337. *Gnathocharax steindachneri,* USNM 278995, 2 specimens. *Rhaphiodon vulpinus,* USNM 231549, 3 specimens. *Triportheus angulatus,* USNM 270343, 2 specimens. *Triportheus* sp., USNM 280498, 4 specimens; USNM 258079, 2 specimens.

Acknowledgments

A number of the specimens of *Moojenichthys myersi* that served as the basis for this paper was collected during a collaborative FFCLRP-USP and USNM expedition in the state of Bahia, Brazil. The success of the collecting effort was assured by the enthusiasm of Susan L. Jewett (USNM), Hertz F. Santos, Maura H. Manfrin, Eliseu B. Dias, and Eduardo Castadelli, Jr. (all of FFCLRP-USP) who unstintingly assisted in the often difficult fishing efforts. Hertz F. Santos made a special second trip into the region of the type-locality to collect additional material of the species, including an extensive series that included most of the larger individuals reported on in this paper. Figures 5 to 7 were prepared by Mr. Theophilus B. Griswold. Sandra Raredon and Jeffrey Howe assisted in the research efforts at USNM. Ms. India Moreira (MNRJ) arranged for the loan of the holotype and paratype of *Moojenichthys myersi,* and Mr. Luis Paulo S. Portugal (MZUSP) and Dr. Naércio A. Menezes (MZUSP) facilitated our examination of those specimens. This paper was improved by the suggestions of Dr. Stanley H. Weitzman (USNM), Dr. Wayne C. Starnes (USNM), Dr. William L. Fink (University of Michigan, Museum of Zoology), Dr. Darrell J. Siebert (British Museum (Natural History)), and Mrs. Marilyn Weitzman (USNM). We thank all of the above for their assistance.

Extensive logistical support for the expedition that collected most of the specimens of *Moojenichthys myersi* was provided by FFCLRP-USP. Funding for that collecting effort was provided through the Neotropical Lowland Research Program of the International Environmental Sciences Program of the Smithsonian Institution. That program also supported the research associated with this project both at museums in Brazil and at the Smithsonian Institution.

Literature Cited

Castro, R. M. C. 1981. *Engraulisoma taeniatum,* um novo gênero e espécie de Characidae da bacia do Rio Paraguai (Pisces, Ostariophysi).—Papéis Avulsos de Zoologia, São Paulo 34(11):135–139.

Cope, E. D. 1872. On the fishes of the Ambiyacu River.—Proceedings of the Academy of Natural Sciences of Philadelphia (for 1871):257–269.

Cuvier, G. & A. Valenciennes. 1849. Histoire naturelle des poissons. Volume 22:1–395.

Fink, W. L., & S. H. Weitzman. 1974. The so-called cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae).—Smithsonian Contributions to Zoology 172:1–46.

Fowler, H. W. 1906. Further knowledge of some heterognathous fishes. Part II.—Proceedings of the Academy of Natural Sciences of Philadelphia (for 1906):431–488.

Géry, J. 1972. Poissons characoïdes des Guyanes, I. Généralitées. II. Famile des Serrasalmidae.—Zoologische Verhandelingen 122:1–250.

———. 1977. Characoids of the world. TFH Publications, Neptune City, New Jersey, 672 pp.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, & G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms.—Bulletin of the American Museum of Natural History 131(4):339–456.

Howes, G. J. 1976. The cranial musculature and taxonomy of characoid fishes of the tribes Cynodontini and Characini.—Bulletin of the British Museum (Natural History), Zoology 29:203–248.

———. 1982. Review of the genus *Brycon* (Teloestei: Characoidei).—Bulletin of the British Museum (Natural History), Zoology 43(1):1–47.

Miquelarena, A. H., & J. R. Casciotta. 1982. Presencia en la Argentina de *Clupeacharax anchoveoides* Pearson, 1924.—Limnobios 2(5):333–335.

Miranda-Ribeiro, P. de. 1941. Notas para o estudo dos characinídos brasileiros (Peixes—Gênero *Chalcinus* Cuv. & Val. 1849).—Papeis Avulsos do Departamento do Zoologia 1(18):159–174.

———. 1956. On a new genus and new species of South American fishes.—Proceedings of the 14th International Congress of Zoology, Copenhagen, 16(Vertebrates):546–547.

Myers, G. S. 1940. Suppression of *Acropsis* and *Chalcinus*, two preoccupied generic names of South American fresh-water fishes.—Stanford Ichthyological Bulletin 1(5):170.

Ortega, H., & R. P. Vari. 1986. Annotated checklist of the freshwater fishes of Peru.—Smithsonian Contributions to Zoology 437:1–25.

Pearson, N. E. 1924. The fishes of the eastern slope of the Andes. I. The fishes of the Rio Beni basin, Bolivia, collected by the Mulford Expedition.—Indiana University Studies 11(64):1–63.

Poll, M. 1957. Les genres des poissons d'eau douce de l'Afrique.—Annales du Musée Royal du Congo Belge, Series Zoologiques 54:1–191.

Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi.—1. Cyprinoidea.—Annals and Magazine of Natural History, ser. 8, 8:14–32.

Roberts, T. R. 1969. Osteology and relationships of the characoid fishes, particularly the genera *Hepsetus, Salminus, Hoplias, Ctenolucius,* and *Acestrorhynchus*.—Proceedings of the California Academy of Sciences, fourth series, 36(15): 391–500.

———. 1973. Osteology and relationships of the Prochilodontidae, a South American family of characoid fishes.—Bulletin of the Museum of Comparative Zoology 145(4):213–235.

———. 1974. Osteology and classification of the neotropical characoid fishes of the families Hemiodontidae (including Anodontinae) and Parodontidae.—Bulletin of the Museum of Comparative Zoology 146(9):411–472.

Sazima, I. 1983. Scale-eating in characoids and other fishes.—Environmental Biology of Fishes 9(2): 87–101.

Schultz, L. P. 1944. The fishes of the family Characinidae from Venezuela, with descriptions of seventeen new forms.—Proceedings of the United States National Museum 95:235–367.

Starks, E. C. 1930. The primary shoulder girdle of the bony fishes.—Stanford University Publications, University Series, Biological Sciences 6(2): 149–239.

Stewart, D. J., R. Barriga S., & M. Ibarra. 1987. Ictiofauna de la cuenca del Río Napo, Ecuador Oriental: lista anotada de especies.—Politecnica, revista de Información Técnico-Científica, 12(4):9–63.

Vari, R. P. 1977. Notes on the characoid subfamily Iguanodectinae, with a description of a new species.—American Museum Novitates 2612: 1–6.

———. 1979. Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea).—Bulletin of the British Museum (Natural History) 36(5):261–344.

———. 1986. *Serrabrycon magoi*, a new genus and species of scale-eating characid (Pisces: Characiformes) from the upper Río Negro.—Proceedings of the Biological Society of Washington 99(2):328–334.

Weitzman, S. H. 1954. The osteology and relationships of the South American characid fishes of the subfamily Gasteropelecinae.—Stanford Ichthyological Bulletin 4(4):213–263.

———. 1960. The phylogenetic relationships of *Triportheus*, a genus of South American characid fishes.—Stanford Ichthyological Bulletin 7(4): 239–244.

———. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family.—Stanford Ichthyological Bulletin 8(1):1–77.

———. 1964. Osteology and relationships of the South

America characid fishes of the subfamilies Lebiasininae and Erythrininae with special reference to the subtribe Nannostomina.—Proceedings of the United States National Museum 116: 127–170.

———, S. V. Fink, & N. A. Menezes. 1985. Appendix 3. A critique of the monophyly of the Glandulocaudinae. Pp. 112–121 *in* S. H. Weitzman and S. V. Fink, eds., Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). Smithsonian Contributions to Zoology 421:1–121.

———, & W. L. Fink. 1983. Relationships of the neon tetras, a group of South American freshwater fishes (Teleostei, Characidae), with comments on the phylogeny of New World characiforms.—Bulletin of the Museum of Comparative Zoology 150(6):339–395.

———, & R. P. Vari. 1987. Two new species and a new genus of miniature characid fishes (Teleostei: Characiformes) from northern South America.—Proceedings of the Biological Society of Washington 100:640–652.

(RMCC) Departmento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Avenida Bandeirantes 3900, 14049 Ribeirão Preto SP, Brazil; and (RPV) Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 543–549

SCORPAENODES IMMACULATUS, A NEW SPECIES OF SCORPIONFISH (OSTEICHTHYES: SCORPAENIDAE) FROM WALTERS SHOALS, MADAGASCAR RIDGE

Stuart G. Poss and Bruce B. Collette

Abstract.—*Scorpaenodes immaculatus* is described from a single specimen collected in shallow water (40–49 m) at Walters Shoals in the southwestern Indian Ocean. It differs from all known species of the genus in lacking dark markings on the head, body, and fins. The new species is most similar to *Scorpaenodes smithi* Eschmeyer & Rama Rao, but differs from it in the absence of a dark spot over the posterior part of the spinous dorsal fin, the absence of bars and other dark markings over the body, in having a small spine on the upper arm of the preopercle, and in having the upper unbranched rays in the pectoral fin slightly elongate.

A shallow water trawl collection made in December 1988 during cruise 17 of the Soviet oceanographic vessel *Vityaz* in the southwestern Indian Ocean (Collette & Parin 1991) resulted in the discovery of a new scorpionfish of the genus *Scorpaenodes* Bleeker. The new species, represented by a single specimen, was taken in shallow water (40–49 m) at Walters Shoals, an isolated submerged oceanic mountaintop that rises to within 18 m of the surface, 400 nautical miles south of Madagascar and 600 nm east of South Africa (33–35°S, 43°50–56′E).

Scorpaenodes is distinguished from other scorpaenid genera by the following combination of features: a low spinous dorsal fin, usually with XIII spines (sometimes XIV), and absence of an occipital pit and palatine teeth. Like many other scorpionfish genera, it is poorly defined. The genus has been divided by some authors (e.g., Smith 1957), but recent work has followed Matsubara (1943) and Eschmeyer (1969a) in recognizing a single genus. With the description of *Scorpaenodes immaculatus,* the genus now includes about 25 species.

The purposes of this paper are to describe the new species so that the name is available for subsequent analysis of the Walters Shoals fish fauna, and to compare it with other species of the widely distributed genus *Scorpaenodes.* In addition, we take the opportunity to list the described species in the genus (Table 1).

Materials and methods.—Counts and head spine terminology follow those of Eschmeyer (1969b). Measurements were taken as specified in Poss (1982). Scale terminology and the methods of cleaning the scales follow Hughes (1981), except the concentration of sodium hypochlorite was reduced to 0.5%. Scales were photographed using an Olympus SZH binocular light microscope.

The acronym USNM designates the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C., where the holotype and only specimen is deposited; CAS, the California Academy of Sciences in San Francisco which houses much of the comparative material.

Scorpaenodes immaculatus, new species

Figs. 1–3

Holotype.—USNM 307748; 89.2 mm SL; western Indian Ocean, Walters Shoals,

Table 1.—Nominal species of *Scorpaenodes* and their distributions.

Species	Author	Distribution
africanus	Pfaff 1933	eastern Atlantic
africanus	Smith 1958	= *albaiensis*
albaiensis	Evermann & Seale 1907	Indo-West Pacific
arenai	Torchio 1962	Mediterranean Sea
asperrimus	Smith 1958	= *parvipinnis*
brocki	Schultz 1956	= *minor*
caribbaeus	Meek & Hildebrand 1928	western Atlantic
corallinus	Smith 1957	Indo-West Pacific
elongatus	Cadenat 1949	eastern Atlantic
englerti	Eschmeyer & Allen 1971	Easter Island
erinacea	Garman 1903	= *guamensis*
floridae	Hildebrand 1940	= *tredecimspinosus*
guamensis	Quoy & Gaimard 1824	Indo-West Pacific
hirsutus	Smith 1957	Indo-Pacific
immaculatus	Poss & Collette 1990	Walters Shoals
insularis	Eschmeyer 1971	St. Helena
investigatoris	Eschmeyer & Rama Rao 1972	western Indian O.
keelingensis	Marshall 1950	= ?*kelloggi*
kelloggi	Jenkins 1903	western Pacific
littoralis	Tanaka 1917	Indo-West Pacific
minor	Smith 1958	Indo-West Pacific
minutus	Cuvier 1829	= ?*guamensis*
muciparus	Alcock 1889	Indo-West Pacific
parvipinnis	Garrett 1864	Indo-West Pacific
polylepis[1]	Bleeker 1851	= *guamensis*
scaber	Ramsay & Ogilby 1886	= ?*guamensis*
smithi	Eschmeyer & Rama Rao 1972	western Indian O.
steeni	Allen 1977	Western Australia
steinitzi	Klausewitz & Froiland 1970	Red Sea
tredecimspinosa	Metzelaar 1919	western Atlantic O.
tribulosus	Eschmeyer 1969	western Indian O.
varipinnis	Smith 1957	Indian Ocean
xyris	Jordan & Gilbert 1882	eastern Pacific O.

[1] Type-species of *Scorpaenodes* Bleeker 1857.

33°11′S, 43°52′E; 40–49 m; 29-m fish trawl; *Vityaz* Cruise 17, Sta. 2685; 12 December 1988; only known specimen.

Diagnosis.—An entirely red species of *Scorpaenodes* without dark markings on body and fins. It is also separable from other species of *Scorpaenodes* by a combination of differences in spination, counts, and measurements (see below, comparisons).

Description.—Dorsal-fin rays XIV, 8½, (count of XIII, 9½ should be expected). Anal-fin rays III, 5½. Pectoral-fin rays 19, rays 2–8 or 9 branched. Lateral line damaged, but with about 27 scales, with last scale extending over base of caudal fin. Gill rakers 5+1+10 (left); 6+1+10 (right). Caudal fin with 12 branched rays (6 ventral; 6 dorsal), 15 segmented rays (7 ventral; 8 dorsal), and 8 unsegmented, procurrent rays (4 dorsal; 4 ventral). Vertebrae 9 precaudal + 15 caudal = 24.

Head moderately large; relatively deep posteriorly. Infraorbital one with suborbital ridge, but without spine. Three lobes on infraorbital one extending over maxilla, one anteriorly, two posteriorly; none ending in pungent spine. Infraorbital two with strong ridge ending in distinct spine near junction

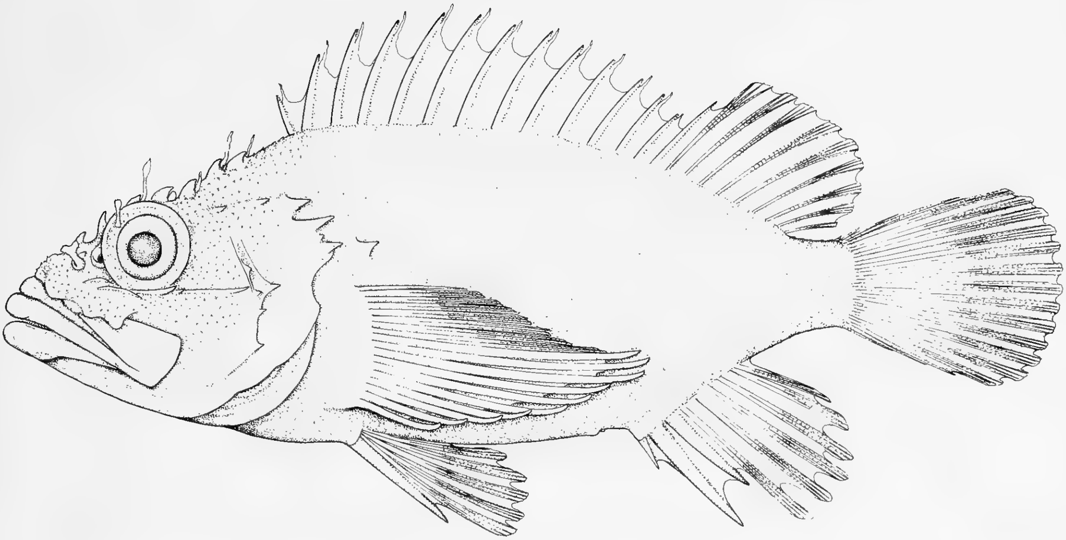


Fig. 1. Holotype of *Scorpaenodes immaculatus* in lateral view (USNM 307748, 89.2 mm SL). Walters Shoals.

with third infraorbital bone. Third infraorbital bone forming strong ridge ending in spine just anterior to preopercular spine. Nasal spine stout, slightly curved. Interorbital broad, shallow, with weak ridges; right ridge ending in small spine. Preocular spine sharp. Supraocular spine stout. Postocular spine strong. Tympanic spine strong. Coronal spines absent. Sphenotic spine absent. Pterotic spine small. Parietal and nuchal spines notably stout; broad at base. Upper posttemporal spine absent. Lower posttemporal spine small. Supracleithral spine prominent. Cleithral spine strong. Posterior margin of the preoperculum with 3 distinct spines: largest at end of suborbital ridge (stay); second ventral to but near first; third larger than second. Fourth and fifth preopercular spines absent. Anterior margin of dorsal arm of preopercle with small spine projecting laterally and slightly posteriorly. Supplemental preopercular spine a small point at base of largest preopercular spine. Operculum with 2 prominent strong spines, extending posteriorly beyond edge of bone. Maxilla extending almost to vertical with posterior border of orbit; without scales. Infraorbital bones and cheek covered with scales. Operculum covered with scales, except posteriorly. Small relatively simple cirri present on many head spines; the longest and most elaborate cirri on supraocular spine.

Body scales of moderate size, with about 50 vertical rows as counted above lateral line (damaged or missing, counted from scale pockets); scales from dorsum with about 40 ctenii in 2 alternating marginal rows and about 4 submarginal rows of ctenial bases in posterior field (Fig. 3a). Underside of head without scales. Scales on posterior part of head and on body ctenoid. Cirri absent on body.

Dorsal fin origin above middle of opercle. Anterior dorsal-fin spines tipped with simple cirri. Anal fin with second spine notably stronger and longer than third. Upper unbranched pectoral-fin rays slightly elongate; extending posteriorly to first segmented anal ray; ventral rays notably thicker. Caudal fin somewhat rounded, but with rays in ventral half slightly longer than those dorsally. Caudal skeleton with haemal spine of second preural centrum broad, weakly ankylosed to second preural centrum, not supporting caudal-fin rays; parhypural broad, free from

Fig. 2. Head of holotype of *Scorpaenodes immaculatus* in dorsal view.

hypurals supporting ventral procurrent rays, partially ankylosed to compound urostylar centrum; hypurals 1 and 2 fused, supporting 6 branched rays and 1 unbranched, autogenous from compound urostylar centrum and hypural 3; hypural 3 supporting 3 branched rays; hypural 4 supporting 2 branched and 1 unbranched ray; hypurals 3 and 4 anky-

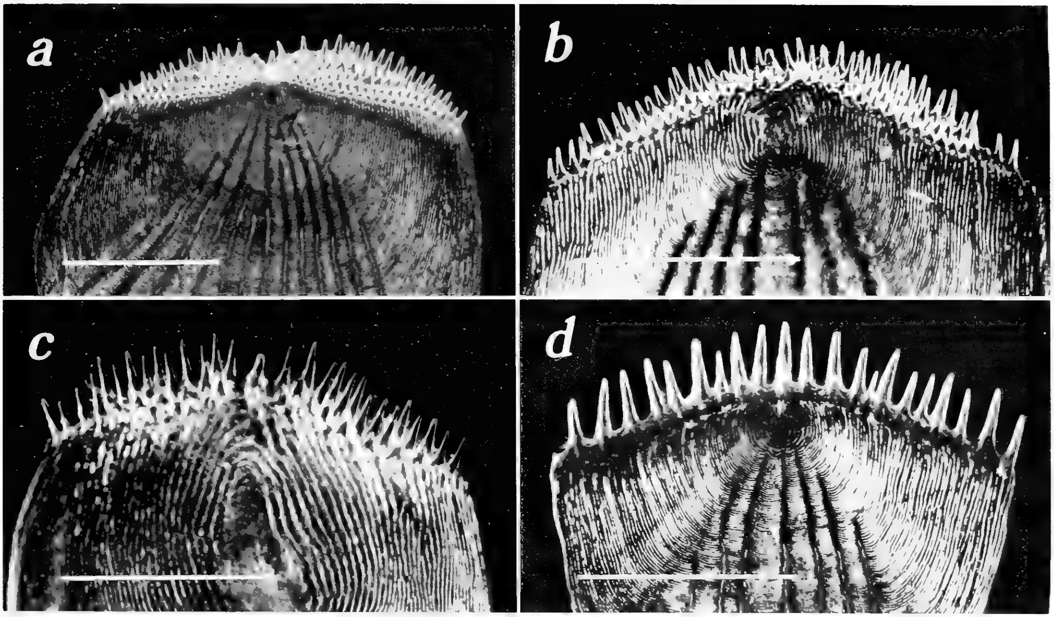


Fig. 3. Comparison of scales from dorsum above lateral line and right pectoral fin in several species of *Scorpaenodes*. a. Holotype of *Scorpaenodes immaculatus* USNM 307748. b. *S. varipinnis,* CAS 48692. c. *S. parvipinnis,* CAS 31352. d. *S. tribulosus,* CAS 24267. Bars represent 1.0 mm. Note differences in number of ctenial bases, size and number of ctenii.

losed only near compound urostylar centrum, distinctly separate posteriorly; hypural 5 autogenous; 3 broad epurals; uroneural long, autogenous; neural spine of second preural centrum broad, short.

Body uniformly red immediately after capture, with small red spots over soft fin rays and no dark brown markings. No dark brown or black spot on posterior part of spinous dorsal fin. Spinous dorsal fin with more red pigment proximally. Body devoid of markings in alcohol.

Measurements for the holotype in mm are as follows (percentage standard length in parentheses): standard length 89.2, head length 38.2(43), snout 11.0(12), orbit 10.1(11), interorbit 6.0(7), upper jaw 19.9(22), postorbit 17.8(20), body depth 31.6(35), predorsal 36.0(40), anal fin 24.6(28), caudal fin 22.6(25), pectoral fin 30.6(34), pelvic fin 22.1(25), first dorsal spine 4.4(5), second dorsal spine 7.3(8), third dorsal spine 9.9(11), fourth dorsal spine 12.2(14), fifth dorsal spine 13.6(15), penultimate dorsal spine 6.6(7), last dorsal spine 9.9(11), first anal spine 7.1(8), second anal spine 18.6(21), third anal spine 14.0(16), maximum width of interorbital ridge 2.3(3), caudal peduncle 9.6(11), snout to second dorsal spine 37.3(42), snout to third dorsal spine 39.6(44), snout to fourth dorsal spine 43.1(48), snout to fifth dorsal spine 46.6(52), first dorsal spine width at midlength 0.5(0.6), interorbital depth 0.9(1), incision of fin membrane at fourth dorsal spine 5.6(6), snout to pelvic insertion 37.7(42), opercular tip to dorsal fin 11.4(13), uppermost preopercular spine 4.3(5), first dorsal spine to fifth dorsal spine 10.1(11), fifth dorsal spine to pelvic insertion 32.7(37), first dorsal spine to pelvic insertion 31.7(36), fifth dorsal spine to last dorsal spine 24.1(27), last dorsal spine to last dorsal ray 16.4(18), last dorsal ray to last anal ray 12.6(14), anal-fin origin to last anal ray 11.8(13), pelvic insertion to anal-fin origin 31.1(35), first dorsal spine to anal-fin origin 46.0(52), last dorsal spine to pelvic insertion 42.4(48), last dorsal spine to last anal ray 21.1(24), last dorsal ray to anal-fin origin 22.8(26), last dorsal spine to anal-fin origin 25.8(29), fifth dorsal spine to anal-fin origin 38.2(43).

Comparisons.—*Scorpaenodes immaculatus* most closely resembles *S. smithi* and *S. investigatoris* but differs from both in lacking any dark markings on head, fins, or body. These three species share the following traits: similar spination on the infraorbital bones, absence or near absence of coronal spines, similar counts and body proportions. With respect to coloration, *S. immaculatus* resembles a specimen identified as *S. smithi* that was photographed by Gloerfelt-Tarp & Kailola (1984:114), but does not fit their description, which noted the presence of a spot on the dorsal fin. Detailed study of geographic variation in *S. smithi* is needed.

Scorpaenodes immaculatus is readily distinguished from its western Indian Ocean congeners by its coloration, among other features. It differs most notably from *S. smithi* in lacking a dark spot in the posterior part of the spinous dorsal fin and the bars and markings present on the body in *S. smithi* (but see below), in having a small spine on the upper arm of the preopercle, in having XIV (if normal) rather than XIII dorsal-fin spines, and in having the upper unbranched rays in the pectoral fin slightly elongate. It differs from *S. investigatoris* in having the upper portion of the pharynx light-colored, rather than dusky-colored. *Scorpaenodes immaculatus* can be separated from *S. tribulosus* in having 3, as opposed to 4–8, spinous points on the suborbital ridge, and with less well-developed ctenii on the scales, a difference especially evident in scales from the chest, maxilla, and interorbital regions, which are thickly covered with ctenoid scales in *S. tribulosus.* It can be quickly distinguished from *S. steinitzi* by having one more dorsal fin spine and fewer segmented dorsal rays (8½ vs. 10), in having 19 as opposed to 16–17 pectoral rays, and lacking coronal spines. *Scorpaenodes immaculatus* has only 3 suborbital spines, unlike *S. parvipinnis,* which typically has from 5 to 10. The new species differs from *S. hirsutus* in having cirri confined to head and fin spines and not widely distributed over the body, in having a deeper body (35% vs. 30–32% SL), in having 3, rather than 4, suborbital spines in a row below the orbit, and in lacking a spine below those in the suborbital row. It can be separated from *S. guamensis* in lacking the large dark spot over the opercle and in not having coronal spines. It lacks the distinct dark spot on the subopercle characteristic of *S. littoralis. Scorpaenodes immaculatus* is distinguishable from *S. varipinnis* in having a wider interorbit (7% vs. 3–4% SL) and in not bearing strong dark markings over the body. It differs widely from *S. albaiensis* and *S. minor* in having well-developed nasal spines, in having a much deeper body (35% vs. 27–30% SL), and in not having the middle pectoral fin rays as abruptly longer as those dorsally.

Scorpaenodes immaculatus differs from *S. insularis,* a species known only from St. Helena in the South Atlantic, in lacking a second spine below the row of 3 spines on infraorbitals 1–3, in having a wider interorbit (7.0% vs. 4.5% SL) and a slightly deeper body (35% vs. 32% SL).

Distribution.—Western Indian Ocean, known only from Walters Shoals.

Etymology.—*immaculatus,* from the Latin meaning unstained, unspotted; in reference to the diagnostic lack of pronounced markings on the body and fins typical of other species of *Scorpaenodes.*

Discussion.—Although scales of *S. immaculatus* taken from the dorsum and immediately above the anterior part of the lateral-line have a broader series of ctenial bases in the posterior field, with respect to ctenial size and number they are otherwise similar to those taken from the same region of the body of most other species assigned to *Scorpaenodes* (Fig. 3). The arrangement in *S. tribulosus* (Fig. 3d) notably contrasts with that of other *Scorpaenodes* in having many fewer and longer ctenii, with little trace of the development of ctenial bases. The presence of abruptly longer middle pectoral-fin rays (relative to those dorsally) was a feature used by Evermann & Seale (1907), Smith (1957), and Schultz (1966) to distinguish species of *Hypomacrus* from other *Scorpaenodes*. However, the intermediate condition observed in *S. immaculatus* is somewhat more pronounced than that figured by Eschmeyer & Randall 1975 for *S. hirsutus* and like that observed in *S. guamensis*-like specimens taken from Madang, Papua New Guinea (SGP observation).

Insular endemism is evident in several other species of *Scorpaenodes,* being known for *S. insularis* (St. Helena), *S. steenei* (Rottnest I., Western Australia), and *S. englerti* (Easter Island). Other shallow-water species, most notably *S. littoralis, S. parvipinnis,* and *S. guamensis,* are among the most broadly distributed of scorpionfishes. Only further collecting will determine if *S. immaculatus* occurs elsewhere. Walters Shoals is one of seven islands and sea mounts extending along the West Wind Drift from Gough and Tristan da Cunha in the South Atlantic to Amsterdam and St. Paul in the southern Indian Ocean. There is a high degree of endemism in the West Wind Drift Islands (Collette & Parin 1991) so *S. immaculatus* should be looked for around the other islands and sea mounts of this chain.

Acknowledgments

N. V. Parin kindly invited B. B. Collette to participate in the cruise of the *Vityaz* that resulted in collecting the unique specimen of *Scorpaenodes immaculatus.* Keiko Hiratsuka Moore prepared Figs. 1 and 2. Robert Allen, Rebbeca Bivings, and Deneen Benford assisted in preparation of the photomicrographs. Drafts of the manuscript were read by William D. Anderson, Jr., William N. Eschmeyer, Thomas A. Munroe and Clive Roberts. This work was supported, in part, through an NSF grant (BSR 8705373) to SGP.

Literature Cited

Collette, B. B., & N. V. Parin. 1991. Shallow-water fishes of Walters Shoals, Madagascar Ridge.—Bulletin of Marine Science (in press).

Eschmeyer, W. N. 1969a. A new scorpionfish of the genus *Scorpaenodes* and *S. muciparus* (Alcock) from the Indian Ocean, with comments on the limits of the genus.—Occasional Papers, California Academy of Sciences 76:1–11.

———. 1969b. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae).—Occasional Papers, California Academy of Sciences 79:1–130.

———, & J. E. Randall. 1975. The scorpaenid fishes of the Hawaiian Islands, including new species and new records (Pisces: Scorpaenidae).—Proceedings of the California Academy of Sciences 40(11):265–334.

Evermann, B. W., & A. Seale. 1907. Fishes of the Philippine Islands.—Bulletin of the [U.S.] Bureau of Fisheries 26:49–110.

Gloerfelt-Tarp, T., & P. Kailola. 1984. Trawled fishes of southern Indonesia and northwestern Australia. Australian Development and Assistance Bureau, Directorate General Fisheries, Indonesia, and German Agency for Technical Cooperation, 406 pp.

Hughes, D. R. 1981. Development and organization of the posterior field of ctenoid scales in the Platycephalidae.—Copeia 1981(3):596–606.

Matsubara, K. 1943. Studies on the scorpaenoid fishes of Japan. (II). Transactions Sigenkagaku Kenkyusyo, pp. 171–486.

Poss, S. G. 1982. A new species of the aploactinid fish genus *Kanekonia* from Halmahera, Indonesia and a redescription of *Kanekonia florida.*—Japanese Journal of Ichthyology 28(4):1–6.

Schultz, L. P. 1966. Fishes of the Marshall and Marianas Islands, vol. 3, United States National Museum Bulletin 202, 176 pp.

Smith, J. L. B. 1957. The fishes of the family Scorpaenidae in the Western Indian Ocean. Part I. The sub-family Scorpaeninae.—Ichthyological Bulletin, Rhodes University (4):49–69.

(SGP) Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39564; (BBC) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 550–557

CYPHOCHARAX PANTOSTICTOS, A NEW SPECIES (PISCES: OSTARIOPHYSI: CHARACIFORMES: CURIMATIDAE) FROM THE WESTERN PORTIONS OF THE AMAZON BASIN

Richard P. Vari and Ramiro Barriga S.

Abstract.—*Cyphocharax pantostictos,* a species of curimatid characiform with a distinctive pattern of dark spots arranged in longitudinal series along the sides of the body, is described as new from the Río Napo, Río Putumayo, Río Ucayali, and Río Nanay in Ecuador and northern Peru. *Cyphocharax multilineatus* (Myers), the only other species in that questionably monophyletic genus with a similar pigmentation pattern has dark wavy horizontal lines, rather than discrete spots arranged in horizontal patterns. The dark body pigmentation in the two species also differs in its relative position on the scales. The pigmentation pattern and overall external appearance of *C. pantostictos* are nearly identical to that of *Steindachnerina fasciata* (Vari & Géry) a species endemic to the upper Rio Madeira system in Brazil. The two species can be readily distinguished on the basis of a series of meristic and morphometric features, and in differences in the portion of buccopharyngeal complex on the roof of the oral cavity. A series of polarized characters indicate furthermore that the two species are not closely related.

The myriad drainage systems, range of stream gradients, and complexity of aquatic habitats found in the drainage basins of the western portions of the Amazon basin are reflected in the remarkable diversity of the fish fauna in that region (Ortega & Vari 1986, Stewart et al. 1987). This region is also one of the areas of greatest diversity for the family Curimatidae, involving both species widely distributed within the Amazon basin (e.g., *Curimata aspera* Günther (Vari 1988: fig.8) and *C. vittata* Kner (Vari 1989b:42)), or ranging north and south of that system into the Río Orinoco or Río de La Plata systems (e.g., *Steindachnerina guentheri* (Eigenmann & Eigenmann) (Vari 1990)). Other curimatids in this area of high species diversity have much more restricted ranges (e.g., *Steindachnerina quasimodoi* Vari & Vari (see Vari & Vari 1989:477)) and are known only to occur in the region that Kullander (1986:40) termed the "Western Amazonian endemic area" based on distributional data from various neotropical genera of the perciform family Cichlidae. In the course of investigations of the fish fauna of eastern Ecuador and northern Peru we independently collected a distinctive species of curimatid with an unusual pigmentation pattern consisting of seven or eight longitudinal series of dark spots along the sides of the body. This material first appeared to represent a major extension in the known distribution of *Curimata fasciata* which Vari & Géry (1985) described from the Rio Madeira system in Brazil, a considerable distance southeast of the region from which the Ecuadorian and Peruvian specimens originated. More recently Vari (1989a:tables 2, 3), in an analysis of intrafamilial phylogenetic relationships, restricted *Curimata* to a single lineage within the family and reassigned *fasciata* to *Steindachnerina* Fowler (1906) on the basis of a series of derived characters. Further examination of our specimens surprisingly showed that they neither constitute a major range extension for *Steindachnerina fasciata,* nor do they even represent a species of *Steindachnerina.* Rather they are a species of *Cyphocharax* Fowler (1906) previously unknown to science. This new curimatid is described herein and is yet another fish species with a known range limited to the Western Amazonian endemic area identified by Kullander.

Materials and methods.—Counts and measurements were made following methods outlined in Vari (1989b, 1989c, 1990). Ranges for meristic and morphometric features include values of all examined specimens. The values in square brackets are those of the holotype. Subunits of the head are presented as proportions of head length (HL). Head length itself and measurements of body parts are presented as proportions of standard length (SL).

The following abbreviations for institutions are used: Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Stanford University, collections now deposited at CAS (CAS-SU); Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Indiana University, collections now deposited at various repositories (IU); Museo de Biologia, Universidad Central de Venezuela, Caracas (MBUCV); Museo de Biología de la Escuela Politécnica Nacional, Quito (MEPN); Muséum d'Histoire Naturelle, Geneva (MHNG); Museu Nacional, Rio de Janeiro (MNRJ); Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP); Naturhistoriska Riksmuseet, Stockholm (NRM); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Cyphocharax pantostictos, new species
Figs. 1, 4

Diagnosis.—The new species is assigned to *Cyphocharax,* a genus that Vari (1989a: 58–59) noted was not defined on the basis of known derived features. *Cyphocharax* of that classification was rather an assemblage of species lacking the derived features diagnostic of the three other genera (*Steindachnerina, Curimatella* Eigenmann & Eigenmann, and *Pseudocurimata* Fernández-Yépez) which together with *Cyphocharax* form an unresolved terminal polytomy in Vari's hypothesis of intrafamilial relationships within the Curimatidae. The absence of identified synapomorphies for *Cyphocharax* increases the likelihood that the genus may not be monophyletic. Ongoing studies by the senior author focus on the question of the monophyly of *Cyphocharax* and its subunits. In the interim we assign the new species to *Cyphocharax* given that *C. pantostictos* shares the synapomorphies for the clade formed by *Cyphocharax, Steindachnerina, Curimatella,* and *Pseudocurimata,* but lacks the derived features that diagnose each of *Steindachnerina, Curimatella,* and *Pseudocurimata.* The striking pattern of seven or eight horizontal series of prominent dark spots aligned along the center of the body scales is unique to the *Cyphocharax pantostictos* within the genus (Fig. 1). Only one other *Cyphocharax* species, *C. multilineatus* (Myers 1927) of the Río Negro system in Venezuela and Brazil, has a pattern of horizontal dark body pigmentation reminiscent of that in *C. pantostictos.* The pattern of dark body pigmentation in *C. multilineatus* (Fig. 2) differs from that in *C. pantostictos* in forming solid wavy horizontal lines rather than a series of discrete rotund spots (compare Figs. 1 and 2). Furthermore, the dark stripes in *C. multilineatus* are positioned along the area of overlap of horizontal rows of scales along the body, rather than being aligned along the center of the scale rows as are the spots in *C. pantostictos.* Thus the patterns of longitudinal dark pigmentation on the bodies in the two species are apparently non-homologous. *Cyphocharax multilineatus* also has a discrete dark band across the mid-

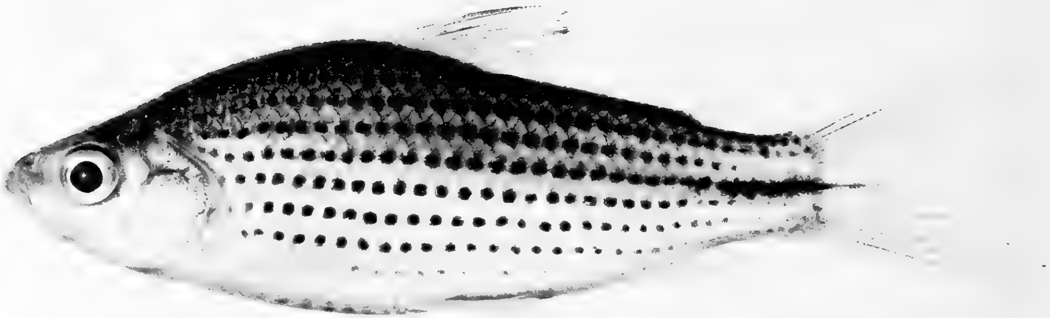


Fig. 1. *Cyphocharax pantostictos,* new species, holotype, USNM 306594, 72.4 mm SL; Ecuador, Napo, Laguna de Jatuncocha.

lateral surface of the head anterior and posterior to the orbit, a pigmentation pattern lacking in *C. pantostictos. Cyphocharax pantostictos,* in turn, is characterized by a well-developed, mid-lateral, horizontally elongate patch of dark pigmentation on the caudal peduncle that is absent in *C. multilineatus.* It is likely that various meristic and morphometric features further distinguish *C. pantostictos* within *Cyphocharax.* Identification of those characters must await the completion of revisionary studies within that speciose genus.

The overall pigmentation pattern and overall external appearance of *C. pantostictos* are strikingly similar to that of one other member of the Curimatidae, *Steindachnerina fasciata* (Fig. 3), an endemic of the Rio Madeira basin, and have lead to misidentifications of the two species. *Cyphocharax pantostictos* lacks the derived features that diagnose *Steindachnerina* (see Vari 1989a: 58, 1990), and lacks the intrageneric synapomorphies for the clades that include *S. fasciata* (see Vari 1990 for details). One of the most obvious differences between the two species involves the form of the buccopharyngeal complex on the roof of the oral cavity. *Cyphocharax pantostictos* has three simple longitudinal fleshy folds in that region. *Steindachnerina fasciata,* in contrast, has a mass of lobulate fleshy bodies that extend ventrally into the oral cavity, a hypothesized derived condition unique to a

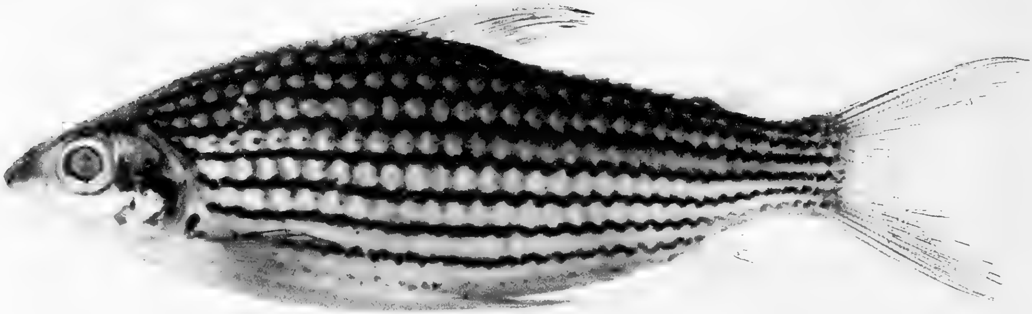


Fig. 2. *Cyphocharax multilineatus,* USNM 269987, 111.8 mm SL; Venezuela, Territorio Federal Amazonas, Departamento Río Negro, Caño Tremblador where crossed by road from San Carlos de Río Negro to Solano.

Fig. 3. *Steindachnerina fasciata,* MNRJ 11208, 89.6 mm SL, holotype of *Curimata fasciata* Vari and Géry; Brazil, Território de Rondônia, Município de Ouro Preto do Oeste, Rio Romari (or São Domingo) near Nova União.

subunit of *Steindachnerina* (see Vari 1989a: 31–35, 1990, for a discussion of the buccopharyngeal complex).

The two species also differ in various meristic and morphometric values including the number of vertebrae (31 in *Cyphocharax pantostictos* versus 32 to 34, typically 33, in *Steindachnerina fasciata*), the number of scales in a longitudinal series to the hypural joint (29 to 31 versus 32 to 37), the number of scale rows above the lateral line to the origin of dorsal fin (4½ versus 5½ or 6½), the relative length of the pelvic fin (0.20–0.23 of SL versus 0.23–0.25), and the relative gape width (0.24–0.28 of HL versus 0.28–0.32).

Description.—Body moderately elongate, somewhat compressed. Dorsal profile of head straight overall, slightly convex anteriorly. Dorsal profile of body smoothly convex from posterior portion of head to origin of dorsal fin; straight or slightly convex, posteroventrally slanted at base of dorsal fin, greatly convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Pre-pelvic region very obtusely flattened, scales of that area not notably enlarged relative to those on lateral surfaces of body. Median pre-pelvic scale series somewhat irregular, particularly near origin of pelvic fin. No distinct median keel posterior to origin of pelvic fin. Barely discernable secondary obtuse keel on each side of post-pelvic portion of body about two scales dorsal of ventral midline.

Greatest body depth at origin of dorsal fin, depth 0.35–0.40 [0.37], relatively deeper in larger specimens; snout tip to origin of dorsal fin 0.47–0.52 [0.50]; snout tip to origin of anal fin 0.83–0.85 [0.83]; snout tip to origin of pelvic fin 0.52–0.57 [0.56]; snout tip to anus 0.78–0.79 [0.78]; origin of dorsal fin to hypural joint 0.54–0.58 [0.56]. Margin of dorsal fin rounded posteriorly; anteriormost rays approximately two to two and one-half times length of ultimate ray. Margin of pectoral fin pointed; length of pectoral fin 0.18–0.21 [0.20], extending slightly over one-half distance to vertical line through origin of pelvic fin. Margin of pelvic fin pointed, length of pelvic fin 0.20–0.23 [0.22], tip reaches to anus in holotype, falls somewhat short of that point in larger specimens. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays about two and one-half times length of ultimate ray. Caudal peduncle depth 0.12–0.14 [0.14].

Head profile distinctly pointed anteriorly, head length 0.29–0.33 [0.31]; upper jaw somewhat longer than lower, mouth subterminal; snout length 0.27–0.31 [0.30]; nares of each side very close, anterior rotund, posterior crescent-shaped with aperture partially closed by thin flap of skin separating nares; orbital diameter 0.27–0.32 [0.31]; adipose eyelid present, moderately developed, with rotund opening over center of eye; length of postorbital portion of head 0.42–0.46 [0.44]; gape width 0.24–0.28 [0.27]; interorbital width 0.39–0.43 [0.43].

Pored lateral-line scales from supracleithrum to hypural joint 29 to 31 [29]; all scales of lateral line pored, canals in scales straight; 2 or 3 pored scales extend beyond hypural joint onto caudal-fin base; 4½ [4½] scales in transverse series from origin of dorsal fin to lateral line; 3½ to 4½ [4] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 [ii,9]; anal-fin rays ii,7 or iii,7 [ii,7]; pectoral-fin rays 13 to 15 [15]; pelvic-fin rays i,8 or i,7,i [i,7,i].

Total vertebrae 31 in 8 specimens.

Color in life.—(Based on photograph of paratype (USNM 280573) from the Río Nanay of Peru taken shortly after capture.) Overall coloration silvery with slightly olive-grey cast on dorsal portions of head and body. Series of black spots arranged in horizontal series along dorsal and lateral surfaces of body. Distinct black mid-lateral stripe on caudal peduncle. Fins hyaline.

Color in alcohol.—See Fig. 1 for preserved color pattern. Available specimens largely lacking guanine on scales. Overall ground coloration yellowish-tan, darker on dorsal portions of head and body. Scales on lateral and dorsal surfaces of body with dark patch of pigmentation on each scale; size of spots largest mid-laterally; overall intensity of spots not as pronounced in smaller individuals. Spots forming 7 or 8 horizontal series, dorsal most series not apparent in smaller specimens. Series of dark spots on scales less developed posteriorly on scale rows ventral of lateral line; very poorly developed in series starting immediately dorsal to origin of pectoral fin. Intense dark spots also progressively less pronounced in horizontal series dorsal to lateral line. Patches of dark pigmentation located on center of scale, with midpoint of spots lying medial of margin of preceding scale. Scales dorsal to lateral line with secondary area of diffuse dark pigmentation posterior to discrete central dark spot; secondary dark pigmentation increasingly pronounced on dorsal portions of body. Dark pigmentation patches on scales along lateral line merging posteriorly into distinct horizontal stripe on mid-lateral surface of caudal peduncle; stripe continuing onto base of middle caudal-fin rays. Deeper lying, dusky band extends along mid-lateral surface of body from supracleithrum to caudal peduncle.

Caudal fin with small streak of dark pigmentation on basal portions of middle rays; basal two-thirds of fin somewhat more dusky than remainder of fin. Median and paired fins somewhat dusky.

Distribution.—Río Napo, Río Putumayo, Río Ucayali, and Río Nanay systems in Ecuador and northern Peru (Fig. 4).

Ecology.—Two of the specimens from Peru (USNM 280573, NRM SOK/1986293.5292) were collected in acidic black waters among grass and submerged vegetation. The specimens from the holotype locality were collected in submerged vegetation in blackwater of pH 5.5 at a depth of 1.5 m. The Río Yasuni specimens came from a slow flowing turbid stream with a pH of 6.0 lacking submerged vegetation.

Etymology.—Pantostictos, from the Greek for "spotted all over" refers to the prominent dark spots on the lateral and dorsal surfaces of the body.

Remarks.—As noted above, *Cyphocharax pantostictos* is very similar in body form and pigmentation to *Steindachnerina fasciata* which is apparently endemic to upper portions of the eastern drainages of the Rio Madeira basin in Brazil (see Vari 1990:fig.

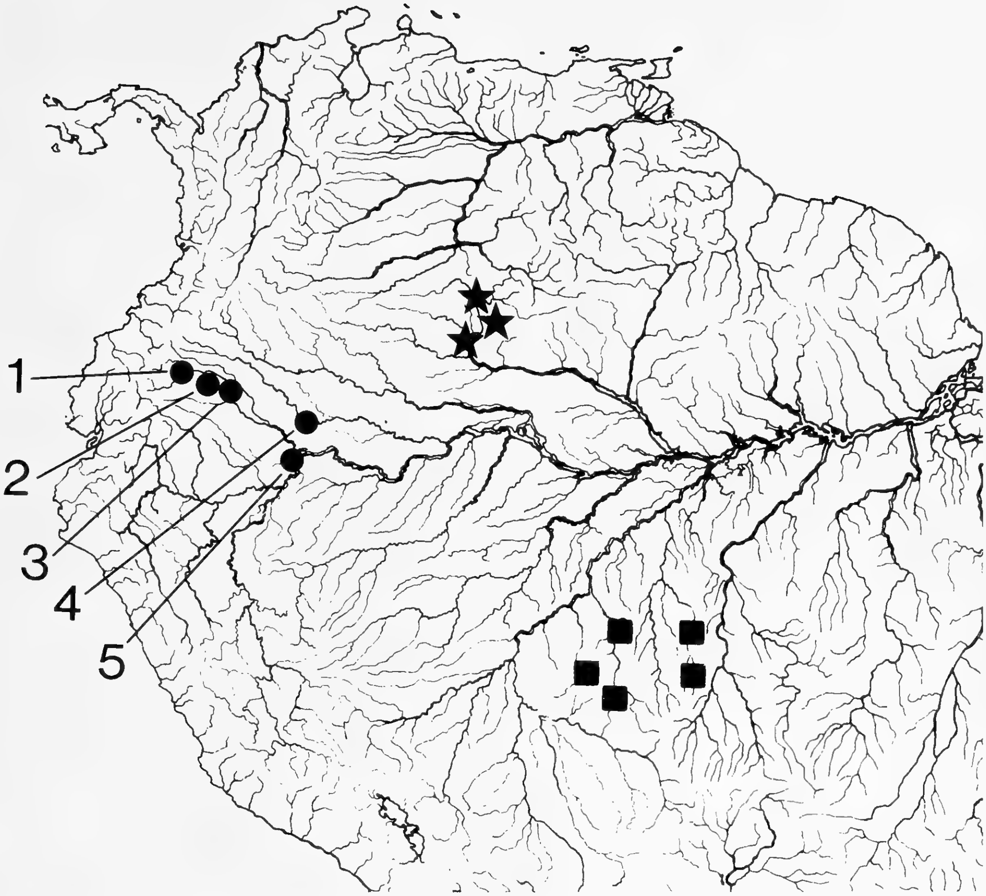


Fig. 4. Map of Amazon basin and adjoining areas showing distribution of *Cyphocharax pantostictus* (dots; localities: 1 = Río Napo above Coca; 2 = Río Yasuni; 3 = Laguna Jatuncocha, type locality; 4 = Río Putumayo, El Estrecho; 5 = Río Nanay, Nanay beach), *Steindachnerina fasciata* (squares), and *Cyphocharax multilineatus* (stars) (see under "Material examined" for additional locality information).

40). Nonetheless those two species differ in many meristic and morphometric features, and *Cyphocharax pantostictos* furthermore lacks the derived characters that both define *Steindachnerina* and clades within the genus that include *S. fasciata* (see Vari (1990) for details).

Such pronounced superficial similarities between two distantly related species would at first consideration apparently represent a case of intergeneric mimicry. Interestingly, however, there is no overlap in the distributions of the two species, whose known ranges are separated by over two thousand river kilometers. Thus mimicry would not appear to be involved in the remarkable external resemblance between *Cyphocharax pantostictos* and *Steindachnerina fasciata.*

Material examined.—10 specimens, 34.4–98.2 mm SL.

Holotype.—Ecuador: Napo. Laguna de Jatuncocha (01°00′S, 75°29′W), collected by R. Barriga, 29 Sep 1988, USNM 306594, 72.4 mm SL.

Paratypes.—Ecuador: Napo. Laguna de Jatuncocha (1°00′S, 75°29′W) collected with holotype, MEPN 4554, 1 specimen, 74.9 mm SL. Estero Culebrero, tributary of Río

Yasuni (0°54′45″S, 76°13′03″W) collected by R. Barriga, 9 May 1988, USNM 305617, 1 specimen, 98.2 mm SL; MEPN 4557, 1 specimen, 81.8 mm SL. Río Napo, 2.7 km along river above the bridge at Coca (0°29.0′S, 77°04.0′W), collected by D. Stewart, R. Barriga, and M. Ibarra, 2 Oct 1983, USNM 305616, 1 specimen, 66.7 mm SL; MEPN 4558, 1 specimen, 63.0 mm SL.

Peru: Loreto. Río Nanay, Nanay beach along river west of Iquitos (approx. 3°50′S, 073°11′W), collected by R. P. Vari, H. Ortega, A. Gerberich, and J. A. Louton, 17 Aug 1986, USNM 280573, 1 specimen, 72.0 mm SL. Small stream approx. 65 km upstream from mouth of Río Nanay, collected by P. Fromm et al., 18 Aug 1989, ANSP 164981, 1 specimen, 34.4 mm SL. Río Putumayo drainage, El Estrecho, Quebrada de Las Granjas, collected by S. O. Kullander et al., 16 July 1986, NRM SOK/1986293.5292, 1 specimen, 94.0 mm SL. Along road from Genero Herrera towards Peruvian-Brazilian border, Río Ucayali drainage, collected by P. Fromm et al., 23 Aug 1989, ANSP 164980, 1 specimen, 39.3 mm SL.

Other material examined.—*Cyphocharax multilineatus.* Brazil: Amazonas. Rio Negro below Daraá, USNM 274102, 1. Rio Negro at Bucuri, CAS 58605, 1 (holotype of *Curimatus multilineatus* Myers, formerly IU 17672); CAS-SU 58986, 1. Rio Paduari, MZUSP 21161, 1.

Venezuela: Territorio Federal Amazonas. Caño La Esmeralda, tributary of Río Orinoco, SE of La Esmeralda, MBUCV V-4479, 1. Rio Mawarinuma (0°55′N, 66°10′W), AMNH uncat., 5. Río Urumi, tributary to Río Negro upstream of Santa Lucia (1°17′N, 66°51′W), USNM 270241, 1. Caño Tremblador where crossed by road from San Carlos de Río Negro to Solano, USNM 269987, 7. Río Barria (0°50′N, 66°10′W), MBUCV V-14898, 1.

Steindachnerina fasciata. Brazil: Território de Rondônia, Rio Romarí (or São Domingo) near Nova União, Munícipio of Ouro Preto do Oeste, MNRJ 11208, 1 (holotype of *Curimata fasciata*); USNM 270377, 4 (paratypes of *Curimata fasciata*); MNRJ 11271, 4 (paratypes of *Curimata fasciata*). Jiparaná, Rio Urupá, tributary of Rio Jiparaná, USNM 273306, 3. Rio Machado system, 20 km upstream of Jiparaná, USNM 295126, 1. Mato Grosso. Rio Aripuanã, above Cachoeira de Dardanelos (approx. 10°19′42″S, 59°12′30″W), USNM 270375, 2 (paratypes of *Curimata fasciata*); INPA, 3 (paratypes of *Curimata fasciata*). Rio Aripuanã, approximately 10 km above Cachoeira de Dardanelos, Cidade de Humboldt, USNM 270376, 2 (paratypes of *Curimata fasciata*); INPA, 2 (paratypes of *Curimata fasciata*); BMNH 1985.2.5:1–2, 2 (paratypes of *Curimata fasciata*); MZUSP 28724, 2 (paratypes of *Curimata fasciata*). Rio Aripuanã, above Cachoeira das Andorinhas, MHNG 2226.24, 6 (paratypes of *Curimata fasciata*).

Acknowledgments

Research associated with this study in Peru was supported by the Neotropical Lowland Research Program of the International Environmental Sciences Program of the Smithsonian Institution. Collecting activities in Peru were made possible by the generous assistance of Prof. Hernán Ortega (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos) and the Consejo Nacional de Ciencia y Tecnologia of Peru. Prof. Ortega and Dr. Andrés Urteaga (Universidad Nacional de la Amazonía Peruana) facilitated and participated in collecting efforts that resulted in the capture of the new species. Mr. William G. Saul directed my attention towards material of the new species in the ANSP holdings. Dr. Jerry A. Louton (USNM) and Mr. Andrew Gerberich (USNM) contributed to the success of the expedition. Dr. Sven O. Kullander and Mr. E. Åhlander (NRM) arranged for the loan of a series of curimatids which included the specimen of *Cyphocharax pan-*

tostictos from the Río Putumayo. Figures 1 to 3 were prepared by Mr. Theophilus Britt Griswold (USNM). This paper benefitted from the comments and suggestions of Dr. Stanley H. Weitzman (USNM) and Dr. Thomas A. Munroe (National Marine Fisheries Service, Systematics Laboratory), and two anonymous reviewers.

Literature Cited

Fowler, H. W. 1906. Further knowledge on some heterognathus fishes, Part. I.—Proceedings of the Academy of Natural Sciences of Philadelphia 58:293–351.

Kullander, S. O. 1986. Cichlid fishes of the Amazon River drainage of Peru. Swedish Museum of Natural History, Stockholm, 431 pp.

Myers, G. S. 1927. Descriptions of new South American fresh-water fishes collected by Dr. Carl Ternetz.—Bulletin of the Museum of Comparative Zoology 68:107–135.

Ortega, H., & R. P. Vari. 1986. Annotated checklist of the freshwater fishes of Peru.—Smithsonian Contributions to Zoology 437:1–25.

Stewart, D., R. Barriga S., & M. Ibarra. 1987. Ictiofauna de la cuenca del río Napo, Ecuador oriental: lista anotada de especies.—Politecnica, Revista de Información Técnico-Científica, Quito 12(4):9–63.

Vari, R. P. 1988. The Curimatidae, a lowland neotropical family (Pisces: Characiformes); distribution, endemism and phylogenetic biogeography. Pp. 313–348 *in* P. E. Vanzolini, and W. Ronald Heyer, eds., Neotropical distribution patterns: proceedings of a workshop. Academia Brasiliera de Ciências, Rio de Janeiro.

———. 1989a. A phylogenetic study of the neotropical Characiform family Curimatidae (Pisces: Ostariophysi).—Smithsonian Contributions to Zoology 471:iv+1–25.

———. 1989b. Systematics of the neotropical Characiform genus *Curimata* Bosc (Pisces: Characiformes).—Smithsonian Contributions to Zoology 474:iii+1–63.

———. 1989c. Systematics of the neotropical Characiform genus *Psectrogaster* Eigenmann and Eigenmann (Pisces: Characiformes).—Smithsonian Contributions to Zoology 481:iii+1–42.

———. 1990. Systematics of the neotropical Characiform genus *Steindachnerina* Fowler (Pisces: Ostariophysi).—Smithsonian Contributions to Zoology (in press).

———, & J. Géry. 1985. A new curimatid fish (Characiformes: Curimatidae) from the Amazon basin.—Proceedings of the Biological Society of Washington 98:1030–1034.

———, & A. W. Vari. 1989. Systematics of the *Steindachnerina hypostoma* complex (Pisces, Ostariophysi, Curimatidae), with the description of three new species.—Proceedings of the Biological Society of Washington 102:468–482.

(RPV) Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; and (RBS) Departamento de Ciencias Biológicas, Escuela Politécnica National, Quito.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 558–572

THE GENUS *AXIANASSA* (CRUSTACEA: DECAPODA: THALASSINIDEA) IN THE AMERICAS

Brian Kensley and Richard Heard

Abstract.—The genus *Axianassa* Schmitt is redefined, based on external morphological characters. Descriptions and figures of the two previously described species *A. intermedia* Schmitt from Curaçao and Puerto Rico, and *A. mineri* Boone from the Pacific Bay of Panama, and three new species, *A. arenaria* from the Gulf of Mexico, *A. jamaicensis* from Jamaica, and *A. canalis* from the Panama Canal, are provided. The species are distinguished primarily on differences in the structure of the antennal acicle, abdominal pleura, and first pereopods. An overview of the family Laomediidae (= senior synonym of Axianassidae) is presented.

Schmitt (1924) described the genus and species *Axianassa intermedia* for which he established the monotypic family Axianassidae. Since that time only one other species, *A. mineri* Boone, 1931, from the Pacific coast of Panama has been described. Until the present study a total of five specimens was known for the genus, which has been alternately placed in the families Axianassidae or the Laomediidae (see references in synonymies for these families under Systematics). Three more species of *Axianassa* are now described from the Gulf of Mexico, Jamaica, and the Panama Canal, but the total number of specimens is still only nine, suggesting that the species are nowhere particularly abundant, that their microhabitats are not often sampled, or that their populations are not readily accessible to conventional collecting methods.

Systematics

Family Laomediidae Borradaile, 1903

Laomediidae Borradaile, 1903:540.—De Man, 1928:15.—Gurney, 1938:332 [larval stages], 343 [key].—Chace, 1939: 529.—Balss, 1957:1578, 1580.—Wear & Yaldwyn, 1966:2, 3.—Yaldwyn & Wear, 1970:384; 1972:127.—Le Loeuff & Intes, 1974:20.—Poore & Griffin, 1979:224.—Goy & Provenzano, 1979:351.—Ngoc-Ho, 1981:247 [larval stages].—Williams, 1984:189.—Konishi, 1989:15 [larval stages].

Axianassidae Schmitt, 1924:76.—De Man, 1928:15.—Gurney, 1938:343 [key].—Balss, 1957:1580.—Wear & Yaldwyn, 1966:2.—Yaldwyn & Wear, 1972:127.—Le Loeuff & Intes, 1974:20.

Diagnosis.—Carapace with linea thalassinica present; cervical groove distinct. Several elongate cleaning setae present on posterior margin of scaphognathite of maxilla 2. Epipod of maxilliped 3 with serrate margin (reduced in *Axianassa*). Epipods present on pereopods 1–4. Pleopod 1 ♀ uniramous; pleopod 1 ♂ absent; appendix interna absent from pleopods.

Axianassa Schmitt, 1924

Axianassa Schmitt, 1924:76.—Balss, 1957: 1580.

Type species.—By monotypy, *Axianassa intermedia* Schmitt, 1924:77, pl. 8, figs. 4, 5, text fig. 7. Gender: feminine.

Diagnosis.—Body poorly calcified, integument thin. Rostrum short, anteriorly rounded, weakly to moderately developed. Eyestalks short, cornea poorly defined, eyes poorly pigmented, generally not, or barely reaching anteriorly beyond rostral apex. Antennules with article 3 of peduncle elongate, slender; superior flagellum longer than inferior. Antennal scale usually well developed and dagger-like; article 4 of peduncle elongate, slender. Mandible with palp of 3 articles, two basal articles incompletely fused; incisor area having several cusps; molar moderately developed, with several tubercles. Maxilla 1 with strongly setose endite. Maxilla 2, scaphognathite bearing 5 elongate setae extending posteriorly into branchial chamber. Exopods present on maxillipeds 1 and 2. Epipods present on maxillipeds 1–3 and pereopods 1–4. Single podobranch present on maxillipeds 2 and 3 (rudimentary on maxilliped 1) and pereopods 1–3; single rudimentary arthrobranch on maxilliped 1, 2 arthrobranchs on maxillipeds 2 and 3, and pereopods 1–4. Pereopod 1, chelae of similar size but dissimilar in chela-palm proportions and dentition of cutting edges of dactylus and propodal finger. Dactyli of pereopods 3–5 flexed, with posterior margin becoming dorsal in position. Pereopod 5 base not covered by carapace, lacking branchiae. Pleopods 2–5 biramous, rami narrowly lanceolate; lacking appendices internae. Uropodal rami lacking sutures, outer ramus with variable weak spination. Telson lacking spination.

Distribution.—The genus is known only from the tropical and subtropical waters of the northeastern Pacific (Panama) and the northwestern Atlantic (Gulf of Mexico and Caribbean).

Axianassa intermedia Schmitt, 1924
Figs. 1, 2, 3

Axianassa intermedia Schmitt, 1924:77, pl. 8, figs. 4, 5, text fig. 7.—De Man, 1928: 17, pl. 1, fig. 2.—Gurney, 1938:332.—Goy & Provenzano, 1979:351.

Material.—Syntypes, National Museum of Natural History, Smithsonian Institution, USNM 57512, 2 ♀ cl.6.8 mm, 7.8 mm, ♂ cl. 6.1 mm, from muddy creek, Spanish Harbor, Curaçao.—USNM 110451, 1 ♂, cl. 5.5 mm, Punta Arenas, Puerto Rico.

Description.—Carapace strongly rounded dorsally but unarmed, with linea thalassinica somewhat grooved; cervical groove clearly defined; rostrum anteriorly rounded, barely surpassing cornea of eyes. Abdomen thin-walled, tergites bearing scattered setae; somite 1 narrowing ventrally, pleuron poorly defined, rounded, lacking any ventral extension; somites 2 and 3 subequal in middorsal length; somites 4–6 decreasing in length. Telson with greatest width slightly more than middorsal length, bearing marginal plumose setae, lateral and posterior margins not clearly separated.

Cornea weakly pigmented, with tiny tubercle distally. Antennular peduncle, articles 1 and 2 together about ⅝ length of article 3; latter slender, elongate-cylindrical; inferior flagellum of about 14 articles, reaching to distal end of antennal peduncle article 5; superior flagellum of about 28 articles, almost twice length of inferior flagellum. Antennal acicle slender, dagger-like, with small tooth on mesial margin; peduncle article 4 slender, elongate-cylindrical, almost reaching distal margin of merus of pereopod 1; flagellum about 3 times carapace length.

Mouthparts as illustrated. Mandible with cutting edge of 7 cusps; raised molar area on mesial face bearing 4 rounded tubercles; palp of 3 articles, articles 1 and 2 partially fused, article 3 bearing numerous stiff setae on outer surface. Maxilla 2, scaphognathite bearing 5 elongate setae on posterior margin. Maxilliped 1, endopod unsegmented, paddle-shaped, distally broadly rounded; exopod bipartite, longer proximal part widening distally, flagellar part about half length of proximal half, bearing plumose setae. Maxilliped 2, endopod pediform, of 5 articles, distal article inserted obliquely on

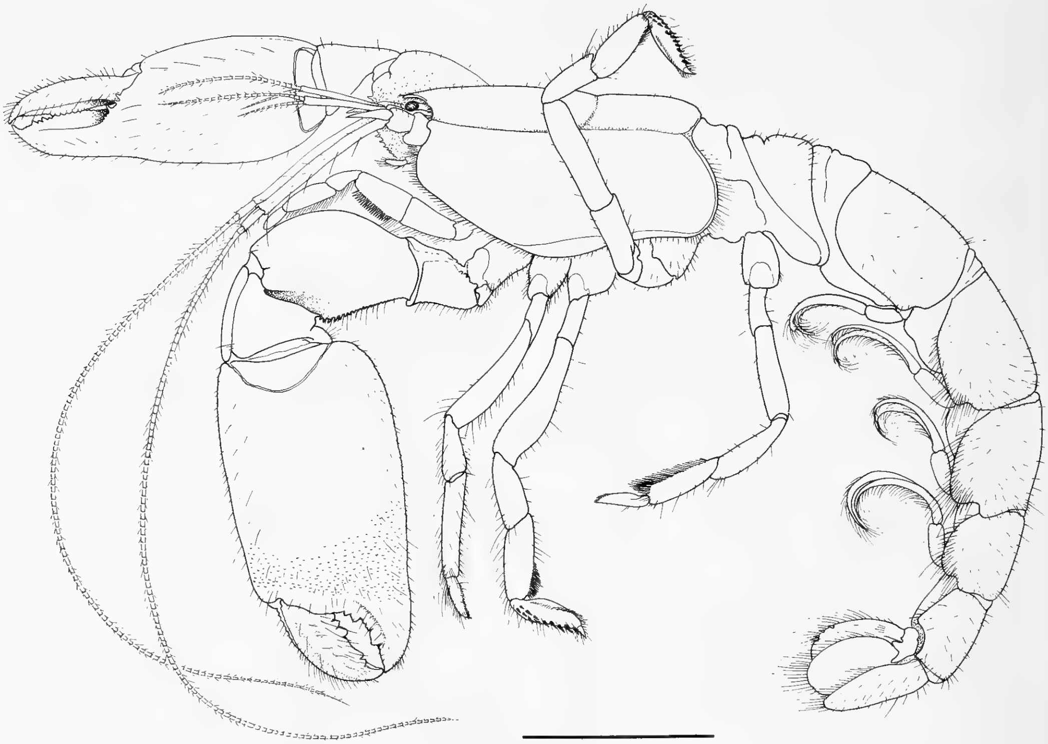


Fig. 1. *Axianassa intermedia,* syntype ♂ in lateral view. scale = 5 mm.

penultimate article; exopod bipartite, proximal part distally broadened, flagellar part more than half length of proximal, bearing plumose setae. Maxilliped 3, endopodal articles strongly setose on mesial margins; basis with single tooth on lateral surface; ischium having dentate crest on mesial surface bearing 15 teeth; merus with band of dense short mesiodistal fusiform setae.

Pereopods 1 asymmetrical; ventral margin of ischium obscurely toothed or tuberculate; merus distally expanded, ventral margin toothed, teeth becoming larger distally, suture along dorsal margin; carpus with longitudinal suture on dorsal surface, small tooth ventrodistally; both chelae carinate along dorsal margin of propodus; larger chela broader, and fingers relatively shorter, than smaller chela, outer surface of propodus at base of finger finely granulate, fixed finger with 2 or 3 large teeth on cutting edge, dactylus strongly curved, with rounded ridge on outer surface, about 5 strong teeth on cutting edge; smaller chela lacking granulations on outer surface, row of small teeth on propodus at base of dactylus on both mesial and lateral surface, cutting edges of fingers more evenly serrate than in larger chela.

Pereopod 2, merus, carpus, and propodus bearing elongate setae on posterior margins; dactylus with posterior margin bearing row of fine spinules. Pereopod 3, propodus with posterodistal band of dense stiff setae; dactylus flexed, with row of about 17 stout corneous spines on posterior surface, sinuous row of fine short spinules on anterior margin. Pereopod 4 similar to pereopod 3, but with merus relatively shorter. Pereopod 5 flexed anteriorly, propodus bearing broad 'pad' of fine setae, those along posterior margin becoming more elongate distally, posterodistal margin bearing several small teeth; dactylus with posterior margin sin-

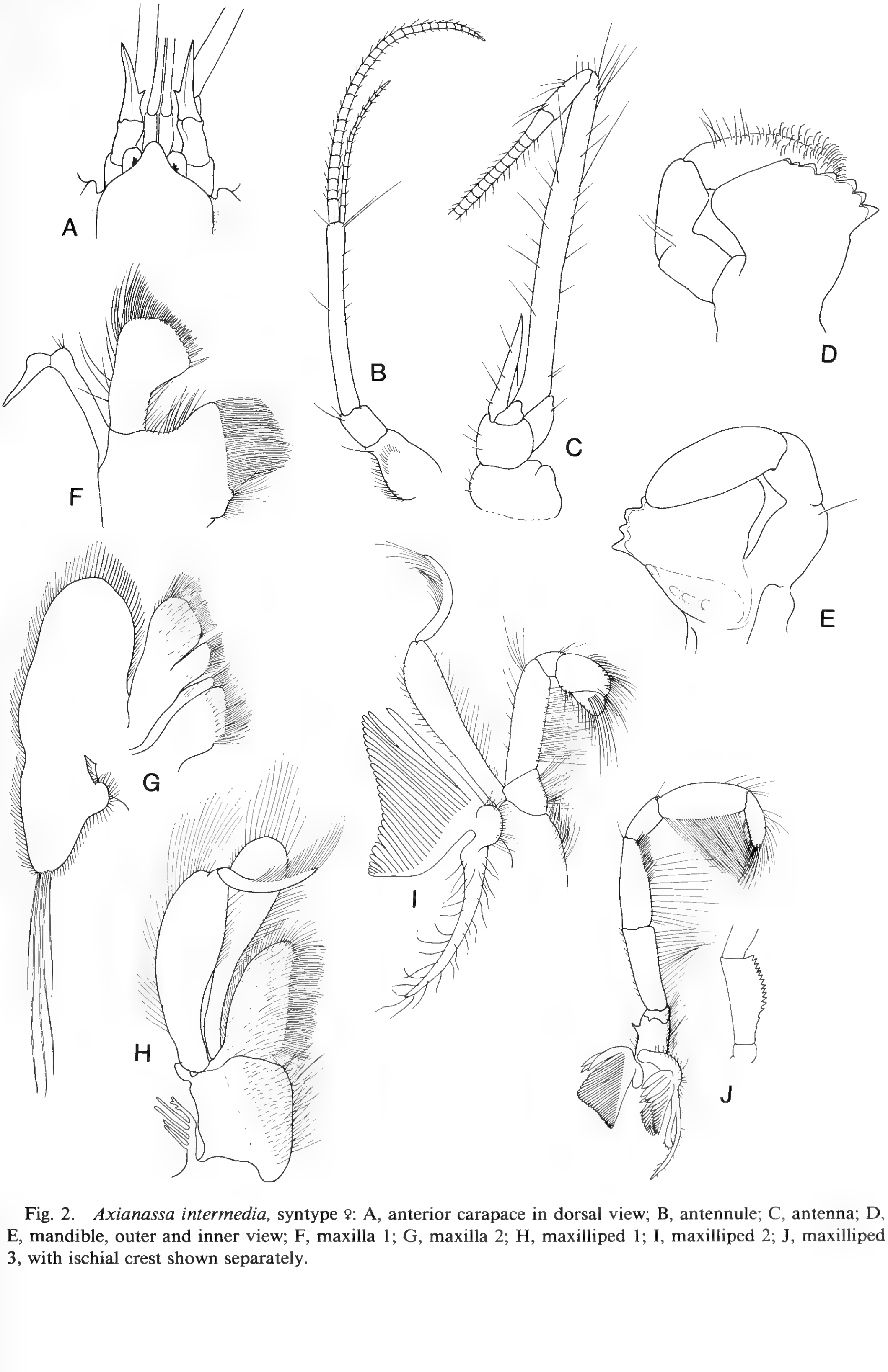


Fig. 2. *Axianassa intermedia,* syntype ♀: A, anterior carapace in dorsal view; B, antennule; C, antenna; D, E, mandible, outer and inner view; F, maxilla 1; G, maxilla 2; H, maxilliped 1; I, maxilliped 2; J, maxilliped 3, with ischial crest shown separately.

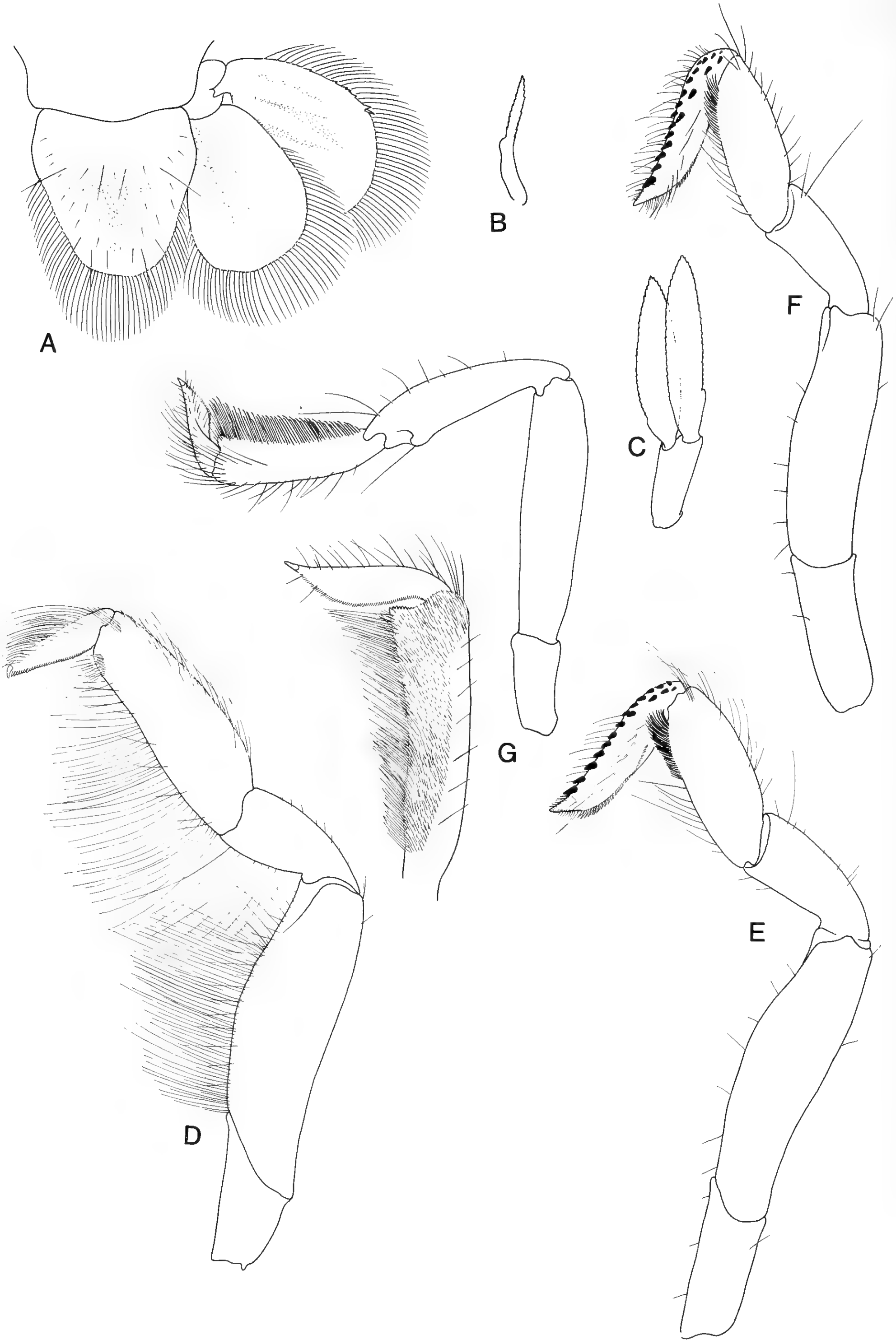


Fig. 3. *Axianassa intermedia,* syntype ♀: A, telson and right uropod in dorsal view; B, pleopod 1; C, pleopod 2; D, pereopod 2; E, pereopod 3; F, pereopod 4; G, pereopod 5, with propodus and dactylus enlarged.

uous, lined with row of tiny spinules. Lateral uropodal ramus ovate, lacking suture, lateral margin bearing 3–5 small fixed teeth, distalmost largest and having mobile spine internal to it.

Variation.—Pereopod 1, spination on ventral margin of merus: USNM 110451: ♂ cl 5.5 mm—strong row of spines on both chelipeds. USNM 57512: ♀ cl 7.8 mm—spines strong on larger chela, almost obsolete on smaller chela. ♀ cl 6.8 mm—spines fairly strong on larger chela, smaller chela missing. ♂ cl 6.1 mm—spines strong on both chelae.

Axianassa mineri Boone, 1931
Fig. 4

Axianassa mineri Boone, 1931:157, fig. 10.—Goy & Provenzano, 1979:351.

Material.—Holotype, American Museum of Natural History, AMNH 8-III-1926-6403, ♀ cl 6.1 mm, Pacheca Island, Pearl Islands, Bay of Panama (Pacific coast), under intertidal stones on rocky and gravelly beach.

Description.—Carapace with linea thalassinica somewhat grooved; cervical groove clearly defined; rostrum barely defined, anterior margin of carapace broadly rounded, not reaching beyond cornea of eyes. Abdomen thin-walled, bearing few setae on posteroventral region of pleura; somite 1 half length of 2, pleuron ventrally indistinct, rounded; somites 2–4 subequal in length, somites 5 and 6 decreasing in length. Telson about ⅛ longer than greatest width, posteriorly broadly rounded.

Cornea subterminal, faintly demarked from eyestalk, pigmentation lost after prolonged preservation, with tiny tubercle distally. Antennular peduncle articles 1 and 2 about ⅓ length of article 3, latter slender, elongate-cylindrical; inferior flagellum of about 14 articles, just reaching beyond antennal peduncle article 5; superior flagellum of about 25 articles, about ⅓ longer than inferior flagellum. Antennal acicle short, apically bifid; peduncle article 4 slender, elongate-cylindrical, slightly longer than distance between rostral apex and cervical groove of carapace; flagellum ¼ longer than carapace.

Mouthparts typical of genus. Maxilliped 3, articles strongly setose on posterior margins; ischium with mesial crest bearing about 14 teeth, crest continuing on proximal merus bearing 3 teeth; merus with one marginal tooth in proximal half and 2 teeth in distal half of posterior margin; carpus with single distal tooth on posterior margin.

Pereopod 1, left chela missing; right leg with ischium finely denticulate on posterior margin; merus inflated, with 3 small teeth proximally and single small tooth distally on posterior margin; carpus with distal rounded process on posterior margin; chela with dactylus equal in length of propodal palm, outer surface of palm smooth except for faint patch of low granulations at base of fixed finger, inner surface somewhat more granulate at base of fixed finger; latter with 4 triangular proximal teeth on cutting edge, followed by several low rounded teeth distally almost to apex; dactylus with cutting edge bearing even row of rounded teeth. Pereopod 2, dactylus with row of fine spinules on posterior margin. Pereopod 3, propodus with pad of short stiff setae distally; dactylus with 37 corneous spines arranged roughly in 3 rows on flexed posterior surface, anteriorly with sinuous row of fine short spinules. Pereopod 4 similar to pereopod 3 but with merus relatively shorter. Pereopod 5, both legs missing.

Lateral uropodal ramus ovate, with single submarginal tooth laterally, 3 marginal teeth and 1 mobile spine on rounded distolateral margin, 1 marginal and 1 submarginal tooth distally; inner ramus with single small tooth on dorsal surface, single tooth on distal margin.

Axianassa arenaria, new species
Fig. 5

Material.—Holotype, USNM 211490, ♂ cl 6.2 mm, Gulf of Mexico, MAFLA (Mis-

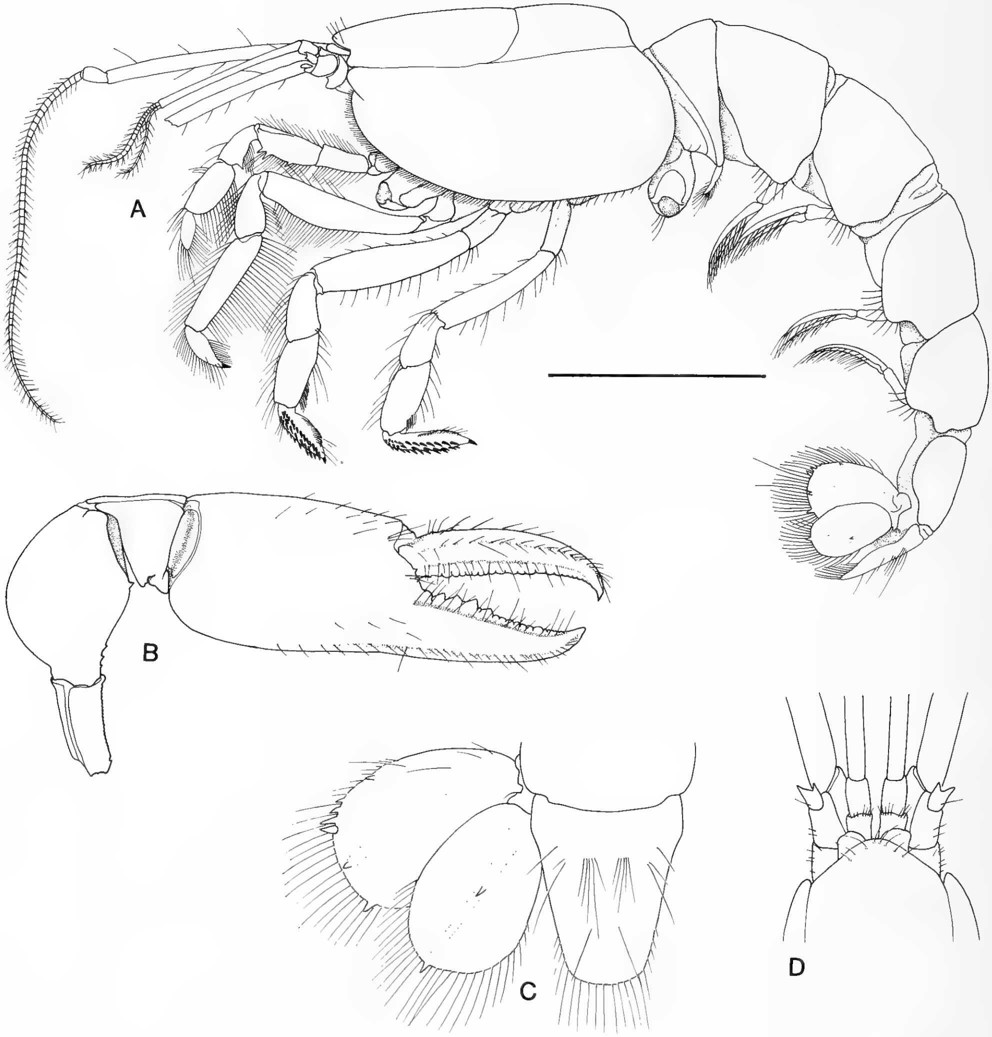


Fig. 4. *Axianassa mineri,* holotype ♂: A, lateral view, scale = 5 mm; B, right pereopod 1; C, telson and left uropod; D, anterior carapace in dorsal view.

sissippi-Alabama-Florida BLM program) sta 2315, 28°33′59″N, 84°20′09″W, 38 m, fine silty sand bottom.—Paratype, USNM 211491, ♂ cl 7.0 mm (pleon somite 6 and telson missing), Gulf of Mexico, MAFLA sta 2209, 27°52′30″N, 83°33′59″W, 34 m, clayey and sandy silt bottom.

Description.—Carapace with linea thalassinica grooved; cervical groove clearly defined; rostrum narrowing to rounded anterior margin with tiny papilla at midpoint, reaching well beyond cornea of eyes. Abdominal somite 1 about half middorsal length of somite 2, pleuron tapering ventrally to somewhat calcified spiniform process. Somites 2 and 3 subequal in length, somites 4, 5, and 6 shorter, subequal; pleura of somites 2–5 with acute posteroventral tooth. Telson middorsal length almost 1.5 times greatest width; tapering to broadly rounded posterior margin.

Cornea not clearly demarked, moderately

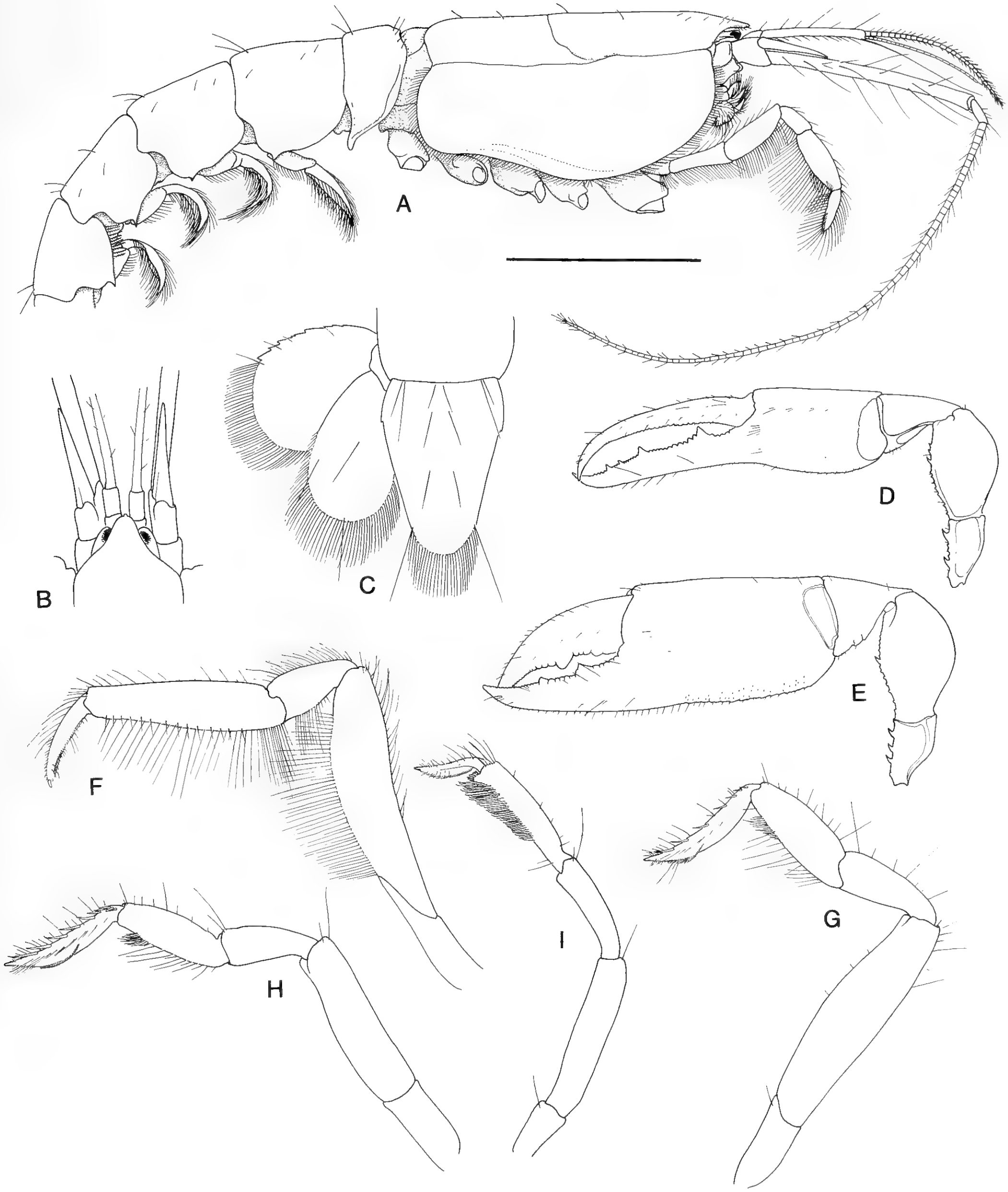


Fig. 5. *Axianassa arenaria*: A, paratype ♂ in lateral view, scale = 5 mm; B, anterior carapace in dorsal view; C, telson and left uropod in dorsal view; D, right pereopod 1, inner view; E, left pereopod 1, outer view; F, pereopod 2; G, pereopod 3; H, pereopod 4; I, pereopod 5.

pigmented. Antennular peduncle articles 1 and 2 together slightly less than half length of article 3; latter slender, elongate-cylindrical; inferior flagellum of 18 articles, ⅔ length of superior flagellum; latter of about 30 articles. Antennal acicle narrowly triangular, lacking tooth on mesial margin; peduncle article 4 slender, elongate-cylindrical, equal in length to distance from rostral tip to cervical groove of carapace; flagellum 1⅔ carapace length including rostrum.

Mouthparts typical of genus. Maxilliped 3, basis with strong mesiodistal tooth; ischium with mesial crest bearing about 17 teeth; 5 distal articles heavily setose on posterior margins.

Pereopod 1, ischium with 2 or 3 strong teeth on posterior margin; merus inflated, with posterior margin bearing single strong tooth in distal half plus several small denticulations; carpus with 1 or 2 blunt tubercles on posterodistal margin; left and right chelae of equal length, left chela more robust than right; left chela, fingers ⅔ length of propodal palm, latter with low granulations on proximoposterior surface, cutting edge of fixed finger with 2 strong triangular teeth and series of small rounded teeth reaching almost to apex; dactylus with strong proximal tooth, second strong tooth at about midlength, rest of cutting edge bearing low rounded teeth almost to apex; right chela, fingers about ⅓ longer than propodal palm; propodal fixed finger with 2 strong triangular teeth, rest of cutting edge bearing row of small rounded teeth; dactylar cutting edge bearing uniform row of small rounded teeth; tapering and curved distally. Pereopod 2, 4 distal articles strongly setose on posterior margins; dactylus about ⅝ length of propodus, with row of very small spinules on posterior margin. Pereopod 3, dactylus flexed, with row of 10 spines on posterior margin, spines becoming progressively more elongate distally; close-packed sinuous fringe of spinules on anterior margin. Pereopod 4 similar to pereopod 3, but merus relatively shorter. Pereopod 5, propodus with band of densely packed spinules, broadening distally, on posterior margin; dactylus flexed, with close-packed row of short spinules on anterior margin.

Outer ramus of uropod with several serrations on outer margin; inner ramus unarmed; both rami bearing dense row of plumose marginal setae.

Etymology.—The specific epithet 'arenaria' meaning sandy, refers to the fine sandy habitat of this species.

Axianassa jamaicensis, new species
Fig. 6

Material.—Holotype, USNM 155732, ♂ cl 6.0 mm, St. James, Montego Bay, Jamaica, intertidal, taken from burrow in sandy bottom, coll. C. B. Wilson, 7 Feb 1910.

Description.—Carapace lightly calcified, dorsally strongly rounded, free margins of branchiostegite bearing row of setae; cervical groove clearly defined; linea thalassinica somewhat grooved; rostrum anteriorly rounded, surpassing cornea of eyes. Abdomen thin-walled, with scattered setae especially on posteroventral angles of pleura; somite 1 with pleuron narrowing ventrally, rounded and poorly defined, lacking any spine-like ventral extension; somite 2 longest, somites 3–5 subequal in length, somite 6 about ⅙ longer than somite 5. Greatest telsonic width only slightly less than middorsal length; posterior margin broadly rounded, bearing marginal plumose setae.

Cornea not clearly demarked from eyestalk, weakly pigmented, with poorly defined mesiodistal tubercle. Antennular peduncle with articles 1 and 2 together half length of article 3; latter slender, elongate-cylindrical; inferior flagellum of about 11 articles, slightly less than half length of superior flagellum; latter of 24 articles. Antennal acicle narrowly triangular, with small tooth at about midlength of mesial margin; peduncle article 4 slender, elongate-cylindrical, about ⅔ length of carapace plus rostrum; flagellum about 3 times carapace length.

Mouthparts, and disposition of exopods, epipods, and branchiae as in *A. intermedia.* Maxilliped 3, endopodal articles strongly setose on posterior margins; basis with single strong mesiodistal spine; mesial crest of ischium bearing 10 teeth.

Pereopod 1, chelae of similar size, dissimilar in proportions and armature; left leg,

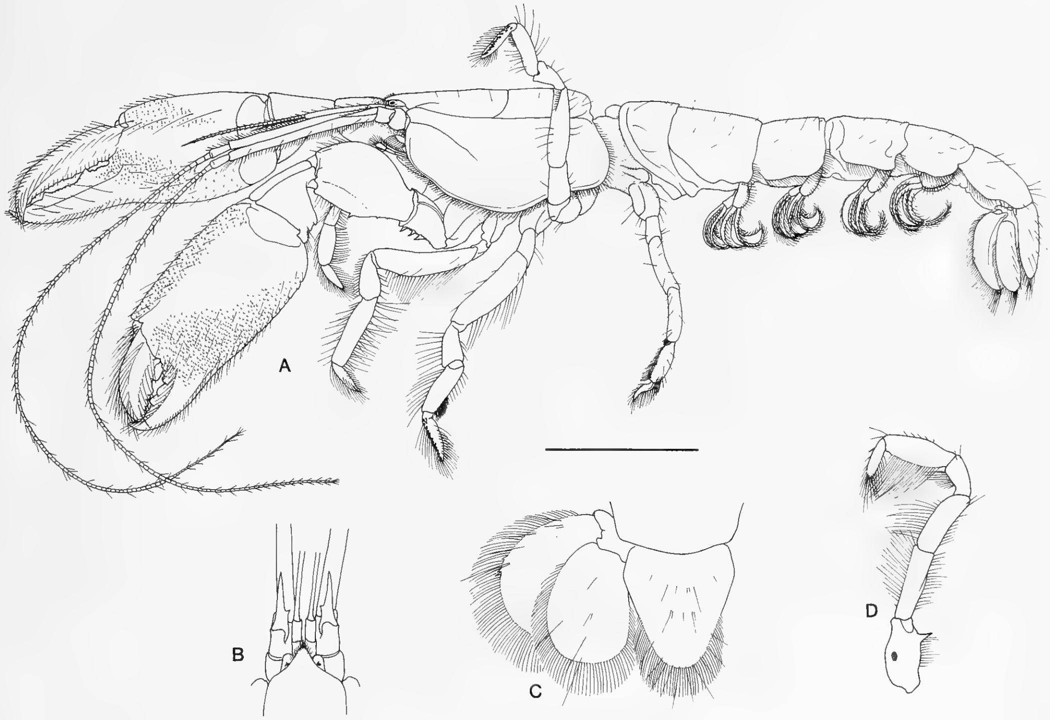


Fig. 6. *Axianassa jamaicensis:* A, holotype ♂ in lateral view, scale = 5 mm; B, anterior carapace in dorsal view; C, telson and left uropod in dorsal view; D, maxilliped 3.

ischium with 3 strong spines on posterior margin; merus inflated, with single spine at midlength of posterior margin and few proximal denticulations; carpus with blunt distal tubercle and shoulder on posterior margin; propodus with marked patches of granulations along anterior (upper) surface, at base of fixed finger and along posterior surface, fixed finger with 4 strong rounded teeth on cutting edge; dactylus slightly more than half length of propodal palm, with proximal molar-like process and distal row of low rounded teeth. Right leg, merus, ischium, and carpus as in left; granulations of propodus similar but not as extensive as in left, cutting edge with large triangular distal and proximal tooth, row of low rounded teeth between; dactylar cutting edge bearing even row of low rounded teeth. Pereopod 2, 4 distal articles bearing numerous marginal setae; dactylus with row of fine spinules on posterior margin. Pereopod 3, propodus with dense posterodistal band of setae; dactylus flexed, with single row of about 16 corneous spines on posterior margin; row of fine spines in sinuous row on anterior margin. Pereopod 4 similar to pereopod 3, but merus relatively shorter; flexed dactylus bearing about 16 corneous spines in single row distally, double row proximally, on posterior margin. Pereopod 5, propodus bearing band of dense short setae; dactylus flexed, setose, lacking spines.

Outer uropodal ramus ovate, with 2 teeth and single mobile spine on outer margin; inner and outer rami bearing dense fringe of plumose setae.

Etymology.—The specific epithet refers to Jamaica, the type locality of the species.

Axianassa canalis, new species
Fig. 7

Material.—Holotype, USNM 125897, ♂ cl 10.9 mm, Panama Canal, seaward of

Thatcher Ferry Bridge, from dredge flume, coll. H. O. Wright, 16 Mar 1967.

Description.—Carapace with linea thalassinica grooved; cervical groove clearly defined; rostrum tapering, anteriorly narrowly rounded, reaching well beyond cornea of eyes. Abdomen thin-walled, terga and pleura bearing fairly dense pile of very short setules; somite 1 somewhat more than half middorsal length of somite 2, pleuron produced ventrally into strong, calcified spiniform process, anteroventral margin bearing few short spinules; somite 2, pleuron ventrally broad, bearing few submarginal spinules; somites 3–6 subequal in length, pleura each bearing dense fringe of marginal and submarginal setae, and few spinules anteroventrally, ventral margins sinuous. Telson length subequal to greatest width, posteriorly broadly rounded, bearing numerous short scattered spinules dorsally.

Cornea not clearly demarked, moderately pigmented. Article 3 of antennular peduncle slender, elongate-cylindrical, twice length of articles 1 and 2 together; inferior flagellum of at least 14 articles, less than half length of superior flagellum; latter of about 44 articles. Antennal acicle narrowly triangular, with tooth on mesial margin; peduncle article 4 slender, elongate-cylindrical, bearing row of short spinules along ventral surface; flagellum missing.

Mouthparts typical of genus. Maxilliped 3, basis with strong mesiodistal tooth; ischium with band of fusiform setae on posterior margin, 9 slender teeth on mesial crest; posterior margins of 5 distal articles strongly setose.

Pereopod 1, both legs missing. Pereopod 2, both legs missing. Pereopod 3, propodus with dense band of setae on posterodistal margin; dactylus flexed, with row of 11 slender spines on posterior margin, becoming more slender distally; fringe of short spinules on anterior margin. Pereopod 4 similar to but shorter than pereopod 3, dactylus with row of 13 slender spines on posterior margin. Pereopod 5, both legs missing.

Outer uropodal ramus ovate, bearing single marginal tooth on lateral margin, outer half of dorsal surface bearing short scattered spinules; inner ramus ovate, with outer half of dorsal surface bearing short scattered spinules; both rami bearing marginal plumose setae.

Etymology.—The specific epithet "canalis" meaning a canal, refers to the type locality of this species.

Characters for the separation of the five known species of the genus *Axianassa* are presented in the following key. Since the combined number of specimens for all species in the genus is only nine, the following key cannot account for intraspecific variability. With more material, some features used in the key and diagnoses may prove to be of limited value in distinguishing the species.

Key to the species of *Axianassa*

1. Antennal acicle long, dagger-like, apically acute 2
– Antennal acicle short, apically bifid .... *mineri*
2. Pleura of abdominal somites 2–5 having single posteroventral tooth; antennal acicle lacking tooth on mesial margin .... *arenaria*
– Pleura of abdominal somites 2–5 unarmed; antennal acicle with tooth on mesial margin 3
3. Abdominal somite 1 produced ventrally into spiniform process ... *canalis*
– Abdominal somite 1 ventrally rounded 4
4. Ischium of pereopod 1 armed with 3 strong teeth on posterior margin ... . *jamaicensis*
– Ischium of pereopod 1 lacking strong teeth, posterior margin finely denticulate .... *intermedia*

Discussion

Since 1924 when Schmitt created the family Axianassidae for his new genus and

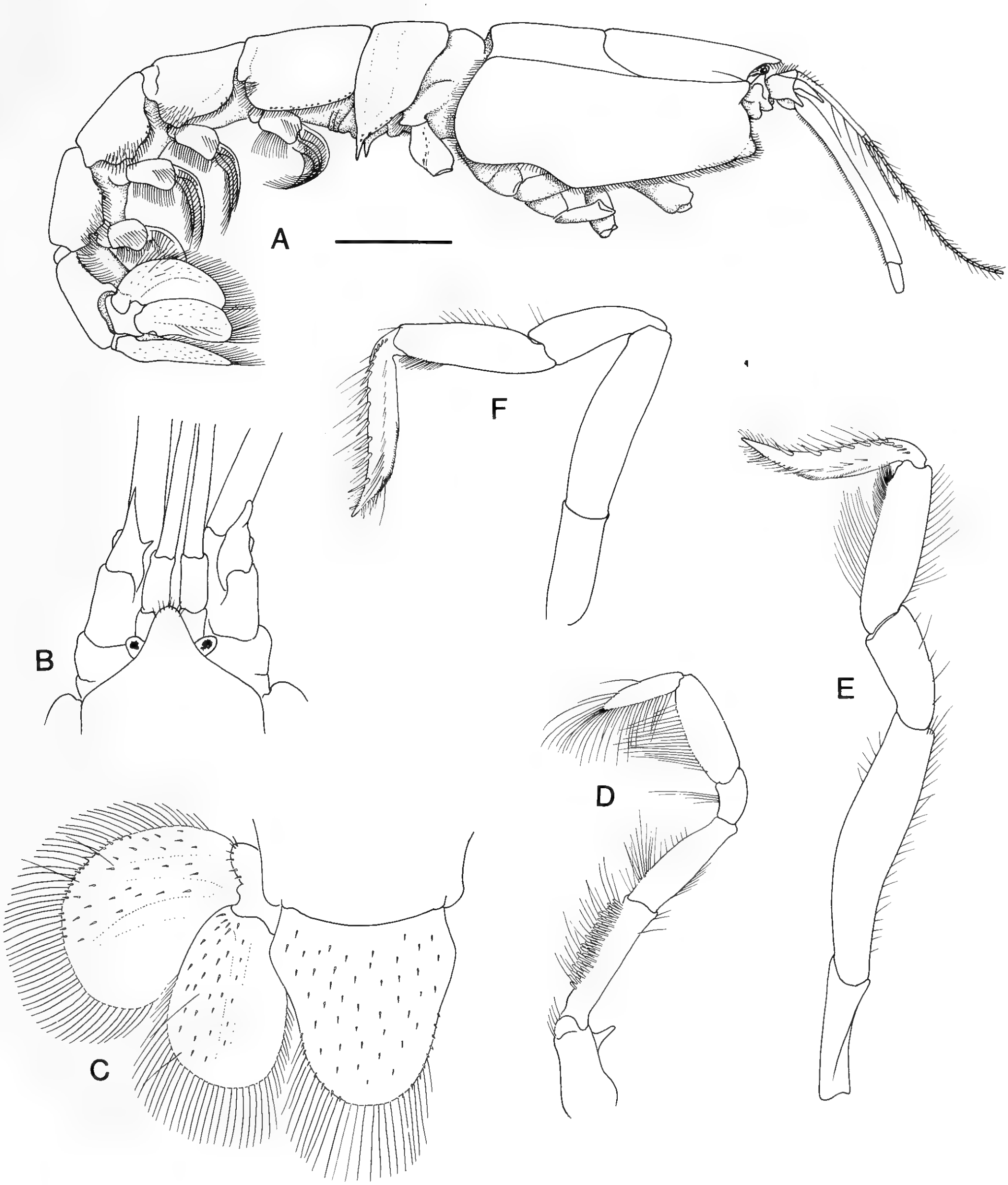


Fig. 7. *Axianassa canalis:* A, holotype ♂ in lateral view, scale = 5 mm; B, anterior carapace in dorsal view; C, telson and left uropod; D, maxilliped 3; E, pereopod 3; F, pereopod 4.

species *Axianassa intermedia,* the position and validity of the family Axianassidae have been questioned by several authors (De Man 1928, Balss 1957; Le Loeuff & Intes 1974, Ngoc-Ho 1981), who included the genus in the earlier family Laomediidae. Others have retained the Axianassidae (Wear & Yaldwyn 1966, Poore & Griffin 1979), while Goy & Provenzano (1979:351) explicitly excluded *Axianassa* from the Laomediidae. Gurney (1938) retained the Axianassidae, based on his studies of larval forms. Chace (1939),

Table 1.—Comparison of the genera of the Laomediidae.

Character	*Axianassa*	*Laomedia*	*Jaxea*	*Naushonia*	*Laurentiella*
rostrum	unarmed	armed	armed	armed	?unarmed
antennular ped. art. 3	elongate	short	elongate	short	short
antennal acicle	spiciform (reduced)	reduced	reduced	well-dev.	spiciform
antennal ped. art. 4	elongate	short	elongate	short	elongate
maxilla 2 elongate setae	5	5	7	10	7
maxilliped 3 exopod	absent	present	present	present	absent
exopods on pereopods	0	2–5 (reduced)	0	0	0
pereopod 1	chelate dissimilar	chelate dissimilar	chelate similar	subchelate similar	chelate dissimilar
pereopod 2	simple	subchelate	subchelate	simple	simple
pereopods 3 & 4	twisted	twisted	?twisted	unflexed	twisted
dactyl	band of spines	band of spines	no band of spines	no band of spines	band of spines
	corneous spines	no corneous spines	no corneous spines	no corneous spines	corneous spines
pereopod 5	subchelate	subchelate	subchelate	simple	subchelate
uropodal sutures	absent	on both rami	on both rami	on both rami	on outer ramus on

in dealing with the species of *Naushonia,* divided the Laomediidae into the subfamilies Laomediinae and Naushoniinae, based on the structure of the uropods, antennal scale, and fifth pereopods, but did not refer to *Axianassa.* Le Loeuff & Intes (1974) added the new genus *Laurentiella* to the family Laomediidae. Five genera have now been included in this family: *Jaxea* Nardo, 1847, *Laomedia* De Haan, 1849, *Naushonia* Kingsley, 1897, *Axianassa* Schmitt, 1924, and *Laurentiella* Le Loeuff & Intes, 1974. Clearly, a critical reexamination of the relationships of these genera is necessary, along with their relationship to the rest of the thalassinidean families.

Table 1 has been compiled for comparison of some of the characters of the five laomediid genera. For each genus, the relevant column of character states may be regarded as its diagnosis.

Unfortunately, information on larval morphology and development for laomediids is limited. The larval types for species in two genera, *Jaxea* and *Naushonia,* have been definitely identified and described by Wear & Yaldwyn (1966) and Goy & Provenzano (1979), respectively. There have been three published reports of laomediid larvae taken in plankton samples from the western Atlantic. In one of these reports based on plankton samples from the southwestern Gulf of Mexico, Ngoc-Ho (1981) tentatively identified the laomediid larvae present as "*Axianassa* sp." and discussed their similarity to the known larvae of the family Upogebiidae. Ngoc-Ho's material appears to be similar and possibly congeneric with the laomediid larvae reported by Gurney (1938) from Brazilian waters and by Truesdale & Andryszak (1983) from the northern Gulf of Mexico off Louisiana. However, until larvae hatched from eggs of *Axianassa* females can be examined and critically compared with the larvae from these previous plankton studies, Ngoc-Ho's generic identification must be considered tentative. Sakai & Miyake (1964) reported on the first zoea of *Laomedia astacina,* and noted its greater similarity to larval stages of *Jaxea* and *Naushonia* than to those of *Laomedia.* Konishi (1989), in a compilation of the known information on thalassinidean larval development, concluded that the upogebiids are intermediate between the more primitive axiids and the more advanced laomediids, and that the earlier reported *Axianassa* zoea (Ngoc-Ho 1981) had more primitive characters than the typical laomediids. While larval features are undoubtedly of value in the question of thalassinidean phylogeny, conclusions about phylogeny based on such features alone should be avoided; rather, larval characters should be considered along with morphological, biological, ecological, and molecular evidence, to build a strong basis for phylogenetic inference.

Acknowledgments

We are grateful to Dr. Harold Feinberg (American Museum of Natural History, New York) for the loan of material, and to Ms. Debbie Roney who inked the whole animal drawings of Figs. 4–7. Our sincere thanks are due to A. B. Williams, National Marine Fisheries Service, for his critical reading of the manuscript.

Literature Cited

Balss, H. 1957. Decapoda (Zehnfusser) Part 12.—Dr. H. G. Bronns Klassen und Ordnungen des Tierreichs 5(1)7:1505–1672.

Boone, L. 1931. A collection of anomuran and macruran Crustacea from Panama and the fresh waters of the Canal Zone.—Bulletin of the American Museum of Natural History 633(2): 137–189.

Borradaile, L. A. 1903. On the classification of the Thalassinidea.—Annals and Magazine of Natural History (7)12:534–551.

Chace, F. A., Jr. 1939. On the systematic status of the crustacean genera *Naushonia, Homoriscus,* and *Coralliocrangon.*—Annals and Magazine of Natural History (11)3:524–530.

Goy, J. W., & A. J. Provenzano, Jr. 1979. Juvenile morphology of the rare burrowing mud shrimp *Naushonia crangonoides* Kingsley, with a review of the genus *Naushonia* (Decapoda: Thalassinidea: Laomediidae).—Proceedings of the Biological Society of Washington 92(2):339–359.

Gurney, R. 1938. Larvae of decapod Crustacea. Part 5. Nephropsidea and Thalassinidea.—Discovery Reports 17:291–344.

Haan, W. de. 1833–1850. Crustacea. *In* P. F. von Siebold, Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit. Leiden, i–xxxi, ix–xvi, 1–243, pls. A–J, L–Q, 1–55.

Kingsley, J. S. 1897. On a new genus and two new species of macrurous Crustacea.—Bulletin of the Essex Institute 27:95–99.

Konishi, K. 1989. Larval development of the mud shrimp *Upogebia (Upogebia) major* (De Haan) (Crustacea: Thalassinidea: Upogebiidae) under laboratory conditions, with comments on larval characters of thalassinid families.—Bulletin of the National Research Institute of Aquaculture, Nansei 15:1–17.

Le Loeuff, P., & A. Intes. 1974. Les Thalassinidea (Crustacea, Decapoda) du Golfe de Guinée. Systématique–écologie.—Cahiers ORSTOM 12(1): 17–69.

Man, J. G. de. 1928. The Decapoda of the Siboga-Expedition. Part 7. The Thalassinidae and Callianassidae collected by the Siboga–Expedition with some remarks on the Laomediidae.—Siboga–Expeditie monographie 39a6:1–187.

Nardo, G. D. 1847. Sinonimia moderna della specie registrate nell' opera initolata: Descrizione de' Crostacei, de' Testacei e de' Pesci che abitano le Laguna e Golfo Veneto, rappresentati in figure dall' Abate S. Chiereghini Ven. Clodiense, applicata per commissione governativa. Venice, xi, 128 pp.

Ngoc-Ho, N. 1981. A taxonomic study of the larvae of four thalassinid species (Decapoda, Thalassinidea) from the Gulf of Mexico.—Bulletin British Museum of Natural History (Zoology) 40(5):237–273.

Poore, G. C. B., & D. J. G. Griffin. 1979. The Thalassinidea (Crustacea: Decapoda) of Australia.—Records of the Australian Museum 32(6):217–321.

Sakai, K., & S. Miyake. 1964. Description of the first zoea of *Laomedia astacina* de Haan (Decapoda Crustacea).—Science Bulletin of the Faculty of Agriculture, Kyushu University 21(1):83–87.

Schmitt, W. L. 1924. Bijdragen tot de kennis der fauna van Curaçao. Resultaten eener reis van Dr. C. J. van der Horst in 1920. The macruran, anomuran and stomatopod Crustacea.—Bijdragen tot de Dierkunde 23:61–81.

Truesdale, F. M., & B. L. Andryszak. 1983. Occurrence and distribution of reptant decapod crustacean larvae in neritic Louisiana waters: July 1976.—Contributions in Marine Science 26:37–53.

Wear, R. G., & J. C. Yaldwyn. 1966. Studies on thalassinid Crustacea (Decapoda, Macrura Reptantia) with a description of a new *Jaxea* from New Zealand and an account of its larval development.—Zoology Publications from Victoria, University of Wellington 41:1–27.

Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Washington, D.C., Smithsonian Institution Press, 550 pp.

Yaldwyn, J. C., & R. G. Wear. 1970. Preliminary description of a new burrowing mud-shrimp from eastern Australia (Crustacea, Macrura, Reptantia, Laomediidae).—Australian Zoologist 15(3):384–385.

———, & ———. 1972. The eastern Australian, burrowing mud-shrimp *Laomedia healyi* (Crustacea, Macrura Reptantia, Laomediidae) with notes on larvae of the genus *Laomedia*.—Australian Zoologist 17(2):126–141.

(BK) Department of Invertebrate Zoology, National Museum of Natural History, NHB-163, Smithsonian Institution, Washington, D.C. 20560; (RH) Gulf Coast Research Lab, P.O. Box 7000, Ocean Springs, Mississippi 39564–7000.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 573–597

ON THE CRAYFISHES (DECAPODA: CAMBARIDAE) OF THE NECHES RIVER BASIN OF EASTERN TEXAS WITH THE DESCRIPTIONS OF THREE NEW SPECIES

Horton H. Hobbs, Jr.

Abstract.—Among the 13 crayfishes recorded here from the Neches River basin in eastern Texas are three that are previously undescribed: *Procambarus* (*Girardiella*) *nigrocinctus, P.* (*G.*) *kensleyi,* and *P.* (*Ortmannicus*) *nechesae.* The first has its closest affinities with *P.* (*G.*) *tulanei* Penn, the second with *P.* (*G.*) *parasimulans* Hobbs and Robison, and the third is a close relative of *P.* (*O.*) *geminus* Hobbs. Present also in the Basin is a member of the genus *Cambarellus,* two representatives of the genus *Cambarus,* two belonging to the genus *Fallicambarus,* a member of the genus *Faxonella,* and four other species of *Procambarus.* New locality records are cited for all of them.

With the intent of stimulating an interest in the crayfish fauna of Texas, the late George Henry Penn, Jr., and I summarized (1958) all of the information available to us concerning the crayfishes of Texas and provided a key to the species and subspecies recognized at that time. Unfortunately, few contributions extending our knowledge of the fauna have appeared since. Among them is that of Rollin D. Reimer (1969) whose unpublished dissertation contains descriptions of several unnamed new taxa and records that are in need of further attention. One of the species ("*Procambarus* species E") included in the dissertation was cited as occurring in the Navasota River basin by Reimer & Clark (1974) in their summary of the decapod crustaceans occurring in that basin. In the following year this crayfish was described under the name of *Procambarus* (*Girardiella*) *curdi* by Reimer (1975). Two of the species described herein were almost certainly recognized by Reimer and were cited by him as occurring in the Neches River basin: his "*Procambarus* species F" is almost certainly conspecific with *P.* (*Girardiella*) *nigrocinctus* described below, and his *Procambarus* species G" embraces, if it is not identical with, *P.* (*G.*) *kensleyi* which is also described herein. As noted by Hobbs & Robison (1982:545), reluctance exists in describing crayfishes that almost certainly were recognized as undescribed by Dr. Reimer, but receiving no response to repeated attempts to communicate with him, descriptions of these two species are included here.

Hobbs (1971) described *Procambarus* (*Ortmannicus*) *texanus* from the fish hatchery near Smithville, Bastrop County, but no records of its presence elsewhere have been reported. Unpublished is a detailed study of the life histories of two crayfishes occurring in southeastern Texas by Albaugh (1973). A new species belonging to the genus *Procambarus* was described by Albaugh (1975) and another of the genus *Cambarellus* by Albaugh & Black (1973). In 1986, I was greatly surprised to learn of the existence of a crayfish pest in the eastern prairie section of Texas that had caused concern to farmers and to residents with lawns for a number of years, if not for generations. How *Fallicambarus* (*F.*) *devastator* Hobbs & Whiteman (1987) escaped earlier attention of students of crayfishes remains unanswered to date. In attempting to obtain information on the distribution and biology of this crayfish (See Hobbs & Whiteman 1990), specimens of other species of cambarids, including three that were previously undescribed, were found within and bordering its range. Their occurrence within the area frequented by *F.* (*F.*) *devastator* are recorded herein.

It would be desirable to compare the crayfish fauna of the Neches River basin with that of other river systems along the western Gulf Slope as has been so admirably done for the freshwater fishes by Conner & Suttkus (1986). Unfortunately the crayfish fauna has not been determined for a single stream between the Mississippi River and the Rio Grande. Certainly the present report does not represent a complete inventory of the crayfishes of the Neches Basin. The only survey of a Texas watershed that has produced a perhaps near-exhaustive list of the crayfishes occurring within it is the study of Reimer & Clark (1974) on the Navasota watershed, a tributary of the Brazos River. They found ten species of crayfishes, six of which are reported herein to occur also in the Neches Basin: *Cambarellus* (*Pandicambarus*) *puer* Hobbs, 1945, *Fallicambarus* (*C.*) *hedgpethi* (Hobbs, 1948) (=*F.* (*C.*) *fodiens* (Cottle, 1863); see Hobbs & Robison 1989), *Cambarus* (*L.*) *ludovicianus* Faxon, 1884, "*Procambarus* species A" (=*P.* (*Girardiella*) *curdi*), *P.* (*Ortmannicus*) *acutus* (Girard, 1852) , and *P.* (*Scapulicambarus*) *clarkii* (Girard, 1852). I am aware of no records for *Procambarus* (*Capillicambarus*) *incilis* Penn (1962), *P.* (*G.*) *simulans* (Faxon, 1884), *P.* (*G.*) species B, and *Orconectes* (*Buannulifictus*) *palmeri longimanus* (Faxon, 1898) in the Neches watershed.

Perhaps this exposure of the comparative richness of the crayfish fauna of the Neches River basin will induce a more thorough survey by others of the crayfishes frequenting this and neighboring watersheds.

Family Cambaridae

Subfamily Cambarellinae

Cambarellus (*Pandicambarus*) *puer* Hobbs

Cambarellus puer Hobbs, 1945:469.
Cambarellus (*Pandicambarus*) *puer*.—Fitzpatrick, 1983:268.

New record.—Jasper Co.: Edge of creek 9.2 mi (14.7 km) NW of US Hwy 190 on St Rte 63, 3 ♂ II, 2 ♀, 17 Apr 1987, G. B. Hobbs & HHH.

Subfamily Cambarinae

Cambarus (*Lacunicambarus*) *diogenes* Girard

Cambarus diogenes Girard 1852:88.
Cambarus (*Lacunicambarus*) *diogenes*.—Hobbs, 1969:110.

New records.—Newton Co.: 2.7 mi (4.3 km) NW of Newton (Courthouse) on US Hwy 190, 2 j♀, 11 Nov 1987, Brian F. Kensley & HHH. Polk Co.: 6.2 mi (9.9 km) NE of Farm Rd 3152 on Rd 350, 1 ♀, 13 Nov 1987, BFK & HHH. Tyler Co.: 2.7 mi (4.3 km) E of Horse Pen Creek on US Hwy 190, 2 ♂ II, 2 ♀, 13 Nov 1987, BFK & HHH.

Remarks.—These specimens belonging to the subgenus *Lacunicambarus* are only tentatively assigned to this species. The ranges and limits of variation of the few described members of this species group are currently receiving a long-needed review by Raymond F. Jezerinac. All of the specimens cited were obtained from burrows.

Cambarus (*Lacunicambarus*) *ludovicianus* Faxon

Cambarus diogenes var. *Ludoviciana* Faxon, 1884:144.
Cambarus (*Lacunicambarus*) *ludovicianus*.—Hobbs, 1990.

New records.—Angelina Co: 5.6 mi (9 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♀, 15 Apr 1987, GBH & HHH. Jasper Co.: 9.0 mi (14.4 km) SW of Jasper on US Hwy 190, 2 j♂ 1 j♀, 16 Apr 1987, GBH & HHH. Polk Co.: 12 mi (19.2 km) E of Livingston on US Hwy 190, 2 j♀, 16 Apr 1987, GBH & HHH. 12.5 mi (20 km) E of Livingston on US Hwy 190, 1 ♀, 16 Apr 1987, GBH & HHH. 7.0 mi (11.2 km) W of US Hwy 287 on Farm Rd 1745, 1 ♂ I, 2 ♀, 12 Nov 1987, R. Armentrout, J. David, BFK, HHH. San Augustine Co.: 19.4 mi (31 km) NE of Zavalla on US Hwy 69, 1 ♂ II, 1 ♀, 17 Apr 1987, GBH & HHH. 1.7 mi (2.7 km) NE of San Augustine on Farm Rd 353, 8 Nov 1987, 1 ♂ II, BFK & HHH.

Remarks.—See "Remarks" under *Cambarus* (*L.*) *diogenes* which are also applicable here. All of the specimens cited were obtained from burrows.

Fallicambarus (*C.*) *fodiens*

Astacus fodiens Cottle 1863:217.
Cambarus hedgpethi Hobbs, 1948:224.
Fallicambarus (*Creaserinus*) *fodiens.*—Hobbs, 1973:463.—Hobbs & Robison, 1989:672.

New records.—Angelina Co.: southeastern part of Lufkin, 1 ♀, 13 Apr 1987, Mike Whiteman & HHH. 3 mi (4.8 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ I, 6 ♀, 14 Apr 1987, GBH & HHH. 4.2 mi (6.7 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ I, 3 ♀, 1 j♂, 14 Apr 1987, GBH & HHH. 5.6 mi (9 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ I, 1 ♂ II, 8 ♀, 14 Apr 1987, GBH & HHH; 3 ♂ II, 5 ♀, 1 j♂, 1 j♀, 15 Apr 1987, GBH & HHH. 7.7 mi (12.3 km) NW of Hwy 59 on Farm Rd 2497, 2 j♂, 1 j♀, 15 Apr 1987, GBH & HHH; 4 j♂, 2 j♀, 9 Nov 1987, BFK & HHH. Jasper Co.: 0.3 mi (0.5 km) N of Angelina River on St Rte 63, 2 ♂ II, 1 ♀, 11 Nov 1987, BFK & HHH. 0.2 mi (0.3 km) SE of Angelina River on St Rte 63, 2oII, 11 Nov 1987, BFK & HHH. 3.1 mi (5 km) SE of Angelina River on St Rte 63, 1 ♂ I, 1 ♀, 1 j♂, 4 ovig. ♀, 11 Nov 1987, BFK & HHH. Polk Co.: 5.0 mi (8 km) W of Livingston on US Hwy 190, 1 ♂ II, 13 Nov 1987, BFK & HHH. Trinity Co.: 4 mi (6.4 km) SW of Farm Rd 357 on Rd 2262, 1 ♂ II, 16 Nov 1987, BFK & HHH. 9.0 mi (14.4 km) SW of Farm Rd 357 on Rd 2262, 1 ♂ II, 1 ♀, 16 Nov 1987, BFK & HHH. 10.6 mi (17 km) SW of Farm Rd 357 on Rd 2262, 1 ♀, 16 Nov 1987, BFK & HHH.

Remarks.—This crayfish has been treated in considerable detail by Hobbs & Robison (1989). All of the adult specimens cited here were obtained from burrows, most of the juveniles from temporary roadside pools.

Fallicambarus (*Fallicambarus*) *devastator* Hobbs & Whiteman

Fallicambarus (*Fallicambarus*) *devastator* Hobbs & Whiteman, 1987:403.

New records.—8 localities in Angelina, Houston, Polk, Trinity, and Tyler counties (see Hobbs & Whiteman 1990). Except for a few specimens in one locality obtained near or at the mouths of burrows at night, all were removed from burrows that were excavated.

Faxonella beyeri (Penn)

Orconectes (*Faxonella*) *beyeri* Penn, 1950: 166.
Faxonella beyeri.—Creaser, 1962:3.

New record.—Angelina Co.: 4.2 mi (6.7 km) NW of US Hwy 59 on Farm Rd 2497, 3 ♂ I, 48 ♂ II, 48 ♀, 14 Apr 1987, GBH & HHH. 5.6 mi (9 km) NW of US Hwy 59 on Farm Rd 2497, 2 ♂ I, 7 ♂ II, 8 ♀, 15 Apr 1987, GBH & HHH. Jasper Co.: 8.7 mi (13.9 km) NW of St Rte 63 on US Hwy 190, 1 j♀, 17 Apr 1987, GBH & HHH. San Augustine Co. 19.4 mi (31 km) NE of Zavalla on St Rte 147, 1 ♂ I, 2 ♀, 17 Apr 1987, GBH & HHH.

Remarks.—Specimens of this species from the Neches River Basin are distinctly larger than any members of the species that I have examined from elsewhere. The largest first form male and female, both from the last locality cited, have carapace lengths of 18.2 and 19.6 mm, respectively. All of the specimens cited were taken from among vegetation in open water.

Procambarus (*Girardiella*) *curdi* Reimer

Procambarus species E.—Reimer 1969:64.
Procambarus species A.—Reimer & Clark, 1974:171.
Procambarus (*Girardiella*) *curdi* Reimer, 1975:22.

New records.—Angelina Co.: ditch at jct of farm rds 287, 1336, & 324 in SW part of Lufkin, 16 j♂, 21 j♀, 13 Apr 1987, MW,

Table 1.—Measurements (mm) of *Procambarus* (*G.*) *nigrocinctus.*

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	37.5	42.2	31.2
Postorbital length	29.2	33.4	23.3
Width	2.1	2.2	1.6
Height	17.5	20.5	13.3
Areola:			
Width	2.1	2.2	1.6
Length	11.1	13.5	9.3
Rostrum:			
Width	5.9	6.6	4.9
Length	—	10.5	9.1
Right chela:			
Length, palm mesial margin	10.4	8.7	4.8
Palm width	11.4	9.9	5.7
Length, lateral margin	31.5	26.2	15.8
Dactyl length	18.5	16.2	9.3
Abdomen:			
Width	14.7	18.1	11.9
Length	39.4	42.1	32.2

GBH, HHH. 2.4 mi (3.8 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ II, 3 ♀, 1 j♂, 6 j♀, 14 Apr 1987, GBH & HHH. 5.6 mi (9 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ II, 4 ♀, 1 j♂, 1 j♀, 14 Apr 1987, GBH & HHH; 2 ♂ II, 2 ♀, 4 j♂, 5 j♀, 15 Apr 1987, GBH & HHH. 7.7 mi (12.3 km) NW of US Hwy 59 on Farm Rd 2497, 2 ♀, 4 j♂, 3 j♀, 15 Apr 1987, GBH & HHH; 2 ♂ I, 3 ♂ II, 2 ♀, 1 j♂, 5 j♀, 9 Nov 1987, BFK & HHH. 0.3 mi (0.5 km) W of Farm Rd 326 on Rd 1475, 1 ♀, 1 j♂, 10 Nov 1987, BFK & HHH. Angelina County Airport, 1 ♀, 10 Nov 1987, BFK & HHH. 1.3 mi (2.1 km) W of Shawnee Creek on Farm Rd 1818, 13 j♂, 11 j♀, 11 Nov 1987, BFK & HHH. NW city limits of Zavalla on US Hwy 69, 1 ♀, 1 ♀ with young, 11 Nov 1987, BFK & HHH. Polk County: 15.1 mi (24.2 km) SE of Trinity on St Hwy 356, 1 j♀, 16 Apr 1987, GBH & HHH. 2.4 mi (3.8 km) W of Tyler Co line on US Hwy 190, 1 ♀, 13 Nov 1987, BFK & HHH. 1.8 mi (2.9 km) N of Farm Rd 350 on Rd 3152, 1 j♀, 13 Nov 1987, BFK & HHH.

Remarks.—This crayfish does not shun sandy soil in which the burrows, consisting of a single shaft and lacking conspicuous chambers, spiral to depths of as much as one meter. Whereas most of the specimens cited were retrieved from burrows, a few were found in roadside pools, several of which were temporary.

Procambarus (*Girardiella*) *nigrocinctus*, new species

Figs. 1, 2a, Table 1

Procambarus species F.—Reimer, 1969:68.

Diagnosis.—Body pigmented, eyes well developed. Rostrum with marginal spines, lacking median carina. Carapace with strong cervical spine. Areola 4.5 to 6.2 (mean 5.4 ± 0.77) times as long as broad and constituting 28.5 to 31.6 (mean 30.0 ± 1.20) percent of total length of carapace (36.8 to 40.9, mean 39.1 ± 1.42, percent of postorbital carapace length). Suborbital angle very weak and obtuse; hepatic area with few small tubercles; branchiostegal spine comparatively strong. Antennal scale about 2.5 times as long as broad, widest at about midlength. Mesial surface of palm of chela bearded; ventral surface tuberculate, tubercles present along proximal half of ventral surface of dactyl. Ischium of third pereiopod in first form male with simple strong hook overreaching basioischial articulation; hook opposed by small setiferous tubercle on corresponding basis; coxa of fourth pereiopod lacking caudomesial boss. First pleopods of first form male reaching coxae of third pereiopods, symmetrical, bearing proximomesial spur and somewhat produced cephalic shoulder at base of terminal elements, lacking lateral subterminal setae, setae on caudoproximal ridge directed caudally, not flared; terminal elements (all sclerotized at least distally) consisting of (1) straight, tapering, subspiculiform, distally directed mesial process; (2) short, acute, distally directed cephalic process; (3) strong, acute, cephalocaudally flattened, and distally disposed central projection not overreaching (4) conspicuous, somewhat tapering, obliquely positioned caudal element; latter consisting of caudomesially excavate lamelliform lobe and lacking distinct digitiform prominence. Lamelliform lobe and central projection reaching almost same level distally. Female with annulus ventralis freely movable, about 1.3 times as long as broad, and subrhomboidal (but tilted) in outline; cephalomedian trough broadening rapidly posteriorly by strong dextral divergence of dextral wall; sinus originating adjacent to wall near midlength of annulus, and, after extending mesially to median line, following sinuous course caudally, ending on caudomedian surface of annulus; cephalic part of sinistral wall bordering trough tuberculate. Preannular plate poorly developed; first pleopods present.

Holotypic male, form I.—Cephalothorax (Fig. 1a, l, 2a) subcylindrical. Second segment of abdomen distinctly narrower than thorax (14.7 and 18.1 mm). Areola 5.3 times as long as broad and with 4 or 5 punctations in narrowest part. Cephalic section of carapace approximately (rostrum broken) 2.4 times as long as areola, latter comprising about 29.5% of total length of carapace (38.0% of postorbital carapace length). Surface of carapace punctate dorsally, strongly granulate laterally; most tubercles in hepatic area little, if any, larger than granules on branchiostegites. Rostrum broad basally, tapering gently anteriorly from level of orbit (apical part of rostrum missing in holotype but in other specimens gradually diminishing in width to well developed marginal spines; slightly upturned tip reaching ultimate podomere of antennular peduncle); margins not thickened; dorsal surface, lacking median carina, concave with punctations scattered between submarginal rows. Subrostral ridges weak and evident in dorsal view only slight distance anterior to posterior margin or orbit. Postorbital ridges prominent, each ending anteriorly in corneous spine. Suborbital angle weak and obtuse. Branchiostegal spine and cervical spine well developed.

Abdomen (Figs. 1k, 2a) subequal in length to carapace in all specimens. Cephalic section of telson with 3 spines in each caudolateral corner, lateral and mesial ones fixed. Cephalic lobe of epistome (Fig. 1i) campanulate with slightly irregular, weakly-thickened anterolateral margins; main body of epistome with distinct fovea. Ventral surface of proximal podomere of antennular peduncle with small spine near midlength. Antennal peduncle with well developed spine on both basis and ischium; flagellum almost reaching midlength of telson. Antennal scale (Fig. 1m) 2.5 times as long as broad, widest near midlength; greatest width of lamellar area 1.7 times that of thickened lateral part.

Third maxilliped extending slightly distal to spine on ventral surface of basal podomere of antennule, ventral surface of podomeres proximal to propodus largely obscured by long plumose setae; lateral surface of all except distalmost part of merus hidden in lateral aspect.

Right chela (Fig. 1p) subovate in cross section, somewhat depressed; palm about 1.1 times as broad as length of mesial margin; latter little more than one-third total length of chela; entire palm studded with tubercles, although those on and adjacent to mesial surface hidden by beard of plumose setae; 7 or 8 tubercles present in mesialmost row, all except proximal and distalmost well obscured by tufts of plumose setae, row flanked by several somewhat irregular rows of tubercles; ventral ridge adjacent to base of dactyl bearing 1 tubercle larger than most others on ventral surface of palm; dorsolateral tubercles conspicuously smaller and more depressed than those more mesially located on dorsal surface. Both fingers with low median longitudinal ridges dorsally and ventrally, ridges flanked

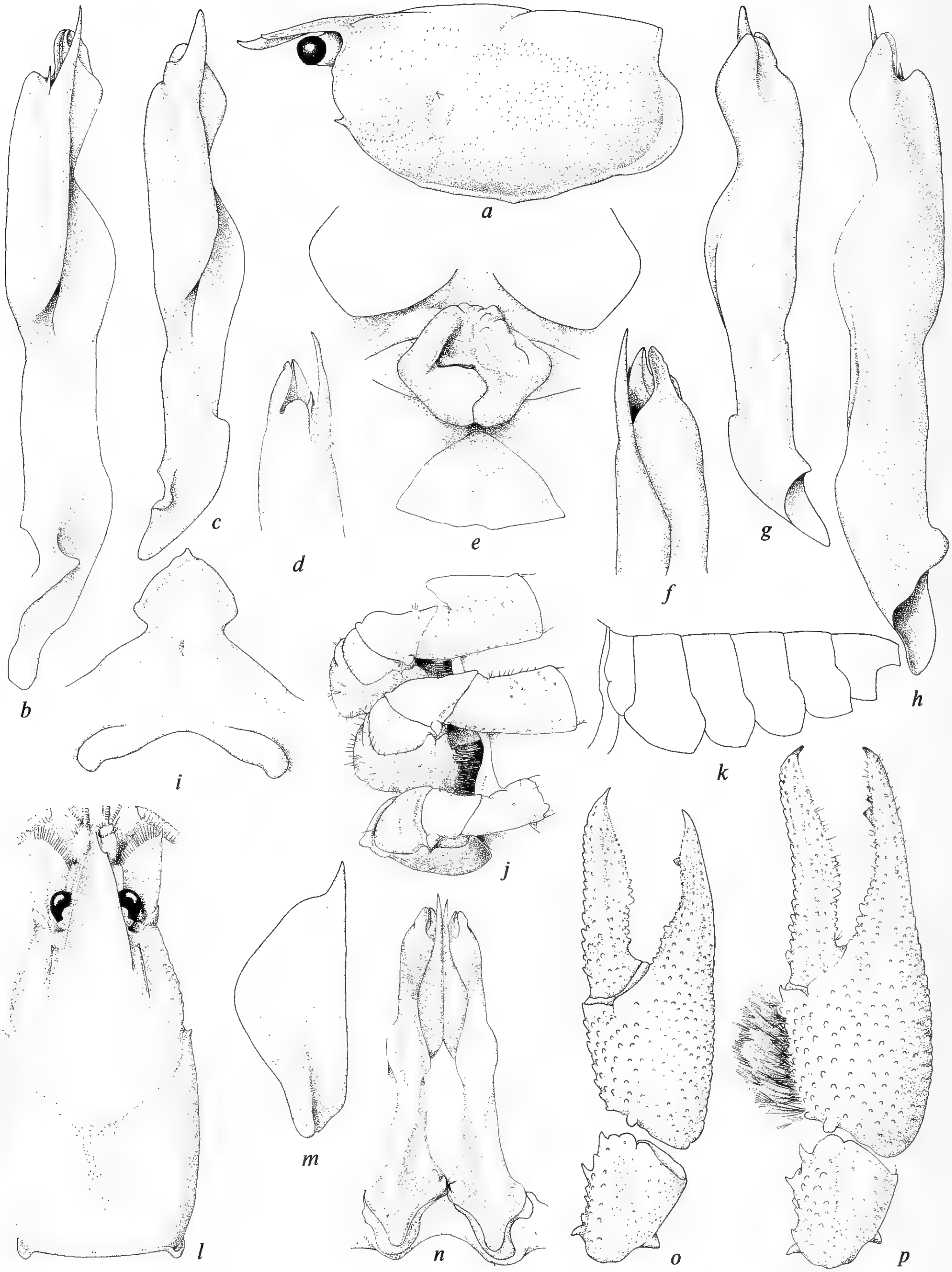
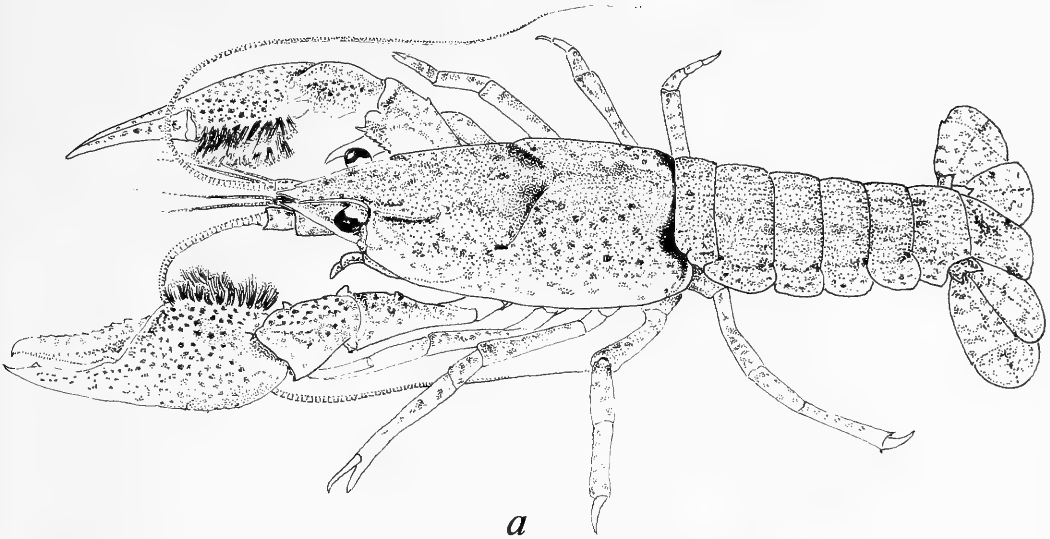


Fig. 1. *Procambarus* (*Girardiella*) *nigrocinctus* (all from holotype except c and g which are from morphotype, and e and o from allotype): a, Lateral view of carapace (rostrum broken, reconstructed on basis of other specimens); b, c, Mesial view of first pleopod; d, Cephalic view of apical part of first pleopod; e, Annulus ventralis and adjacent sternites; f, Caudal view of apical part of first pleopod; g, h, Lateral view of first pleopod; i, Epistome; j, Basal podomeres of third, fourth, and fifth pereiopods; k, Lateral view of abdomen; l, Dorsal view of carapace (rostrum broken, reconstructed on basis of other specimens); m, Antennal scale; n, Caudal view of first pleopods; o, p, Dorsal view of distal podomeres of cheliped.



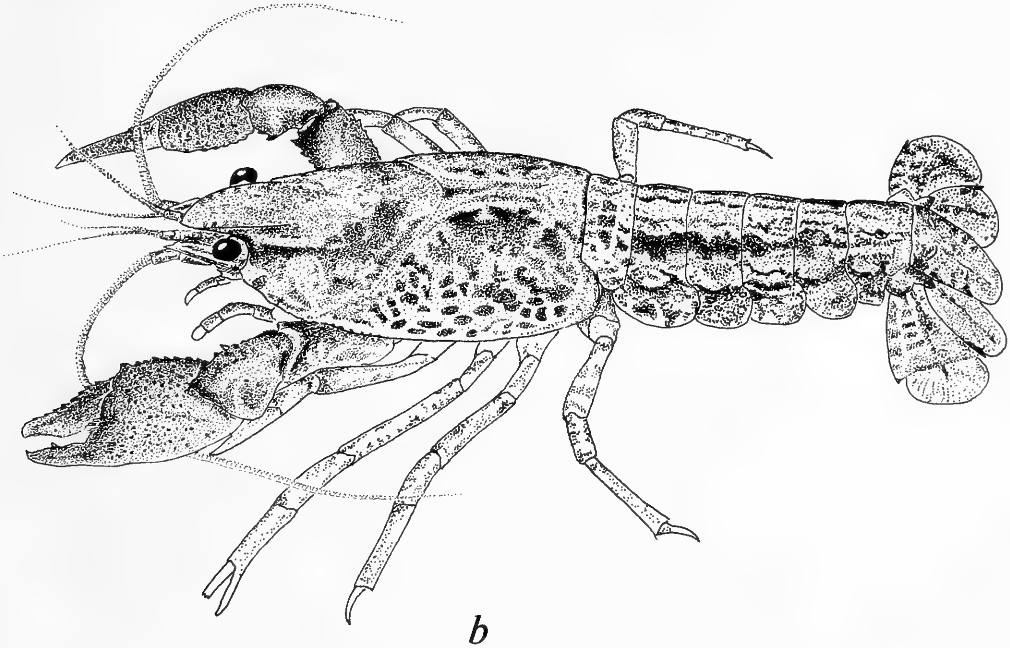


Fig. 2. Dorsolateral views of new crayfishes: a, *Procambarus* (*Girardiella*) *nigrocinctus*; b, *Procambarus* (*Girardiella*) *kensleyi*.

by tubercles along proximal half and by setiferous punctations along distal half. Opposable margin of fixed finger with row of 23 (left chela with 20) tubercles (more distal ones too small to be included in Fig. 1p), fifth from base largest, those distal to fifth decreasing in size to ultimate, which located twice length of corneous tip of finger from apex; row of 3 (2 on left) strongly cornified tubercles borne more ventrally on opposable margin in distal third of finger; longitudinal band of minute denticles extending almost entire length, broadening in area between rows of tubercles in distal third of finger; lateral margin with row of tubercles almost reaching midlength of finger. Opposable margin of dactyl with row of 17 (left with 12) tubercles, 7th (5th on left) from base largest, along proximal two-thirds of finger, few additional contiguous small tubercles on dorsal side of row, and distal to 17th (12th on left) tubercle, dorsal row of 4 and ventral one of 3 small tubercles continuing distally separated by band of minute denticles reaching base of corneous tip of finger; denticle band beginning at base of finger interrupted by principal tubercular row; mesial surface of finger with subserrate row of 17 (15 on left) tubercles.

Carpus of cheliped longer than broad with very shallow oblique furrow flanked mesially by squamous tubercles and laterally by scattered punctations; mesial surface with 2 acute tubercles somewhat larger than others and ventromesial triangular patch of tubercles with apex directed toward large, strongly acute tubercle on ventromesial distal margin of podomere; another similar strong tubercle on ventrodistal margin flanking articular condyle; otherwise ventral and lateral surfaces sparsely setose punctate.

Merus tuberculate dorsally with 2 strong, spiniform tubercles short distance proximal to distal margin; lateral, and most of mesial surfaces sparsely punctate, although distomesial surface with few small tubercles; ventral surface of podomere with mesial row of 15 tubercles and lateral one of 8 followed by oblique row of 4 joining distal ends of lateral and mesial rows; few additional tubercles present between and to the sides of the longitudinal rows. Strong spine present on distolateral angle. Ischium with row of 5 small tubercles ventromesially.

Hook on ischium of 3rd pereiopod (Fig. 1j) simple, heavy, overreaching basioischial articulation, and opposed by weak, setiferous tubercle on corresponding basis. Coxa of 4th pereiopod lacking caudomesial boss, that of 5th with small triangular one.

Sternum between 3rd, 4th, and 5th pereiopods moderately deep; ventrolateral margins with plumose setae obscuring much of 1st pleopods.

First pleopods (Fig. 1b, d, f, h, n) as described in "Diagnosis."

Uropods with both lobes of basal podomere bearing acute spines; mesial ramus with weak median carina but with well developed, distinctly-premarginal distomedian spine; distolateral spine strong.

Allotypic female.—Differing from holotype, other than in secondary sexual features, in following aspects: apex of rostrum reaching slightly beyond midlength of ultimate podomere of antennular peduncle; in respect to total carapace length, areola proportionately longer (32.0% of carapace length, 40.0% of postorbital carapace length) than in any other specimens available, but apical part of rostrum probably regenerated; cephalic section of telson with 2 fixed spines in each caudolateral corner; cephalic lobe of epistome subtriangular with irregular cephalolateral margins; 3rd maxilliped slightly overreaching basal podomere of antennule; mesial margin of palm of right chela (Fig. 1o) (left chela partly regenerated) lacking beard; opposable margin of fixed finger of chela with row of 11 tubercles, distalmost lying proximal to large tubercle situated ventral to level of row, denticles dispersed in single row; opposable margin of dactyl with row of 16 tubercles, 6th from base largest, 2nd row lacking, and denticles, for most part, arranged in single row, mesial surface with row of 15 tubercles, more distal ones not so well developed as in holotype; merus with ventromesial row of 13 tubercles, and 4 in row on ischium.

Annulus ventralis (Fig. 1e) as described in "Diagnosis." Preannular plate inconspicuous, deeply embedded in sternum, and consisting of narrow calcified arch, anteromedian part fusing with sternite XIII. Postannular sclerite subtriangular 1.7 times as broad as long and wider than, but only 0.7 as long as, annulus and bearing shallow, median longitudinal depression. First pleopod comparatively well developed, overreaching cephalic margin of annulus when abdomen flexed.

Morphotypic male, form II.—Differing from holotype in following respects: apex of acumen reaching distal extremity of antennular peduncle; spines on body and on preoral appendages more strongly developed than in holotype and allotype; antennal scale broadest slightly proximal to midlength; beard on mesial surface of palm less well developed but clearly evident; opposable margin of fixed finger with row of 10 tubercles, 4th from base largest, corresponding margin of dactyl with row of 12 tubercles, 5th from base largest, and 2 more ventral tubercles near midlength of finger; mesial margin of dactyl with row of 13 tubercles; ventral surface of merus of cheliped with lateral row of 8 tubercles, mesial one of 12, and distal connecting row of 4; ischium of cheliped with ventromesial row of 4 tubercles; hooks on ischia of 3rd pereiopods very small, tuberculiform. First pleopod (Fig. 1c, g) with shoulder on cephalodistal margin much weaker than that in holotype and not produced; mesial process much heavier than that in holotype, cephalic process not clearly distinguishable from cephalic rim partly encircling and forming part of bulbous central projection; caudal process well developed but, like other terminal elements, non-corneous.

Color notes.—Holotype (Fig. 2a): Predominant coloration tan with brown markings, most in form of small spots. Cephalic region of carapace tan with small brown spots and few pale ones along lateral rostral and postorbital ridges; latter with dark brown line extending along ventrolateral margin. Mandibular adductor region with complex patterns of fine spots forming paired semielliptical splotches abutting cervical groove. Thoracic region spotted like cephalic region and with conspicuous, paired, almost black, semielliptical splotches at posterior dorsolateral extremity; splotches narrowing and converging mesially into narrow transverse band. Abdomen similarly spotted but with darker pigments forming paired dorsolateral lines from first through basal part of 6th terga, and bases of pleura set off by scalloped sublinear series from which paler subtriangular patches extending laterally onto pleura; other spots scattered between lines and patches. Telson and uropods with anastamosing maculations exhibiting same color contrasts. Antennular and antennal peduncles and antennal scale spotted; flagella of both appendages tan. Third maxillipeds cream. Chelipeds similar in color to carapace (i.e., cream tan with brown spots) except tan reduced almost to cream over much of carpus, propodus, and dactyl; major tubercles on merus and carpus and those on mesial margin of palm and on fingers at least tipped with cream; those scattered over dorsum of merus, carpus, and palm very dark brown; both fingers fading from base distally to distinctly pinkish orange distal fourth. Setal tufts on mesial surface of palm tan. Second through 5th pereiopods cream basally but with spots and splotches of grayish tan from merus through propodus.

Coloration of female differing in no remarkable way from that of male.

Type locality.—Jack Creek, a tributary of the Neches River, at State Route 94, about 3.0 mi (4.8 km) WSW of Lufkin Perimeter Route 287, Angelina County, Texas. There the creek was some 2 to 8 m wide, no more than 0.7 m deep, and flowed with a moderate current over a sandy and rocky bottom. The sometimes clear, weak-coffee colored water was slightly cloudy in November. Adult crayfish were found under the bridge among rocks and debris that had accumulated adjacent to the pilings. Just downstream from the bridge a stand of *Myriophyllum* was present in a sun-drenched area, and from the debris in this clump, a few juveniles were taken. Several burrows along the bank were examined, but no crayfish was found in them. Shading the creek were trees belonging to the genera *Liquidambar, Quercus, Pinus, Acer,* and *Salix.* The population in the area of the bridge is rather small, for only five adult specimens were collected on two visits to the locality, 16 April 1987 and 9 November 1987. Juveniles were far more common in April than in November.

Disposition of types.—The holotype, allotype, and morphotype (♂ I, ♀, ♂ II) are deposited in the National Museum of Natural History (Smithsonian Institution), nos. 219436, 219437, and 219438, respectively, as are the paratypes consisting of 1 ♂ I, 2 ♂ II, 3 ♀, 22 j♂, and 30 j♀.

Size.—The largest specimen available is the allotypic female which has a carapace length of 42.2 (postorbital carapace length 33.4) mm despite the fact that the anterior part of the rostrum is apparently regenerated perhaps shorter than it would have been had it not been injured. The smaller of the two first form males has corresponding lengths of 37.3 and 28.9 mm. Ovigerous females or ones carrying young have not been collected.

Range and specimens examined.—This crayfish has been collected in only five localities, all in the Neches River basin in Angelina and Jasper counties, Texas. Angelina County: (1) Type locality, 1 ♂ I, 1 ♂ II, 1 ♀, 6 j♂, 18 j♀, 16 Apr 1987, GBH & HHH; 1 ♂ I, 1 ♀, 1 j♀, 9 Nov 1987, BFK & HHH. (2) Jack Creek at Farm Road 2497, SW of Lufkin, 8 j♂, 6 j♀, 14 Apr 1987, GBH & HHH; 1 ♂ II, 2 ♀, 1 j♂, 1 j♀, 9 Nov 1987, BFK & HHH. (3) Moccasin Creek at Farm Rd 2497, 4.9 mi (7.8 km) SE of jct with St Rte 94, 1 ♂ II, 6 j♂, 3 j♀, 9 Nov 1987 BFK & HHH. (4) Pool in roadside ditch on Farm Rd 2407, 1.2 mi (1.9 km) SE of intersection with St Rte 94, 1 j♀. 9 Nov 1987, BFK, HHH. Jasper County: (5) Sand-bottomed creek at St Rte 63, 1.1 mi (1.8 km) SE of Angelina River, 1 j♂, 11 Nov 1987, BFK & HHH. Almost certianly Reimer's "*Procambarus* species F" is conspecific with this crayfish (unfortunately, these specimens have not been available to me); he reported its presence in Anderson County : (6) 4.1 mi E of Slocum. Nacodoches County: (6) 5 mi E of Nacogoches; (7) 4 or 5 mi NW of Nacodoches; (8) 9 mi W of Nacogoches; (10) 2.5 mi SW of Garrison, Polk County: (11) 2 mi S of Corrigan. Smith County: (12) 3.5 mi N of Troup. Shelby County: (13) 13 mi N, 2 mi W of San Augustine.

Variations.—With so few adult specimens, and these from nearby localities, it is not surprising that the range of variation noted among them seems very small. One of the most conspicuous variations occurs in the relative development of the beard on the mesial margin of the palm of the chela: it is much the longest and densest in first form males, but it appears in the young by the time they have attained a carapace length of 10 mm. It becomes more obvious with succeeding molts in both sexes, and in at least some juvenile males approaching the molt that will take them into first form, the setal tufts are little, if any, better developed than they are in adult females. In some of the latter, the beard is reduced to a few small patches of setae that scarcely rise above the level of the adjacent tubercles, as occurs in the allotype. The chief differences noted in the rostrum seem to be associated with injury, primarily the loss of part or all of the acumen, and in several specimens, including both first form males, the acumen is either absent or has obviously been broken and regenerated, its tip not attaining the distal extremity of the antennular peduncle. The areola in specimens with carapace lengths of at least 27.8 mm ranges from 4.5 to 6.2 times as long as broad and comprises from 28.5 to 32.0% of the total length of the carapace (37.4 to 40.9% of postorbital length). The spines on the carapace and chelipeds are almost always well developed, although occasionally one or more may be shorter than the average (asymmetry in degree of development suggests that some reductions might well be associated with injury and regeneration). The spines in the caudolateral corners of the cephalic section of the telson vary in size and number: there may be two, three, or four in each corner, but only one, that immediately mesial to the fixed lateral spine, in each corner is movable. The differences noted in the secondary sexual features deserve no comment.

Relationships.—The color pattern, the bearded chelae, the comparatively broad areola, and the proximity of the range to that of *Procambarus* (*Girardiella*) *tulanei* Penn, 1953, attest to the assumed close relationship existing between *P.* (*G*) *nigrocinctus* and that species. They are both "speckled" and, although less well defined in *tulanei,* corresponding dark areas (line on lateral flank of postorbital ridges; large area over and adjacent to the mandibular adductor region; and parts of the dark band on the caudal margin of the carapace) are comparable. The areolae of the primary types of *P. tulanei,* according to Penn's measurements, range from 7.8 to 9.0 times as long as wide, in all of the available adults of *P. nigrocinctus,* from 4.5 to 6.2. The ranges of the two are contiguous, for *P. tulanei* has been found as far west in Louisiana as the Sabine River basin, which parallels the Neches watershed immediately to the west. Insofar as is known, however, their ranges are allopatric.

The presence of marginal spines on the rostrum, well developed cervical spines, a distinct dark band at the caudal margin of the carapace, and a first pleopod of the male in which the central projection does not overreach the lamelliform lobe of the caudal process will serve to distinguish *P.* (*G.*) *nigrocinctus* from all other members of the subgenus *Girardiella.*

Ecological note.—All except one of the specimens available to us were taken from streams. The single juvenile female obtained at locality 4, however, came from what appears to be a permanent roadside pool that appeared to be distant from a body of flowing water.

Etymology.—Niger (L.) = black + Cinctus (L.) = girdle; alluding to the narrow black band across the caudal margin of the carapace.

Table 2.—Measurements (mm) of *Procambarus* (*G.*) *kensleyi.*

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	31.8	33.5	31.3
Postorbital length	25.5	27.0	24.9
Areola:			
Width	2.1	2.4	1.6
Length	10.2	10.3	9.8
Rostrum:			
Width	5.2	6.3	5.2
Length	7.3	7.5	7.7
Right chela:			
Length, palm mesial margin	8.0	6.3	5.2
Palm width	8.3	8.2	6.6
Length, lateral margin	23.3	20.0	18.6
Dactyl length	13.4	11.7	11.0
Abdomen:			
Width	13.5	14.8	12.5
Length	32.8	37.2	31.7

Associates.—Collected with this crayfish in one or more localities were: *Procambarus* (*Ortmannicus*) *a. acutus* (Girard, 1852), *P.* (*Girardiella*) *curdi* Reimer, 1975, *P.* (*Scapulicambarus*) *clarkii* (Girard, 1852), *P.* (*O.*) *nechesae* n. sp., and *Fallicambarus* (*C.*) *fodiens* (Cottle, 1863).

Procambarus (*Girardiella*) *kensleyi,* new species

Figs. 2b, 3, Table 2

Procambarus species F.—Reimer, 1969:73 [in part?].

Diagnosis.—Body pigmented, eyes well developed. Rostrum without marginal spines, lacking median carina. Carapace without cervical spine. Areola 4.0 to 6.2 (mean 5.1 ± 0.81) times as long as broad and constituting 30.4 to 34.7 (mean 32.2 ± 1.26) percent of total length of carapace (36.9

to 42.9, mean 40.1 ± 1.63, percent of postorbital carapace length). Suborbital angle obtuse; hepatic area weakly tuberculate; branchiostegal spine rather weak. Antennal scale about 2.2 times as long as broad, widest slightly distal to midlength. Mesial surface of chela not bearded, ventral surface tuberculate, tubercles present along proximal half of ventral surface of dactyl. Ischium of third pereiopod in first form male with simple hook overreaching basioischial articulation; hook not opposed by tubercle on corresponding basis; coxa of fourth pereiopod lacking caudomesial boss. First pleopods of first form male reaching coxae of third pereiopods, symmetrical, bearing proximomesial spur, and subangular shoulder at base of terminal elements lacking lateral subterminal setae; setae on caudoproximal ridge directed caudally, not flared; terminal elements (all sclerotized at least distally) consisting of (1) straight, tapering, subspiculiform, distally-directed mesial process; (2) very short, acute, distally-directed cephalic process; (3) strong, cornified, acute, cephalocaudally-flattened, distally-disposed central projection not overreaching (4) prominent, distally-cornified, flattened, obliquely-positioned caudal element, latter consisting of caudomesially excavate lamelliform lobe with small digitiform prominence situated in caudomesial concavity. Lamelliform lobe and central projection reaching almost same level distally. Female with annulus ventralis freely movable, about 1.2 times as broad as long, and subrhomboidal (but tilted) in outline; moderately deep cephalomedian trough, flanked by smooth to tuberculate ridges, broadening posteriorly, dextral wall flaring more strongly than sinistral one; sinus originating in caudodextral part of trough, forming symmetrical loop caudodextrally over tongue and fossa, then turning caudosinistrally across median line before curving caudally and slightly dextrally and ending just anterior to caudal margin of annulus. Preannular plate poorly developed; first pleopods present.

Holotypic male, form I.—Cephalothorax (Fig. 2b, 3a, l) subcylindrical. Second segment of abdomen distinctly narrower than thorax (13.5 and 15.9 mm). Areola 4.9 times as long as broad and with room for 4 or 5 punctations across narrowest part. Cephalic section of carapace 2.1 times as long as areola, latter comprising 32.1% of total length of carapace (40.0% of postorbital carapace length). Surface of carapace punctate dorsally, hepatic area mostly tuberculate and lateral and ventrolateral parts of branchiostegites granulate, anteroventral branchiostegal region tuberculate. Rostrum broad, gradually tapering from base to level of distal extremity of proximal podomere of antennule, anteriorly contracting more rapidly to apex, which reaching almost midlength of ultimate podomere of antennular peduncle; margins not thickened and without spines or tubercles; dorsal surface, lacking median carina, concave with punctations scattered between prominent submarginal rows. Subrostral ridges weak and not evident in dorsal aspect. Suborbital angle inconspicuous and obtuse. Branchiostegal spine moderately well developed; cervical spine represented by small tubercle.

Abdomen (Figs. 2b, 3k) shorter than carapace. Cephalic section of telson with 2 spines in each caudolateral corner, lateral one fixed. Cephalic lobe of epistome (Fig. 3i) subtriangular with irregularly crenulate anterolateral margins; main body of epistome with distinct fovea. Ventral surface of proximal podomere of antennular peduncle with small spine near midlength, mesial margin of peduncle with plumose setae, especially 2 more distal podomeres. Antennal peduncle with small spine on both basis and ischium, distal 3 podomeres bearing prominent mesial fringe of plumose setae; flagellum reaching fourth abdominal tergum. Antennal scale (Fig. 3m) about 2.2 times as long as broad, widest slightly distal to midlength; greatest width of lamellar area about 2 times that of thickened lateral part.

Third maxilliped almost reaching distal end of proximal podomere of antennule;

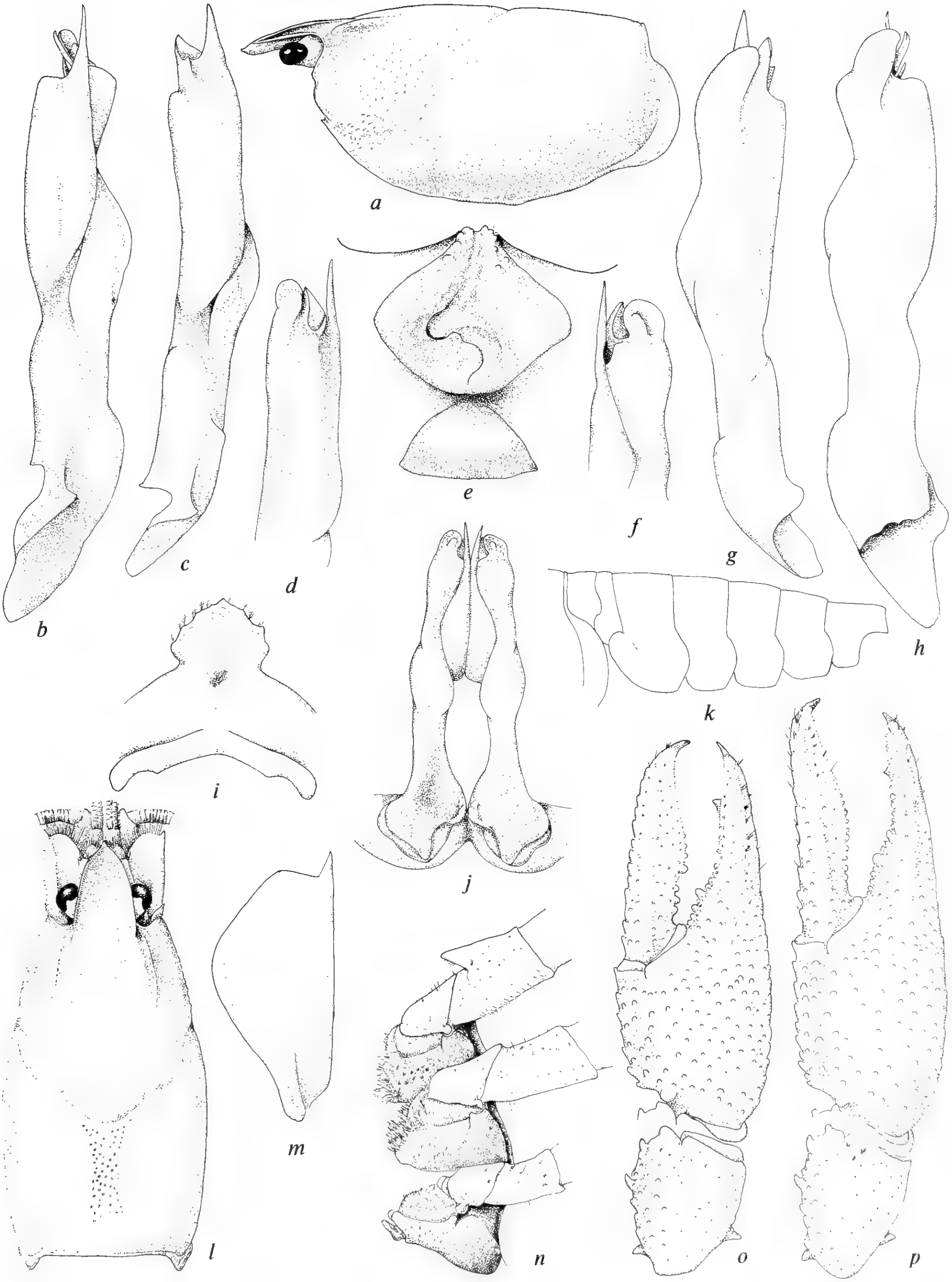


Fig. 3. *Procambarus* (*Girardiella*) *kensleyi* (all from holotype except c and g from morphotype, e and o from allotype, and j from topotypic first form male): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Cephalic view of distal part of first pleopod; e, Annulus ventralis and adjacent sclerites; f, Caudal view of distal part of first pleopod; g, h, Lateral view of first pleopod; i, Epistome; j. Caudal view of first pleopods; k, Lateral view of abdomen; l, Dorsal view of carapace; m, Antennal scale; n, Basal podomeres of third, fourth, and fifth pereiopods; o, p, Dorsal view of distal podomeres of cheliped.

ventral surfaces of ischium and merus studded with dense mat of plumose setae; lateral surface of all except distalmost part of merus hidden in lateral aspect.

Right chela (fig. 3p) (left regenerated) subovate in cross section, moderately depressed; palm slightly broader than length of mesial margin; latter slightly more than one-third total length of chela; entire palm studded with tubercles; 7 present in each of 3 mesialmost rows; ventral ridge opposite base of dactyl with 1 tubercle larger than others on ventral surface. Both fingers with low median longitudinal ridges dorsally and ventrally, ridges flanked by tubercles proximally and setiferous punctations distally. Opposable margin of fixed finger with row of 17 small tubercles along proximal three-fourths of finger, sixth from base largest (more distal ones very small); larger ("locking") tubercle present below distalmost tubercle of row; band of minute denticles extending from base of finger to base of corneous tip between and distal to tubercles; lateral margin with row of tubercles reaching midlength of finger (not visible in Fig 3p). Opposable margin of dactyl with row of 12 comparatively small tubercles, fifth from base largest, along proximal two-thirds of finger; band of minute denticles extending from base of finger to base of corneous tip between and distal to tubercles; mesial surface of finger with row of 12 tubercles, distalmost just proximal to corneous tip.

Carpus of cheliped longer than broad with shallow oblique furrow flanked mesially by tubercles and few punctations and laterally by widely spaced punctations; mesial surface with 2 tubercles larger than others, one just distal to midlength and other at dorsodistal angle, 9 additional ones present in proximal half; ventral surface with few squamous tubercles and punctations proximal to 3 subacute tubercles on distal margin.

Merus tuberculate dorsally with 2 strong spiniform tubercles near distal margin; mesial surface with few tubercles near distal extremity, otherwise it and lateral surface with scattered punctations; ventral surface with mesial row of 14 tubercles, lateral one of 10, and oblique distal row of 4; tufts of short plumose setae present between rows; short, heavy, spiniform tubercle on distolateral extremity. Ischium with row of 4 tubercles ventromesially and another of 3 dorsally.

Hook on ischium of third pereiopod (Fig. 3n) simple and overreaching basioischial articulation, not opposed by tubercles on corresponding basis. Coxa of fourth pereiopod without caudomesial boss, that of fifth with small rounded one.

Sternum between third, fourth, an fifth pereiopods moderately deep, ventral marginal fringe of plumose setae concealing much of first pleopods.

First pleopods (Fig. 3b, d, f, h, j) as described in "Diagnosis."

Uropods with both lobes of basal podomere bearing acute spines; mesial ramus with premarginal distomedian spine at end of keel and strong lateral spine.

Allotypic female.—Differing from holotype, other than in secondary sexual features, in following respects: areola 30.7% of carapace length (38.1% of postorbital carapace length); rostrum reaching distal end of penultimate podomere of antennular peduncle; flagellum of antenna reaching fifth abdominal tergum; chela (Fig. 3o) with 6 tubercles present in mesialmost row on palm, 5 in adjacent dorsal row and 6 in adjacent ventral row; opposable margin of fixed finger with row of 9 tubercles, fourth from base largest; corresponding margin of dactyl with 9; opposable margins of both fingers with single longitudinal row of minute denticles; mesialmost of 3 tubercles on ventral surface of carpus of cheliped situated more dorsally; merus with ventromesial row of 15 tubercles, ventrolateral one of 11, and oblique distal row of 3; only 2 tubercles present on dorsal margin of ischium.

Annulus ventralis (Fig. 3e) as described in "Diagnosis."

Morphotypic male, form II.—Differing

from holotype in following respects: areola 6.1 times as long as broad and consisting of 31.3% of length of carapace, 39.3% of postorbital length; abdomen slightly longer than carapace; cephalic section of telson with 3 (right) or 4 (left) spines in each caudolateral corner; anterolateral margins of cephalic lobe of epistome almost smooth; antennal flagellum reaching base of telson; setae on third maxilliped less dense and most of merus visible in lateral aspect; row on mesial margin of palm of chela flanked by row of 6 tubercles dorsally and one of 7 ventrally; opposable margin of fixed finger with row of 11 tubercles, fourth from base largest; corresponding margin of dactyl with row of 13 tubercles; denticles on both fingers arranged in single row; carpus with tubercles situated more similar to those in allotype; ventromesial angle of merus with row of 15 tubercles, 8 in lateral row, and 4 in oblique row; ischium with ventromesial row of 5 tubercles; hook on ischium of third pereiopod and boss on coxa of fifth markedly reduced; setae on ventrolateral margins of sternites XII and XIII much less well developed.

First pleopods (Fig. 3c, g) with reduced setation; terminal elements disposed as in holotype (cephalic process slightly more posteriomesially situated), and while shorter, more stocky and none corneous.

Color notes.—(Based on recently molted first form male from Trinity County, Texas; see Fig. 2b for pattern.) Basic colors dark tan with reddish brown markings. Rostrum dark tan with few small brown splotches, some of which anastomosing in basal area; postorbital ridges with brown stripe flanking ventrolateral border and merging with anastomosing splotches forming anterior part of irregular longitudinal stripe; lateral part of cephalic region with mosaic dark brown pattern. Suborbital angle encompassed by cream-colored splotch extending over antennal and mandibular regions. Thoracic region with ill-defined, irregular stripe dorsolaterally and with distinctive spotted pattern laterally (spots and background fading ventrally); areola mostly tan but with dark branchiocardiac grooves and submedian elongate spot anteriorly. Caudal ridge almost black; caudal flange gray. Abdomen with tan dorsomedian stripe from first to anterior half of sixth abdominal tergum; stripe flanked by irregular, very narrow brown stripe, and it, in turn, by broader dorsolateral ones continuous with irregular ones on branchiostegites; third pair of brown stripes formed by ventrally convex arcs across bases of pleura, these flanked dorsally and ventrally by mosaic of pale anastomosing splotches. Telson and uropods all tan with light reddish brown and cream spots; proximal podomere of uropods edged in dark brown, spines on telson and uropodal rami also dark brown. Antennular and antennal peduncles and antennal scale with dark brown margins; flagella light brown with olive suffusion distally. Dorsum of chelipeds from merus distally tan with dark brown to black tubercles, ventral surface mostly pinkish cream to pinkish tan; tips of fingers purplish. Remaining pereiopods light pinkish tan with darker tan to brown splotches dorsally; distal part of merus and carpus darker than more proximal and distal podomeres, which pinkish cream dorsally and ventrally. Setal tufts on third maxillipeds cream.

Type locality.—Roadside ditch on gentle slope 4.6 mi (7.4 km) NW of US Highway 59 on Farm Road 2497, Angelina County, Texas. There the crayfish were collected from simple burrows 0.5 to 0.8 m deep and topped by chimneys eight to 25 cm tall. The soil was a sandy clay supporting grasses and sedges. Dominant among the trees in the adjacent woods were *Liriodendron tulipifera* and members of the genera *Pinus* and *Quercus.*

Disposition of types.—The holotype, allotype, and morphotype (♂ I, ♀, ♂ II) are deposited in the National Museum of Natural History (Smithsonian Institution), nos. 219772, 219973, and 219774, respectively, as are the paratypes consisting of 4 ♂ I, 3 ♂ II, 8 ♀, 1 j♂, and 3 j♀.

Size.—The largest specimen available is a female from Tyler County, Texas, having a carapace length of 40.9 mm (postorbital length 32.8 mm). The largest and smallest first form males have corresponding lengths of 36.3 (28.9) mm and 30.6 (25.2) mm. Measurements are not available for females carrying eggs or young, neither of which has been collected.

Range and specimens examined.—This crayfish has been found in eleven localities in eastern Texas as follows (The specimens in those collections preceded by asterisks are excluded from the type series.): Angelina County: (1) Type locality, 2 ♂ I, 2 ♂ II, 3 ♀, 1 j♀, 14 Apr 1987, GBH & HHH. *(2) Roadside ditch 5.6 mi (9.0 km) NE of US Hwy 59 on Farm Rd 2497, 1 j♂, 2 j♀, 14 Apr 1987, GBH & HHH. Jasper County: (3) Roadside ditch on St Rte 63, 0.7 mi (1.1 km) NW of Farm Rd 255, 1 ♂ I, 2 ♂ II (one molted to form I on 10 Feb 1988), 2 ♀, 11 Nov 1987, BFK & HHH. (4) Roadside ditch on US Hwy 190, 1.5 mi (2.4 km) E of County Courthouse, 1 ♀, 12 Nov 1987, BFK & HHH. Newton County: *(5) Pool in roadside ditch 6.3 mi (10.1 km) NW of Newton on US Hwy 190, 13 juv, 11 Nov 1987, BFK & HHH. (6) Roadside ditch 2.7 mi (4.3 km) NW of Newton on US Hwy 190, 1 ♂ II, 1 j♂, 1 j♀, 11 Nov 1987, BFK & HHH. Panola County: *(7) Roadside ditch 9 mi (14.4 km) S of Carthage on US Hwy 96, 2 j♂, 17 Apr 1987, GBH & HHH (tentatively assigned to this species). San Augustine County: (8) Burrow in creek bank 1.7 mi (2.7 km) NE of San Augustine on Farm Rd 353, 1 ♀, 8 Nov 1987, BFK & HHH. Trinity County: (9) Burrow in creek bank on Farm Rd 2262 9.0 mi (14.4 km) SW of Farm Rd 357, 1 ♂ II (molted to form I in laboratory), 1 j♀, 14 Nov 1987, BFK & HHH. Tyler County: (10) Floodplain of Horsepen Creek on US Hwy 190, about 1.5 mi (2.4 km) E of Polk Co line, 1 ♀, 13 Nov 1987, BFK & HHH. (11) Floodplain of Big Cypress Creek on US Hwy 190, about 4 mi (6.4 km) E of Polk Co line, 1 ♀, 12 Nov 1987, BFK & HHH.

Should Reimer's "*Pocambarus* species G" prove to be conspecific with this crayfish, a number of localities cited by him expands the range of the species into western Louisiana and southwestern Arkansas. The identy of specimens from the localities offered by him should be confirmed.

Variations.—With so few specimens available from all of the localities, there is no way to determine whether the few variations noted are individual ones or typical of the populations of which they were members. No attempt is therefore made to note in which locality/ies these features were exhibited. The antennal scale may be broadest at midlength or slightly more distally; the third maxillipeds are all hirsute, but some decidedly more so than others; the suborbital angle varies from being almost obsolete to almost acute, but in none of the specimens is it prominent; differences noted in the first pleopod of the first form males include reduction or absence of a proximomesial spur, a reduction in the cephalic process that renders it a virtual rudiment, and in one specimen the central projection slightly surpasses the caudal process distally; the annulus ventralis exhibits much variability in the nature of the ridges bordering the cephalomedian trough: they may be smooth and quite approximate so that their opposing slopes are almost vertical or, like the allotype (Fig. 3e), they may be tuberculate with their crests more widely separated. While there are variations in the numbers of tubercles elsewhere and, to some extent, in their distribution, most fall within the range cited for the primary types. Tubercles on the dorsolateral margin of the ischium of the third maxilliped are absent in many crayfishes but here range in number from 2 to 5.

Relationships.—*Procambarus* (*G.*) *kensleyi* has its closest affinities with *P.* (*G.*) *parasimulans* Hobbs & Robison (1982). In both of them the areola is broad (no more than nine times as long as wide) and short (constituting a maximum of 35% of the Carapace length), the opposable margin of the dactyl of the cheliped lacks a well defined excision in the basal third, the dorsolateral surface of the palm of the chela is tuberculate, the central projection of the first pleopod of the first form male neither clearly overreaches nor projects laterally beyond the caudal process. They differ in that in *P.* (*S.*) *kensleyi* the areola is more densely punctate, the rostrum is almost always more tapering, the mesial margin of the antennular peduncle and the ventral and ventrolateral surfaces of the third maxilliped are strongly hirsute, the cephalic process of the first pleopod does not extend beyond midlength of the central projection which extends as far distally as the caudal element, and the latter is less tapering.

Ecological notes.—Even though all of the adult specimens belonging to this species that have been collected came from burrows, I am reluctant to state that it is a primary burrower, largely because of the simplicity of their domiciles which consist of a single subvertical, slightly sloping or loosely spiraling shaft that leads to a very slight enlargement at depths of 0.6 to 1.8 m. In most of the localities, the soil consisted of clay or sandy clay overlain by sand, occasionally by as much as 30 cm. Whereas no adults were found in open water, perhaps this reflects the habitats (burrows) selected by the collectors rather than the habitat distribution of the crayfish. More frequently than not, a broad, short areola, such as that possessed by this crayfish, is that of a dweller of well areated streams. The lack of a reduction in the abdomen also suggests that it frequents open water.

Some burrowing crayfishes can be enticed to the air-water interface in burrows (Hobbs, 1981:31), but not one of the specimens available could be lured from the fundus of its single shaft which lacked even one conspicuous chamber.

Etymology.—This crayfish is named in honor of my friend and colleague Brian F. Kensley whose assistance in collecting many of the crayfishes reported here was invaluable.

Table 3.—Measurements (mm) of *Procambarus* (*O.*) *nechesae.*

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	32.6	40.6	32.6
Postorbital length	25.5	20.9	24.7
Width	16.3	19.5	16.0
Height	16.0	19.0	15.1
Areola:			
Width	1.4	1.3	1.5
Length	10.4	12.9	9.6
Rostrum:			
Width	5.6	6.9	5.6
Length	8.0	11.3	8.9
Right chela:			
Length, palm mesial margin	11.4	8.0*	7.9*
Palm width	8.2	7.5*	6.3*
Length, lateral margin	31.8	24.0*	23.8*
Dactyl length	17.5	14.1*	13.7*
Abdomen:			
Width	13.7	17.3	13.0
Length	33.7	43.3	33.8

* Left chela.

Associates.—Co-existing with this crayfish in one or more localities were members of: *Cambarus* (*L.*) *diogenes, C.* (*L.*) *ludovicianus, Fallicambarus* (*C.*) *fodiens, Procambarus* (*G.*) *curdi, Faxonella beyeri, Procambarus* (*O.*) *acutus acutus* (Girard), and *P.* (*Pe.*) *dupratzi* Penn (1953).

Procambarus (*Ortmannicus*) *acutus acutus* (Girard)

Cambarus acutus Girard, 1852:91.
Procambarus (*Ortmannicus*) *acutus acutus.*—Hobbs, 1972:9.

New records.—Angelina Co.: 3.5 mi (5.6 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ II, 1 j♂, 14 Apr 1987, GBH & HHH. 4.2 mi (6.7 km) NW of US Hwy 59 on Farm Rd 2497, 1 ♂ I, 3 j♂, 2 j♀, 14 Apr 1987, GBH

& HHH. trib. Moccasin Creek at Farm Rd 2497, 4.9 mi (7.8 km) SE of St Rte 94, 1 ♂ II, 9 Nov 1987, BFK & HHH. 1.3 mi (2.1 km) W of Shawnee Creek on Farm Rd 1818, 3 j♂, 1 j♀, 11 Nov 1987, BFK & HHH. Jasper Co.: 8.7 mi (13.9 km) NW of US Hwy 190 on St Rte 63, 1 j♂, 17 Apr 1987, GBH & HHH. 9.2 mi (14.7 km) NW of US Hwy 190 on St Rte 63, 3 ♂ II, 2 ♀, 17 Apr 1987, GBH & HHH. Newton Co.: 6.3 mi (10.1 km) NW of Newton on US Hwy 190, 1 j♂, 2 j♀, 11 Nov 1987, BFK & HHH. Polk Co.: 7 mi (11.2 km) W of US Hwy 287 off Farm Rd 1745 (David Farm), 2 ♂ II, 4 j♂, 4 j♀, 12 Nov 1987, J. David, RA, BFK, & HHH. Trinity Co.: 4 mi (6.4 km) SW of Farm Rd 357 on Rd 2262, 1 j♂, 1 j♀, 14 Nov 1987, BFK & HHH.

Remarks.—The specimens cited here were taken from sluggish streams, roadside pools, and from burrows consisting of single, subvertical shafts.

Procambarus (*Ortmannicus*) *nechesae*, new species

Fig. 4, Table 3

Diagnosis.—Body pigmented, eyes well developed. Rostrum of adults with or without marginal spines but lacking median carina. Carapace with small cervical spine or tubercle. Areola 7.3 to 10.9 (mean 8.8 ± 1.20) times as long as wide and constituting 29.1 to 32.4 (mean 30.9 ± 1.03) percent of total length of carapace (38.0 to 42.3, mean 40.8 ± 1.20 percent of postorbital length). Suborbital angle very weak and obtuse; postorbital ridges with cephalic spine or tubercle sometimes abraded; hepatic area weakly tuberculate; branchiostegal spine small to vestigial. Antennal scale little more than twice as long as broad, widest at about midlength. Ischia of third and fourth pereiopods with simple hooks, hooks of third distinctly overreaching basioischial articulation and lacking opposing tubercle on basis, that of fourth almost reaching articulation and opposed by strong tubercle on basis; coxa of fourth pereiopod with strong caudomesial boss, that of fifth much smaller and flattened. First pleopod of first form male reaching coxa of third pereiopod, asymmetrical, provided distolaterally with rounded prominence (caudal knob) bearing conspicuous tuft of subapical setae; terminal elements consisting of (1) mesial process tapering from base to acute tip, directed caudolaterally and extending distally to about tip of caudal process; (2) acute cephalic process directed caudally, hooding (3) beaklike central projection which also directed caudally; and (4) caudal process, arising from caudolateral extremity of shaft, bladelike with acute tip and directed caudodistally. Annulus ventralis about twice as broad as long, with nearly straight caudal margin and strongly arched cephalically; sinuous sinus arising near cephalic margin, progressing caudosinistrally in cephalic third of annulus before turning caudally and finally caudodextrally ending on prominent protruding submedian tongue-like prominence. Sternum immediately anterior to annulus with low tubercles flanking median line. Unadorned postannular sclerite subtriangular, almost two-thirds as broad as annulus. First pleopod present in female.

Holotypic male, form I.—Cephalothorax (Fig. 4a, k) subcylindrical in section. Abdomen narrower than thorax (16.7 and 20.5 mm). Greatest width of carapace slightly greater than height at caudodorsal margin of cervical groove. Areola 8.3 times longer than wide with 1 or 2 punctations in narrowest part. Cephalic section of carapace about 2.1 times as long as areola, length of latter 31.9% of entire length of carapace (40.8% of postorbital carapace length). Surface of carapace punctate dorsally, granulate laterally. Rostrum slightly deflected ventrally with slender converging margins, its acute apex reaching slightly beyond midlength of penultimate podomere of antennular peduncle; margins neither thickened nor provided with spines or tubercles, faintly contracted at base of short acumen; dorsal surface concave with many fine setiferous

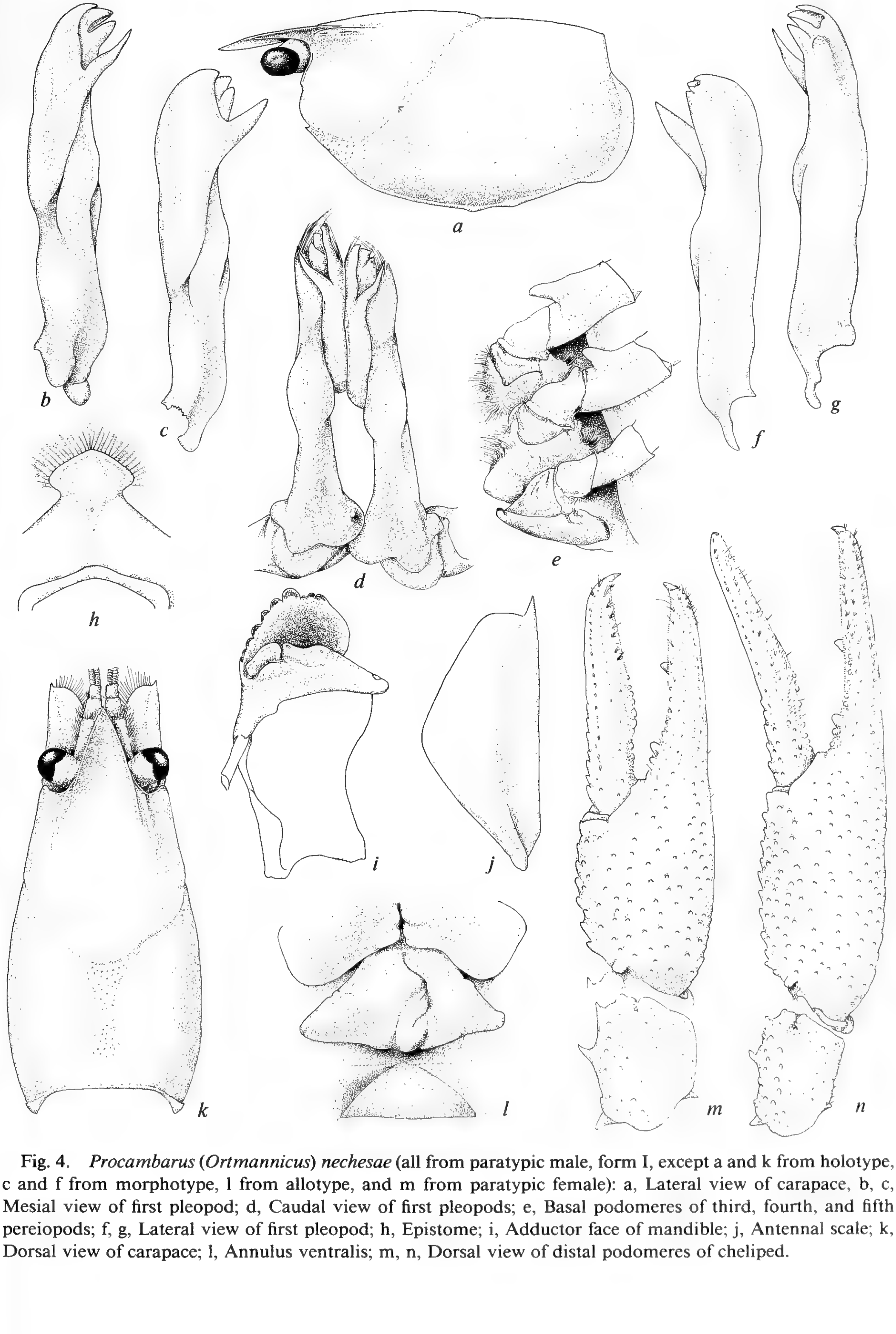


Fig. 4. *Procambarus* (*Ortmannicus*) *nechesae* (all from paratypic male, form I, except a and k from holotype, c and f from morphotype, l from allotype, and m from paratypic female): a, Lateral view of carapace, b, c, Mesial view of first pleopod; d, Caudal view of first pleopods; e, Basal podomeres of third, fourth, and fifth pereiopods; f, g, Lateral view of first pleopod; h, Epistome; i, Adductor face of mandible; j, Antennal scale; k, Dorsal view of carapace; l, Annulus ventralis; m, n, Dorsal view of distal podomeres of cheliped.

punctations. Subrostral ridge evident in dorsal aspect for only short distance anterior to caudal margin of orbit. Postorbital ridge well developed, grooved dorsolaterally and bearing small tubercle at cephalic extremity. Suborbital angle very small and obtuse. Branchiostegal spine also small. Cervical spine represented by small tubercle.

Abdomen and carapace subequal in length. Pleura of third through fifth segments very broadly rounded, almost truncate ventrally but lacking posteroventral angles. Cephalic section of telson with 2 spines in each caudolateral corner, lateral ones immovable; caudal margin of caudal section with shallow median excavation. Cephalic lobe of epistome (like Fig. 4h) broadly triangular with slightly elevated cephalolateral margins heavily fringed with plumose setae, central area convex; distinct anteromedian fovea present on main body. Ventral surface of proximal podomere of antennular peduncle with spine at midlength. Antenna with comparatively weak spiniform tubercles on basis and ischium; flagellum extending almost to end of telson. Antennal scale (like Fig. 4j) almost 2.5 times as long as broad, widest at about midlength; greatest width of lamella about 1.8 times width of thickened lateral part.

Mandible (like Fig. 4i) as illustrated. Third maxilliped extending cephalically to base of penultimate podomere of antennule; ischium not produced distolaterally, its ventral surface studded with plumose setae.

Right chela (like Fig. 4n) subovate in cross section, not strongly depressed. Mesial surface of palm with row of 8 tubercles subtended by additional rows of more squamous ones dorsally and ventrally; tubercles present over all except ventrolateral part of palm and also present on basal parts of both fingers. Both fingers with low, rounded longitudinal ridges dorsally and ventrally, all poorly defined except for being flanked by rows of setiferous punctations. Opposable margin of fixed finger with dorsal row of 9 (10 on left) tubercles, third from base largest, on proximal half of finger, and ventral row of 6, fifth much larger than others, in middle third of finger; lateral margin with row of setiferous punctations. Opposable margin of dactyl with dorsal row of 11 tubercles in proximal half and ventral row of 13 (8 and 18, respectively, on left); mesial margin with row of 5 (7 on left) tubercles proximally followed by row of setiferous punctations. Mesial surface of dactyl with subserrate row of tubercles along proximal two-fifths. Carpus of cheliped longer than broad with distinct oblique furrow dorsally, tuberculate mesially and dorsomesially; mesial surface with 3 tubercles somewhat larger than others: 1 proximally, 1 near midlength, and another distally; ventral surface with usual 2 tubercles on distal margin, otherwise setiferous.

Merus tuberculate dorsally, distomesially, and ventrally; 1 premarginal tubercle larger than others on dorsodistal surface; ventral surface with mesial row of 16 tubercles and lateral one of 11, 3 forming oblique distal row joining lateral and mesial rows. Ischium with ventromesial row of 3 tubercles.

Hooks on ischia of third and fourth pereiopods (like Fig. 4e) simple, that on third overreaching basioischial articulation, that on fourth not overreaching articulation but opposed by prominent tubercle on corresponding basis. Coxa of fourth pereiopod with prominent, subvertically oriented caudomesial boss; that of fifth with smaller one strongly compressed in longitudinal plane of body. Sternum between third, fourth, and fifth pereiopods comparatively deep with mat of plumose setae extending mesially from ventrolateral margins.

First pleopods (like Fig. 4b, d, g) as described in "Diagnosis." Uropod with both lobes of basal podomere bearing small acute spine; both rami with distolateral spines, and distomedian spine on mesial ramus situated distinctly proximal to subtruncate distal margin.

Allotypic female.—Differing from holotype, except in secondary sexual characters, as follows: apex of rostrum almost reaching distal extremity of antennular peduncle; small corneous marginal spines flanking base of short, narrow acumen; suborbital angle almost obsolete; left cervical spine very small but with sharp apex; abdomen slightly longer than carapace; chelipeds perhaps regenerated but similar to chela of paratypic female (like Fig. 4m); comparatively few plumose setae on third maxilliped; mesial surface of palm with row of 6 tubercles subtended by dorsal one of 6 and ventral one of 3; opposable margin of fixed finger with single row of 9 tubercles, third from base largest, on proximal half of finger with larger more ventrally located one almost at midlength; single row of minute denticles extending between tubercles and continuing to base of corneous tip of finger; opposable margin of dactyl with row of 13 tubercles, sixth from base largest, in proximal half (left with 12, fourth from base largest), minute denticles as on fixed finger; tubercles on mesial surface of dactyl weaker than those in holotype; merus with 2 premarginal tubercles larger than others on dorsodistal surface, ventral surface with mesial row of 12 tubercles and lateral one of 11, oblique row inseparable from lateral; ischium with mesial row of 4 (2 very small) tubercles. (See Table 3 for measurements.)

Annulus ventralis (Fig. 41) as described in "Diagnosis."

Morphotypic male, form II.—Differing from holotype in following respects: rostral margins bearing minute tubercles at base of slender, short acumen, latter reaching ultimate podomere of antennular peduncle; abdominal pleura with posteroventral extremities (especially of sixth segment) angular; flagella of antennae broken; third maxilliped, probably regenerated at least in part, reaching midlength of proximal podomere of antennular peduncle, comparatively few plumose setae present; mesial surface of palm of chelae with mesialmost row of 6 tubercles, 6 in that on dorsal flank, and 4 in that on ventral flank; fixed finger of right chela with row of 10 tubercles (13 on left), third from base largest; opposable margin of dactyl with upper row of 19 (15 on left) and lower row of 8 (9 on left); mesial surface of carpus of cheliped with additional tubercle between proximalmost and that near midlength; ventral surface of merus with mesial row of 14 tubercles and lateral one of 15 (left with 12 and 14 respectively); ischium with only 2 tubercles marking mesial row in holotype. Hooks on ischia of third and fourth pereiopods and bosses on fourth and fifth much reduced.

First pleopods (Fig. 4c, f) with all terminal elements positioned as in holotype; mesial process comparatively much heavier, remaining ones smaller and not nearly so clearly differentiated as in holotype; subapical setae and shoulder much less prominent. Juvenile oblique suture clearly defined on shaft.

Type locality.—Semi-permanent pool in roadside ditch on Farm Road 2497, 1.2 mi (1.9 km) SE of intersection with State Route 94, southwest of Lufkin, Angelina County, Texas. The pool of grayish cloudy water, some 3 by 13 and no more than one-half m in depth, was excavated in a sandy clay soil and is situated adjacent to a wooded area in which *Pinus* and *Quercus* are the dominant plants; grasses and a few sedges are present in the open ditch adjacent to the pool. Both on 13 Apr and 9 Nov 1987, two other crayfishes, *Procambarus* (*Girardiella*) *curdi* and *Fallicambarus* (*Creaserinus*) *hedgpethi* shared the pool with *P.* (*O.*) *nechesae.*

Disposition of types.—The holotype, allotype, and morphotype (♂ I, ♀, ♂ II) are deposited in the National Museum of Natural History (Smithsonian Institution), numbers 219733, 219735, and 219734, respectively, as are the paratypes consisting of 2 ♂ I, 9 ♂ II, 8 ♀, 6 j♂, and 10 j♀.

Size.—The largest specimen available is a first form male having a carapace length of 40.8 mm (postorbital carapace length 31.2 mm); the smallest has corresponding lengths of 30.8 and 24.2 mm. Length of females carrying eggs or young are not available because of lack of such specimens.

Range and specimens examined.—This crayfish has been found at the following localities in the Neches River basin of Angelina and Trinity counties, Texas. Angelina County: (1) Type locality, 1 ♂ I, 1 ♂ II, 1 ♀, 15 Apr 1987, GBH & HHH; 1 ♂ II, 9 Nov 1987, BFK & HHH. (2) Burrows in flooded roadside ditch in southeastern Lufkin, 1 ♂ I, 1 ♀, 13 Apr 1987, Mike Whiteman & HHH. (3) Drainage ditch and pool at Angelina County Airport, about 5 mi (8.0 km) S of Lufkin, 1 ♂ I, 4 ♂ II, 4 ♀, 6 j♂, 10 j♀, 13 Apr 1987, Harold Brockman, MW, & HHH. (4) Roadside pool at junction of Farm Road and road into airport, about 3.5 mi (5.6 km) S of Lufkin, 13 Apr 1987, MW & HHH; 1 ♂ II, 1 ♀ 10 Nov 1987, BFK & HHH. Trinity County: (5) Caney Creek, 12 mi (19.2 km) NE of Trinity on St Rte 94, 1 ♂ II, 16 Apr 1987, BFK & HHH.

Variations.—Perhaps the most conspicuous of the variations noted is in the rostrum, which in some of the juvenile specimens is not so strongly contracted anteriorly and bears prominent marginal spines; in most of the specimens there is at least a trace of these spines, but in a few of the larger individuals there is hardly an indentation along the gently contracting margins. In most specimens the antennal scale is broadest at about midlength, but occasionally the greatest width is clearly more proximal, and as for the length, the apices reach to or beyond the tip of the acumen. Cervical spines, like the marginal spines on the rostrum, may be strong in juveniles, but may be reduced to tubercles or even become, at most, rudimentary in the adults. The epistome is usually little different from that illustrated for a paratype in Fig. 4h, but in the small male from locality 5 its shape approaches that of an isosceles triangle. The ventrolateral surface of the ischium of the third maxilliped may be almost hidden by the dense mat of plumose setae borne on it, or the setae may be comparatively small, sparse, or so inconspicuous that the podomere appears almost naked. The telson bears 2 to 4 spines in the caudolateral corner of the cephalic segment. Variations in the secondary sexual characters are almost all so slight that they are not noteworthy, but the proximomesial angle of the first pleopod of the male does show a conspicuous variation which in some is produced into a conical prominence (as in right member of Fig. 4d) that is reminiscent of, if not homologous to, the proximomesial spur typical of several species groups, but not of most members of *Ortmannicus.*

Relationships.—*Procambarus* (*O.*) *nechesae* has its closest relationships with *Procambarus* (*O.*) *geminus* Hobbs (1975), *P.* (*O.*) *lecontei* (Hagen, 1870), and *P.* (*O.*) *texanus* Hobbs (1971). This is most clearly revealed in the short, caudally bent terminal elements of the first pleopod of first form males and in the configuration of the annulus ventralis. *Procambarus* (*O.*) *nechesae* resembles *P.* (*O.*) *geminus* more closely than it does the other two, but it may be distinguished from this crayfish and *P.* (*O.*) *lecontei* by the less strongly reflexed (40 to 50 degrees instead of 80 to 90 degrees) terminal elements of the first pleopod of the male, by the strong tubercle on the basis of the fourth pereiopod which opposes the hook on the corresponding ischium, and usually by the more strongly tapered margins of the rostrum. (Some of the females of *P.* (*O.*) *nechesae* and *P.* (*O.*) *geminus* are virtually impossible to distinguish.) The new crayfish differs from *P.* (*O.*) *texanus* in several striking respects: the areola is usually broader (7.3 to 10.9, avg. 8.8, as opposed to 8.5 to 16.4, avg. 12.8, times longer than broad); the first pleopods of the male are strongly asymmetrically situated with their proximomesial extremities overlapping as opposed to being almost symmetrically disposed; there is a strong tubercle on the basis of the fourth pereiopod that opposes the hook on the corresponding ischium in *P.*

nechesae that is lacking in *P. texanus*; the sternum in the female of the former is much more weakly tuberculate than that of the latter, and the tongue-like prominence, so conspicuous on the caudomesial part of the annulus ventralis of *P. nechesae,* is represented at most by a rudiment in *P. texanus.* These three species constitute a closely allied group and may well represent geographic races of a single species. Until their ranges are more clearly determined and evidence of gene exchange between them is found, assigning them specific rank seems preferable to me.

Ecological notes.—All of the known members of this species, except the single small male collected in Caney Creek (locality 5), were collected from burrows consisting of a single subvertical shaft or from temporary or semi-permanent pools in roadside ditches. Caney Creek, flowing over a bed-rock bottom, is a clear stream 3 to 10 m wide and with depths exceeding 1 m. The single specimen, the only crayfish obtained at that locality, was found under a rock adjacent to the shore. It seems likely to me that it had wandered or perhaps was washed into this unlikely habitat during a period of high water.

Etymology.—The name is derived from the Neches drainage basin, the only watershed in which it has been collected.

Crayfish associates.—Taken from the same pool, or dug from burrows adjacent to those occupied by *P.* (*O.*) *nechesae* were members of the following species: *Fallicambarus* (*F.*) *devastator, F.* (*Creaserinus*) *fodiens, Procambarus* (*Scapulicambarus*) *clarkii, P.* (*Girardiella*) *curdi,* and *P.* (*G.*) *nigrocinctus.*

Procambarus (*Pennides*) *dupratzi* Penn

Procambarus dupratzi Penn, 1953:1.
Procambarus (*Pennides*) *dupratzi.*—Hobbs, 1972:10.

New records.—Jasper Co.: Small creek 0.3 mi (0.5 km) E of St Rte 63, 16 mi (25.6 km) N of jct with US Hwy 90, 1 ♂ I, 1 ♂ II, 3 j♂, 4 j♀, 17 Apr 1987, GBH & HHH. Polk Co.: Menard Creek 16 mi (25.6 km) W of Tyler Co line on US Hwy 190, 2 ♂ II, 1 ♀, 10 j♂, 9 j♀, 12 Nov 1987, BFK & HHH. Tyler Co.: Russell Creek at US Hwy 287, 7 ♂ II, 5 ♀, 8 j♂, 3 j♀, 12 Nov 1987, BFK & HHH.

Remarks.—The specimens cited here were taken from lotic habitats in which the water was translucent but coffee-colored.

Procambarus (*Scapulicambarus*) *clarkii* (Girard)

Cambarus Clarkii Girard, 1852:91.
Procambarus (*Scapulicambarus*) *clarkii.*—Hobbs, 1972:12.

New records.—Angelina Co.: SE part of Lufkin, 2 ♂ I, 1 ♀, 13 Apr 1987, MW & HHH. Trib to Moccasin Creek at Farm Rd 2497, 1 ♀, 4 j♂, 3 j♀, 4.9 mi (7.8 km) SE of St Rte 96, 9 Nov 1987, BFK & HHH. Polk Co.: Menard Creek on US Hwy 190, 16 mi (25.6 km) W of Tyler Co line, 1 j♀, 13 Nov 1987, BFK & HHH. Creek 5 mi (8 km) W of Livingston on US Hwy 190, 1 j♂, 13 Nov 1987, BFK & HHH. Trinity Co.: 4.0 mi (6.4 km) SW of Farm Rd 357 on Rd 2262, 1 ♀, 1 j♂, 1 j♀, 16 Nov 1987, BFK & HHH.

Remarks.—Except for the adult specimens from the first locality listed, which were dug from shallow, flooded, burrows, all were found either in creeks or in a roadside pool.

Acknowledgments

Thanks are extended to the following persons for their assistance in collecting the specimens on which this report is based: Bob Armentrout, Extension Agent for Tyler County, Texas; Hal Brockman of the Soil Conservation Service in Lufkin, Texas; my wife, Georgia B. Hobbs; Brian F. Kensley of the National Museum of Natural History; and Mike Whiteman, Extension Agent for Angelina County, Texas. For their criticisms of the manuscript I am indebted to J. F. Fitzpatrick, Jr., University of South Alabama, H. H. Hobbs III, Wittenberg University; and Brian F. Kensley.

Literature Cited

Albaugh, Douglas W. 1973. Life histories of the crayfishes *Procambarus acutus* and *Procambarus hinei* in Texas. Unpublished Ph.D. dissertation, Texas A&M University, xiii + 135 pp.

———. 1975. A new crawfish of the genus *Procambarus,* subgenus *Capillicambarus,* from Texas, with notes on the distribution of the subgenus.—Tulane Studies in Zoology and Botany 19(1 & 2):1–7.

———, & Joe B. Black. 1973. A new crawfish of the genus *Cambarellus* from Texas, with new Texas distributional records for the Genus (Decapoda, Astacidae).—Southwestern Naturalist 18(2):177–185.

Conner, John V. & Royal D. Suttkus. 1986. Zoogeography of freshwater fishes of the western Gulf Slope of North America. Chapter 12. Pp. 413–456 *in* Charles H. Hocutt and E. O. Wiley, eds., The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Cottle, T. J. 1863. Two species of *Astacus* found in upper Canada.—Canadian Journal of Industry, Science, and Arts (n.s.) 45:216–219.

Creaser, Edwin P. 1962. Notes on homologies and genetic relationships in the Cambarinae crayfishes. 7 pp. [Privately printed].

Faxon, Walter. 1884. Descriptions of new species of *Cambarus,* to which is added a synonymical list of the known species of *Cambarus* and *Astacus.*—Proceedings of the American Academy of Arts and Sciences 20:107–158.

———. 1898. Observations on the Astacidae in the United States National Museum and in the Museum of Comparative Zoology, with descriptions of new species.—Proceedings of the United States National Museum 20(1136):643–694.

Fitzpatrick, J. F., Jr. 1983. A revision of the dwarf crawfishes (Cambaridae, Cambarellinae).—Journal of Crustacean Biology 3(2):266–277.

Girard, Charles. 1852. A revision of the North American Astaci, with observations on their habits and geograpical distribution.—Proceedings of the Academy of Natural Sciences of Philadelphia 6:87–91.

Hagen, Herman A. 1870. Monograph of the North American Astacidae.—Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College 3:viii + 109 pp.

Hobbs, Horton H., Jr. 1945. Two new species of crayfishes of the genus *Cambarellus* from the Gulf coastal states, with a key to the species of the genus (Decapoda, Astacidae).—American Midland Naturalist 34(2):466–474.

———. 1948. A new crayfish of the genus *Cambarus* from Texas, with notes on the distribution of *Cambarus fodiens* (Cottle).—Proceedings of the United States National Museum 98(3230):223–231.

———. 1969. On the distribution and phylogeny of the crayfish genus *Cambarus. In* Perry C. Holt, Richard L. Hoffman, and C. Willard Hart, Jr., eds., The distributional history of the biota of the Southern Appalachians, Part I: Invertebrates.—Virginia Polytechnic Institute, Research Division Monograph 1:93–178.

———. 1971. New crayfishes of the genus *Procambarus* from Alabama and Texas (Decapoda: Astacidae).—Proceedings of the Biological Society of Washington 84(11):81–94.

———. 1972. The subgenera of the crayfish genus *Procambarus* (Decapoda: Astacidae).—Smithsonian Contributions to Zoology 117:1–22.

———. 1973. New species and relationships of the members of the genus *Fallicambarus.*—Proceedings of the Biological Society of Washington 86(40):461–481.

———. 1975. New crayfishes (Decapoda: Cambaridae) from the southern United States and Mexico.—Smithsonian Contributions to Zoology 201:1–34.

———. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 318:viii + 549 pp.

———. 1990. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae).—Smithsonian Contributions to Zoology 480:iii + 236 pp.

———, & Henry W. Robison. 1982. A new crayfish of the genus *Procambarus* from southwestern Arkansas.—Proceedings of the Biological Society of Washington 95(3):545–553.

———, & ———. 1989. On the crayfish genus *Fallicambarus* (Decapoda: Cambaridae) in Arkansas, with notes on the *fodiens* complex and descriptions of two new species.—Proceedings of the Biological Society of Washington 102(3):651–697.

———, & Mike Whiteman. 1987. A new, economically important crayfish (Decapoda: Cambaridae) from the Neches River Basin, Texas, with a key to the subgenus *Fallicambarus.*—Proceedings of the Biological Society of Washington 100(2):403–411.

———, & ———. 1990. Notes on the burrows, behavior, and color of the crayfish *Fallicambarus (F.) devastator* (Decapoda: Cambaridae).—Southwestern Naturalist (in press).

Penn, George H., Jr. 1950. A new crawfish of the genus *Orconectes* from Louisiana (Decapoda: Astacidae).—Journal of the Washington Academy of Sciences 40(5):166–169.

———. 1953. Two new crawfishes of the genus *Procambarus* from Texas, Louisiana, and Arkansas

(Decapoda, Astacidae).—American Museum Novitates 1636:1–10.

———. 1962. A new crawfish of the *Hinei* Section of the genus *Procambarus* (Decapoda, Astacidae).—Crustaceana 3(3):222–226.

Penn, George H., Jr., & Horton H. Hobbs, Jr. 1958. A contribution toward a knowledge of the crayfishes of Texas (Decapoda, Astacidae).—Texas Journal of Science 10(4):452–483.

Reimer, Rollin D. 1969. A taxonomic study of the Gracilis Section of the Genus *Procambarus.* Unpublished Ph.D. Dissertation, Tulane University, New Orleans, Louisiana, 190 pp.

———. 1975. *Procambarus* (*Girardiella*) *curdi,* a new crawfish from Arkansas, Oklahoma, and Texas (Decapoda, Astacidae).—Tulane Studies in Zoology and Botany 19(1, 2):22–25.

———, & William J. Clark. 1974. Decapod crustaceans of the Navasota River system in central Texas.—Southwestern Naturalist 19(2):167–178.

Department of Invertebrate Zoology National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 598–601

PANOPEUS MARGENTUS, A NEW CRAB FROM THE ARGENTINE WARM TEMPERATE SUBREGION (DECAPODA: XANTHIDAE)

Austin B. Williams and E. E. Boschi

Abstract.—*Panopeus margentus* new species, a xanthid crab from warm, temperate, marine Argentine waters is described, illustrated, and compared with the recently described *Panopeus mirafloresensis* from the Pacific side of the Panama Canal. The first male pleopods and carapace of these species are similar and resemble these features in *P. bermudensis.* Notes on associated xanthids are given.

An unidentified Argentine species of crab belonging to the brachyuran family Xanthidae (family Panopeidae Ortmann, 1893, sensu Guinot 1978, and subfamily Panopeinae Ortmann, 1893, sensu Martin & Abele 1986) has been known to the junior author for a number of years. Boschi (1964) described and illustrated brachyurans from Argentine marine waters, including xanthid species belonging to the genera *Platyxanthus, Pilumnoides,* and *Pilumnus,* and he (1979) added *Panopeus* sp. from the warm temperate region of Buenos Aires and northern Patagonia to this array in an annotated checklist of decapods from the region. Williams (1984) treated species of the *Panopeus "herbstii* complex," which has representatives in Brazil and Uruguay, but at that time were not known from Argentina. Description of the species listed by Boschi (1979) as *Panopeus* sp. is the central subject of this paper.

Type materials are deposited in the crustacean collection of the United States National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.

Panopeus margentus, new species
Fig. 1a–e

Material.—Argentina: USNM 239191. Holotype ♂ (damaged carapace and right chela), Escollera Norte, Mar del Plata, Province of Buenos Aires, E. Boschi, 18 Jan. 1964.—239192, Paratypes, 7 ♂, 15 ♀ ovig., same.—239193. Paratypes, 1 ♂, 1 ♀ ovig., Escollera Norte, Mar del Plata Puerto, Risso, Jan. 1964.—239194, Allotype ♀ ovig., Mar del Plata, E. Boschi, 18 Jan. 1964.—239195, Paratypes, 3 ♂, 4 ♀ ovig., same. Specimens in all of these collections are very brittle, and legs are detached from most of them.

Description.—Carapace (Fig. 1a) wider than long, surface smooth, regions faintly indicated, margins finely granular; few lightly granular transverse lines, sinuous epibranchial line more or less evident, less evident arcuate line leading toward but not continued on 4th anterolateral tooth, faint oblique lines on mesogastric lobes still less evident. Faint shallow and sinuously transverse depression near posterior ⅓ passing between meso- and metabranchial, mesogastric and cardiac regions, another faint depression curving posteromesially from juncture of 3rd and 4th anterolateral teeth, and still another similar groove coursing from between 4th and 5th anterolateral teeth to join transverse groove; slight submarginal swelling on metabranchial region near coxa of 5th leg. Front with V-shaped median notch, each transverse half shallowly concave; orbital regions broad, moderately raised and cut by 2 nearly equal fissures; coalesced 1st and 2nd anterolateral teeth separated by well defined but variable notch (progressively developed with increasing age); 1st tooth narrower than 2nd and exceeding it, posterior slope straight to slightly concave; 2nd tooth bluntly triangular, posterior margin arcuate; 3rd and 4th teeth broader, each with anterior margin shorter than posterior, tip rounded, rectilinear, or occasionally subacuminate; 5th tooth much smaller, acute or rounded (sometimes on either side of same specimen) and directed laterally; posterodorsal margin slightly and unevenly granular.

Abdomen of mature ♂ with segments 3 to 5 fused and narrowing distally, segment 6 free; telson narrowly subtriangular. Abdomen of mature ♀ ovate in outline, 6 segments free, 4th broadest, 6th longest in midline; telson broadly subtriangular.

Chelipeds (Fig. 1a–c) not markedly asymmetrical; microscopically granular except for smooth fingers, carpus unevenly granular and sometimes faintly rugose, with mesial lobelike tooth stout and rounded; hand with outer surface variably marked by broad shallow groove between dorsal crest and swollen palm, lower margin sinuous; curved dactyl of each chela longer and more slender than stout wedge shaped fixed finger, occlusive edge of each rather sharp; major dactyl with strong blunt basal tooth and 1 or more less prominent triangular teeth distal to it; triangular tooth on fixed finger, sometimes compound, closing against distal edge of basal tooth on dactyl, other smaller teeth variable; fingers of minor chela each with tooth row somewhat uneven, not strongly developed.

Male first pleopod (Fig. 1d–e) obscurely trilobed at tip; accessory process much reduced, not exceeding membranous collar nearly surrounding it, being perhaps a modification of median process, subterminal lateral tooth present; terminal tract of short spinules on lateral rim of collar, subterminal row of about 8 spinules on folded edge of shaft just proximal to collar, grading proximad from long to short, and scattered shorter spinules on shaft proximal to these.

Measurements in mm.—Holotype ♂, carapace length 7.7, width 10.6; Allotype ♀, same, 6.7, 9.5; Paratypes (239192), same, ♂ 7.7, 10.9, ♀ 8.2, 11.7.

Color.—Color of fingers extending onto distal part of palm, color boundary sharply defined but both fingers and palm faded in specimens available for study.

Known range.—Limited to the type locality.

Remarks.—The holotype and allotype, although damaged, are the most complete specimens in the material examined. The carapace of the holotype ♂ has been punctured in two places, the carpus of the major chela has been broken, and the minor chela has been detached from the body, but no essential features are lost through these damages. The allotype ♀ lacks the left fifth leg. The first pleopod of the holotype has the accessory process blunted at the tip, and spines on the membranous collar surrounding it are swollen, presumably because of poor preservation. Pleopods on ♂ paratypes show both the accessory process and features of the collar in a better state of preservation.

The first pleopods of *Panopeus margentus* bear some resemblance to those of *Panopeus mirafloresensis* Abele & Kim, 1989 from the Pacific side of the Panama Canal (see also Martin & Abele 1986: fig. 2A), as do features of the carapace. Otherwise, the species is comparable in these regards with *Panopeus bermudensis* Benedict & Rathbun, 1891 (see Martin & Abele 1986).

Associated with the material studied are three other xanthid species. *Panopeus meridionalis* Williams, 1984, is represented by 1 ♀, cl 9.7, cw 13.2 mm, a specimen with characters less definitely expressed than those of larger individuals of the species known previously only from the Montevideo region of Uruguay. *Pilumnoides hassleri* A. Milne Edwards, 1880 (see Guinot &

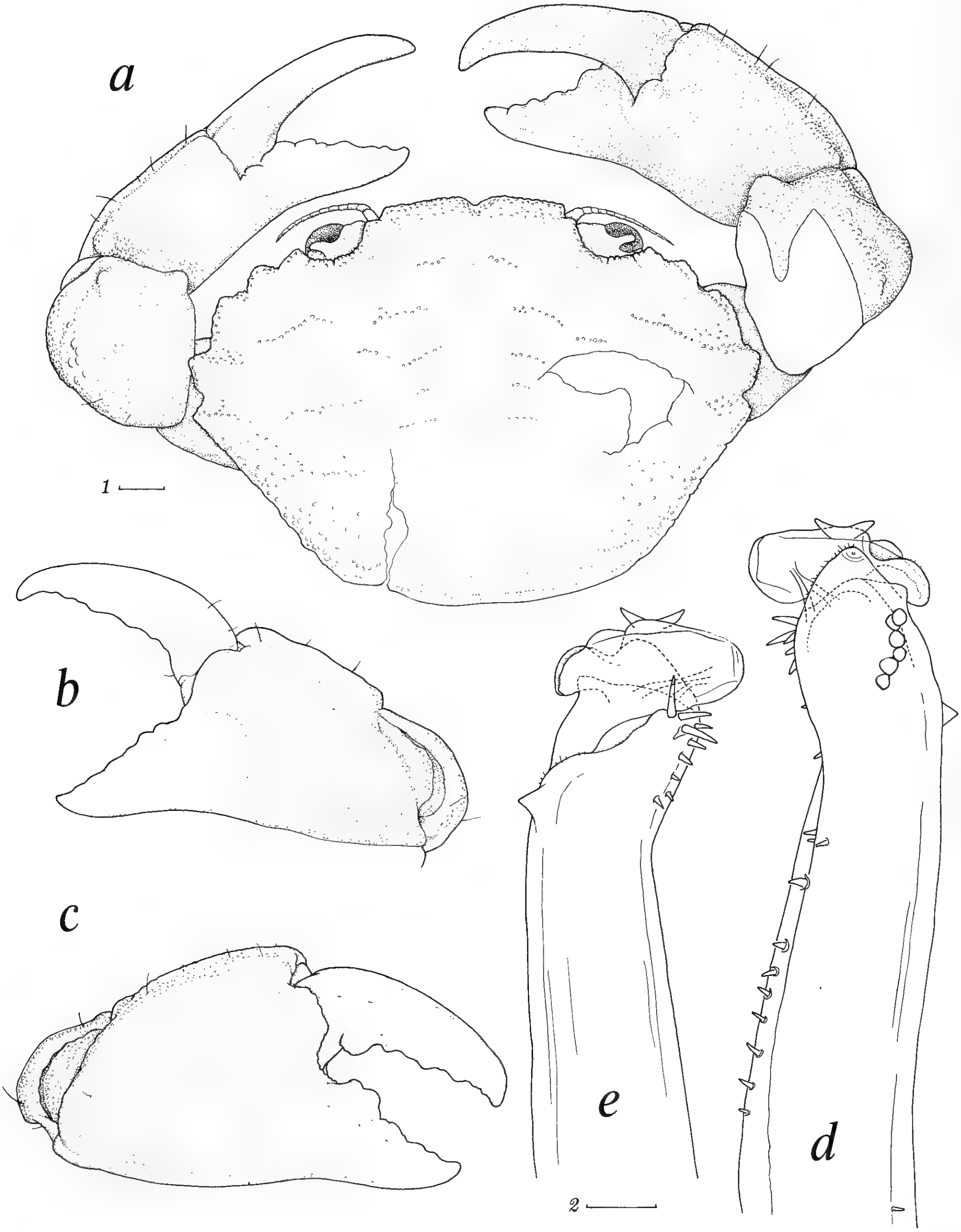


Fig. 1. *Panopeus margentus* new species, holotype ♂: *a,* dorsal view showing carapace and chelipeds, broken exoskeleton indicated; *b,* minor; and *c,* major chelae in frontal view; first pleopod, *d,* abdominal; and *e,* sternal views. Scales: 1 = 1 mm, 2 = 0.1 mm.

Macpherson 1987) is represented by 1 ♂, cl 9.7, cw 13.2 mm. *Pilumnus reticulatus* Stimpson, 1860 is represented by 1 fragmentary ♂, cl 5.9, cw 7.9 mm, which is seemingly closest to the variant *forma tessellata* discussed by Rathbun (1930) and Boschi (1964).

Etymology.—The specific name is a construct from the Latin equivalent of Mar del Plata, "mare," sea, and "argentum," silver, treated as a masculine noun.

Acknowledgments

The manuscript has been critically reviewed by F. A. Chace, Jr., R. B. Manning, and M. Vecchione. The illustrations were rendered by Keiko Hiratsuka Moore.

Literature Cited

Abele, L. G., & W. Kim. 1989. The decapod crustaceans of the Panama Canal.—Smithsonian Contributions to Zoology 482:1–50.

Boschi, E. E. 1964. Los crustaceos decapodos Brachyura del litoral bonaerense (R. Argentina).—Boletin del Instituto de Biologia Marina 6:1–76.

———. 1979. Geographic distribution of Argentinian marine decapod crustaceans. *In* A. B. Williams, ed., Symposium on the composition and evolution of crustaceans in the cold and temperate waters of the World Ocean.—Bulletin of the Biological Society of Washington 3:134–143.

Guinot, D. 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyoures.—Bulletin Biologique de la France et de la Belgique, n.s. 112(3):211–292.

———, & E. Macpherson. 1987. Révision du genre *Pilumnoides* Lucas, 1844, avec description de quatre espècies nouvelles et création de Pilumnoidinae subfam. nov. (Crustacea Decapoda Brachyura).—Bulletin du Muséum National d'Histoire Naturella, Paris, s. 4, 9 (sect. A, 1): 211–247.

Martin, J. W., & L. G. Abele. 1986. Notes on male pleopod morphology in the brachyuran crab family Panopeidae Ortmann, 1893, sensu Guinot (1978) (Decapoda).—Crustaceana 50(2):182–198.

Ortmann, A. 1893. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VII Theil. Abtheilung: Brachyura (Brachyura genuina Boas). II. Unterabteilung: Cancroidea, 2 Section: Cancrinea, 1. Gruppe: *Cyclometopa.*—Zoologische Jahrbücher. Abtheilung für Systematik, Geographie und Biologie der Thiere 7:411–495, pl. 17.

Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae.—United States National Museum Bulletin 152:i–xvi, 1–609, 230 pl.

Williams, A. B. 1984. The mud crab *Panopeus herbstii,* s.l. Partition into six species (Decapoda: Xanthidae).—Fishery Bulletin, U.S. 81(4, for 1983):863–882.

(ABW) National Marine Fisheries Service-NOAA Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (EEB) Instituto Nacional de Investigacion y Desarrollo Pesquero, Casilla de Correo 175, 7600 Mar del Plata, Argentina.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 602–607

A NEW SPECIES OF *CHACEON* FROM NEW ZEALAND (CRUSTACEA: DECAPODA: GERYONIDAE)

Raymond B. Manning, Elliot W. Dawson and W. Richard Webber

Abstract.—*Chaceon yaldwyni,* new species, is described from material collected off New Zealand in 1040–1045 and 1228–1276 m. It is the second species from the central Pacific characterized by laterally compressed dactyli on the walking legs. It differs from the other species known from the area, *Chaceon bicolor* Manning & Holthuis, 1989, by the slenderness of its legs in combination with characters of leg spinulation.

Among material of the commercially important crab genus *Chaceon* taken in New Zealand waters are two specimens, one from northeast of the Chatham Islands and the second from deeper water east of the North Island, that represent an undescribed species, characterized below. The holotype and paratype have been deposited in the National Museum of New Zealand (NMNZ).

Abbreviations used in the account below include cb for carapace width, including lateral spines, cl for carapace length on the midline, P5 for fifth pereopod, and FV for Fishering Vessel.

Chaceon yaldwyni, new species
Figs. 1–3

"second species."—Webber et al., 1990:10.

Material.—New Zealand: Northeast of Chatham Islands, 43°40.4′S, 174°09.6′W to 43°26.6′S, 174°05.5′W, 1040–1045 m, leg. Henry Kavale, FV *Oyang 86,* Sta. 33, 14 Apr 1988: 1 ♂, holotype (NMNZ Cr. 6048).—Off Portland Island, Mahia Peninsula, 39°51.9′S, 177°55.3′E to 39°48.9′S, 177°55.6′E, 1228–1276 m, leg. Alan Hart, FV *Willwatch,* Sta. WIL/163/89, 19 Oct 1989: 1 ♀, paratype (NMNZ Cr. 6468).

Diagnosis.—A moderately large *Chaceon,* cl to 105 mm, cb to 128 mm, with well-developed anterolateral teeth on the carapace in adults and with laterally compressed dactyli on the walking legs. Carapace 1.2–1.3 times broader than long, moderately inflated, distinctly convex from front to back, surface appearing smooth, pitted posterolaterally, not tuberculate. Median pair of frontal teeth short, rounded, separated by U-shaped emargination, medians extending further forward than laterals. Anterolateral teeth well-developed but not spiniform, second and fourth smaller than remainder. Distance from first to second tooth slightly less than distance from third to fourth tooth, distance from first to third less than distance from third to fifth. Suborbital tooth strong, visible in dorsal view, extending about to level of lateral frontal tooth; suborbital margin evenly curved, with some low, rounded tubercles. Cheliped: merus with sharp spine subdistally and with distal dorsal spine; carpus rough dorsally, with distal outer spine, denticulate anterior margin, and with strong, distinct inner spine; propodus roughened on dorsal and outer surfaces, with trace of distal dorsal spine on larger chela. Meri of posterior 3 walking legs with distal dorsal spine. Dactyli of walking legs laterally compressed, height at midlength greater than width. P5: merus 5.11–5.25 times longer than high and 0.5–0.6 times cb, with distal dorsal spine; carpus with erect spinules dorsally; propodus distinctly longer than dactylus, 4.9 times longer than high.

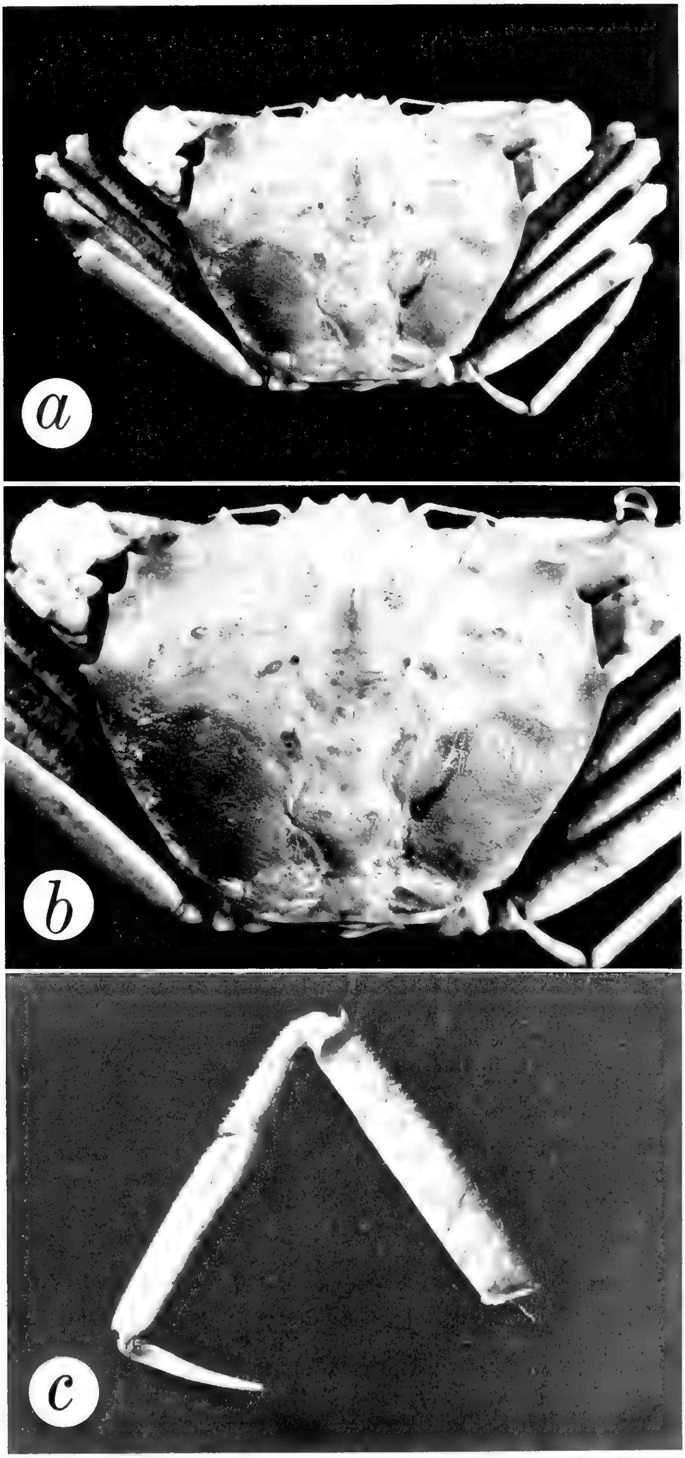


Fig. 1. *Chaceon yaldwyni,* male holotype, cb 128 mm: *a,* dorsal view; *b,* carapace; *c,* P5.

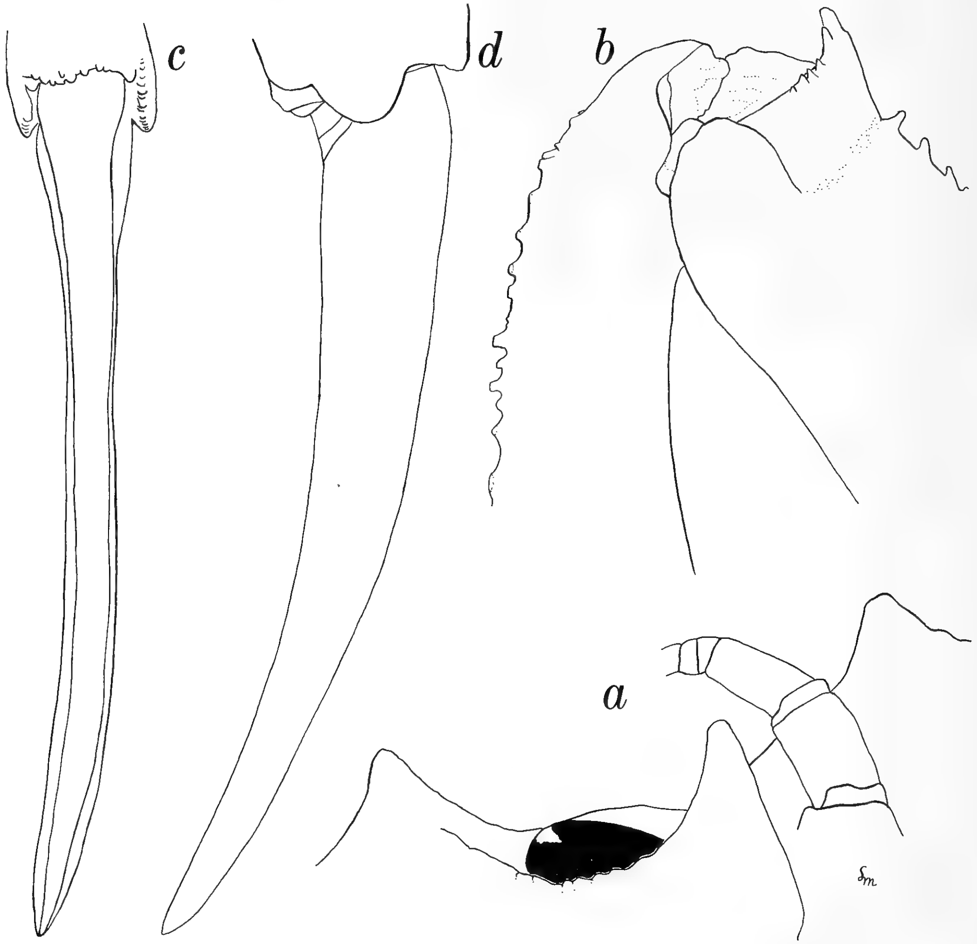


Fig. 2. *Chaceon yaldwyni,* male holotype, cb 128 mm: *a,* ventral view of orbit; *b,* merocarpal articulation of P5; *c,* dactylus of P5, dorsal view; *d,* dactylus of P5, posterior view.

Size.—Male holotype, cl 105 mm, cb 128 mm; female paratype, cl 72 mm, cb 92 mm.

Color.—The carapace of both specimens, when fresh, was a fairly uniform yellowish-red, in contrast to *C. bicolor,* in which, despite its name, the color ranges from a uniform tan to varying shades of purple forming a distinctive pattern on the carapace (see color figures of *C. bicolor* in Sakai (1978:pl. 2, fig. D).

Remarks.—Manning & Holthuis (1989: 75) listed five species of *Chaceon* known from the Indo-West Pacific region, two from the Pacific Ocean, three from the Indian Ocean. Three of these species resemble *C. yaldwyni* in having laterally compressed dactyli on the walking legs: *C. bicolor* Manning & Holthuis (1989) from the central and southwestern Pacific, *C. crosnieri* Manning & Holthuis (1989) from Madagascar, and *C. paulensis* (Chun) (1903) from Amsterdam Island, southern Indian Ocean.

Chaceon yaldwyni resembles both *C. crosnieri* and *C. paulensis* in having distinct meral spines on the walking legs. It further resembles *C. crosnieri* in having the carapace, especially the protogastric regions, distinctly inflated, so that the carapace is arched in lateral view; the carapace is much more inflated dorsally in *C. crosnieri* than in *C. yaldwyni.*

Chaceon yaldwyni differs from *C. crosnieri* in having more strongly developed anterolateral spines on the carapace and longer walking legs, with a line of erect spinules on the carpus.

This new species differs from *C. paulensis* in having the carapace much more inflated and in having much shorter anterolateral spines on the carapace. In *C. paulensis* the second and fourth anterolateral spines are well developed in adults, whereas in *C. yaldwyni* they are reduced in relation to the other anterolateral spines.

In the New Zealand region, *C. bicolor* is the more commonly found species of *Chaceon.* It is known from east and northeast of the North Island (Webber et al. 1990), whereas *C. yaldwyni* is only known at present from two areas, in one of which *C. bicolor* also occurs, although at shallower depths. *Chaceon yaldwyni* differs from *C. bicolor* principally in having quite strikingly slender legs in relation to body size and with strong carapace spines (although such spines have their counterparts in some specimens of *C. bicolor,* also, particularly in very young specimens tentatively identified with *C. bicolor*). Measurements of the proportions of the propodus of the walking legs give an index of this slenderness which can serve as a basis of comparison of the two species of *Chaceon* known from New Zealand waters.

A linear regression analysis of the length/height ratio of the propodus of P5 on carapace length for a total sample of 25 specimens of *Chaceon* available to us gave a low positive correlation coefficient (*r*) of 0.174. In contrast, omitting the two specimens of *C. yaldwyni* with the distinctly higher length/height ratios, the analysis yielded a high positive correlation coefficient of 0.775 (Fig. 3). The analysis includes all adult specimens previously determined as *C. bicolor.*

A comparison of the means of the P5 length/height ratios gave a *t* value of 3.879. For 23 degrees of freedom, the probability of obtaining a value of *t* greater than 2.807 is 0.01. Hence, the difference between the means is judged to be significant at the 1% level. In other words, the observed difference in propodus slenderness reflects, 99% of the time, a real difference between *C. bicolor* (*n* = 23) and *C. yaldwyni* (*n* = 2) so far as statistical discrimination based on the small sample sizes allows.

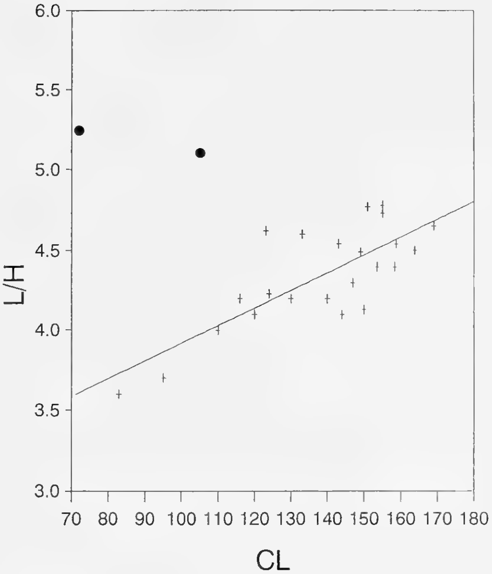


Fig. 3. Length/height ratio (L/H) of propodus of fifth leg (P5) in relation to carapace length (CL) in *Chaceon bicolor* (+) and *C. yaldwyni* (●); regression line applies to *C. bicolor* only.

Chaceon yaldwyni also appears to differ from *C. bicolor* in having much more strongly developed anterolateral spines on the carapace, a longer, sharper suborbital tooth, and in having distinct distal dorsal spines on the meri of the walking legs in the adult. Meral spines are present in juveniles from New Caledonia identified with *C. bicolor* by Manning & Holthuis (1989); these juveniles, however, might well belong to *C. yaldwyni* or even another species rather than to *C. bicolor,* as they were not taken together with *C. bicolor* but in deeper water near areas where *C. bicolor* was collected. However, *C. bicolor* shows variability in its P5 distal meral spines, which, so far as New Zealand specimens are concerned, can range from mere protuberances to distinct low spines. Similarly, the dorsal margin of the carpus of P5 may vary from being quite smooth to bearing low spinules. These features certainly are much more pronounced in both of our specimens of *C. yaldwyni.*

It would be useful to be able to distinguish smaller *C. bicolor* from *C. yaldwyni* of the same size, but only two of the 23 specimens of *C. bicolor* available to us have carapace lengths of less than 100 mm. With only two specimens of *C. yaldwyni* so far known, it is hardly valid to attempt to establish any limits for its population mean in comparison with the mean of the sample. However, the limits for the population mean of the length/height ratios of the P5 propodus, the measure of leg slenderness, derived from a sample of 23 *C. bicolor* at the 95% confidence level ($P = 0.05$) is 4.206 to 4.467 (mean 4.337). For *C. yaldwyni* such a limit is 4.293 to 6.07. The specimens of *C. bicolor* closest in size to the known *C. yaldwyni* have cl and length/height ratio of the P5 propodus of 83 mm and 3.6, 95 mm and 3.7, and 110 mm and 4.0 whereas in *C. yaldwyni* these values are 72 mm and 5.25 and 105 mm and 5.11. It might be expected, then, that smaller *C. bicolor* will be distinguishable by having proportionately stouter legs, in addition to a variable degree of conspicuousness of the carpal spinules, the distal meral spine, and the compression of the dactylus on the walking legs.

So far as taxonomic discrimination is concerned, the two populations of *Chaceon* found in New Zealand waters can be distinguished at the species level, even if some subjectivity may be needed in the determination of smaller individuals of *C. bicolor* in New Zealand using the range of morphological diagnostic criteria proposed by us.

The genus *Chaceon* now comprises 22 species. Manning & Holthuis (1989) listed 19 nominal species, and subsequently two other species have been named, *Chaceon chilensis* Chirino-Gálvez & Manning (1989), from Chile, and *C. ramosae* Manning, Tavares, & Albuquerque (1989), from Brazil.

The female paratype of *C. yaldwyni,* cl 72 mm, cb 92 mm, has enlarged, open vulvae with slightly blackened edges and longitudinal markings posteriorly consistent with the abrasive action of male pleopods. Size at sexual maturity might possibly be further evidence for the distinctness of *C. yaldwyni,* although, in the case of the West African *C. maritae* (Manning & Holthuis) (1981), Melville-Smith (1989) has suggested that mature females may moult more than once and continue to grow extremely slowly.

Name.—This species is named for John C. Yaldwyn, recently retired Director of the National Museum of New Zealand.

Distribution.—Known only from New Zealand.

Acknowledgments

We thank John Yaldwyn for his comments on the manuscript. Henry Kavale and Alan Hart collected the specimens, and we thank them for their interest. The line drawings were done by Lilly K. Manning, who also prepared the figures for publication. Simon Dawson prepared Fig. 3.

Literature Cited

Chirino-Gálvez, L. A., & R. B. Manning. 1989. A new deep-sea crab of the genus *Chaceon* from Chile (Crustacea, Decapoda, Geryonidae).—Proceedings of the Biological Society of Washington 102:401–404.

Chun, C. 1903. Aus den Tiefen der Weltmeeres, 2nd edition. Gustav Fischer, 592 pp.

Manning, R. B., & L. B. Holthuis. 1981. West African brachyuran crabs.—Smithsonian Contributions to Zoology 306, 379 pp.

———, & ———. 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae).—Proceedings of the Biological Society of Washington 102:50–77.

———, M. S. Tavares, & E. F. Albuquerque. 1989. *Chaceon ramosae,* a new deep-water crab from Brazil (Crustacea: Decapoda: Geryonidae).—

Proceedings of the Biological Society of Washington 102:646–650.

Melville-Smith, R. 1989. A growth model for the deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia.—Crustaceana 56(3):279–292.

Sakai, T. 1978. Decapod Crustacea from the Emperor Seamount Chain.—Researches on Crustacea 8 (supplement):1–39, pls. 1–4.

Webber, R., E. Dawson, & B. Stephenson. 1990. The deep-sea red crab—a new resource?.—New Zealand Professional Fisherman 3(6):10–11.

Note added in proof: A reference to *Chaceon yaldwyni* (as *Chaceon* sp.) taken northeast of the Chatham Rise in 962 meters came to our attention while this manuscript was in proof. The citation of this species was in:

1990. Fishes collected by the R/V Shinkai Maru around New Zealand. Japan Marine Fishery Resource Center, Tokyo, 410 pp.

The account of the crustaceans in this volume apparently is by M. Takeda, but the pagination of Takeda's article is unknown to us.

(RBM) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (EW) Research Associate, Natural History Unit, National Museum of New Zealand, P.O. Box 467, Wellington, New Zealand (formerly New Zealand Oceanographic Institute, DSIR, Wellington); (WRW) Crustacea Department, Natural History Unit, National Museum of New Zealand, P.O. Box 467, Wellington, New Zealand.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 608–613

A NEW CRAYFISH (DECAPODA: CAMBARIDAE) FROM SOUTHEASTERN TEXAS

Horton H. Hobbs, Jr. and H. H. Hobbs III

Abstract.—*Procambarus* (*Ortmannicus*) *zonangulus* is described from Jefferson, Hardin, and Orange counties Texas. It may be distinguished from its closest relatives: *P.* (*O.*) *texanus* Hobbs, *P.* (*O.*) *lecontei* (Hagen), and *P.* (*O.*) *geminus* Hobbs by the attenuated distal part of the first pleopod of the male and a strong cephalomesial shoulder situated proximal to the caudodistally disposed terminal elements.

Some years ago one of us (HHH, Jr) became aware of the variation that exists in populations of crayfishes that were being identified as members of *Procambarus* (*Ortmannicus*) *acutus acutus* (Girard, 1852), and that opinion was stated in the most recent checklist of the American crayfishes (Hobbs 1989). With the accumulation of collections of these crayfishes from Maine to Mexico and northward to Minnesota, the two of us began a study of the cluster of species currently included in the "complex."

The description of this crayfish, while premature in terms of the scope of our project, is offered to enable David L. Bechler, of Lamar University, Beaumont, Texas, and the late Xuehuai Deng of East China Normal University, Peoples' Republic of China, to associate the results of their studies with a taxon that will be employed in our revision. A review of the literature involving this crayfish, a summary of its range, and geographic variations are anticipated to be included in our study of the complex.

Procambarus (*Ortmannicus*) *zonangulus*, new species

Fig. 1, Table 1

Diagnosis.—Body pigmented, eyes well developed. Rostrum of adults with or without minute marginal tubercles but lacking median carina. Carapace with cervical tubercle scarcely larger than others in row on caudoventral flank of cervical groove. Areola 13.1 to 29.0 (mean 19.15 ± 3.89; $n = 42$) as long as wide, constituting 32.0 to 37.1 (mean 33.86 ± 1.17; $n = 42$) percent of total length of carapace and 41.0 to 46.8 (mean 42.79 ± 1.22; $n = 42$) percent of postorbital length. Suborbital angle very weak and obtuse; postorbital ridges with or without inconspicuous cephalic tubercle; hepatic area tuberculate; branchiostegal spine small and acute. Antennal scale approximately twice as long as broad, widest slightly distal to midlength. Ischia of third and fourth pereiopods with simple hooks, hooks of third distinctly overreaching basioischial articulation and lacking opposing tubercle on basis, that of fourth almost attaining articulation and not opposed by tubercle on basis; coxa of fourth pereiopod with strong caudomesial boss, that of fifth much smaller and flattened. First pleopods of first form male reaching coxae of third pereiopods, symmetrical, and conspicuously tapering distally; cephalomesial margin with well developed, rounded hump projecting cephalomesially. Terminal elements consisting of: (1) tapering acute mesial process directed caudodistally and inclined laterally; (2) cephalic process, obscuring central projection in cephalic aspect, corneous, acute, tapering from broad base, inclined mesially, and directed caudally, its apex lying mesial to central projection; (3) caudal element consisting of corneous, tapering, acute caudal process lying almost against caudal surface of central projection and comparatively inconspicuous, non-corneous, setiferous caudal knob at lateral base of cephalic process; and (4) corneous central projection, largest of corneous terminals, inclined mesially and tapering to subacute apex which directed caudodistally and slightly laterally. Annulus ventralis more than twice as broad as long, dextral half elevated little more than sinistral; sinus originating on median line, disappearing beneath dextral wall and emerging on caudal flank of dextrally oriented tongue near midlength where crossing median line and turning almost caudally before forming arc and extending caudomesially onto conspicuous posteromedian prominence and terminating before reaching caudal extremity of latter. Sternum immediately anterior to annulus strongly cleft and multituberculate. Unadorned postannular sclerite approximately half width of annulus, subtriangular. First pleopods present in female.

Holotypic male, form I.—Cephalothorax (Fig. 1a, m) ovate in section, taller than broad. Abdomen narrower than thorax (17.1 and 20.5 mm). Greatest width of carapace slightly less than height at caudodorsal margin of cervical groove. Areola 20.4 times as long as wide with no more than 1 punctation in narrowest part. Cephalic section of carapace 1.9 times as long as areola, length of latter 34.0% of entire length of carapace (42.6% of postorbital carapace length). Surface of carapace punctate dorsally, granulate to tuberculate laterally. Rostrum slightly deflected ventrally with converging slender margins, acute apex of short acumen reaching midlength of ultimate segment of antennular peduncle; minute marginal tubercles marking base of acumen; dorsal surface concave with many fine setiferous punctations. Subrostral ridges evident in dorsal aspect for short distance anterior to caudal margin of orbit. Postorbital ridges well developed, grooved dorsolaterally and bearing small acute tubercle at cephalic extremities.

Table 1.—Measurements (mm) of *Procambarus* (*O.*) *zonangulus.*

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	42.0	49.8	39.0
Postorbital length	33.6	40.0	30.2
Width	20.5	24.5	19.5
Height	21.0	24.1	18.3
Areola:			
Width	0.7	1.0	1.0
Length	14.3	17.6	13.1
Rostrum:			
Width	7.0	9.2	6.9
Length	10.5	11.6	10.6
Right chela*			
Length, palm mesial margin	16.0	12.5	12.1
Palm width	12.5	13.5	8.4
Length, lateral margin	48.7	40.5	35.0
Dactyl length	29.2	25.0	20.2
Abdomen:			
Width	17.1	21.9	15.8
Length	42.1	48.2	40.0

* Left chela in morphotype.

Suborbital angle very small and obtuse. Branchiostegal spines small. Cervical spines represented by small acute tubercles scarcely larger than neighboring ones on caudal flank of cervical groove.

Abdomen (Fig. 1j) subequal in length to carapace. Pleura of third through fifth segments subtruncate to rounded with caudoventral extremities subangular on third and fourth. Cephalic section of telson with 3 spines in each caudolateral corner, middle one in both clusters movable; caudal margin of caudal section with shallow median excavation. Cephalic lobe of epistome (Fig. 1l) ovate with elevated free margins; central area subplane and sparsely punctate; distinct anteromedian fovea present on main body. Ventral surface of proximal podomere of antennular peduncle with spine slightly proximal to midlength. Antenna with small spiniform tubercles on basis and

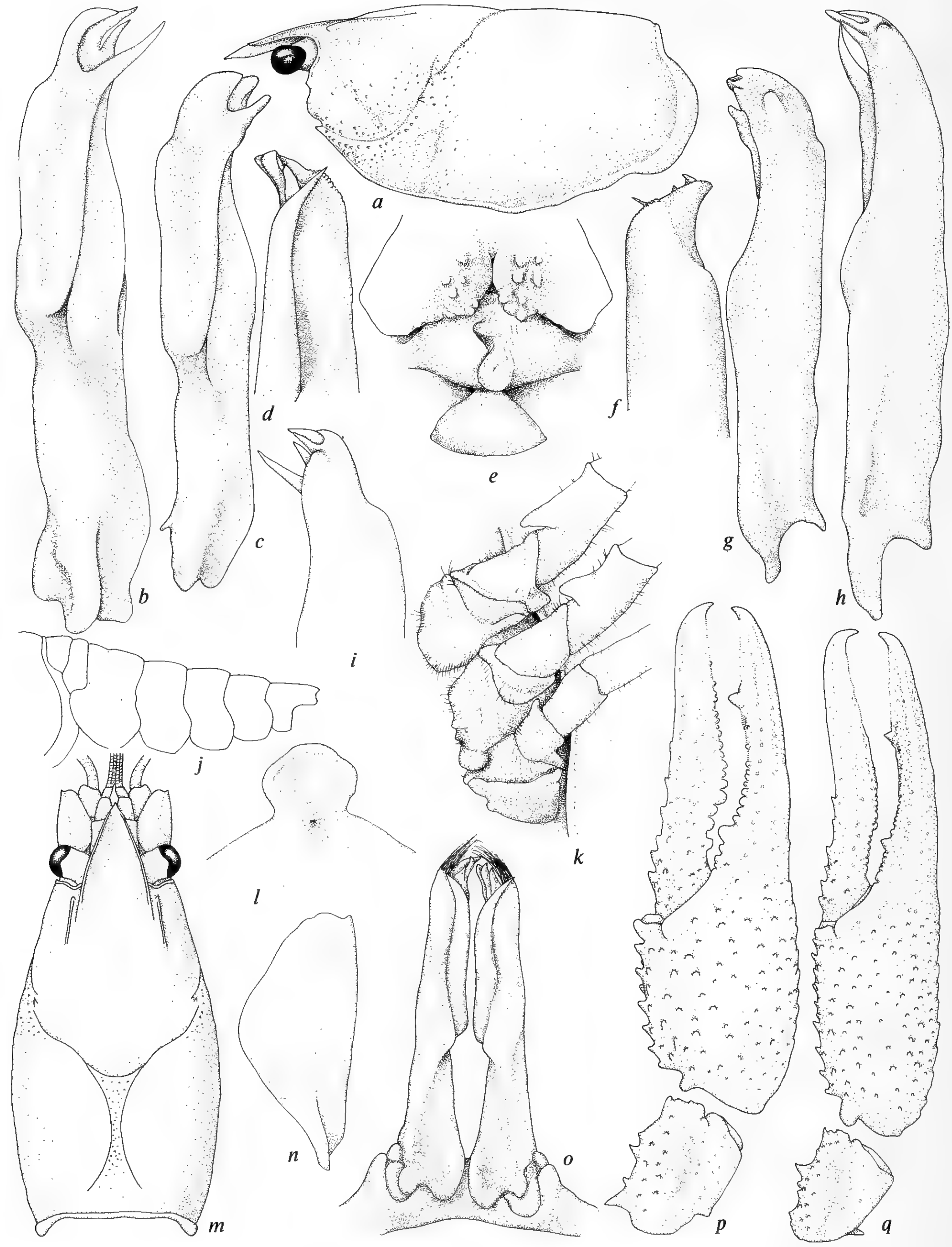


Fig. 1. *Procambarus* (*Ortmannicus*) *zonangulus* (all from holotype except c and g from morphotype, e and p from allotype, and o from paratypic first form male): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Caudal view of distal part of first pleopod; e, Annulus ventralis and adjacent sternites; f, Cephalic view of distal part of first pleopod; g, h, Lateral view of first pleopod; i, Caudolateral view of distal part of first pleopod; j, Lateral view of abdomen; k, Proximal podomeres of third, fourth and fifth pereiopods; l, Epistome; m, Dorsal view of carapace; n, Antennal scale; o, Caudal view of first pleopods; p, q, Dorsal view of distal podomeres of cheliped.

ischium; flagella overreaching caudal margin of telson. Antennal scale (Fig. 1n) 2.2 times as long as broad, widest slightly distal to midlength; greatest width of lamella almost twice width of thickened lateral part.

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

Right chela (Fig. 1q) subovate in cross section, not strongly depressed. Mesial surface of palm with row of 8 tubercles subtended dorsally by additional row and ventrally by only few tubercles. Entire palm moderately tuberculate, but ventrolateral tubercles much reduced and some replaced by punctations. Dorsal and ventral longitudinal ridges scarcely evident on either finger. Opposable surface of fixed finger with dorsally situated row of 24 (32 on left) tubercles along proximal three-fifths and lower row of 14 (15 on left), one of which much larger than other tubercles on finger; broad band of minute denticles situated between rows of tubercles and extending to base of corneous tip of finger; except for few tubercles proximoventrally, finger otherwise smooth except for longitudinal rows of setiferous punctations. Opposable margin of dactyl with upper row of 32 (29 on left) tubercles on proximal three-fifths and lower row of 17 (15 on left); broad band of minute denticles present between rows and extending distally to base of corneous tip of finger; dorsal and ventral surfaces with few tubercles in basal portion, otherwise with few longitudinal rows of setiferous punctations; mesial surface of finger with row of 6 (4 on left) tubercles along proximal fourth followed distally by row of setiferous punctations reaching base of corneous tip. Carpus of cheliped longer than broad with prominent oblique furrow dorsally, tuberculate mesially and dorsomesially; mesial surface with 3 (2 on left) tubercles larger than others, two near midlength and one distomesially; ventral surface with usual 2 tubercles on distal margin. Merus tuberculate dorsally, distomesially, and ventrally; 2 premarginal tubercles larger than others on dorsodistal surface; ventral surface with mesial row of 16 (15 on left) tubercles and lateral one of 14 (13 on left). Ischium with ventromesial row of 4 tubercles.

Hooks on ischia of third and fourth pereiopods (Fig. 1k) simple, that on third overreaching basioischial articulation, that on fourth almost reaching articulation and unopposed by prominent tubercle on corresponding basis. Coxa of fourth pereiopod with prominent subvertically oriented caudomesial boss; that of fifth with smaller one strongly compressed in longitudinal plane of body (when legs positioned at right angles to longitudinal axis). Sternum between third, fourth, and fifth pereiopods comparatively deep with mat of plumose setae extending mesially from ventrolateral margins.

First pleopods (Fig. 1b, d, f, h, i, o) as described in "Diagnosis." Uropod with both lobes of basal podomere bearing small acute spine; both rami with distolateral spines, and distomedian spine on mesial ramus situated distinctly proximal to subtruncate distal margin.

Allotypic female.—Differing from holotype, except in secondary sexual characters, as follows: acumen of rostrum, marked basally by sudden but shallow contraction of rostral margins reaching base of ultimate podomere of antennular peduncle; tubercles at cephalic extremities of postorbital ridges rounded; suborbital angle vestigial; branchiostegal spine tuberculiform; pleura of third through fifth abdominal segments angular posteroventrally; cephalic lobe of epistome more nearly subtriangular with anteromedian prominence; mesial surface of palm of chela (Fig. 1p) with row of 6 (7 on left) tubercles; opposable surface of fixed finger with single row of 13 (left with 10 tubercles, latter with additional large one at base of distal fourth; opposable margin of dactyl with single row of 14 (13 on left) tubercles and mesial margin with row of 5; ventral surface of merus of cheliped with mesial row of 14 (13 on left) tubercles and lateral row with 15 (13 on left). Ventromesial surface of ischium with 4 (3 on left) tubercles.

Annulus ventralis (Fig. 1e) as described in "Diagnosis."

Morphotypic male, form II.—Differing from holotype in following respects: greatest width of carapace slightly more than height at caudodorsal margin of cervical groove; narrowest part of areola with 2 punctations; acumen reaching base of ultimate segment of antennular peduncle; marginal tubercles at base of acumen much more strongly developed; cephalic section of telson with 2 spines in each caudolateral corner, mesial pair movable; antennal scale with acute distolateral spine and broadest slightly proximal to midlength; longitudinal ridges on fixed finger of chela more distinct, opposable margin with dorsal row of 14 tubercles and ventral row of only 3; opposable margin of dactyl with corresponding rows of 22 and 11 tubercles, mesial surface with row of 4 tubercles along proximal fourth; ventral surface of merus of cheliped with mesial row of 17 tubercles and lateral one of 14; ischium of cheliped with ventromesial row of 5 tubercles; hooks on ischia of third and fourth pereiopods much smaller, neither overreaching articulation with corresponding ischium; bosses on coxae of fourth and fifth pereiopods weaker. First pleopod (Fig. 1c, g) with apical section much more stocky and while all terminal elements described for holotype present, all reduced and none corneous.

Type locality.—Dishman Road at Tram Road north of Meeker, Jefferson County, Texas 30°7′N, 94°15′W). Roadside ditch, occasionally drying, with sedges and grasses, bordered by *Salix niger.*

Disposition of types.—The holotype, allotype, and morphotype (USNM 220297, 220298, and 220299, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes, consisting of 24 ♂ I, 2 ♂ II, 8 ♀, 2 j♀.

Specimens examined.—(1) Type locality: 16 ♂ I, 7 ♀, 27 May 1989, coll. Edmund Farmer and David L. Bechler. (2) Massey Lake Slough and unnamed slough, Hardin County, Texas (Lat. 30°7′, Long. 94°12′), 3 ♂ I, 1 ♀, 2 j♀, 12 May 1989, coll. DLB, Lynn Sadler, Roy King. (3) The Crawdad Farm, Mauriceville, Orange County, Texas: 5 ♂ I, 27 May 1989, coll. Boyce and Sharon Ward. (4) Pond adjacent to Neches River at Beaumont, Orange County, Texas: 1 ♂ I, 3 ♂ II, 1 ♀, 26 Sept 1953, coll. R. J. Baldauf.

Relationships.—*Procambarus* (*Ortmannicus*) *zonangulus* has its closest affinities with *P.* (*O.*) *texanus* Hobbs (1971), which has been reported from a single locality in Bastrop County, Texas. More distant affinities exist with *P.* (*O.*) *lecontei* (Hagen, 1870) and *P.* (*O.*) *geminus* Hobbs (1975). Among the features in which it differs from the latter two are a much narrower, less densely punctate areola, a rostrum with more strongly convergent margins and weaker marginal spines; the first pleopods are symmetrical and, except for the caudal process, the terminal elements of the first pleopod of the first form male are directed caudally at approximately right angles to the main shaft of the appendage. This crayfish differs from *P.* (*O.*) *texanus* chiefly in features of the first pleopod, especially in the first form male: the distal part of the pleopod is strongly tapering; the cephalomesial shoulder proximal to the terminal elements is much more strongly developed; the central projection and caudal process are proportionally longer, and more tapering.

Etymology.—Zona (L.) = belt + Angulus (L.) = bay or gulf, noting its range in the gulf coastal area of the United States.

Acknowledgments

Our thanks are extended to David L. Bechler, Lamar University, for providing us with most of the specimens selected to be included in the type series of this crayfish and to Raymond B. Manning, Smithsonian

Institution, for his criticisms of the manuscript.

Literature Cited

Girard, Charles. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution.—Proceedings of the Academy of Natural Sciences of Philadelphia 6:87–91.

Hagen, Hermann A. 1870. Monograph of the North American Astacidae.—Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College 3:viii+109 pp.

Hobbs, Horton H., Jr. 1971. New crayfishes of the genus *Procambarus* from Alabama and Texas (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 84:81–94.

———. 1975. New crayfishes (Decapoda: Cambaridae) from the southern United States and Mexico.—Smithsonian Contributions to Zoology 201:1–34.

———. 1989. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae and Parastacidae).—Smithsonian Contributions to Zoology 480:iii + 236 pp.

(HHH, Jr) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (HHH III) Department of Biology, P.O. Box 720, Wittenberg University, Springfield, Ohio 45501.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 614–616

POMATOGEBIA, A NEW GENUS OF THALASSINIDEAN SHRIMPS FROM WESTERN HEMISPHERE TROPICS (CRUSTACEA: UPOGEBIIDAE)

Austin B. Williams and Nguyen Ngoc-Ho

Abstract.—A new genus, *Pomatogebia,* is proposed for 3 species of thalassinidean shrimps from the tropical western Atlantic and eastern Pacific that are specialized for burrowing in massive stony corals. The caudal part of the shrimp's abdomen is shaped as an operculum that can be inserted from within the burrow system into its entrance, the exoskeletal surface mimicking that of the coral. *Pomatogebia operculata* (Schmitt, 1924), placed in *Upogebia* until now, becomes the type species of the new genus.

A tropical western Atlantic thalassinidean shrimp, identified until now as *Upogebia operculata* Schmitt, 1924, is specialized for commensal existence in several species of massive stony corals (Kleemann 1984, Scott et al. 1988). The shrimps at an early stage of development commence excavation of burrows in host corals and establish themselves eventually as male–female pairs that grow into maturity while becoming confined in the burrows. The caudal part of the shrimp's abdomen is shaped as an operculum or plug, with a surface mimicking that of the host coral. In this specialization and in morphology of the carapace and appendages, this shrimp and two other species in the tropical eastern Pacific differ from related shrimps in the region. Indeed, there are no other upogebiids in the world known to be specialized in this manner, and we regard this structural novelty as worthy of generic rank.

Pomatogebia, new genus
Fig. 1a–c

Diagnosis.—Carapace anterior to cervical groove more or less flattened dorsally and armed on its gastric ⅔ with field of spines grading from strong anteriorly to weak or obsolescent posteriorly; spines irregularly distributed but tending to arrangement in rows that diverge posteriorly, many with tufts of setae emerging anterior to base. Gastric region projected into broadly subtriangular rostrum barely exceeding short eyestalks and bearing pair of subterminal spines, similar spine at each posterolateral corner where rostrum merges with gastric field. Lateral margin of spine field flanked on each side by poorly developed furrow, and that in turn by imperfectly developed lateral ridge bearing crest of about 8–11 spines grading from strong anteriorly to obsolescence posteriorly. Incomplete orbital margin concave in dorsal portion; postorbital margin spineless.

Abdomen broadly and smoothly arched dorsally on segments 1–4, segment 4 with dense fringe of setae on posterior margin and transverse band across anterior half; pleura of segment 1 narrowly rounded posterolaterally, those of 2–5 broadly rounded, margins unspined; dense fine setae in tracts on pleura of segments 3–4, tuft on posterolateral corner of 2 and anterolateral corner of 5; segment 6 irregularly rectangular, broader than long, its lateral margin scalloped anteriorly and adapted posteriorly for articulation with base of uropod; dorsal sur-

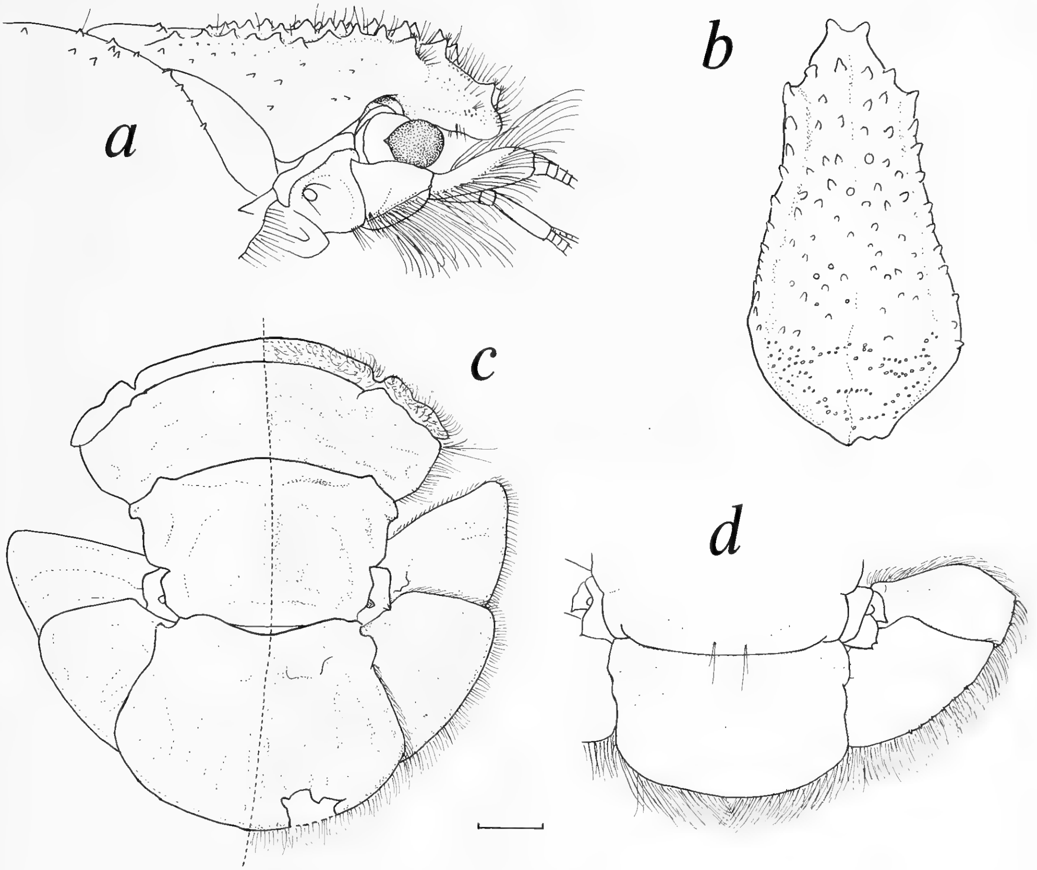


Fig. 1. *Pomatogebia operculata* (Schmitt): *a,* Cephalic region, lateral; *b,* Anterior carapace, dorsal; *c,* Caudal opercular complex, abdominal segments 5–6, telson and uropods; Paratype ♀, USNM 57952, Barbados, Lesser Antilles, West Indies. *Upogebia affinis* (Say): *d,* Telson, left uropods and posterior margin of abdominal segment 6; ♂, USNM 31289, near Bluffton, South Carolina, USA. Scale = 1 mm.

face of segments 5 and 6 ornamented with symmetrical pattern of meandering rugae.

Tail fan with exposed aspect generally concave. Telson with sides diverging posteriorly and posterior margin convex, stiffened with radiating longitudinal ribs; exopod and endopod of uropods bearing similar radiating ribs. Entire tail fan with dense fringe of setae on distal margin, forming together with segments 5 and 6 an almost circular operculum when fully extended.

Maxilliped 1 with an epipod, maxilliped 3 lacking even rudimentary epipod.

Chelipeds equal, rather slender, more slender in females than in males; articles spineless; fixed finger nearly as long as dactyl, toothed proximally, rather stout and gently curved; dactyl curved, setose, stouter than fixed finger, abruptly tapered to tip and hooking beyond tip of opposed finger. Pereopods 2–5 spineless.

Type species.—*Upogebia operculata* Schmitt, 1924.

Etymology.—From the Greek "pomatos," operculum, for the operculate caudal complex, and the stem "gebia," from *Upogebia,* underground digger. The gender is feminine.

Remarks.—The operculate abdomen best distinguishes *Pomatogebia operculata* and its two sister species in the eastern Pacific, *P. rugosa* (Lockington, 1878) and *P. cocosia* (Williams, 1986), from members of the genus *Upogebia* Leach, 1814, distributed worldwide in shallow temperate and tropical seas and currently containing 78 recognized species. *Pomatogebia* has a multiribbed telson with convex posterior margin and divergent lateral margins, and the rami of the uropods are also ribbed. *Upogebia* does not have an operculate abdomen; the telson (Fig. 1*d*) is basically rectangular, with straight or slightly concave posterior margin and lateral margins straight, somewhat sinuous, or slightly convergent distally, never divergent, and although reinforced by a variously developed transverse proximal ridge confluent with low submarginal lateral ridges, never displays multiple longitudinal ribbing (see Williams 1986).

In addition to the two above mentioned genera, three other genera are currently recognized in the family Upogebiidae: *Tuerkayogebia* Sakai, 1982 (Japan, 1 species), *Wolffogebia* Sakai, 1982 (Malay Peninsula-northwestern Australia, 3 species), and *Gebiacantha* Ngoc-Ho, 1989 (Réunion, Indonesia, and New Caledonia, 11 species).

Acknowledgments

We thank Fenner A. Chace, Jr., Bruce B. Collette, and Raymond B. Manning for critical review of the manuscript, and Keiko Hiratsuka Moore for rendering the drawings.

Literature Cited

Kleemann, K. 1984. Lebensspuren von *Upogebia operculata* (Crustacea, Decapoda) in karibischen Steinkorallen (Madreporaria, Anthozoa).—Beiträge zur Paläontologie von Österreich, Institut für Paläontologie der Universität Wien, No. 11:325–49.

Leach, W. E. [1814.]. Crustaceology. *In* Edinburgh encyclopaedia. Edinburgh, 76:383–437, pl. 221.

Lockington, W. N. 1878. Remarks upon the Thalassinidea and Astacidea of the Pacific coast of North America, with description of a new species.—Annals and Magazine of Natural History 5(2):299–304.

Ngoc-Ho, N. 1989. Sur le genre *Gebiacantha* gen. nov., avec la description de cinq espèces nouvelles (Crustacea, Thalassinidea, Upogebiidae).—Bulletin du Muséum National d'Histoire Naturelle, Section A, Série 4, 11(1):117–145.

Sakai, K. 1982. Revision of Upogebiidae (Decapoda, Thalassinidea) in the Indo-West Pacific region. Researches on Crustacea, The Carcinological Society of Japan, Special No. 1:1–106.

Schmitt, W. L. 1924. Report on the Macrura, Anomura and Stomatopoda collected by the Barbados-Antigua Expedition from the University of Iowa in 1918.—University of Iowa Studies in Natural History 10(4):65–99, pls. 1–5.

Scott, P. J. B., H. M. Reiswig, & B. M. Marcotte. 1988. Ecology, functional morphology, behaviour, and feeding in coral- and sponge-boring species of *Upogebia* (Crustacea: Decapoda: Thalassinidea).—Canadian Journal of Zoology 66(2):483–495.

Williams, A. B. 1986. Mud shrimps, *Upogebia*, from the eastern Pacific (Thalassinoidea: Upogebiidae).—San Diego Society of Natural History, Memoir 14:1–60.

(ABW) National Marine Fisheries Service-NOAA Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (NN-H) Muséum National d'Histoire Naturelle, Laboratoire de Zoologie (Arthropodes), 61 Rue de Buffon, 75231 Paris, CEDEX 05, France.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 617–623

GITANA DOMINICA, A NEW SPECIES FROM THE CARIBBEAN SEA (AMPHIPODA: AMPHILOCHIDAE)

James Darwin Thomas and J. L. Barnard

Abstract.—The new species *Gitana dominica* is described from Dominica in the Lesser Antilles; it is the first record of the genus from the western Atlantic Ocean. The new species differs from its closest relative, *Gitana calitemplado,* from California, in the shorter and posteroventrally excavate coxa 1. *Gitana* is reviewed.

Gitana is reviewed and followed by the description of the new species. The first name after each species in the review is the author of the species with date of publication; additional dates or information in parentheses refer to more modern comprehensive references to the several species; numbers in brackets refer to geographic distribution codes described by Barnard & Barnard (1983); those codes represent a universal geographic descriptive system but codes for these species are not included therein and are modernized and presented herein for the first time.

Gitana Boeck

Gitana Boeck, 1871:132 (*Gitana sarsi* Boeck, 1871, designated by Sars, 1895: 229, "Remarks.").—Stebbing, 1906: 155.—Lincoln, 1979:162.

Diagnosis.—Mandibular molar large, cushion-shaped, triturative. Lower lip ordinary. Palp of maxilla 1 uniarticulate. Maxilla 2 ordinary. Outer plate of maxilliped weakly excavate or not, palp articles 1–2 equal or not strongly different in length. Gnathopods 1–2 small, more or less carpochelate, poorly subchelate or almost simple, palms very oblique, dactyls lacking large inner nodiform process. Urosomite 3 poorly alate.

Variables.—Inner plate of maxilla 2 rather thin (*longicarpa*) but broader than outer; gnathopods simple (*rostrata, longicarpa,* etc.), gnathopod 2 scarcely carpochelate (*longicarpa, rostrata*; etc.).

Relationship.—Like *Gitanopsis* but palp of maxilla 1 uniarticulate. Like *Amphilochopsis* but gnathopod 2 feeble.

Species.—See important notes on biogeography and taxonomy in Chevreux (1911), Chevreux & Fage (1925), Gurjanova (1951), Krapp-Schickel (1982), Ledoyer (1973), Schellenberg (1942), Stephensen (1938).

Gitana abyssicola Sars, 1895 (Ledoyer, 1973), eastern Atlantic, warm-temperate to boreal [355];
Gitana bilobata Myers, 1985, Fiji [576];
Gitana calitemplado J. L. Barnard, 1962, 1964, northeastern Pacific warm-temperate [370];
Gitana dominica Thomas & Barnard, herein, Caribbean, Leeward Islands [491];
Gitana gracilis Myers, 1985, Fiji [576];
Gitana liliuokalaniae J. L. Barnard, 1970, Hawaiian Islands [381];
Gitana longicarpa Ledoyer, 1977, northeastern Mediterranean, bathyal [348B];
Gitana rostrata Boeck, 1871 (Sars, 1895) boreal east Atlantic, bathyal [240B];
Gitana sarsi Boeck, 1871 (Sars, 1895) (= *Gitana sabrinae* Stebbing, 1878) (Lincoln, 1979) amphi-Atlantic, Mediterranean, warm-temperate to arctic ocean [355].

Biogeography.—Marine, cold and warm northeast Atlantic, warm mid to east Pacific, 0–575 m, 9 species.

Gitana dominica, new species
Figs. 1–3

Etymology.—dominica, noun in apposition, from the type locality.

Diagnosis.—Rostrum large (see Fig. 1B) and downturned; lateral cephalic lobes broadly rounded; eyes large and pigmented deep orange in life. Articles 1–2 of antenna 1 of equal length, article 3 shorter, accessory flagellum forming small articulate scale.

Labrum almost symmetrically and deeply lobed. Right lacinia mobilis slender and bifid, left broad and multitoothed. Outer lobes of lower lip widely spread, unnotched, apices each with articulate "salivary spout"; faint inner lobes present.

Coxa 1 spout-shaped, with weakly excavate posteroventral margin and weakly bifid apically. Carpi of gnathopods 1–2 medium-short, propodi much longer; carpus of gnathopod 1 with short posterodistal lobe, of gnathopod 2 with medium lobe extending along posterior fifth of propodus but not appressed to it; palms obsolescent but barely distinct and armed with sparse spinules. Pereopodal dactyls simple, locking spines paired and unspecialized. Article 2 of pereopods 5–7 of diverse sizes, of 5–6 setose but not serrate posteriorly, of pereopod 7 setulose and serrate posteriorly.

Epimera 1 and 3 with rounded-quadrate posteroventral corner, epimeron 2 with small posteroventral tooth. Outer ramus of uropod 1 barely shorter than inner ramus, of uropod 2 one third shorter. Telson about two-thirds as long as peduncle of uropod 3, sharply tapering and pointed.

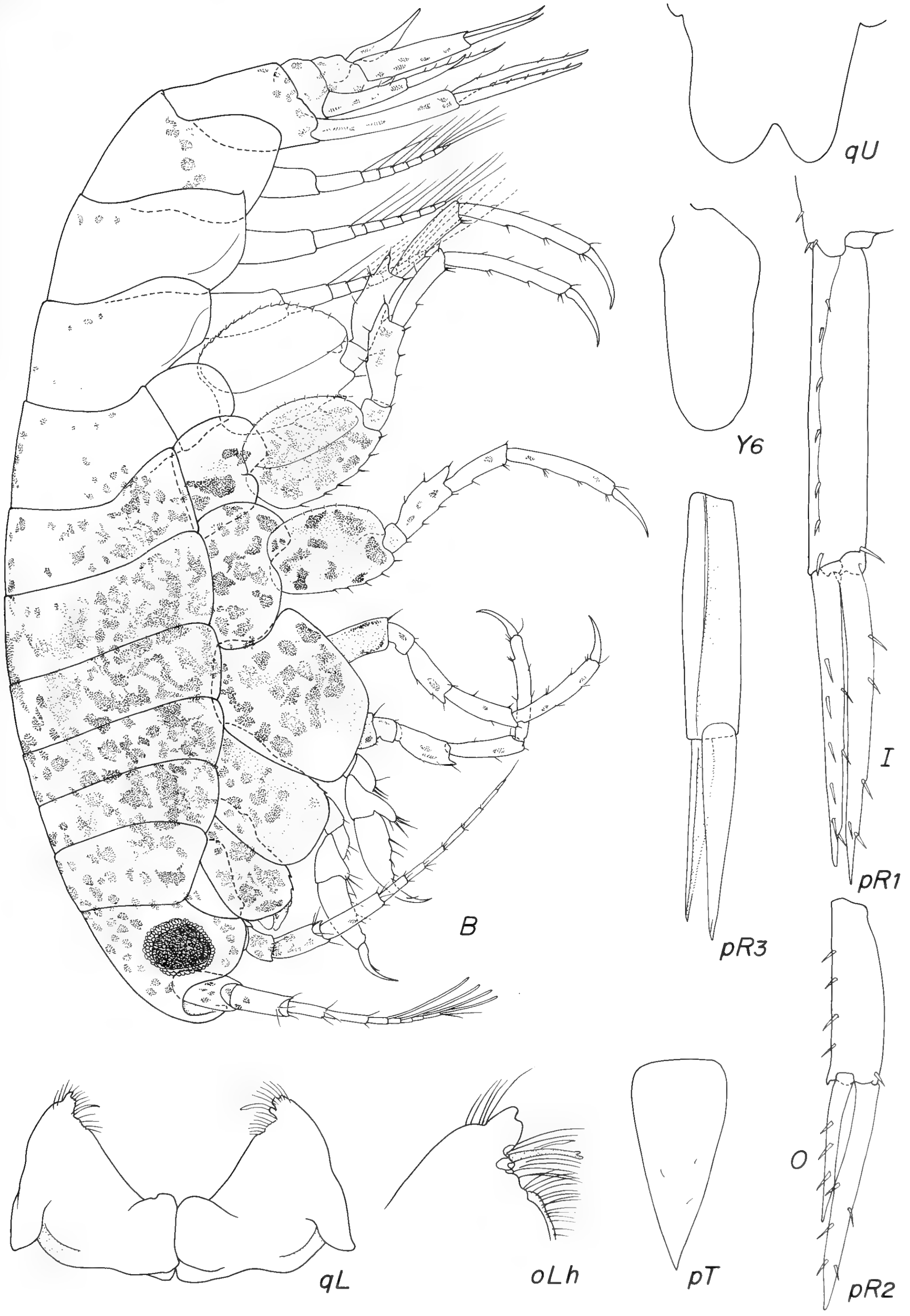
Description.—Apical 3–4 articles of flagellum on antenna 1 each with 3–4 aesthetascs. Incisors multitoothed. Inner plate of maxilla 1 with 1 apical setule, outer plate with 5 medial serrate spine-setae, apicomedial serrate hump and 8 apical spines; uniarticulate palp with 4 apical spines. Inner plate of maxilla 2 with 9 medial setae and small stiff setule; outer plate very slender, with apical spout and 4 setae. Inner plate of maxilliped with subsidiary apical hump bearing apicolateral spine-tooth, incipient apicomedial spine-tooth, and lateral setule inserted below facial pocket, primary truncate margin with 2 apicomedial and one apicolateral spines; outer plate with 3 medial spines, no combs on these plates; dactyl with barely visible nail and 2 minute accessory setules.

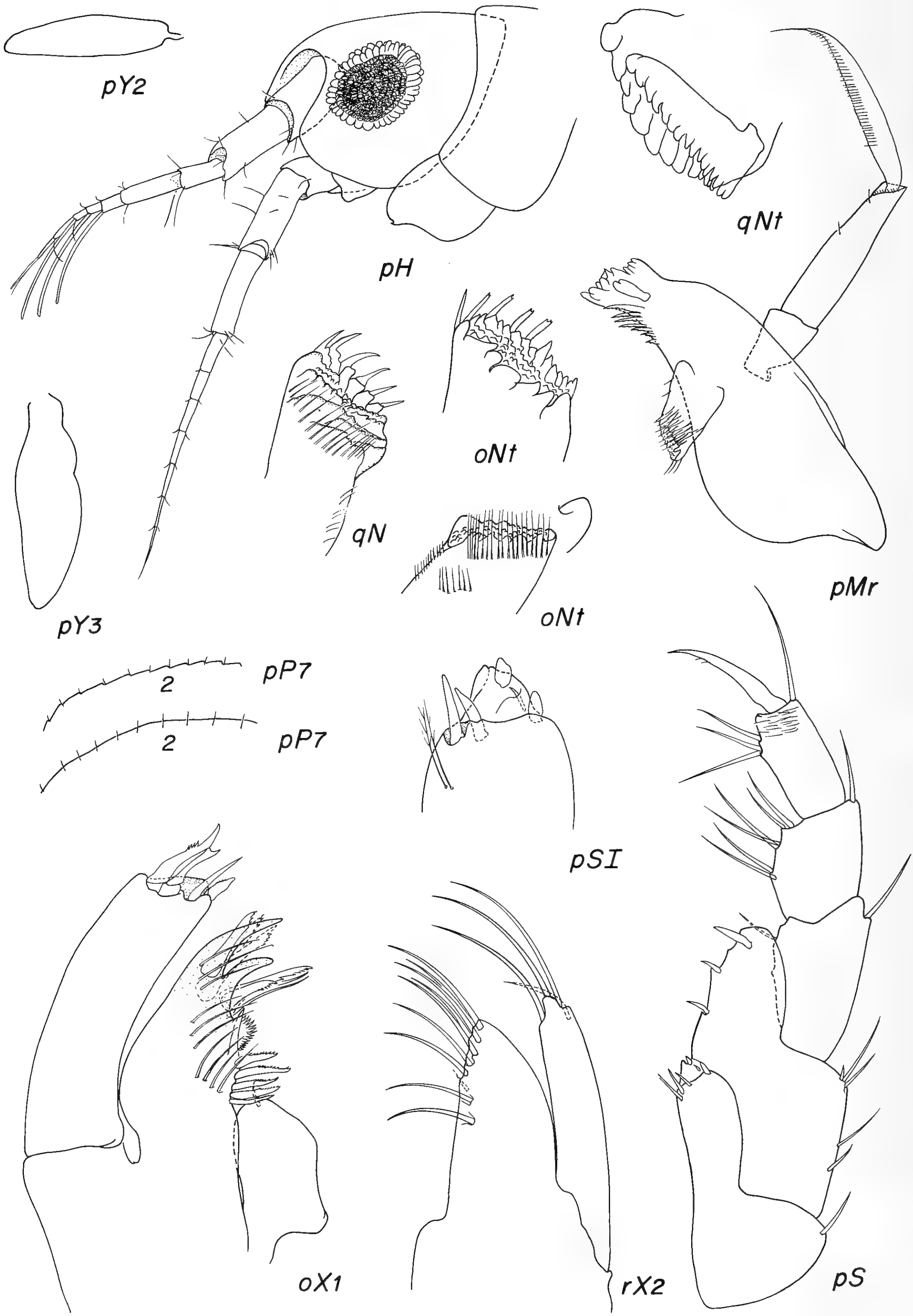
Coxae 2 and 3 with 2 and 3 weak posteroventral serrations. Oostegites 2–4 medium-broad, oostegite 5 small, all sparsely setose. Gills sac-like, on coxae 2–6, gills 2–3 smaller than gills 4–6. Epimera 1–2 with lateral facial ridge.

Color.—Colors cited are from USA National Bureau of Standards ISCC-NBS Color-Name Charts. In life, eyes very orange (48) to deep orange (51); somatic chromatophores dark olive brown (96) but when fully expanded yielding overall cast from 40 power observation of dark gray yellow brown (81); during maximum color rendition anterior part of body from head to posterior margin of segment 6, including coxae, very dark but splotchy; chromatophores not fully joined nor interspersed, thus rendering densely dotted appearance; dense chro-

→

Fig. 1. *Gitana dominica,* figures without lower case letter on left of label = holotype, female "n," 2.01 mm; o = female "o" 1.98 mm; p = male "p" 2.08 mm; q = female "q" 2.10 mm. (Legend: Capital letters in figures refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as described: B, body; C, coxa; D, dactyl; G, gnathopod; H, head; I, inner plate or ramus; L, labium; M, mandible; N, molar, or incisor and lacinia mobilis; P, pereopod; R, uropod; S, maxilliped; T, telson; U, upper lip; W, pleon; Y, gill; Z, oostegite; h, half; t, left.)


qU
Y6
I
pR1
B
pR3
O
pR2
qL
oLh
pT


pY2
pH
qNt
pMr
oNt
qN
oNt
pY3
2
pP7
2
pP7
pSI
oX1
rX2
pS

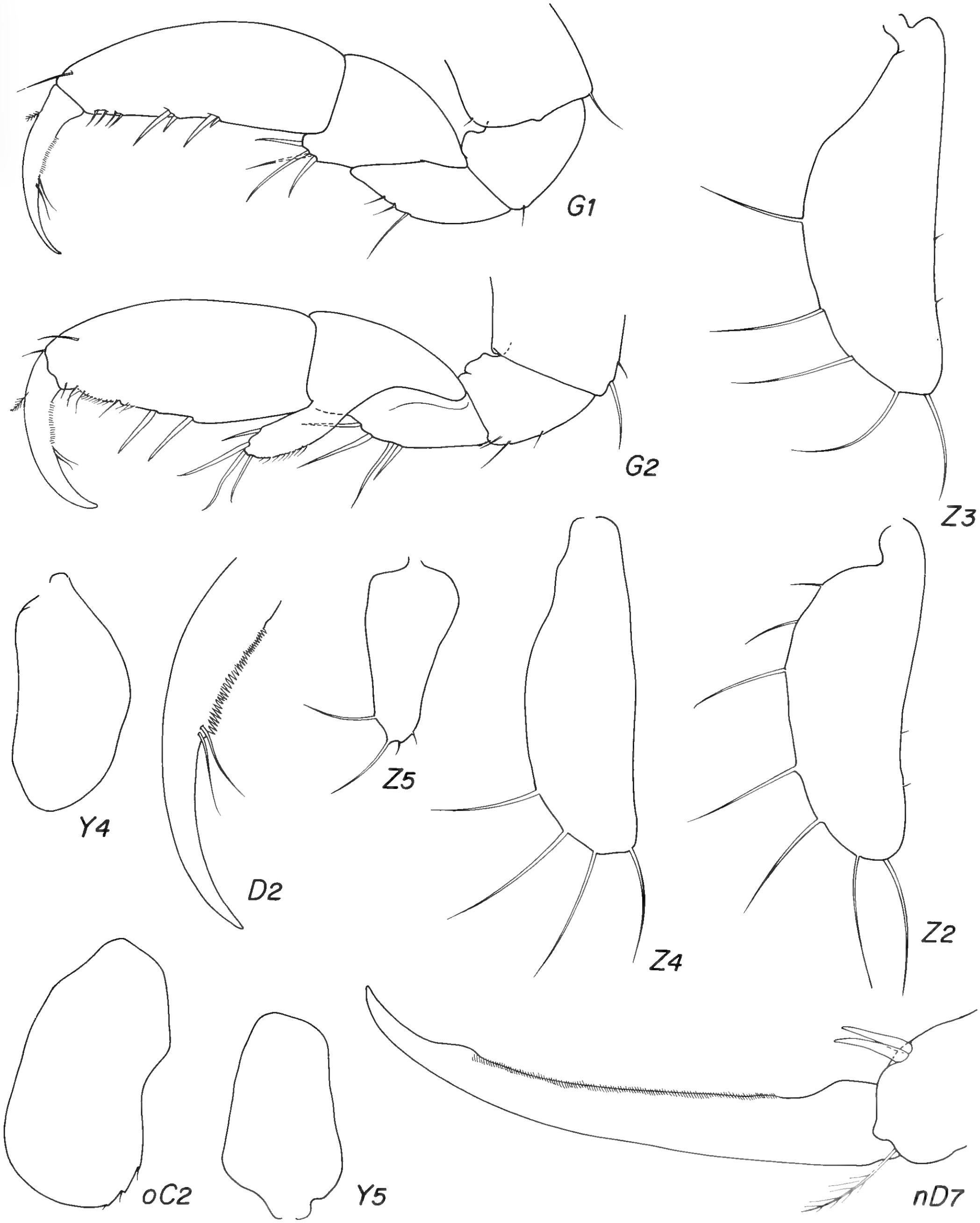


Fig. 3. *Gitana dominica,* figures without lower case letter on left of label = holotype, female "n," 2.01 mm; o = female "o" 1.98 mm.

←

Fig. 2. *Gitana dominica,* figures without lower case letter on left of label = holotype, female "n," 2.01 mm; o = female "o" 1.98 mm; p = male "p" 2.08 mm; q = female "q" 2.10 mm; r = female "r" 2.70 mm.

matophores also in articles 2–3 of pereopods 5–6, article 1 of antenna 1 and articles 1–4 of antenna 2; medium density chromatophores present in urosomites 2–3 and posterior end of urosomite 1, midlateral face of pleonite 3 and peduncles of uropods which, when expanded, provide dark cast; very scattered chromatophores present in some apical articles of pereopods 3–6, pereonite 7, pleonites 1–2, article 2 of antenna 1, article 5 of antenna 2, and telson. Faint pigmentary cast not well organized into giant chromatophores present generally throughout gnathopods, article 2 of pereopods 3–4, coxa 3, article 2 of pereopods 5–6. Anteroventral corner of coxa 4 and pereopod 7 not pigmented. Drawing of holotype body showing principal chromatophores and diffuse casts based on field notes and male "p," the pigment of which was best preserved. Pigment of chromatophores concentrated on death and to some extent broken and contents released to form pigmentary cast. Microhabitat unusual for amphilochids which are generally thought to be slime lappers on sedentary organisms, especially coelenterates.

Holotype.—USNM 242015, female "n" 2.01 mm (Figs. 1–3).

Type locality.—JDT-DOM 2A, Pte. Guignard, Dominica, 2 km south of Roseau, sediments amongst reef outcrop, 19 May 1987; coarse quartzose sand with dark mineral inclusions, 6.3 meters, sediment appearing greyish-black; large amount of unicellular algal strands; J. D. Thomas and J. Clark, collectors.

Material.—All paratypes from type locality, female "o" 2.48 mm; female "p" 2.58 mm; female "q" 2.60 mm; female "r" 2.70 mm; male "s" 1.80 mm. Six other specimens from the type locality provisionally labeled as this species are deposited in USNM collections but are not discretely identified and are left undamaged for future examiners.

Relationship.—Our species appears most similar to *Gitana calitemplado.* These two species differ from other species of *Gitana* in the short carpi and relatively long propodi of the gnathopods. This may have generic significance and is a condition so far restricted to species in the western hemisphere. Our species differs from *Gitana calitemplado* in the short, posteroventrally excavate coxa 1.

Differing from *Gitana sarsi* in the shorter carpi of the gnathopods, spout-like shape of coxa 1, and lack of inner notches on the lower lip.

Differing from *Gitana longicarpa* in the downturned rostrum, short carpi of the gnathopods, poorly lobed article 2 of pereopods 5–7, shorter peduncle of antenna 2, unpointed coxa 2, short article 1 of mandibular palp, less extended palp of the maxilliped and shorter broader telson.

Differing from *Gitana abyssicola* in the short carpi of the gnathopods, spout-like coxa 1, slightly larger rostrum and greater difference in relative sizes of article 2 on pereopods 5–7.

Differing from *Gitana rostrata* in the downturned rostrum, short carpi of the gnathopods, thicker peduncle of antenna 2, relatively greater differences in article 2 of pereopods 5–7.

Differing from *Gitana liliuokalaniae* in the relatively long propodi and short carpi of the gnathopods, distinct tooth of epimeron 2, bifid right lacinia mobilis, more elongate peduncle of antenna 1, and spout-like coxa 1.

Differing from *Gitana bilobata* and *Gitana gracilis* in the short carpi of the gnathopods, the much longer antenna 1, and much longer (but normal) coxa 2.

Distribution.—Dominica, 6 m.

Acknowledgments

Fieldwork for this report was supported by Smithsonian's CCRE committee; this is CCRE Contribution No. 260; we thank Dr. Klaus Ruetzler, head of this program, and Mike Carpenter for their assistance. The second author was supported by NSF Grant 8515186. Linda Lutz of Vicksburg, Mississippi, inked our drawings.

Literature Cited

Barnard, J. L. 1962. Benthic marine Amphipoda of southern California: families Amphilochidae, Leucothoidae, Stenothoidae, Argissidae, Hyalidae.—Pacific Naturalist 3:116–163.

———. 1964. Los anfipodos bentonicos marinos de la costa occidental de Baja California.—Revista de la Sociedad Mexicana de Historia Natural 24:205–274, 11 figs., 5 tabs.

———. 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands.—Smithsonian Contributions to Zoology 34:1–286.

———, & C. M. Barnard. 1983. The freshwater Amphipoda of the world.—Mt. Vernon, Virginia, Hayfield Associates, 2 volumes, xix and 849 pp.

Boeck, A. 1871. Crustacea Amphipoda Borealia et Arctica.—Forhandlinger i Videnskabs-Selskabet i Christiania 1870:83–280.

Chevreux, E. 1911. Campagnes de la *Melita.* Les amphipodes d'Algerie et de Tunisie.—Memoire de la Societe Zoologique de France 23:145–285, plates 6–20.

———, & L. Fage. 1925. Amphipodes.—Faune de France 9:1–488, 438 figs.

Gurjanova, E. 1951. Bokoplavy morej SSSR i sopredel'nykh vod (Amphipoda-Gammaridea).—Akademiia Nauk SSSR, Opredeliteli po Faune SSSR 41:1–1029, 705 figs.

Krapp-Schickel, Gitana. 1982. Family Amphilochidae. *In* S. Ruffo, ed., The Amphipoda of the Mediterranean, Part 1, Gammaridea (Acanthonotozomatidae to Gammaridae).—Memoires de l'Institut Oceanographique 13:70–93, figs. 48–63.

Ledoyer, M. 1973. Amphipodes gammariens nouveaux ou peu connus de la region de Marseille.—Tethys 4:881–898, 13 pls.

———. 1977. Contribution a l'etude de l'ecologie de la faune vagile profonde de la Mediterranee nord occidentale 1. Les gammariens (Crustacea, Amphipoda).—Bollettino del Museo Civico di Storia Naturale, Verona 4:321–421.

Lincoln, R. 1979. British marine Amphipoda: Gammaridea. London, British Museum (*Natural History*), vi + 658 pp., 280 figs., 3 pls.

Myers, A. S. 1985. Shallow-water, coral reef and mangrove Amphipoda (Gammaridea) of Fiji.—Records of the Australian Museum supplement 5:1–144, 109 figs.

Sars, G. O. 1895. An account of the Crustacea of Norway with short descriptions and figures of all the species. Christiania: Alb. Cammer-Meyers 1:1–711.

Schellenberg, A. 1942. Krebstiere oder Crustacea IV: Flohkrebse oder Amphipoda.—Die Tierwelt Deutschlands, Jena 40:1–252, 204 figs.

Stebbing, T. R. R. 1878. On two new species of amphipodous crustaceans.—-Annals and Magazine of Natural History, series 5, 2:364–370, pl. 15.

———. 1906. Amphipoda I. Gammaridea.—Das Tierreich 21:1–806, 127 figs.

Stephensen, K. 1938. The Amphipoda of N. Norway and Spitsbergen with adjacent waters.—Tromso Museums Skrifter 3:141–278, figs. 20–31.

USA National Bureau of Standards. ISCC-NBS Centroid Color Charts Standard Sample No. 2106. Supplement to NBS Circular 553. (Version with 257 colors.)

(JDT) Reef Foundation, P.O. Box 569, Big Pine Key, Florida 33043; (JLB) NHB-163, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 624–632

THE JAPANESE AMPHIPOD GENUS *EONIPHARGUS*, REDISCOVERED IN A SOUTH KOREAN CAVE

Jan H. Stock and Young Won Jo

Abstract.—*Eoniphargus*, a monotypic genus, known only from the Tokyo area, Japan, has been rediscovered in cave waters of South Korea. The Korean animals are a new species, *E. glandulatus*, which bridges to a certain extent the gap between *Eoniphargus* and the Indian genus *Indoniphargus*. Their morphology indicates that these genera are more closely related to the Gammaridae than to the Crangonyctidae.

Among a number of stygobiont amphipods collected by the junior author in cave waters of South Korea, a representative of a new species was discovered belonging to a small group of two monotypic genera, *Eoniphargus* Uéno, 1955 (*Eoniphargus* was originally described as a subgenus of *Neoniphargus*, but was elevated to generic rank by Straškraba 1964), and *Indoniphargus* Straškraba, 1967. The former is known from a single locality near Tokyo (Japan), whereas the latter is known from the states of West Bengal and Orissa (India). The Korean taxon bridges to a certain extent the gap between *Eoniphargus* and *Indoniphargus*: of the ten discriminating characters, three agree better with *Indoniphargus*, whereas seven correspond with *Eoniphargus* (Table 1). The resemblance to *Eoniphargus* bears amongst others on the shape of the gnathopods 1 and 2, and the armature of the inner and outer lobes of maxilla 1, both considered of prime importance in amphipod taxonomy. The resemblance to *Indoniphargus* bears on "weak" characters (urosome spination, number of segments in the accessory flagellum, absence of calceoli), known to be variable, sometimes even at infraspecific level. Therefore, the Korean form has been attributed to *Eoniphargus* rather than to *Indoniphargus*.

Eoniphargus and *Indoniphargus* have often been thought related to the crangonyctids or crangonyctoids (e.g., Bousfield 1977:table VI, Bousfield 1982:262, Straškraba 1964:table I, Straškraba 1967). Barnard & Barnard (1983) classify *Eoniphargus* near the gammarids, but *Indoniphargus* near the melitids. Clearly enough, and contrary to what the generic names suggest, these genera are not closely related to the Niphargidae. In our opinion, several points in their morphology prohibit inclusion in the crangonyctids s.l. (= superfamily Crangonyctoidea Bousfield), e.g., the asymmetrical palps of left and right maxillae, the occurrence of spines on the urosome, the 'eulimnogammarid' shape of the gnathopods of *Eoniphargus*, the absence of sternal gills, the absence of a coxal gill on pereiopod 7, the absence of a double row of distally-notched spine teeth on the palm of the two gnathopods, the rather elongate third uropod, the occasional presence of calceoli described as shoe-shaped by Uéno (1955:fig. 1) on antenna 2 of the male. None of these characters alone is sufficient proof of a non-crangonyctid relationship, but in combination they probably show that *Eoniphargus* forms a subgroup of the gammarids (or gammaroids, if one believes in superfamilies in this group).

Eoniphargus glandulatus, new species

Material.—1 ♀ (holotype), 1 ♂ (allotype), 4 paratypes. South Korea, Ondal-gul (gul = cave), Prov. Choongbuk, Danyang-gun,

Table 1.—Comparison of some salient characters of the new Korean taxon (K), *Indoniphargus indicus* (I), and *Eoniphargus kojimai* (E).

	K	I	E
Armature urosomites	spines + setules	spines + setules	setules
A1, acc. flag.	1-segmented	2-segmented	4-segmented
A2 ♂, calceoli	absent	absent	present
Distal segm. Md. palp	long	short	long
Mx.1, inner lobe	broad, with 11 setae	finger-shaped, with 2 setae	broad, with 8 setae
Mx.1, outer lobe	10 spines	8 spines	10 spines
Mx.2, inner lobe, oblique row of setae	present	absent	present
Gn.1 & 2, carpus	non-lobate	lobate	non-lobate
Gn.1 & 2, propodus	elongate	mittenform	elongate
Peduncle uropod 1, ventral spine(s)	absent	present	absent

Youngchoon-myeon, Ha-ri (128°30′E, 37°04′N); pools of 10–20 cm deep in limestone cave, 50–120 m from entrance (dim light to complete darkness); water temperature 12.5°C; 11 Oct 1986; leg. Y. W. Jo and H. J. Lee, ZMA Amph. 108.633.

Description.—Body length of ♀ up to 6 mm, ♂ 4.5 mm. Blind, colourless in alcohol. Body shape as in Fig. 1a. Lateral lobe of head rounded (Fig. 1b); antennal sinus very shallow. Coxal plates 1 to 4 deep, 5 to 7 shallow. Dorsum of metasome with a few setules. Urosomite 1 with variable armature: 1 lateral spine + 1 dorsal setule or 1+1 setules; urosomite 2 with 2 lateral spines, sometimes 1 additional lateral setule, and 1 dorsal setule; urosomite 3 unarmed (Fig. 1h).

Antenna 1 (Fig. 1c): Peduncle segment 1 longest; segment 2 slightly longer than 3. Flagellum with up to 25 segments; short aesthetascs on segments 5 to 22. Accessory flagellum slightly longer than first flagellum segment, 1-segmented.

Antenna 2 (Fig. 1d) with very long, tapering gland cone. Peduncle segments 4 and 5 thin and slender. Flagellum 7-segmented. Calceoli absent (♂, ♀).

Upper lip (Fig. 3c) rounded. Lower lip (Fig. 3d) without inner lobes.

Mandible (Fig. 2a): Molar setae present both on right and left appendage; left lacinia mobilis 5-dentate; right lacinia bifid; 3 spines + 3 plumose setae between molar and incisor of left mandible, 2+2 right. Palp (Fig. 2b) strong; segment 1 unarmed; segment 2 with row of about 10 ventrodistal setae; segment 3 with regular row of c. 15 D-setae, 1 B-setule, 4 E-setae, but without A- or C-setae.

Maxilla 1 (Fig. 2c, d): Palps asymmetrical (left more slender, with 5 slender spines and 1 seta; right more robust, with 6 robust spines and 1 seta). Outer lobe with 10 distal spines, each spine with 4 to 10 medial denticles. Inner lobe rounded-triangular, with 11 plumose setae on medial margin.

Maxilla 2 (Fig. 2e) with oblique row of 14 strong setae on inner lobe.

Maxilliped (Fig. 2f): Inner lobe with 3 short, robust distal spines. Outer lobe with 5 mediodistal spines; medial margin setose.

Gnathopods 1 and 2 with very slight sexual dimorphism (propodus in ♂ slightly larger in size than in ♀; palmar margin in ♂ with more setules than in ♀; largest palmar angle spine of Gn.2 longer in ♂ than in ♀).

Gnathopod 1 (Fig. 3a): Basis with 3 anterior and 5 posterior setae. Carpus unlobed. Propodus of similar shape in both

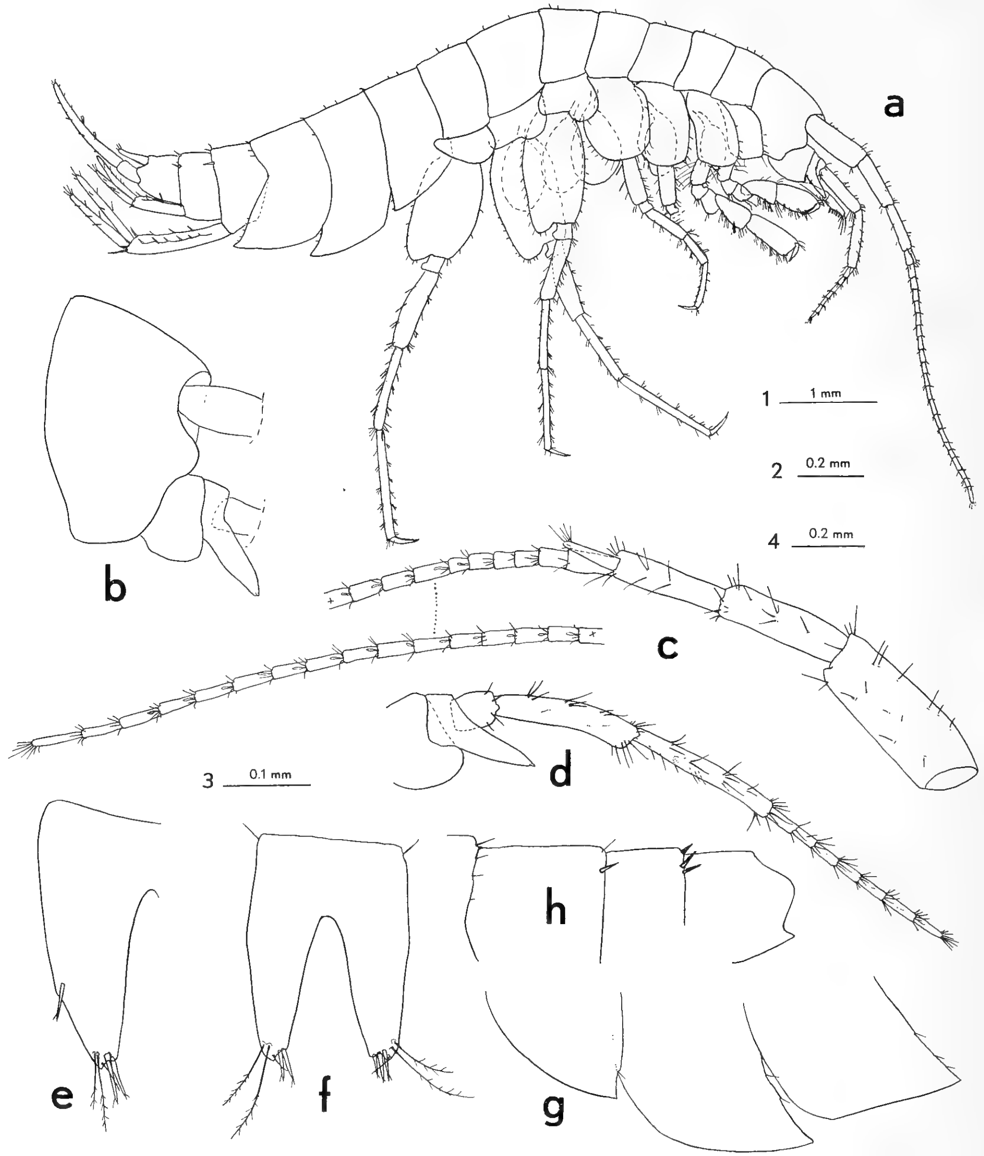


Fig. 1. *Eoniphargus glandulatus:* a, female, from the right, pleopods omitted (scale 1); b, head, ♀ (2); c, antenna 1, ♀ (2); d, antenna 2, ♀ (2); e, telson, left half, ♀ (3); f, telson, ♂ (3); g, epimeral plates, ♂ (2); h, contour of urosome, ♂ (4).

sexes, almost rectangular; 4 palmar angle spines (2 short, 1 medium, 1 very long); palmar margin with setules only (c. 6 in ♀, cf. Fig. 4a; c. 15 in ♂, Fig. 4b); claw slender; dactylus with 2 inner, 1 outer, and 3 distal setae; unguis shorter than dactylus.

Gnathopod 2 (Fig. 3b) slightly longer than Gn.1, but propodus "feebler" in appearance than that of Gn.1. Basis with 2 anterior and 7–9 posterior setae. Carpus more elongate than that of Gn.1. Propodus very narrow and slender in both sexes. Palmar angle with

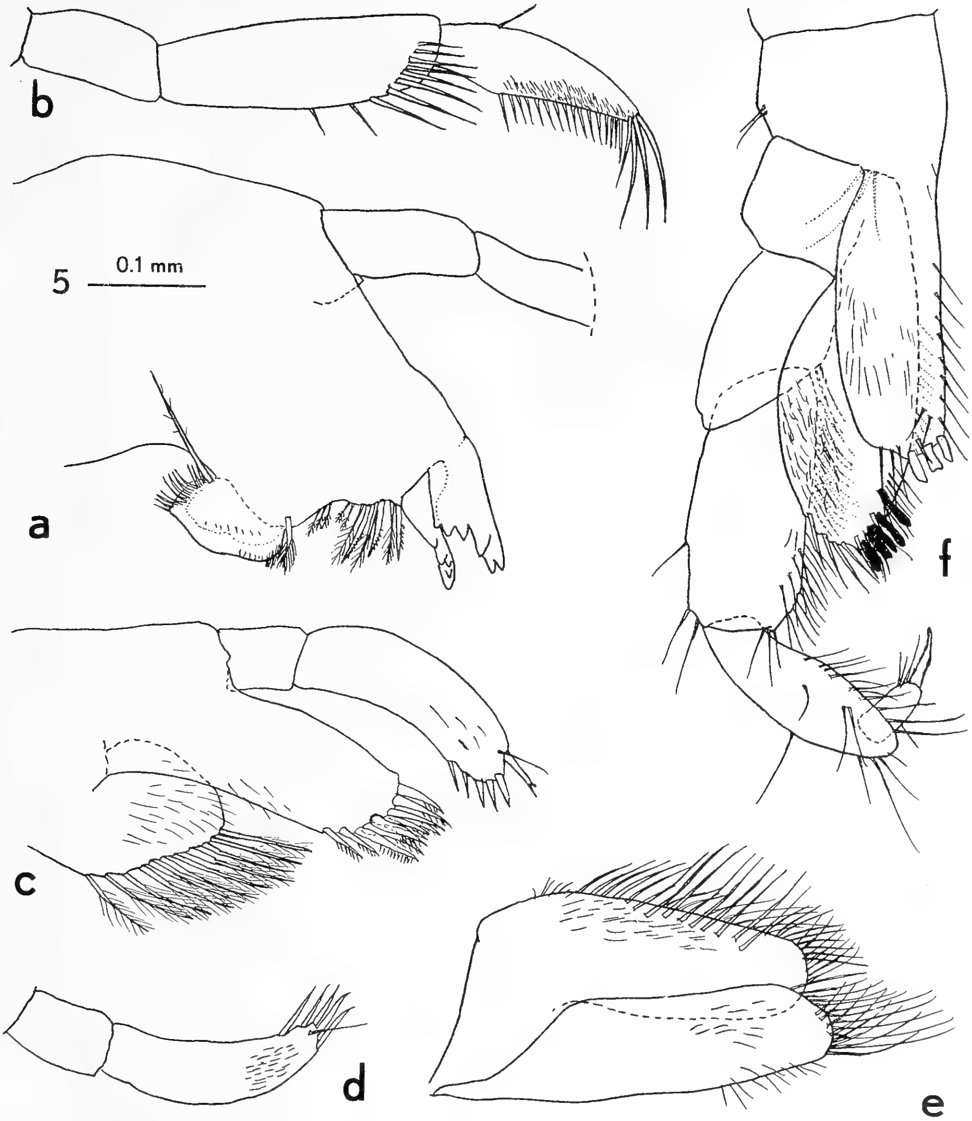


Fig. 2. *Eoniphargus glandulatus* ♀: a, left mandible; b, right mandibular palp; c, right maxilla 1; d, palp of left maxilla 1; e, maxilla 2; f, maxilliped. All scale 5.

4 spines (1 very long); palmar margin with setules only (c. 10 in ♀, Fig. 4c; c. 14 in ♂, Fig. 4d). Armature of claw as in Gn.1.

Pereiopod 3 (Fig. 5a) with long and narrow coxal plate. Distal segment poorly setose/spinose. Claw thin and slender. Coxal plate 4 (Fig. 5b) with shallow posterior emargination; remaining segments of P4 as in P3.

Pereiopods 5 and 6 (Fig. 5c, e) broken in all specimens examined (reconstructed from the fragments in Fig. 1a). P5 shorter than P6, P7 longer than P6. Basis of P5 to P7 with strong posteroventral lobe. Dactylus

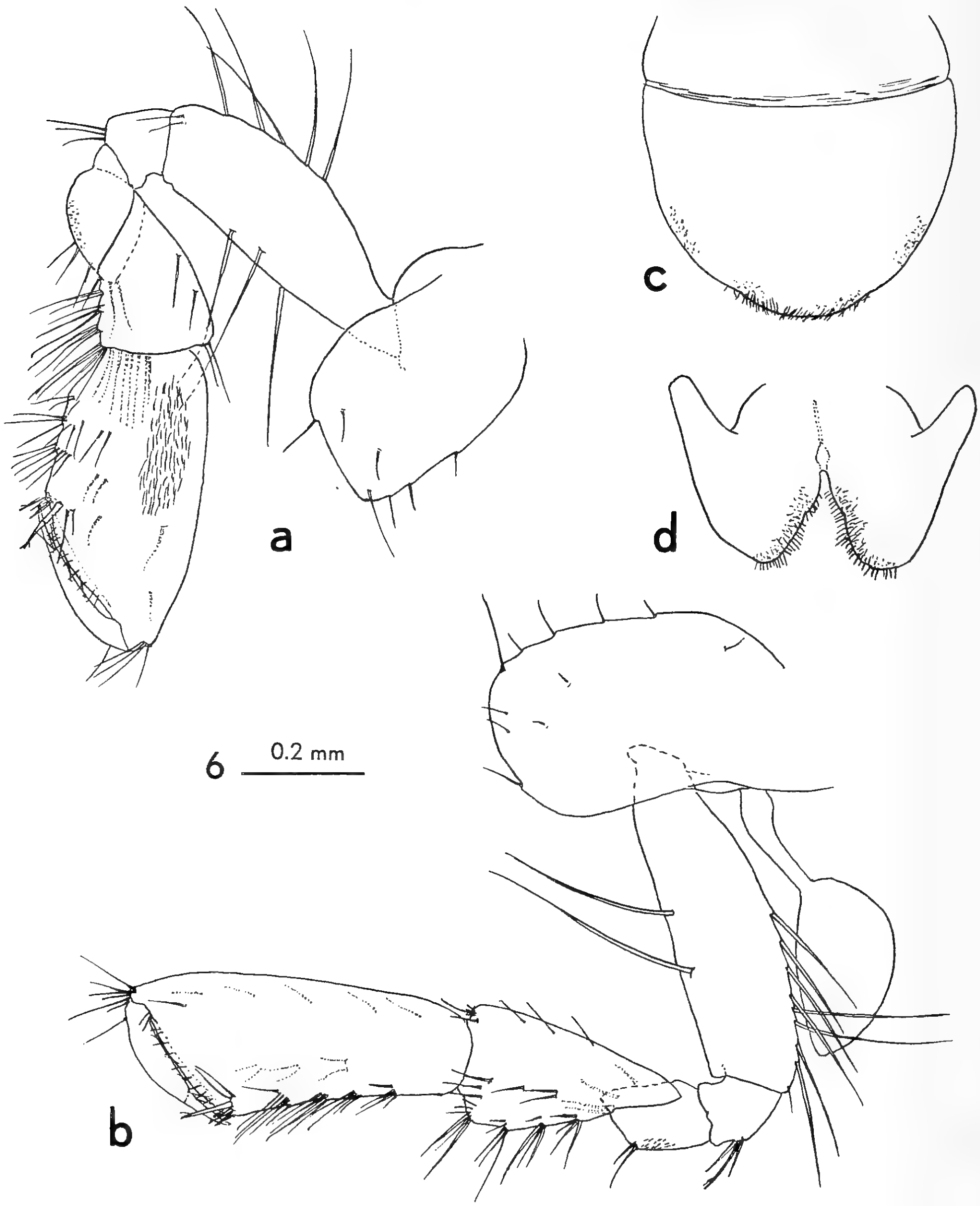


Fig. 3. *Eoniphargus glandulatus:* a, gnathopod 1, ♂ (scale 6); b, gnathopod 2, ♂ (6); c, upper lip, ♀ (5); d, lower lip, ♀ (6).

thin and slender, unguis small (Figs. 5c, 6d). Basis practically without sexual dimorphism (Fig. 5d).

Coxal gills large, ovate, with long basal stalk, present on Gn.2 and P3 through P6. No sternal gills. Oostegites linear, non-setiferous (diapause stage), but with scars indicating insertion of c. 8 setae on margins of distal part (Fig. 5a); present on Gn.2 and P3 through P5.

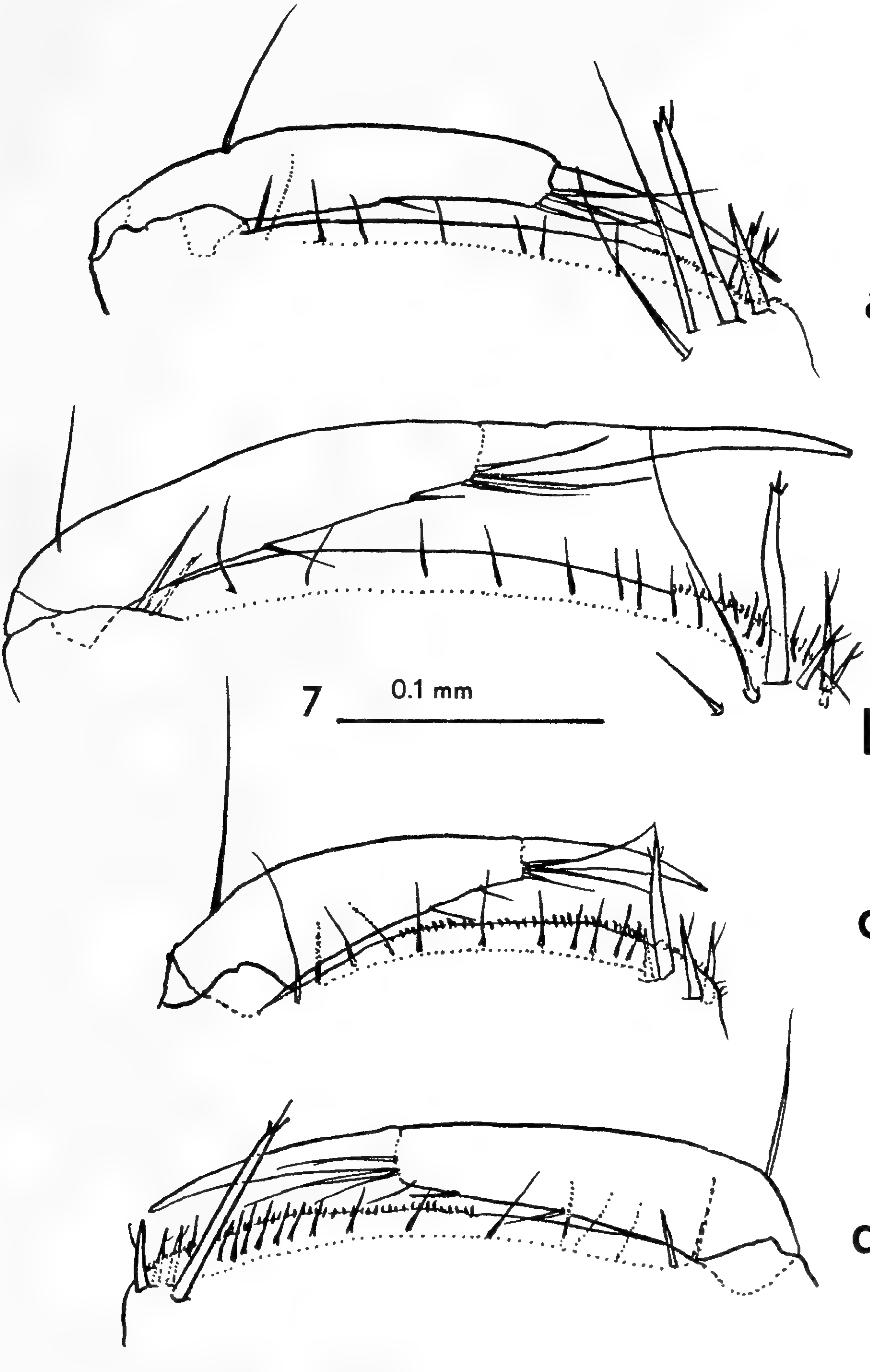


Fig. 4. *Eoniphargus glandulatus:* a, palma of gnathopod 1, ♀; b, palma of gnathopod 1, ♂; c, palma of gnathopod 2, ♀; d, palma of gnathopod 2, ♂. All scale 7.

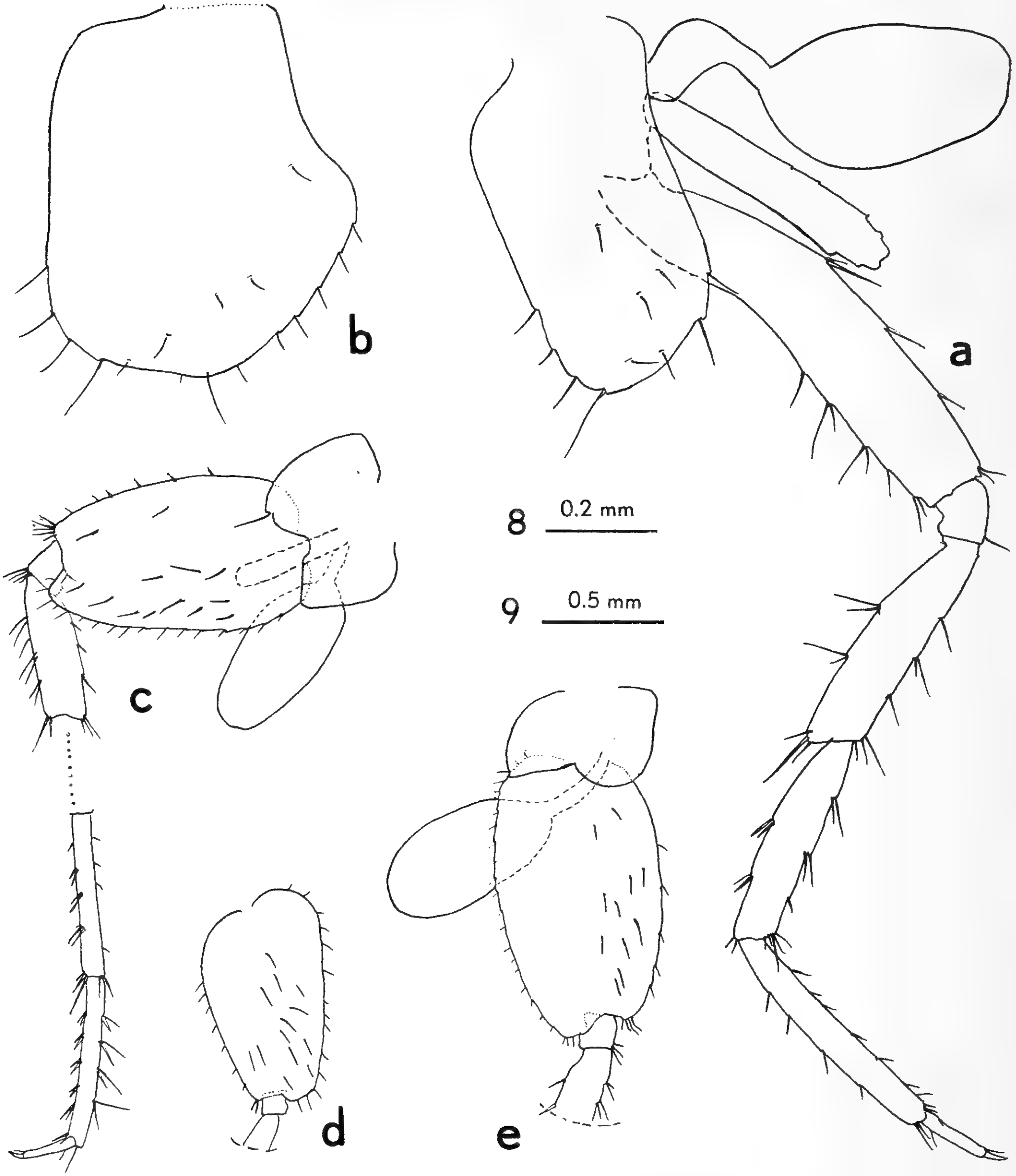


Fig. 5. *Eoniphargus glandulatus:* a, pereiopod 3, ♀ (scale 8); b, coxal plate of pereiopod 4, ♀ (8); c, pereiopod 5, ♀ (9); d, basal segments of pereiopod 5, ♂ (9); e, basal segments of pereiopod 6, ♀ (9).

Epimeral plates with angular posteroventral corners (Fig. 1g), unarmed ventral margins and 1 to 3 setules on posterior margin.

Pleopod peduncle with 2 retinacula (Fig. 6c), shorter than rami. Pleopod 1: both rami 11-segmented. Pleopods 2 and 3 with 11-segmented exopodite and 10-segmented endopodite. All setae of pleopod rami feathered, no clothes-peg spines.

Uropod 1 (Fig. 6a): Peduncle without proximoventral spine; 1 distomedial and 2 distolateral spines; 2 rows of 3 to 6 dorsal

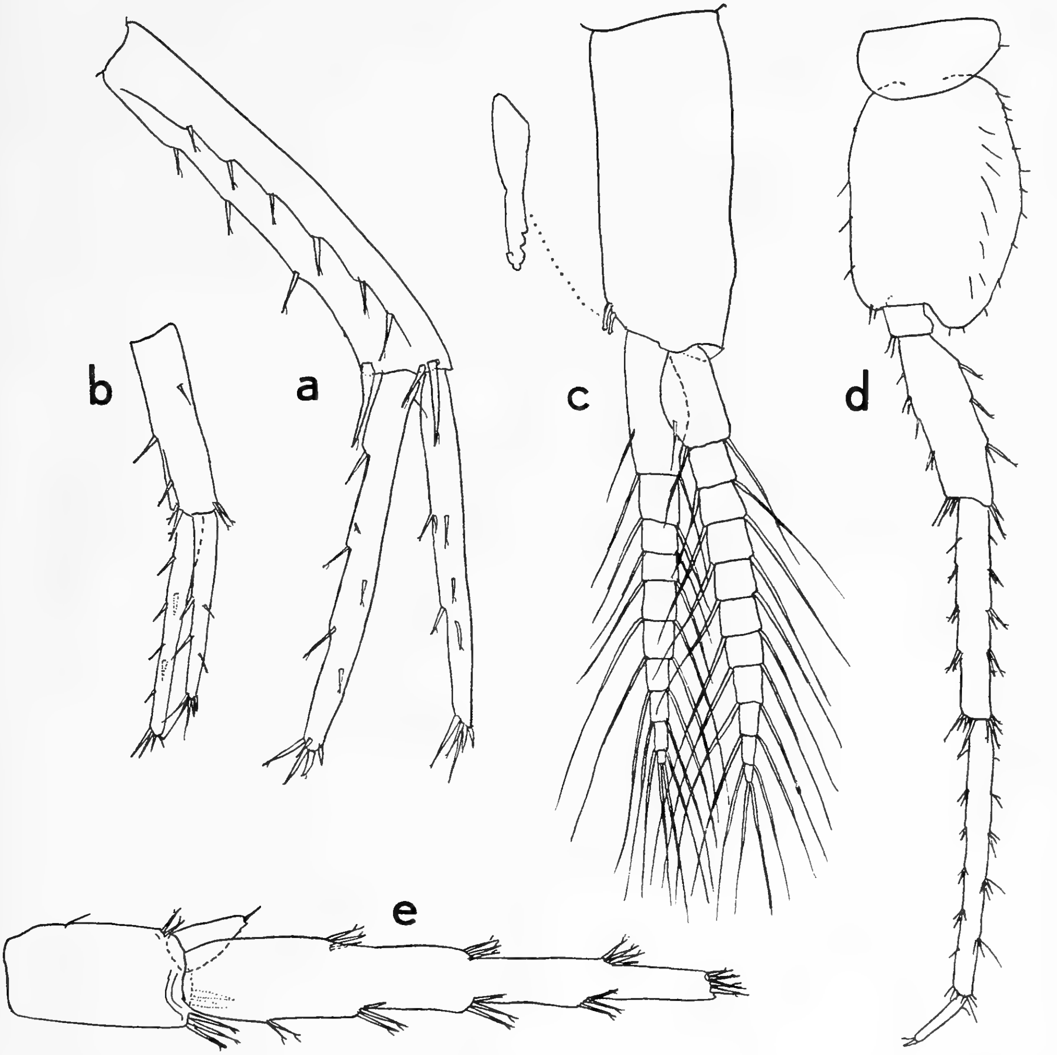


Fig. 6. *Eoniphargus glandulatus* ♀: a, uropod 1 (scale 8); b, uropod 2 (8); c, pleopod 2 (8); d, pereiopod 7 (9); e, uropod 3 (6).

spines. Exopodite slightly shorter than endopodite, both rami with dorsal, lateral and distal spines.

Uropod 2 (Fig. 6b) much shorter than U1, with proximal peduncular spine, but otherwise rather similar.

Uropod 3 (Fig. 6e) not sexually dimorphous, reaching far beyond tip of uropod 1 (Fig. 1a). Exopodite 1-segmented, terminal margin truncate with 4 spines; 4 groups of lateral spines and 3 groups of medial spines; no setae. Endopodite scale-like, small, with 1 distal setule and a minute laterodistal notch.

Telson (Fig. 1e, f) deeply incised (over about 70% of its length); cleft V-shaped, rather wide. Armature variable: a lateral spine may be present or absent; distal armature of each telson lobe consisting of 2 or 3 spines and 1 setule; 2 long, plumose ("sensorial") setae distolaterally on each lobe.

Discussion.—The Korean taxon differs from *Indoniphargus indicus* (Chilton 1923) in the characters listed in Table 1 (see also Straškraba 1967 and Stephensen 1931). From the only species known of *Eoniphargus, E. kojimai* Uéno, 1955, it differs in (1) the monomerous accessory flagellum (4-segmented in *E. kojimai*); (2) the absence of calceoli on the male second antenna; (3) the shape of the exopodite of uropod 3 (with acuminate, unarmed distal end in *E. kojimai*; with truncate, spinose distal end in the new species); (4) the very strongly elongated antennal gland cone; (5) a slightly less elongate carpus of gnathopod 2; (6) the presence of spines on urosomites 1 and 2 (setules only in *E. kojimai*); (7) shorter aesthetascs on the flagellum of antenna 1.

Character states (1) and (2) are frustrating since they are often considered of some taxonomic value. However, the presence or absence of calceoli is a variable character in the genus *Gammarus* (e.g., *G. insensibilis* is permanently devoid of calceoli, cf. Stock 1967, whereas in *G. fossarum* certain populations lack calceoli, cf. Goedmakers 1972). Apparently, the new species is apomorphous in character states (1) and (2), in comparison with *Eoniphargus kojimai.*

Etymology.—The specific name is based on *glandula* (Latin = gland), alluding to the large size of the antennal gland.

Literature Cited

Barnard, J. L., & C. M. Barnard. 1983. Freshwater Amphipoda of the world. Hayfield Associates, Mt. Vernon, Virginia, 1, 2:830 pp.

Bousfield, E. L. 1977. A new look at the systematics of gammaroidean amphipods of the world.—Crustaceana, Suppl. 4:282–316.

———. 1982. Amphipoda. Pp. 254–293 *in* S. P. Parker, ed., Synopsis and classification of living organisms. McGraw-Hill, New York.

Chilton, C. 1923. A blind amphipod from a mine in Bengal.—Records of the Indian Museum 25(2): 195–196.

Goedmakers, A. 1972. *Gammarus fossarum* Koch, 1835: redescription based on neotype material and notes on its local variation (Crustacea, Amphipoda).—Bijdragen tot de Dierkunde 42:124–138.

Stephensen, K. 1931. *Neoniphargus indicus* (Chilton), an Indian fresh-water amphipod.—Records of the Indian Museum 33:13–19.

Stock, J. H. 1967. A revision of the European species of the *Gammarus locusta*-group (Crustacea, Amphipoda).—Zoölogische Verhandelingen Leiden 90:3–56.

Straškraba, M. 1964. *Perthia* n. g. (Amphipoda, Gammaridae) from fresh water of western Australia, with remarks on the genera *Neoniphargus* and *Uroctena.*—Crustaceana 7(3):125–139.

———. 1967. Re-examination of the taxonomic status of *Neoniphargus indicus* Chilton (Amphipoda, Gammaridae) and its zoogeographical relations.—Proceedings of the Symposium on Crustacea, Ernakulam 1:126–132.

Uéno, M. 1955. Occurrence of a freshwater gammarid (Amphipoda) of the *Niphargus* group in Japan.—Bulletin of the Biogeographical Society of Japan 16:146–152.

Institute of Taxonomic Zoology, University of Amsterdam, P.O. Box 4766, 1009 AT Amsterdam, The Netherlands.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 633–642

TAXONOMIC REMARKS ON *SCHIZOBOPYRINA* MARKHAM, 1985, WITH THE DESCRIPTION OF *S. BRUSCAI* (CRUSTACEA: ISOPODA: BOPYRIDAE)

Ernesto Campos and Alma Rosa de Campos

Abstract.—*Schizobopyrina striata* (Nierstrasz & Brender à Brandis, 1929) that infests *Thor algicola* Wicksten, 1987 is reported from the Golfo de California, México. The morphology of the female examined agrees well with that of the lectotype female from San Diego Bay, California. *Schizobopyrina bruscai* is described from a single adult female collected in Bahía Concepción, Baja California Sur, México. This species is a parasite of a new species of *Thor.* It differs from other species of *Schizobopyrina* principally in the pleomeres and pleotelson morphology. In addition, we suggest *Bopyrina platylobata* Bourdon, 1983, from Seram, Seleman Bay and Queensland, should be included within *Schizobopyrina,* and *S. lobata* Bourdon & Bruce, 1983, from Queensland, should be redescribed in order to determine whether this species is correctly placed within this genus.

Resûmen.—El isópodo bopírido *Schizobopyrina striata* (Nierstrasz & Brender á Brandis, 1929) se registra como parásito del camarón carídeo *Thor algicola* Wicksten, 1987 en el Golfo de California. La morfología de la hembra corresponde a la del lectotipo colectado en San Diego Bay, California, EEUU. *Schizobopyrina bruscai* se describe en base a un espécimen hembra adulto que se colectó en Bahía Concepción, Baja California Sur, México. Esta especie es parásita de una especie indescrita de *Thor.* Difiere de otras especies del género *Schizobopyrina* principalmente en morfología de los pleómeros y pleotelson. Adicionalmente se sugiere que *Bopyrina platylobata* Bourdon, 1983, de Seram, Bahía de Seleman y Queensland, debe ser asignada al género *Schizobopyrina,* y que *S. lobata* Bourdon & Bruce, 1983, de Queensland, necesita redescribirse a fín de establecer si su inclusión a este género es correcta.

Markham (1985) proposed the genus *Schizobopyrina* to include 10 species that had been assigned formerly to the closely allied genus *Bopyrina* Kossman, 1881. *Schizobopyrina* has a maxilliped palp, elongate second through fifth oostegites, and at least lateral separation of the six pleomeres. These features contrast with the lack of maxilliped palp, tiny oostegites 2–5 and fusion of pleomeres on the short side in *Bopyrina.* Two species of *Schizobopyrina* have been recorded from American waters only. The type species, *Schizobopyrina urocaridis* (Richardson, 1904), was collected from North Carolina, western Florida, and Belize, while *S. striata* (Nierstrasz & Brender à Brandis, 1929) has been recorded only from San Diego Bay, California (Nierstrasz & Brender à Brandis 1929, Markham 1985).

In the present note we extend the known distribution, report a new host and give additional morphological information for *S. striata,* a species that apparently has not been collected since its description. Concomitantly, a new northeastern Pacific species of *Schizobopyrina* is described.

These species records increase from 12 to 14 the number of bopyrid species reported from the Mexican Pacific (Campos & Campos 1989). In addition, some comments on taxonomy of the Australian species *S. lobata* Bourdon & Bruce, 1983 and *Bopyrina platylobata* Bourdon, 1983 are included. Specimens of *S. striata* and *Schizobopyrina bruscai* described herein have been deposited in the Collection of Invertebrates, Escuela Superior de Ciencias, Universidad Autónoma de Baja California. The terms posteroventral border of head and spur described by Markham (1985) are respectively herein referred as barbula and plectron in agreement with Markham (1988). Information recorded in Table 1 was obtained from the below-noted descriptions and papers of Chopra (1923); Nierstrasz & Brender à Brandis (1923); Shiino (1933, 1939a, 1939b, 1942); Bourdon (1983); Bourdon & Bruce (1983); and Markham (1985).

Schizobopyrina striata
(Nierstrasz & Brender à Brandis, 1929)
Figs. 1, 2

Bopyrina striata Nierstrasz & Brender à Brandis, 1929:40–42, figs. 51–53.

Schizobopyrina striata.—Markham, 1985: 46.

Distribution.—San Diego Bay, California (type locality); upper Golfo de California (new record, herein).

Hosts recorded.—Caridea-Hippolytidae: *Hippolyte californiensis* Holmes, 1895.

Material examined.—One female, Puertecitos, Golfo de California, Baja California, km 72 road San Felipe-San Luis Gonzága 30°30′N, 114°40′W, 23 May 1986, lower midlittoral, E. Campos coll.

New host.—Rubén Ríos (pers. comm.) noted that the host of *S. striata* agrees well with description of *T. algicola* Wicksten, 1987; however, he suggested that Wicksten's species should be considered as a junior synonym of *T. manningi* Chace, 1972. A discussion of this topic will be published by R. Ríos (in prep.).

Description.—Female (Fig. 1A, B). Length 4.0 mm, maximum width 2.0 mm, head length 0.8 mm, pleon length 0.9 mm, body axis distortion 126°.

Head roughly triangular, separated from pereon by a deep groove. Large and indistinctly set-off frontal lamina extending into sub-triangular points and notched on shorter side of body; frontal lamina with medial extensions. Antennae tiny, obscure. Maxilliped (Fig. 2A) with setose palp well developed, articulating with margin (Fig. 2B). Barbula medially produced, with two blunt projections on each side (Fig. 2C). Seven well defined pereomeres dorsally and laterally, inconspicuous ventrally. Coxal plates on pereomeres 1–4 of both sides; dorsolateral bosses on pereomeres 1–4 of long side. Pereopods subequal, increasing slightly in length posteriorly, seventh pereopod with bilobed and pseudoarticulated merus (Fig. 2D). First pair of oostegites asymmetrical (Fig. 2E); right one with falcate posterolateral point, left one with larger and sickle-shaped posterolateral point; internal ridges of both first oostegites unadorned.

Pleon with 5 medially fused pleomeres and pleotelson, latter deeply arcuate and embedded in the fifth pleomere. Four pairs of lanceolate uniramous pleopods; ventral surface of lateral plates of long side bearing tuberculiform projections decreasing posteriorly, conical on first four pleomeres, rounded on fifth one. On short side such projections are not evident. No uropods.

Remarks.—*Schizobopyrina striata* is the only species of this genus recorded from the East Pacific (Markham 1985). It was described by Nierstrasz & Brender à Brandis (1929) from specimens collected in San Diego Bay, California. There are no additional published records to our knowledge. Morphologically our female specimen (Fig. 1A, B) is almost identical to that described and figured in 1929 by Nierstrasz & Brender à

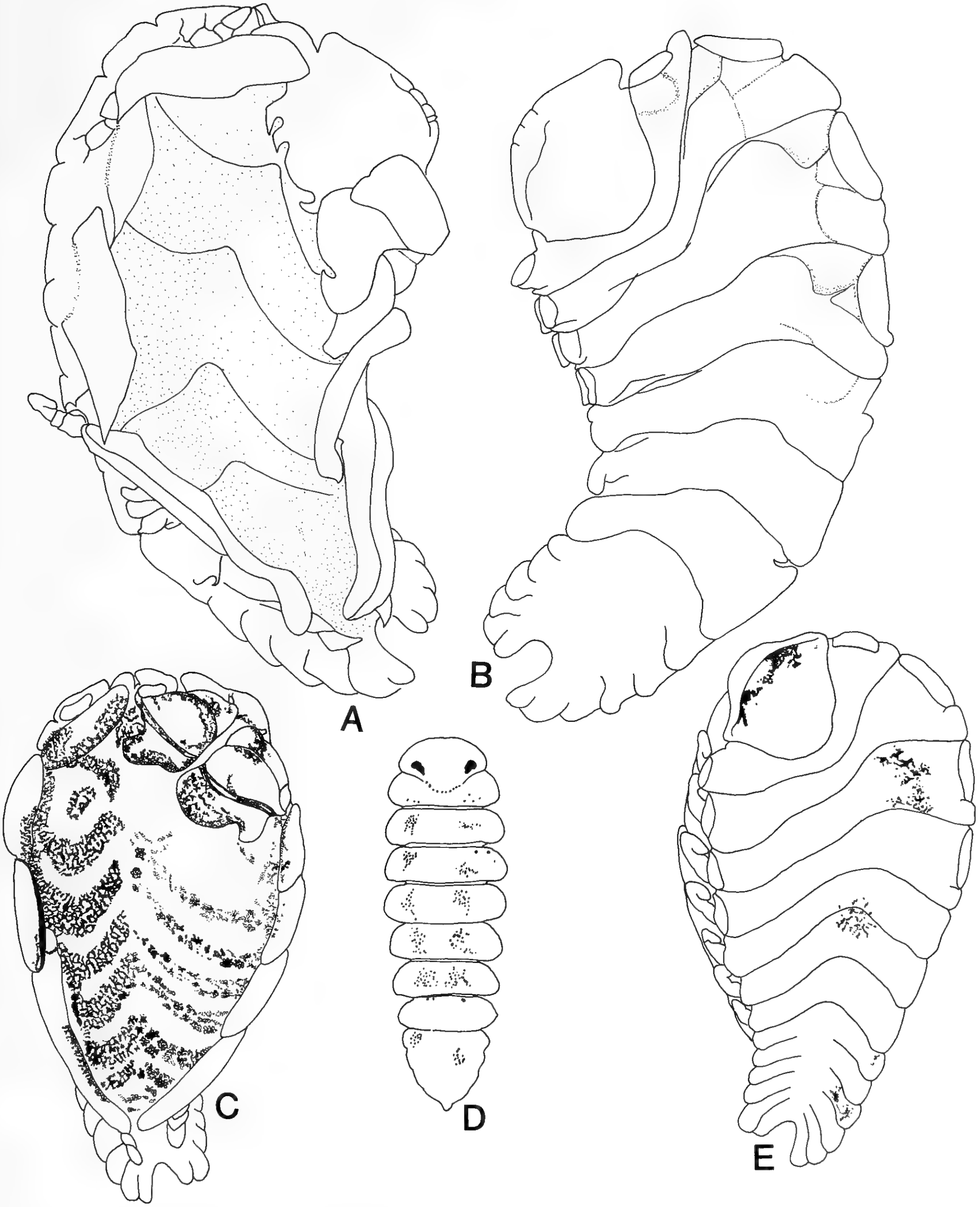


Fig. 1. *Schizobopyrina striata* (Nierstrasz & Brender à Brandis, 1929): A, C, Female ventral view; B, E, Female dorsal view; D, Male. (C–E redrawn from Nierstrasz & Brender à Brandis 1929).

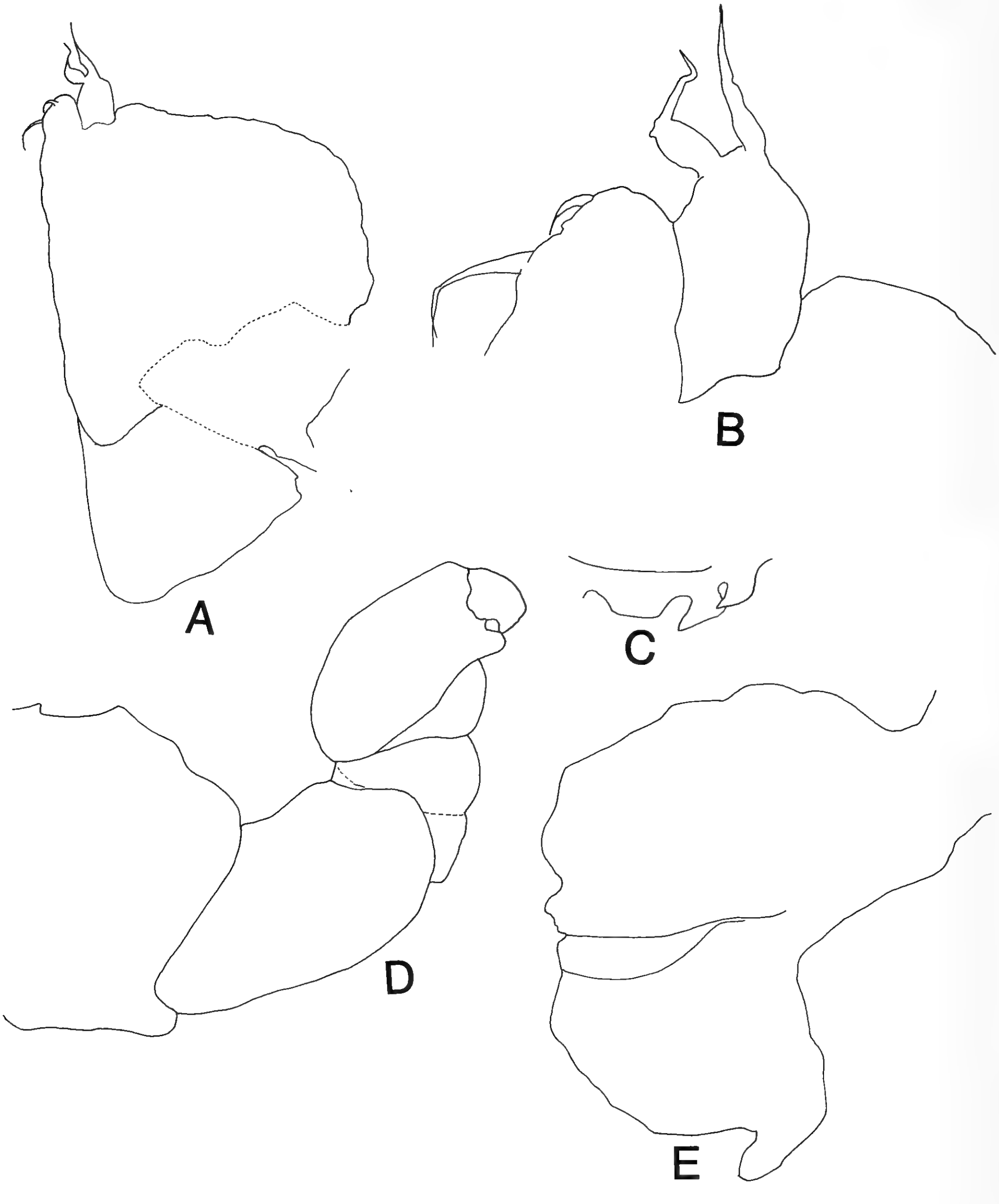


Fig. 2. *Schizobopyrina striata* (Nierstrasz & Brender à Brandis, 1929), Female: A, Maxilliped; B, Maxilliped palp; C, Barbula; D, Pereopod 7; E, Left oostegite 1.

Brandis (fig. 1C, D). Differences occur in the body distortion (126° in our specimen, 85° in the lectotype); the festoons of the frontal lamina (lacking in the lectotype); and the degree of pleonal fusion (more complete in our female). Since we did not collect a male specimen, the original description and figure given by Nierstrasz & Brender à Brandis (1929) is reproduced here (Fig. 1E). The features that they recorded are the following: "mit Augen; Pigmentierung wie auf def Abbildung; Grenze zwischen Cephalon und

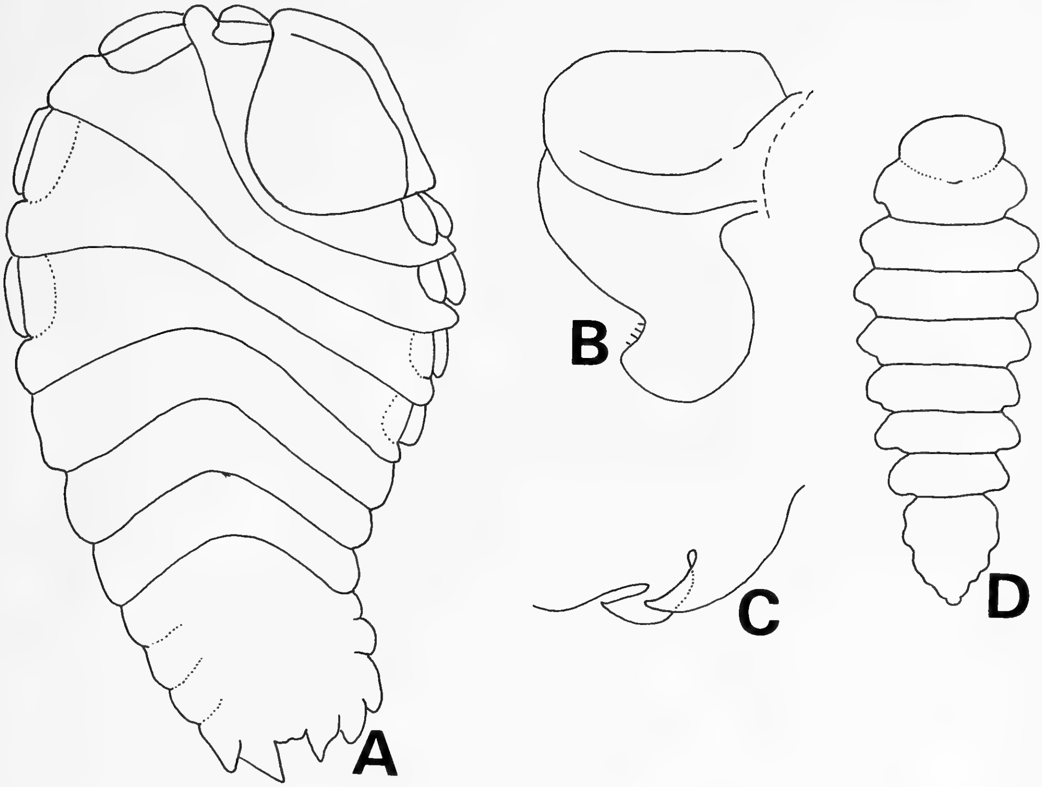


Fig. 3. *Schizobopyrina platylobata* (Bourdon, 1983): A, Female dorsal view; B, Right oostegite 1; C, Barbula; D, Male dorsal view (all redrawn from Bourdon 1983).

Thoracomer II nicht deutlich; Pleon mit kleinem caudalen Fortsatz; Pleomere und Pleotelson verwachsen, I und II aber seitlich angedeutet" (= with eyes; pigmentation as in the illustration. Border between cephalon and first pereomere not clear; pleon with a small caudal process; pleomeres and pleotelson fused, however I and II indicated laterally).

Schizobopyrina platylobata
(Bourdon, 1983), new combination
Fig. 3

Restricted synonymy:

Bopyrina platylobata Bourdon, 1983:867–869, fig. 13a–d.—Bourdon & Bruce, 1983: 99.

Remarks.—Based on the original descriptions and figures recorded in Bourdon (1983) we suggest this species should be included within *Schizobopyrina.* The female (Fig. 5A–C) has (1) the frontal lamina evident, (2) the maxilliped with palp, (3) the barbula with two lanceolate projections, (4) dorsolateral bosses and coxal plates on pleomeres 1–4, (5) elongated oostegites 2–5, and (6) five pairs of laterally indicated pleomeres and pleotelson. The exclusion of *S. platylobata* from *Bopyrina* Kossmann 1881 is because females in this genus have a maxilliped without palp, tiny oostegites 2–5 and complete pleomeral fusion on the short side of body. These features are lacking in *S. platylobata.* The male of this species (Fig. 3D) is almost identical to those described within *Schizobopyrina.*

Schizobopyrina(?) *lobata* Bourdon & Bruce, 1983

Restricted synonymy:

Bopyrina lobata Bourdon & Bruce, 1983: 100–101, fig. 3a–d.—Markham, 1985:46.

Remarks.—Bourdon & Bruce (1983) described this bopyrid and pointed out that the generic position of this species will remain uncertain. Subsequently Markham (1985) excluded this species from *Bopyrina* and included it within *Schizobopyrina.* In agreement with Markham's first action we considered that this isopod is not a species of the genus *Bopyrina*; however, we found in the original description given by Bourdon & Bruce (1983) a partial support to Markham's second action. According to Bourdon & Bruce (1983) *S.*(?) *lobata* has a maxilliped apparently without palp (close to *Bopyrina*), the barbula with single pair of poorly developed projections (like *Bopyrina*) and lack of dorsolateral bosses and coxal plates (similar to *Bopyrina*). In contrast, *Schizobopyrina* possesses a maxilliped palp well defined, the barbula with two pairs of projections, and with dorsolateral bosses or coxal plates or both on pereomeres 1–4. However, the species *lobata* agree well with *Schizobopyrina* in other features, e.g., oostegites 2–5 elongate, pleomeres laterally indicated, frontal lamina visible. The above-mentioned similarities and dissimilarities may suggest this species is intermediate between *Schizobopyrina* and *Bopyrina,* but a redescription is necessary to resolve the systematics of this enigmatic species.

Schizobopyrina bruscai, new species
Figs. 4, 5

Material examined.—One female, holotype, Bahía Concepción, Golfo de California, south side of El Coyote beach, Baja California Sur, México, 26°44′N, 111°55′W, 2 m depth, 6 Oct 1981, Rubén Ríos coll.

Host. According to R. Ríos (pers. comm.) this host is conspecific with *Thor spinosus* recorded by Wicksten (1983) [not Boone 1935]. Ríos (pers. comm.) has found this cariden is an undescribed species of *Thor.*

Description.—Female (Fig. 4A, B). Length 2.2 mm, maximal width 1.1 mm, head length 0.5 mm, pleon length 0.7 mm, body axis distortion 85°.

Head distinct, moderately set into pereon; frontal lamina large, well differentiated from head, extended into lateral lobules, margin on short side of body slightly concave and notched. Antennae inconspicuous; barbula (Fig. 5A) medially produced, with 2 blunt projections. Maxilliped palp large, setose and obscurely articulated (Fig. 5B), plectron projecting, large and slender (Fig. 4C). Pereomeres distinctly separated dorsally and laterally, much less so ventrally. Coxal plates on pereomeres 1–4 of both sides. Dorsolateral bosses on pereomeres 1–4 of long side. Pereopods subequal, increasing a little posteriorly, each of the 7 articles well defined.

First oostegites asymmetrical, left one with posterolateral point short, slender and slightly hooked (Fig. 4D); right one large, broad and hook-shaped (Fig. 5C) internal ridge of both first oostegites slightly ornamented, with setae on distomedial margin. Oostegites 2–5 slender, fifth one larger.

Pleon (Fig. 5D) of 4 distinct pleomeres and pleotelson that are obscurely separated medially; pleotelson notched in middle; 4 pairs of leaf-like and uniramous pleopods diminishing in length posteriorly, first pair suboblong, last three pairs subovate. No uropods.

Distribution.—Known only from the type locality, El Coyote beach, Bahía Concepción, Baja California Sur, México.

Etymology.—This species is named in honor of Richard C. Brusca, for his scientific contributions to the knowledge of the marine fauna of the Golfo de California.

Remarks.—Markham's (1985) diagnosis of the genus *Schizobopyrina* was based on the type species and took into account all 10 species that he included within this ge-

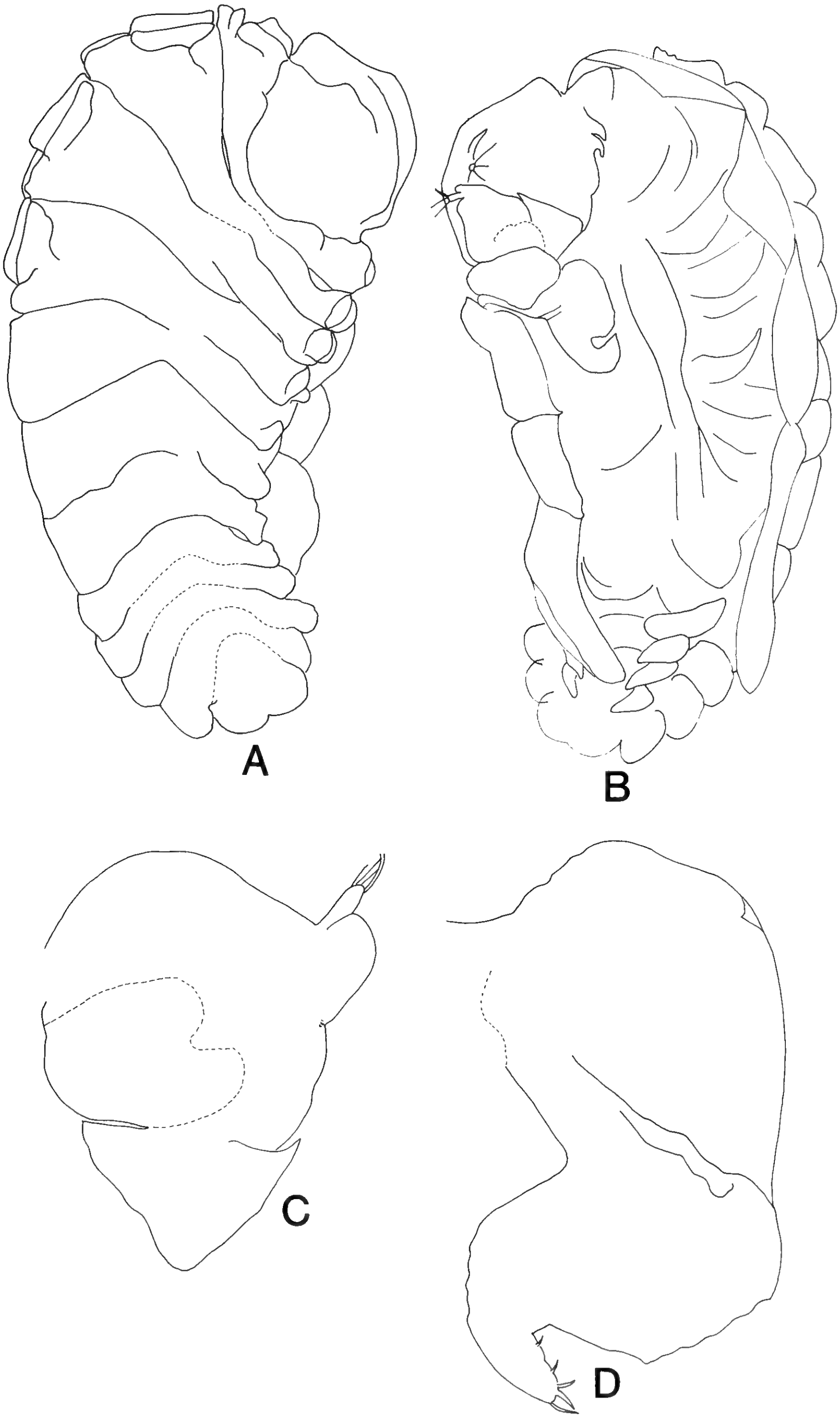


Fig. 4. *Schizobopyrina bruscai,* n. sp., Female holotype: A, Dorsal view; B, Ventral view; C, Maxilliped; D, Left oostegite 1.

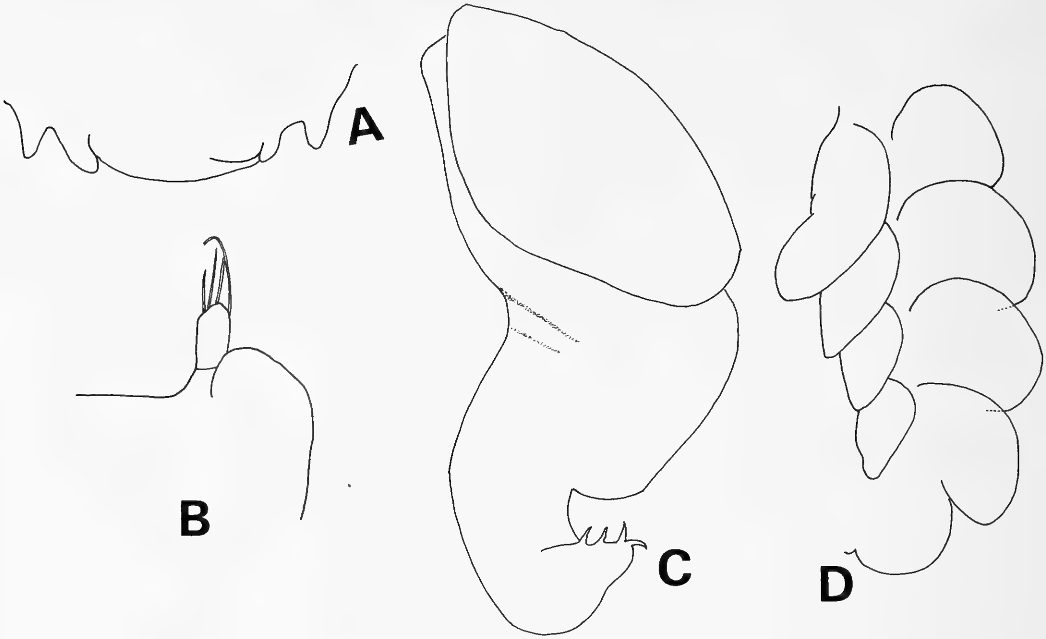


Fig. 5. *Schizobopyrina bruscai,* n. sp., Female holotype: A, Barbula; B, Maxilliped palp; C, Right oostegite; D, Pleon, ventral view.

nus. *Schizobopyrina bruscai* is similar to another congener in its frontal lamina, maxilliped palp, dorsolateral bosses, shape and number of oostegites and number of pleopods. Comparison of the *Schizobopyrina* species, including *S. bruscai,* is recorded in Table 1. *Schizobopyrina bruscai* principally differs from *S. amakusaensis* (Shiino, 1939) [from Amakusa, Kyusyu, Japan], *S. andamica* (Chopra, 1923) [from India and Japan], *S. brachytelson* (Nierstrasz & Brender à Brandis, 1923) [from Dangar, Besar, Saleh Bay], *S. gracilis* Chopra, 1923 [from India and Japan], and *S. lobata* (Bourdon & Bruce, 1983) [from off Caloundra, Queensland], in that the first species has the cephalon separated from the first thoracic somite (Fig. 4A), instead of fused as recorded in the last six species (Table 1). Furthermore, *S. bruscai* possesses 4 pleomeres and pleotelson, while these species, except *S. amakusaensis,* have 5 pleomeres and pleotelson. This last pleomeral trait is also observed in *S. cochinensis* (Chopra, 1923) [from Cochin, India], *S. platylobata* (Bourdon, 1983) [from Seram, Seleman Bay], *S. striata* (Nierstrasz & Brender à Brandis, 1929) [from California and Golfo de California, México) and *S. urocaridis* (Richardson, 1904) [from Atlantic coast of U.S. and Belize], and represents the most evident difference between these last four species and *S. bruscai.* Additional differences are recorded in Table 1.

Schizobopyrina bruscai differs from *S. miyakei* Shiino, 1939, from Palao and Australia, in the margin of pleotelson, bilobed-symmetrical in *S. bruscai,* and from obliquely-continuous to bilobed-asymmetrical in *S. miyakei.* Additionally, *S. bruscai* has the cephalon and first thoracic somite well separated by a deep groove, instead of fused with suture line indicated by a shallow groove as in *S. miyakei.* With regard to the diagnosis of *Schizobopyrina,* Markham (1985) pointed out that this genus possesses six distinct pleomeres (= 5 pleomeres and pleotelson). *S. amakusaensis, S. bruscai,* and *S. miyakei* have 4 pleomeres and pleotelson. This pleonal variation is analogous to that recorded in other genera of Bopyridae

Table 1.—Comparison of selected diagnostic features among species of *Schizobopyrina*. Species marked with (*) have the cephalon and pereomere 1 fused.

	Dorsolateral bosses	Coxal plates	Abdominal pleomeres and pleotelson (PT)	Pleomere V	Margin of pleomere V	Pleotelson margin
S. amakusaensis (*)	present	present	4 + PT	No indicated	No indicated	Rounded continuous
S. andamica (*)	present	present	5 + PT	Extending far beyond telson margin	Angular	Rounded continuous
S. brachytelson (*)	present	present	5 + PT	Extending far beyond telson margin	Angular	Straight continuous
S. bruscai	present	present	4 + PT	No indicated	No indicated	Bilobed
S. cochinensis	indistinct	present	5 + PT	No extending far beyond telson margin	Rounded	Rounded continuous
S. gracilis (*)	absent	present	5 + PT	Extending far beyond telson margin	Rounded	Straight continuous
S. kossmanni (*)	present	present	5 + PT	Slightly extending far beyond telson margin	Angular	Rounded sinuous
S. lobata (*)	absent	absent	5 + PT	No extending far beyond telson margin	Rounded	Asymmetrical bilobed
S. miyakei	present	present	3 + PT 4 + PT	No indicated	No indicated	Obliquely continuous or asymmetrical bilobed
S. platylobata	present	present	5 + PT	Extending far beyond telson margin	Angular	Bilobed
S. striata	present	present	5 + PT	No extending far beyond telson margin	Rounded	Concave continuous
S. urocaridis	present	present	5 + PT	Slightly extending far beyond telson margin	Rounded	Widely rounded

infesting caridean shrimps (e.g., *Bopyrina*, Markham 1985; *Bopyrione*, Bourdon and Markham 1980) and should be included in the diagnosis of *Schizobopyrina*.

Acknowledgments

We are grateful to Rubén Ríos (Centro de Investigación Científica y de Educación Superior de Ensenada) who allowed us to examine and describe *S. bruscai*, and gave us information about taxonomy of the species of *Thor* from the Golfo de California. We are indebted and deeply grateful to Roland Bourdon and John Markham for their support of our bopyrid studies. Our great appreciation is due to Roger Seapy for his criticism of the first draft of this note and to Lon McLanahan and Lady Janie Yeo Kirk for their support during our stay in California State University, Fullerton. This work was sponsored by project "Sistemática y bioecología de los Arthropoda dominantes en áreas selectas del municipio de Ensenada, Baja California" of the Escuela Superior de Ciencias, Universidad Autónoma de Baja California and by the agreement SEP-UABC 089-01-0352.

Literature Cited

Boone, L. 1935. Crustacea: Anomura, Macrura, Euphausiacea, Isopoda, Amphipoda and Echinodermata: Asteroidea and Echinoidea. *In* Scientific results of the world cruise of the yacht "Alva," 1931 William K. Vanderbilt, commanding.—-Bulletin of the Vanderbilt Marine Museum 6:1–264.

Bourdon, R. 1983. Expedition Rumphius II (1975) Crustacés parasites, commensaux, etc. (Th. Monod Ed.). VIII. Crustacés Isopodes (3e partie: Epicarides Bopyridae).—Bulletin du Muséum d'Histoire Naturelle, Paris, Serie 4, 5, Section A, 3:845–869.

———, & A. J. Bruce. 1983. Six bopyrid shrimps (Isopoda, Epicaridea) new to the Australian fauna.—Crustaceana 45:96–106.

———, & J. C. Markham. 1980. A new genus and species of bopyrid isopod infesting alpheid shrimps in the genus *Synalpheus* in the Eastern Atlantic Ocean.—Zoologische Mededelingen (Leiden) 55:221–230.

Campos, E., & A. R. de Campos. 1989. Epicarideos de Baja California: distribución y notas ecológicas de *Probopyrus pandalicola* (Packard, 1879) en el Pacífico oriental.—Revista de Biologia Tropical 37(1):29–36.

Chopra, B. 1923. Bopyrid isopod parasitic on Indian Decapoda Macrura.—Records of the Indian Museum 25:411–550.

Markham, J. C. 1985. A review of the bopyrid isopods infesting caridean shrimps in the northwestern Atlantic Ocean, with special reference to those collected during the Hourglass cruises in the Gulf of Mexico.—Memoirs of the Hourglass Cruises 7(3):1–156.

———. 1988. Description and revision of some species of Isopoda Bopyridae of the north Western Atlantic Ocean. Zoologische Verhandelingen, Leiden 246:1–63.

Nierstrasz, H. F., & G. A. Brender à Brandis. 1923. Die Isopoden der Siboga-Expedition. II. Isopoda Genuina. I. Epicaridea. Siboga-Expeditie Monography 32^{b}: 4 unnum + 1–65.

———, & ———. 1929. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. XLVIII. Epicaridea I.—Videnskabelgie Meddelelser fra Dansk Naturrhistorisk Forening i Kobenhavn 87:1–44.

Shiino, S. M. 1933. Bopyrid from Tanabe Bay.—Memoirs of the College of Science, Kyoto Imperial University, Series B, 7:249–300.

———. 1939a. A bopyrid from Palao.—Palao Tropical Biological Station Studies 24:598–601.

———. 1939b. Bopyrid from Kyusyu and Ryukyu.—Amakusa Marine Biological Laboratory 70:79–99.

———. 1942. Bopyrids from the South Sea Islands with description of a hyperparasitic cryptoniscid.—Palao Tropical Biological Station Studies 2:437–458.

Wicksten, M. K. 1983. A monograph on the shallow water caridean shrimps of the Gulf of California, Mexico.—Allan Hancock Monographs in Marine Biology 134:1–59.

(Postal address) Escuela Superior de Ciencias, Universidad Autónoma de Baja California, Apartado Postal 2300, Ensenada, Baja California, México; Department of Biological Sciences, California State University–Fullerton, Fullerton, California 92634.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 643–648

TRIDENTELLA WILLIAMSI, A NEW SPECIES OF ISOPOD CRUSTACEAN FROM THE BRITISH VIRGIN ISLANDS, WESTERN ATLANTIC (FLABELLIFERA: TRIDENTELLIDAE)

Paul M. Delaney

Abstract.—*Tridentella williamsi,* n. sp., described from the British Virgin Islands, is distinguished from other Atlantic species by its distinctively tuberculate pleotelson. A species list for the genus is given.

Previously only two *Tridentella* species have been described from the Atlantic, *T. virginiana* (Richardson, 1900) and *T. recava* Bowman, 1986. Herein a third Atlantic species, *T. williamsi,* is described from the tropical waters of the Virgin Islands, based on examination of specimens from the United States National Museum of Natural History (USNM).

Family Tridentellidae Bruce, 1984
Genus *Tridentella* Richardson, 1905
Tridentella williamsi, new species
Figs. 1–3

Material.—Caribbean Sea, British Virgin Islands, "fish parasites," two males, 8.5 mm holotype (from *Epinephelus mystacinus*), USNM 239198 and 4.8 mm paratype (from *E. flavolimbatus*), USNM 239199.

Description of male.—Length up to 8.5 mm, about 2.3× as long as wide. Cephalon without tubercles, with small pointed rostrum meeting frontal lamina and slightly separating antennule bases. Eyes large, facets well-developed. Pereonites 1–3 without dorsal ornamentation, 4–7 with small tubercles along posterior margins, 7 with short, incomplete tubercle rows extending medially on lateral margins. Pereon widest at pereonite 3. Coxae 6–7 visible in dorsal view; coxae 6 extending to midlength of pereonite 7, coxae 7 extending to pleonite 2. All coxae without carinae, tubercles, spines or setae (Fig. 1). Pleonites 1–5 with row of tubercles on posterior margins; pleonites 3–4 with additional, short median tubercle row, pleonite 5 with 2 additional tubercle rows. Pleon widest at pleonite 1. Pleonite 1 laterally encompassed by pereonite 7 coxae; pleonite 5 narrow, encompassed laterally by pleonite 4. Pleotelson subtriangular, apex rounded, crenulate, with 6 setae; lateral margins with very large tubercles, dorsum with tubercle row on either side of medial depression, and 2 short tubercle rows near pleotelson base (Fig. 1).

Antennule extending slightly past posterior margin of cephalon (Fig. 1); peduncle article 3 longer than 1 and 2 combined, flagellum of 13–14 articles (Fig. 2A). Antenna extending beyond midlength of pereonite 3 (Fig. 1), peduncle article 5 longest, flagellum of 15 articles (Fig. 2B). Frontal lamina pentagonal, lateral margins slightly concave; clypeus short, very broad; labrum small, not encompassed by clypeus (Fig. 2C). Left mandible with narrow, unicuspid incisor process and triangular, setose molar process; middle palp article longest, with 14 simple setae and 1 plumose marginal seta (hereafter PMS), apical article with 20 simple setae and 1 PMS (Fig. 2D). Maxillule lateral lobe with 5 large apical spines, 5 smaller subapical hooklike spines; medial lobe slender, with simple rounded apex and 1 apical seta (Fig. 2E). Maxilla 2-segmented, apex with many denticles (Fig. 2F). Maxilliped palp articles 1–3 with simple medial marginal setae, distal 3 articles with comblike setae; endite extending to penultimate palp article, without coupling hooks, with single apical seta (Fig. 2G).

Pereopods 1–3 subsimilar, subprehensile. Pereopod 1 stouter than 2–3, ischium with 2 simple spines on distomedial and distolateral angles; merus medial margin with 3 stout bifid spines, 1 bifid and 2 simple setae, distolateral angle with 2 long spines; carpus medial margin with 1 bifid, 2 simple spines; propodus medial margin with 1 bifid, 1 simple seta, and 1 short spine distally, lateral margin with 3 simple setae; dactylus with 1 simple seta at base of unguis on medial margin, lateral margin with 3 simple setae proximal to unguis (Fig. 3A). Pereopods 4–7 slender, ambulatory. Pereopod 4 basis with simple spine on distomedial angle; ischium medial margin with 2 simple setae and 2 spines, distolateral angle with 1 large bifid spine, 1 simple spine; merus medial margin with 1 simple and 9 bifid spines, distolateral angle with 1 simple, 2 bifid spines; carpus distomedial angle with 2 bifid, 2 simple spines, 1 seta; propodus medial margin with 1 bifid, 2 simple spines and 2 simple setae, distolateral margins with 3 simple setae; dactylus with 1 seta at base of unguis on medial margin (Fig. 3B). Pereopod 7 basis with 2 spines on distomedial angle, lateral margin with 8 short setae; ischium medial margin with 4 bifid and 4 simple spines, distolateral angle with 2 plumose setae, 2 bifid spines; merus medial margin with 4 simple and 3 bifid spines, distolateral angle with 3 bifid spines, 1 simple seta; carpus medial margin with 1 simple and 4 bifid spines, distolateral angle with 1 spine, 2 simple and 10 plumose setae; propodus medial margin with 5 bifid spines, distolateral angle with 1 seta; dactylus medial margin with single seta at base of unguis, lateral margin with 3 setae proximal to unguis (Fig. 3C). Penes set distinctly apart on sternite 7.

Pleopods 1–5 rami with PMS as figured, endopod of pleopod 5 naked; exopods of 3–5 with complete or partial transverse sutures. Peduncles of pleopods 1–5 with 1 spine on lateral margins. Peduncles of pleopods 1–5 with 1 spine on lateral margins. Pleopod 1 peduncle with 3 coupling spines, 1 PMS on medial margin; pleopods 2–4 peduncles with 4 coupling spines and 2 PMS on medial margins. Appendix masculina of pleopod 2 rodlike, with pointed apex, arising from proximal medial margin of endopod (Fig. 3D–H).

Uropods extending well beyond pleotelson apex; exopod one-half width of endopod, both rami with scalloped margins inset with PMS, lacking spines. Uropod peduncle with 3 simple setae, 2 PMS on lateral margin, distomedial angle with 3 PMS (Fig. 3I).

Etymology.—This species is named for Ernest H. Williams, Jr. in recognition of his contributions to Caribbean isopod biology.

Remarks.—*Tridentella williamsi* is easily distinguished from the other two Atlantic species by its strongly tuberculate pleotelson and lack of cephalic tubercles. *T. virginiana* (Richardson) has four cephalic tubercles and an unornamented, smoothly rounded pleotelson. *T. recava* Bowman lacks cephalic tubercles, has a pleotelson apex with a distinctive U-shaped excavation, and the pleotelson dorsum is unornamented.

Tridentella williamsi is the 14th species known in the genus, and has a highly ornamented or sculpted pleotelson as do 9 of the other 13 species. *T. williamsi* also lacks the marginal uropodal spines found in five other *Tridentella* species.

Species list.—The currently-known *Tridentella* species and their localities are listed below. See Delaney & Brusca (1985) for synonymies.

1. *T. acheronae* Bruce, 1988; New Zealand.
2. *T. cornuta* Kussakin, 1979; northwest Pacific.
3. *T. glutacantha* Delaney & Brusca, 1985; California.

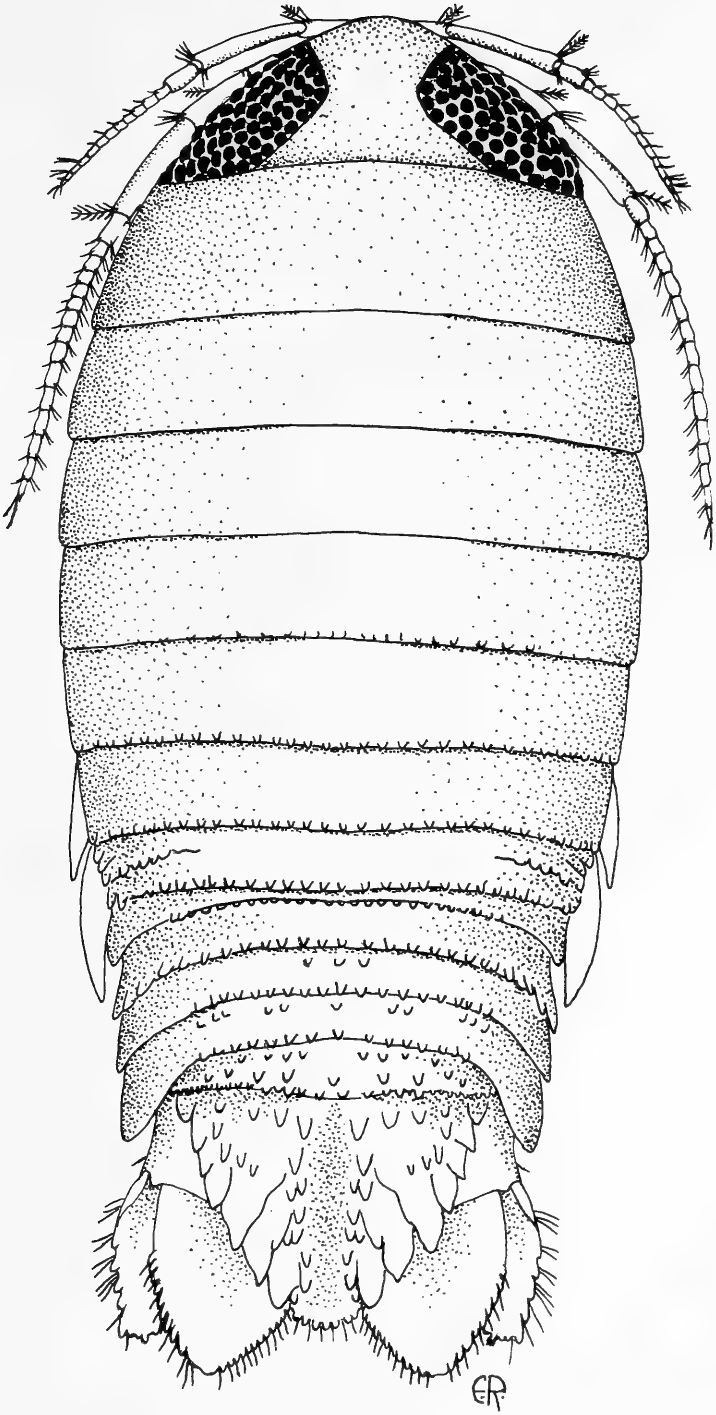


Fig. 1. *Tridentella williamsi*, n. sp., dorsal view of holotype male, USNM 239198, British Virgin Islands.

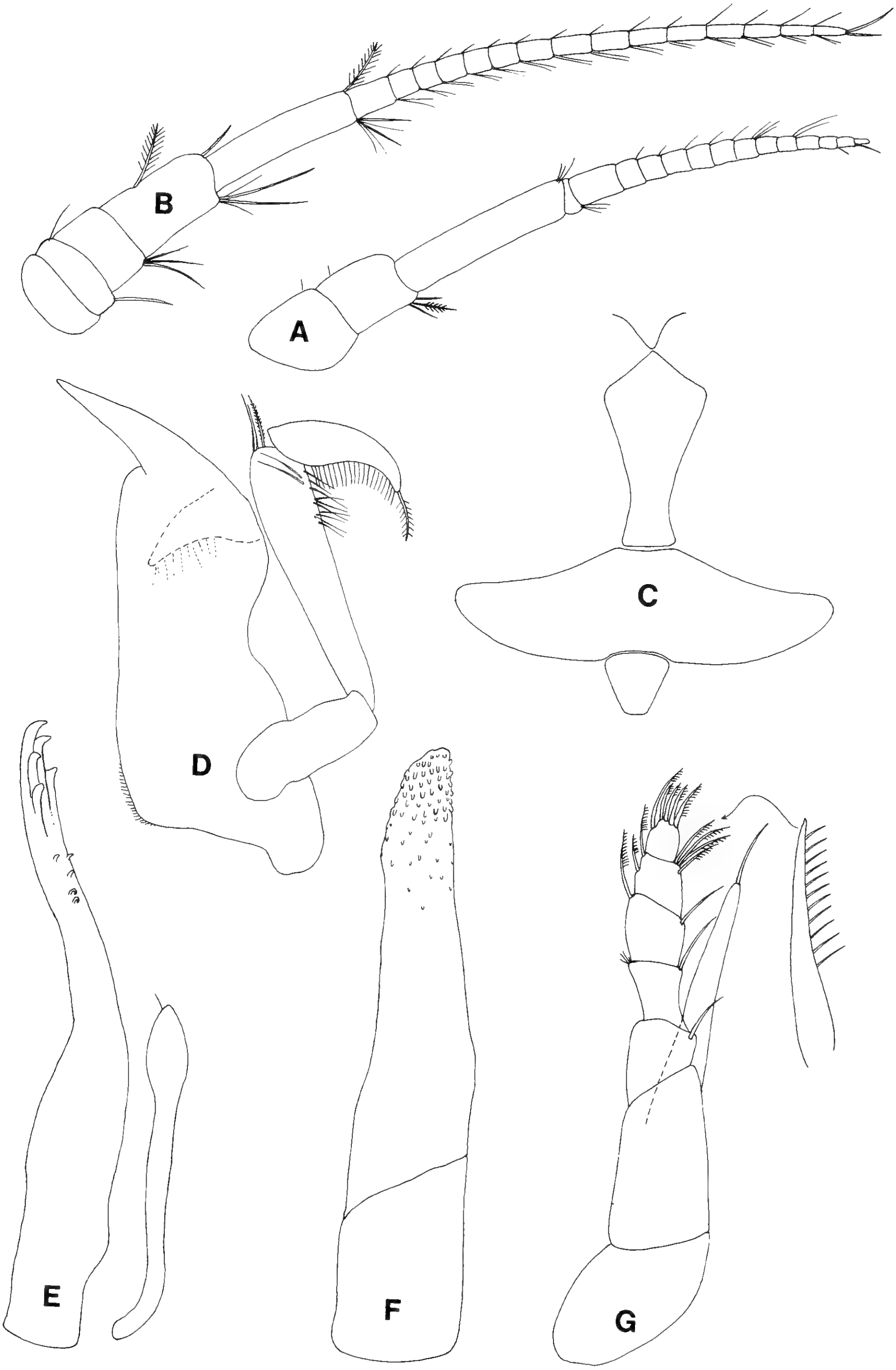


Fig. 2. *Tridentella williamsi,* holotype: A, Antennule; B, Antenna; C, Frontal lamina, clypeus and labrum; D, Left mandible; E, Maxillule; F, Maxilla; G, Maxilliped.

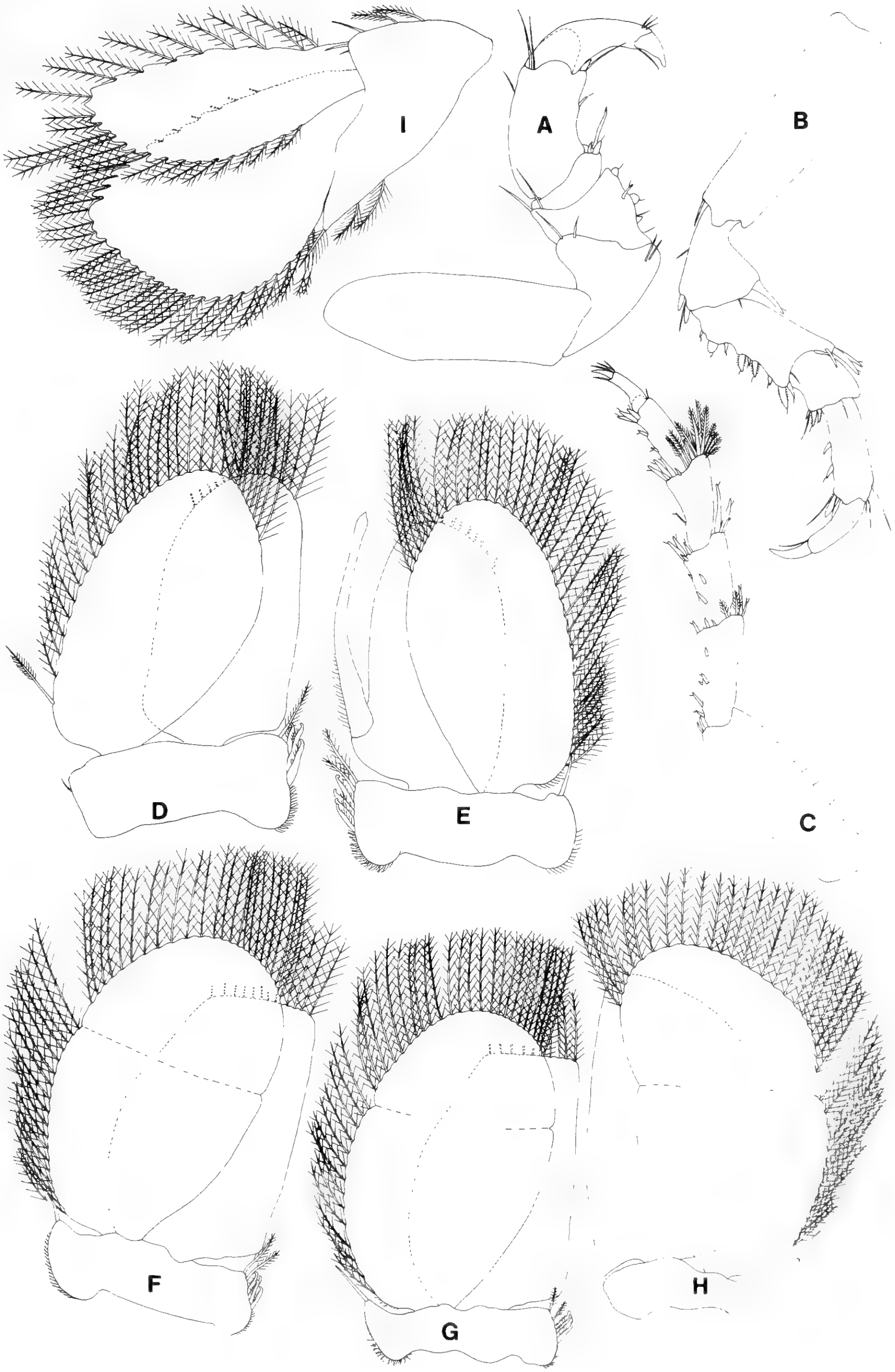


Fig. 3. *Tridentella williamsi,* holotype: A, Pereopod 1; B, Pereopod 4; C, Pereopod 7; D, Pleopod 1; E, Pleopod 2; F, Pleopod 3; G, Pleopod 4; H, Pleopod 5; I, Ventral view of uropod.

4. *T. japonica* Thielemann, 1910; Japan.
5. *T. laevicephalax* Menzies, 1962; southern Chile.
6. *T. ornamenta* (Menzies & George, 1972); Peru-Chile Trench.
7. *T. quinicornis* Delaney & Brusca, 1985; California.
8. *T. recava* Bowman, 1986; New York Bight.
9. *T. saxicola* (Hale, 1925); Australia.
10. *T. sculpturata* Kussakin, 1955; northwest Pacific.
11. *T. tangaroae* Bruce, 1988; New Zealand.
12. *T. virginiana* (Richardson, 1900); Virginia to Nova Scotia.
13. *T. vitae* Bruce, 1984; Fiji.
14. *T. williamsi,* n. sp.; British Virgin Islands, Caribbean.

Acknowledgments

Specimens were loaned to the author by Dr. Thomas E. Bowman (USNM), and Frances Runyan drew the figures. Institutional support provided by the University of the Virgin Islands is gratefully acknowledged. I thank Dr. Ernest H. Williams, Jr. for his correspondence and specimen loan which aided evaluation of this *Tridentella* species. This paper benefited from reviews by several anonymous reviewers.

Literature Cited

Bowman, T. E. 1986. *Tridentella recava,* a new isopod from tilefish burrows in the New York Bight (Flabellifera: Tridentellidae).—Proceedings of the Biological Society of Washington 99:269–273.

Bruce, N. L. 1984. A new family for the isopod genus *Tridentella* Richardson, 1905, with description of a new species from Fiji.—Zoological Journal of the Linnean Society, London 80(4):447–455.

———. 1988. Two new species of *Tridentella* (Crustacea, Isopoda, Tridentellidae) from New Zealand.—National Museum of New Zealand Records 3(7):71–79.

Delaney, P. M., & R. C. Brusca. 1985. Two new species of *Tridentella* Richardson, 1905 (Isopoda: Flabellifera: Tridentellidae) from California, with a rediagnosis and comments on the family, and a key to the genera of Tridentellidae and Corallanidae.—Journal of Crustacean Biology 5(4):728–742.

Hale, H. M. 1925. Review of the Australian isopods of the cymothoid group. Part I.—Transactions of the Royal Society of South Australia 49:128–185.

Kussakin, O. 1955. New for far-eastern waters U.S.S.R.—the warm water families of Isopoda. —Transactions of the Institute of Zoology and Academy of Sciences U.S.S.R. 18:228–234 (text in Russian).

———. 1979. Marine and brackish-water Isopoda of cold and temperate waters of the Northern Hemisphere. I. Flabellifera.—Opredeliteli po Faune SSSR 12:1–470, Academy of Sciences, Leningrad, U.S.S.R. (text in Russian).

Menzies, R. J. 1962. The zoogeography, ecology and systematics of the Chilean marine isopods.—Reports of the Lund University Chile Expedition 1948–49, No. 42, Lunds Universitets Arskriffter, Avd. 2, Bund 57:1–162.

———, & R. Y. George. 1972. Isopod Crustacea of the Peru-Chile Trench.—Anton Bruun Report Number 9:124 pp., Texas A&M Press.

Richardson, H. R. 1900. Synopses of North American invertebrates. VII. The Isopoda.—American Naturalist 34:207–230, 295–309.

———. 1905. Isopods of North America.—United States National Museum Bulletin 54:1–727.

Thielemann, M. 1910. Beitrage zur Kenntnis der Isopodenfauna Ostasiens.—Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse der Koeniglich-Bayerische Akademie der Wissenschaften, Supplementary Volume 2, Abhandling 3:1–109.

Marine Science Program, University of the Virgin Islands, St. Thomas, U.S. Virgin Islands 00802.

(Current address) Life Science Division, Los Angeles County Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 649–654

DESCRIPTION OF THE CRYPTONISCIUM LARVA OF *ENTOPHILUS OMNITECTUS* RICHARDSON, 1903 (CRUSTACEA: ISOPODA: EPICARIDEA) AND RECORDS FROM THE GULF OF MEXICO

Daniel L. Adkison and Sneed B. Collard

Abstract.—*Entophilus omnitectus* is reported from two new host species, *Munida microphthalma* and *M. valida,* and its range in the Atlantic Ocean is extended from the Azores to the northern Gulf of Mexico. The cryptoniscium larva is described and comments on its maturation to the adult male form are presented. *Entophilus omnitectus* is an internal parasite enclosed by a host sheath that is similar to that surrounding the Entoniscidae. Seven of the eleven host specimens were also parasitized by *Aporobopyrina anomala* Markham, 1973 and/or an unidentified rhizocephalan.

A specimen of *Munida valida* Smith, 1883 collected on a University of West Florida training cruise was parasitized by *Entophilus omnitectus* Richardson, 1903, *Aporobopyrina anomala* Markham, 1973 and an unidentified rhizocephalan. The presence of *E. omnitectus* was indicated by a pore near the anterolateral margin of the host's carapace and by swelling and discoloring of the hepatic region of the carapace. This pore is herein referred to as the "larval exit pore" for its presumed function. Galatheoids from subsequent cruises were examined for external signs of infestation noted above and additional *Entophilus omnitectus* specimens were found.

The material examined has been deposited in the collections of the Smithsonian Institution, Washington, D.C. (USNM) and Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg (FSBC).

Entophilus omnitectus Richardson, 1903
Figs. 1, 2

Entophilus omnitectus Richardson, 1903: 53–54, figs. 6–8.—Danforth, 1963:17–18, 40 pls. 3, 7; 1970:13, 72–73, fig. 18.—Bourdon 1976:385–391, figs. 20–23; 1979:511.

Material examined.—Gulf of Mexico. Infesting *Munida valida* Smith, 1883. R/V *Bellows* B8403 sta 4; 22 Mar 1984, coll. S. B. Collard, 15 ft flat trawl, 185–370 m, 29°16.53′N, 29°12.06′W to 29°12.06′N, 87°47.97′W, *Aporobopyrina anomala* 1 ♀, 1 ♂ USNM 240129, *Entophilus omnitectus* 1 ♀ (no ♂) USNM 240128, host with rhizocephalan USNM 240127.—R/V *Oregon II* sta 42230; 13 Nov 1984, coll. T. H. Hansknecht, 55 ft shrimp trawl, 640–685 m, 29°09′N, 87°59′W, 2 hosts each with a pair of branchial and internal bopyrids, *Aporobopyrina anomala* 2 ♀, 2 ♂ USNM 240138, *Entophilus omnitectus* 2 ♀, 1 ♂, 1 cryptoniscium larva USNM 240137.—R/V *Gyre* 86-G-2 sta 42; 28 Feb 1986, coll. D. L. Adkison, 30 ft trawl, 620–850 m, 27°47.0′N, 90°16.9′W to 27°46.5′N, 90°12.5′W, *Entophilus omnitectus* 1 ♀ (gravid), 1 ♂, FSBC I-33079, host FSBC I-33080.—R/V *Gyre* 86-G-2 sta 70; 6 Mar 1986, coll. D. L. Adkison, 30 ft trawl, 600–770 m, 27°43.2′N, 91°15.7′W to 27°43.2′N, 91°19.4′W, *Aporobopyrina anomala* 1 ♀ (gravid), 1 ♂ FSBC I-33081, *Entophilus omnitectus* 1 ♀ (no ♂)

FSBC I-33082, host FSBC I-33083.—R/V *Gyre* 86-G-2 sta 76; 7 Mar 1986, coll. D. L. Adkison, 30 ft trawl, 600–750 m, 27°22.1′N, 93°31.1′W to 27°24.9′N, 93°27.8′W, 2 hosts each with a female branchial and internal bopyrid, *Aporobopyrina anomala* 2 ♀ (gravid), 2 ♂ USNM 240132, *Entophilus omnitectus* 2 ♀ (1 gravid), 1 ♂ USNM 240131, host with rhizocephalan USNM 240130.—R/V *Gyre* 87-G-2 sta 26; 5 Mar 1987, coll. D. L. Adkison, 30 ft trawl, 660–1010 m, 27°42.9′N, 91°16.6′W to 27°43.0′N, 91°19.6′W, *Entophilus omnitectus* 1 ♀ (gravid), 1 ♂ USNM 240134, host with rhizocephalan USNM 240133.—M/V *H.O.S. Citation* sample 4502 sta E2A; 13 May 1985, coll. LGL, trawl, 625 m, 28°35.61′N, 86°46.31′W to 28°35.40′N, 86°46.24′W, *Entophilus omnitectus* 1 ♀, 1 ♂ USNM 240126.—M/V *H.O.S. Citation* sample 4508 sta E2D; 16 May 1985, coll. LGL, trawl, 624–631 m, 28°07.44′N, 85°52.31′W to 28°06.78′N, 85°54.09′W, *Entophilus omnitectus* 1 ♀, 1 ♂ USNM 240124.

Infesting *Munida microphthalma* A. Milne Edwards, 1880. R/V *Gyre* 86-G-2, sta 47; 2 Mar 1986, coll. D. L. Adkison, 30 ft trawl, 430–690 m, 28°06.1′N, 89°58.9′W to 28°03.7′N, 89°58.9′W, *Entophilus omnitectus* 1 ♀, 1 ♂ USNM 240136, host USNM 240135.

Description.—Bourdon (1976) gave excellent descriptions and illustrations of *E. omnitectus* adults. The present material agrees in most details with descriptions of Richardson (1903) and Bourdon (1976) though several differences for the male are noted. The antenna is elongate and more similar to that illustrated by Richardson (1903) than that by Bourdon (1976). All pereopods have five segments. Several males appear to be intermediate between adult and cryptoniscium larva with the pleopodal endopod being a distinct article. Several specimens have a vestigial pleopodal exopod but pereopods are as in mature males. Discussed in greater detail under maturation of the male.

Cryptoniscium larva (Fig. 2): Eyes present. Antennule, biramous; peduncle of 2 articles, distally with a tuft of long setae; basal segment without posterior teeth. Antenna of 9 articles, reaching pereomere 4. Oral cone without terminal sucker. Dorsal cuticular striation not seen, presumed absent. Coxal plates without teeth on posterior and ventral margins; posterior margin weakly scalloped; ventral margin with minute serration; posteroventral corner blunt on pereomere 1, corner becoming elongate on posterior pereomeres. Pereopods increasing in length posteriorly, dactylus with 1 short seta; propodus palm with 2–3 stout spines; carpus distally with 2 long setae and 0–2 stout spines; merus with 1 large spine on posterior margin; ischium and basis grooved to receive distal segments. Pleopods biramous, pleopods 1–3 with 2 setae on distomedial corner of peduncle; exopod quadrate with 1 seta on distolateral corner and 5 long feathered setae; endopod broad, rounded laterally, distally with 5 long feathered setae and distolateral corner with 4 crenations. Pleopod 4 with 2 setae on distomedial corner of peduncle; exopod quadrate with 1 seta on distolateral corner and 4 long feathered setae; endopod quadrate with 4 long feathered setae and distolateral corner with 3 crenations. Pleopod 5, peduncle without setae on distomedial corner; exopod with 1 seta and 4 long feathered setae on distolateral corner; endopod elongate, distally with 4 long feathered setae. Uropod peduncle long, approximately twice length of endopod, distomedial margin with dense band of setae, distomedial corner with 2 strong teeth, distolateral corner with 1 seta; exopod approximately ⅔ length of endopod; endopod with 1 seta on ventral surface. Posterior margin of pleomere 6 entire.

Maturation of the male.—The cryptoniscium larva is larger than the mature male. The larva appears to attain adult form over

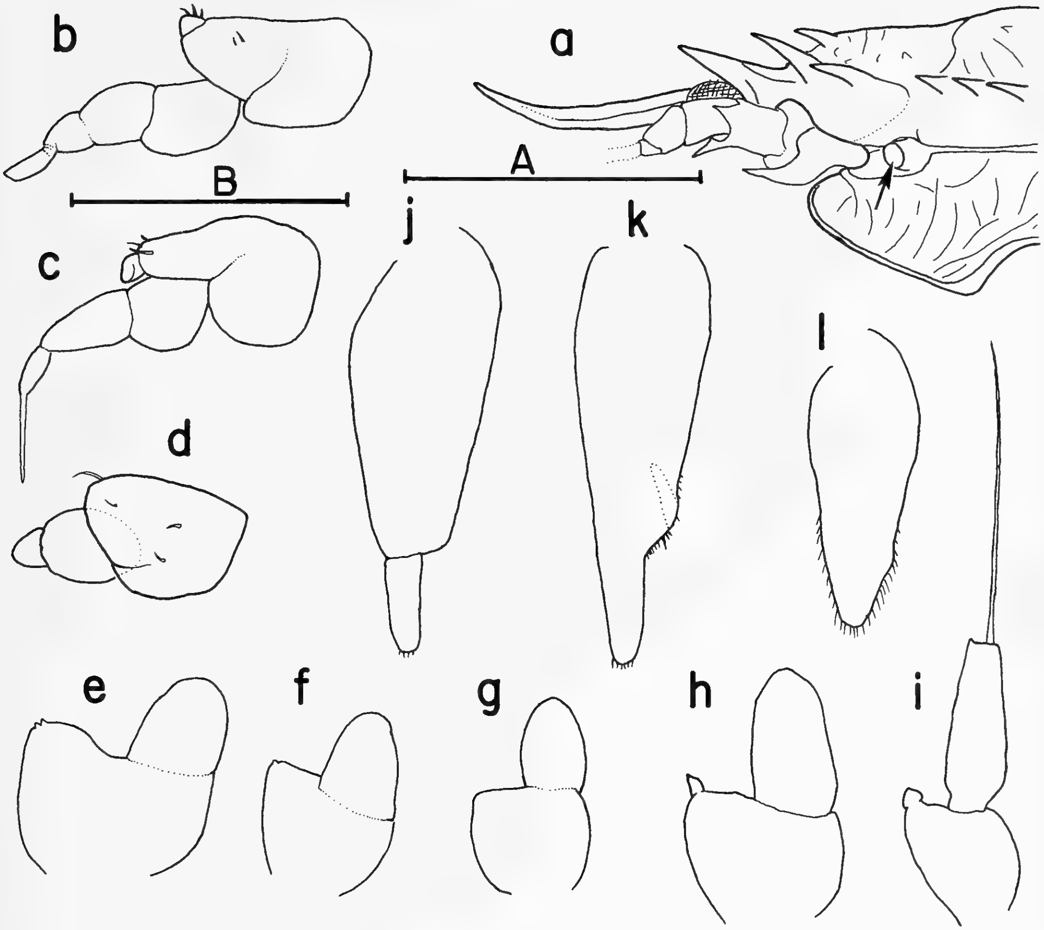


Fig. 1. Host carapace and male of *Entophilus omnitectus*: a, Carapace of *Munida microphthalma* showing exit pore (arrow) of the female *Entophilus omnitectus,* anterolateral view; b–d, Antennae; e, Pleopod 1; f, Pleopod 4; g, Pleopod 5; g, Pleopod 5; h, Pleopod 4; i, Pleopod 5; j–l, Uropod. Scale bar A is 1 cm, for Fig. a; scale bar B is 0.3 mm, for Fig. b to l. Figures from USNM 240136 (host *Munida microphthalma*) a, b, h, i, k. Figures from USNM 240137 c, j. Figures from USNM 240134 d–g, l.

several molts. While pereopods of all male specimens except cryptoniscium larva are of adult form, antennae show variable segmentation. In general, the basal segment of antennule becomes bilobed and then loses its distal articles. Antenna becomes reduced and then loses its flagellar articles, resulting in an appendage of one or two articles. In the adult form, antenna is largely covered by antennule, thus appearing to be the distal articles of antennule.

After the cryptoniscium stage, pleopod setae are lost early except for one long seta on endopod of pleopod 5. This seta reaches nearly to the distal end of the uropod peduncle. Between the cryptoniscium and mature male, two forms of pleopods were found. The first has a free endopod and a vestigial exopod. The later form has a uniramous pleopod with fused endopod. Changes in uropods are similar to those of pleopods. Distal spines, setae and exopod are lost first, followed by the loss of the dense setal band on the peduncle. In one

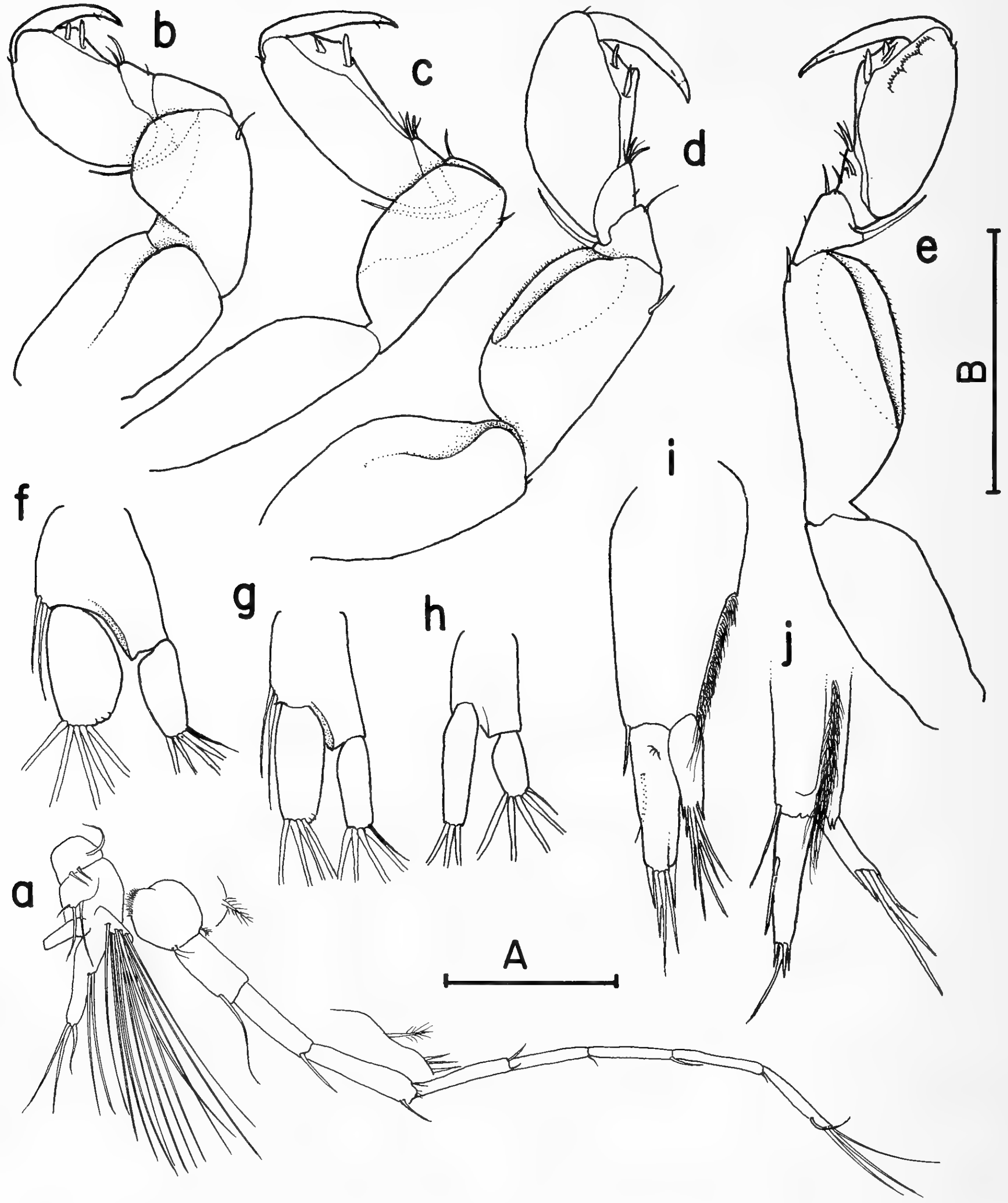


Fig. 2. Cryptoniscium larva: a, Antennae; b, Pereopod 1; c, Pereopod 3; d, Pereopod 5; e, Pereopod 7; f, Pleopod 1; g, Pleopod 4; h, Pleopod 5; i, Uropod, dorsal view; j, Uropod, distal ventrolateral view. Scale bars are 0.3 mm; scale A for Fig. a; scale B for Fig. b to j.

specimen (from *Munida microphthalma*) a deep invagination is present at the location of the dense setal band. Next, the endopod fuses with the peduncle although its location is indicated by the asymmetrical shape of the distal end of the uropod. Last, all indication of the endopod is lost, and the distal end of the uropod is symmetrical.

Distribution.—*Entophilus omnitectus* has a sporadic distribution from off the Hawaiian Islands on *Munida normani* Henderson (type locality; Richardson 1903), off Australia and the Philippines (Bourdon 1976 as unpublished records), off Madagascar Island on *M. incerta* Henderson (Bourdon 1976), off the Azores on *M. sanctipauli* Henderson (Bourdon 1979) and in the Gulf of Mexico on *M. microphthalma* and *M. valida* (reported here).

Position of parasite.—Danforth (1963, 1970) described the position of female *Entophilus omnitectus* as mid-dorsal under the host's carapace. In the present material and those reported by Bourdon (1976), the female *E. omnitectus* is located anterolaterally under the host's carapace, anterior to branchial chamber. The female parasite is oriented with the posterior end of its pleon at the larval exit pore. The long axis of the female is directed obliquely across the host towards the lateral wall on the other side of the host's carapace. The dorsal surface of female parasite is directed toward the ventral surface of host and the brood chamber faces the dorsal surface of the host's carapace. As in Bopyridae and Dajidae, the male is usually found on ventral surface of the female pleon. As previously noted, presence of an adult female parasite is indicated by a swelling on the dorsal surface of the host's carapace and a small pore anterior to branchiostegite region of the carapace.

Female *Entophilus omnitectus* are enclosed in a host-derived sheath that appears similar to but thicker than the sheath surrounding female entoniscid isopods. The host derived-sheath around *E. omnitectus* is in less intimate contact with the female parasite than around female entoniscids (Shiino 1942, Kuris et al. 1980) where the sheath is very difficult to remove without damaging the specimen. Like the entoniscids (Kuris et al. 1980), *Entophilus omnitectus* is clearly an internal parasite.

Discussion.—For the nine hosts with an adult female *E. omnitectus,* female parasite length is 39% (range 33 to 45%) of host carapace length. The length of the two immature female parasites are 19% of host carapace length. In both cases, the host with an immature female had a partly closed larval exit pore and no dorsal swelling of the host carapace. The remains of the previous adult female *E. omnitectus* were found at the larval exit pore in specimen, FSBC I-33082, and the immature female parasite was found in a swelling on the lateral margin of the host carapace dorsal to the larval exit pore. In the other case (USNM 240131), the immature parasite was found in a "normal" position, with its pleon at the partly closed larval exit pore. It is unknown whether the immature females (both without males) were the transformed males of the previous adult female or the result of subsequent infestation.

Entophilus omnitectus has low numbers of large eggs per clutch. The number of eggs in three broods are 435 (USNM 240134), 563 (USNM 240124), and 1524 (FSBC-I33079). One female carried 2228 embryos (USNM 240126). The average egg diameters for four broods were 403 μm (USNM 240124), 438 μm (FSBC-I33079), 548 μm (USNM 240131), and 561 μm (USNM 240134). The number of eggs and clutch volume (calculated by treating eggs as spheres and multiplying egg volume times number of eggs) were not found to be related to length of either female parasite or host. Eggs of *Entophilus omnitectus* are the largest reported for any epicaridean and are within the size range of eggs of other isopods (Stromberg 1971).

Of the 11 hosts infested by *Entophilus omnitectus,* only four were not parasitized by females of other parasites. Six hosts were infested by *Aporobopyrina anomala,* three were infested by an unidentified rhizocephalan, and two were infested by females of all three parasites. One rhizocephalan appears parasitized by a cryptoniscid isopod. Markham (1973) reported the simultaneous infestation of *Munida valida* by a rhizocephalan and *A. anomala.*

The known distribution of *Entophilus omnitectus* is sporadic, no doubt in part due to the relatively subtle inflation of the host carapace when compared to that caused by the branchial bopyrids. The examination of galatheoids using the signs of infestation noted above will turn up more material and should help address the question of whether *E. omnitectus* is a single species or a species complex.

Acknowledgments

We wish to thank Thomas H. Hansknecht for allowing us to use material collected by him on the R/V *Oregon II* and Randall Howard of LGL Ecological Research Associates Inc., Bryan, Texas for allowing the use of material under his care. Material from LGL was collected in the Northern Gulf of Mexico Continental Slope Study with funding by the U.S. Department of Interior, Minerals Management Service, Gulf of Mexico Regional Office, under contract numbers 14-12-0001-30046 and 14-12-0001-30212. We also wish to thank Dr. James M. Brooks, Geochemical and Environmental Research Group, Texas A&M University, College Station, Texas, for allowing one of us (DLA) to make several cruises on the R/V *Gyre* and use material collected on these cruises. Support for R/V *Gyre* time was partially provided by the Marine Chemistry Program of the National Science Foundation (grant OCE83-01538 to Brooks). We wish to thank David Camp of Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida, for confirmation of the identification of the host specimens. We wish to thank Drs. Thomas E. Bowman and John C. Markham for comments on an early draft of this manuscript. The assistance of Dr. Linda Adkison in the preparation of this paper is gratefully acknowledged.

Literature Cited

Bourdon, R. 1976. Epicarides de Madagascar. I.—Bulletin du Muséum National d'Histoire Naturelle, Paris, Ser. 3, No. 371, Zoologie 259:353–392.

———. 1979. Bopyridae de la campagne Biacores (Isopoda: Epicaridea).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Ser. 4, No. 1, Sec. A, 2:507–512.

Danforth, C. G. 1963. Bopyridian (Crustacea, Isopoda) parasites found in the eastern Pacific of the United States. Unpublished Ph.D. Dissertation, Oregon State University, Corvallis, 110 pp.

———. 1970. Epicaridea (Crustacea: Isopoda) of North America.—Ann Arbor, Michigan, University Microfilms, 191 pp.

Kuris, A. M., G. O. Poinar, & R. T. Hess. 1980. Postlarval mortality of the endoparasitic isopod castrator *Portunion conformis* (Epicaridea; Entoniscidae) in the shore crab, *Hemigrapsus oregonensis,* with a description of the host response.—Parasitology 80:211–232.

Markham, J. C. 1973. Six new species of bopyrid isopods parasitic on galatheid crabs of the genus *Munida* in the western Atlantic.—Bulletin of Marine Science 23:613–648.

Richardson, H. 1903. Isopods collected at the Hawaiian Islands by the United States Fish Commission Steamer Albatross.—United States Fish Commission Bulletin for 1903:47–54.

Shiino, S. M. 1942. On the parasitic isopods of the family Entoniscidae, especially those found in the vicinity of Seto.—Memoirs of the College of Sciences, Kyoto Imperial University, Series B 17:37–76.

Stromberg, J.-O. 1971. Contribution to the embryology of bopyrid isopods with special reference to *Bopyroides, Hemiarthrus* and *Pseudione* (Isopoda, Epicaridea).—Sarsia 47:1–46.

(DLA) 1699 Wesleyan Bowman Road, Macon, Georgia 31210; (SBC) Biology Department, University of West Florida, Pensacola, Florida 32514.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 655–662

A NEW SPECIES OF ISOPOD, *AEGA* (*RHAMPHION*) *FRANCOISAE* (FLABELLIFERA: AEGIDAE), FROM THE CLOACA OF AN ASCIDIAN FROM THE GALÁPAGOS ISLANDS

Regina Wetzer

Abstract.—*Aega* (*Rhamphion*) *francoisae,* a new species of Aegidae, is reported from a depth of 316 m in the Galápagos Islands. All 10 specimens of the type series were found in the cloaca of a single ascidian, *Halocynthia hispida* (Pyuridae: Stolidobranchiata). This is the first species of aegid isopod to be reported inhabiting a urochordate. The nature of the relationship is not known.

In November and December 1986 the Harbor Branch Oceanographic Institute and SeaPharm Inc. undertook a collecting expedition in the Galápagos Islands. Chief scientists for the expedition were Drs. Shirley Pomponi and Kenneth Rinehart, while Drs. Richard Brusca and Françoise Monniot undertook studies of the Crustacea and Urochordata, respectively. During this expedition, a single deep-water specimen of the stolidobranchiate ascidian *Halocynthia hispida* (Herdman, 1881) was collected by the *Johnson-Sea-Link* research submersible; the ascidian had 10 specimens of an undescribed aegid isopod in its cloacal chamber.

Members of the family Aegidae are typically predators/parasites on marine fishes and to my knowledge no aegid or any other isopod species have been reported as commensals or parasites in ascidians. In the eastern Pacific this family has been most recently treated by Brusca (1983) and Brusca & Iverson (1985). Knowledge of the Australian aegid fauna has been brought current by Bruce (1983, 1988).

Abbreviations used in this paper are: PMS = plumose marginal setae; LACM = Los Angeles County Museum of Natural History, Los Angeles, California; SDNHM = San Diego Natural History Museum, San Diego, California; USNM = National Museum of Natural History, Washington, D.C.; BMNH = British Museum (Natural History), London.

Aega (*Rhamphion*) *francoisae,* new species

Material examined.—Ten individuals, from one specimen of the solitary ascidian *Halocynthia hispida* (Herdman, 1881) (Family Pyuridae: Order Stolidobranchiata), SeaPharm no. 24-XI-86-3-9V. Ecuador, Galápagos Islands, near Fernandina Island, ca. 0.23°S, 91.32°W, 316 m depth, 24 November 1986. Holotype (SDNHM 2220), female 9.6 mm long (with oostegites). Five paratypes (SDNHM 2221) (2 females 10.7 mm, 10.3 mm both with oostegites; 2 males 9.2 mm, 9.2 mm; 1 manca 4.3 mm). One male paratype each sent to the USNM (250192) (7.4 mm), LACM (86-446.1) (7.5 mm), BMNH (1990:31) (7.8 mm) and the Australian Museum, Sydney (P40180) (8.3 mm).

Diagnosis.—Body unornamented; lateral body margins strongly convex, cephalon and pleon considerably narrower than pereonite 4. With a single frontal plate of uncertain homology (frontal lamina wanting; clypeus and labrum fused?). Antennule article 3 at least 3.5 times longer than article 2. Maxillule with 3 apical spines and 3 subapical spines. Distal article of maxillipedal palp in males with ctenate setae. Pleotelson evenly rounded, without marginal notches. Uropodal endopod without a deep cleft or notch on lateral margin; apex of inner peduncular angle with 1 long circumplumose seta; exopod oblong with prominent, stout, apical spine; endopod subtriangular.

Description.—Body smooth and compact, slightly more than twice as long as wide; pleon narrower than pereon; pleonites progressively narrower posteriorly (Fig. 1A, B). Cephalon wider than long, subtriangular. Eyes large, well pigmented, with distinct facets, covering ⅔ of cephalon but not contiguous. Cephalon produced anteriorly into a small triangular rostrum extending ventrally to separate basal articles of antennules (Fig. 2A). Frontal plate, of uncertain homology (fused clypeus and labrum?), shieldlike, elevated anteriorly on a broad pedicel, with median transverse ridge, sloping downward posteriorly, and separating antennae. Antennules extending to middle of second pereonite; basal articles 1 and 2 somewhat expanded, article 3 3.5–4 times as long as article 2; peduncular articles 2 and 3 with simple and palmate setae; 8–12 flagellar articles, each with 3–4 aesthetascs (not all figured); terminal flagellar article usually with 4 long simple setae and 1 seta bearing fine setules over most of its length (Fig. 2B). Antennae extending to posterior margin of second pereonite; with 5 peduncular articles and 9–10 flagellar articles; peduncular articles 2–5 with simple setae, article 5 also with 3 setae bearing fine setules over most of their length; simple setae on all flagellar articles (Fig. 2C).

Both right and left mandibles with a prominent incisor process; with a rounded, fleshy molar process lacking setation; palp of 3 articles subequal in length, proximal (first) article shorter than middle article; middle article with 5 plumose setae with short setules and 3 simple setae on margin; distal article with row of about 18 simple setae on margin (Fig. 3A). Maxillule with 3 stout apical and 3 subapical spines (Fig. 3B). Maxilla with 2 unequal lobes, each with 3 stout, slightly curved spines (Fig. 3C). Maxillipedal palp of 5 articles; terminal article very short, with 5 curved ctenate setae; article 4 with 5 small recurved marginal spines; article 3 with 4 marginal spines and 1 submarginal spine; article 2 with 2 distolateral spines; article 1 without spines or setae (Fig. 3D). In oostegite-bearing females, proximal maxillipedal palp articles somewhat indistinct and basis expanded into a large plate with PMS as figured (Fig. 3E).

Pereonites 4–6 considerably longer than pereonites 1–3. Pereonite 7 as long as pereonite 3. Coxal plates of pereonites 5–7 visible in dorsal aspect. Pereopods 4–7 considerably longer than 1–3 and increasing in length posteriorly (Fig. 4A–G). Pereopods 1–3 with very few setae. Pereopods 4–7 more spinose than pereopods 1–3, as figured. Pereopods 1–3 with large curved dactyl, as long as propodus, without expanded distal lobe on propodus. Penes small, on sternite 7; fused basally.

Pleon with 5 free pleonites plus pleotelson; pleonite 1 almost entirely covered by pereonite 7; pleonites 2–4 equilength. Pleotelson with 8 short spines on posterior margin and PMS as figured (Fig. 1C). Uropodal exopod oval; endopod subtriangular, without a deep cleft or notch on lateral margin; both with spines and PMS as figured; endopods slightly longer than exopods. Inner angle of peduncle strongly produced, about half length of endopod and with 1 long terminal plumose seta; outer distal angle of peduncle with one dorsal and one ventral spine (Fig. 1D).

Peduncles of pleopods not divided; pleopodal peduncles 1–4 with 3–6 basally plumose coupling spines and 3–9 PMS on inner margin; peduncle of pleopod 5 without coupling spines or PMS; peduncles of pleopods 2–5 with 1 large spine on outer margin (Fig. 5A–F); spine on pleopod 2 often missing (probably broken off). Pleopodal rami undivided; all pleopods with PMS as figured; density of PMS more-or-less equal on all exopods, but decreasing posteriorly on en-

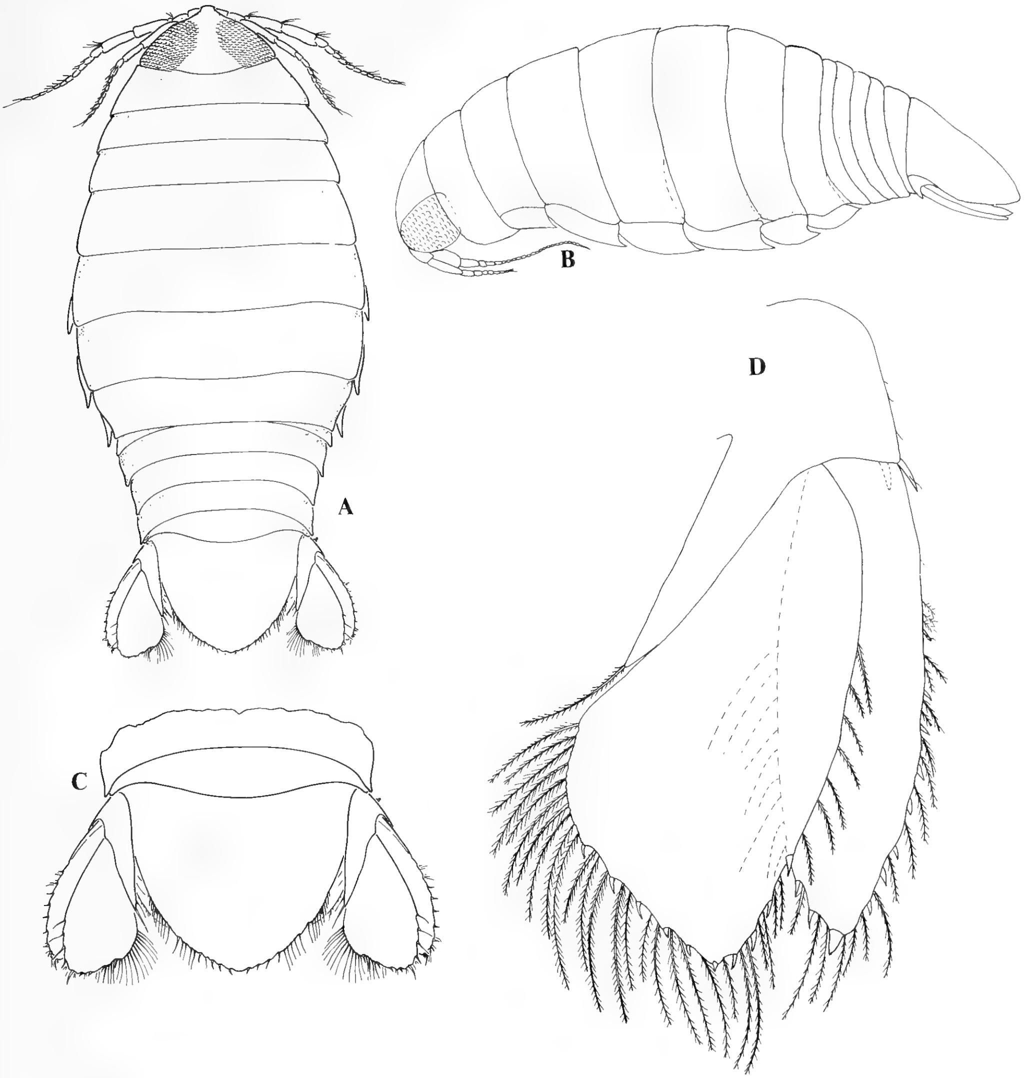


Fig. 1. *Aega francoisae* n. sp. A, dorsal view of holotype (female); B, lateral view of male paratype (9.2 mm); C, pleotelson of holotype; D, left uropod of female paratype (10.7 mm).

dopods and absent on pleopod 5 endopod; endopod of pleopod 5 with proximal lobe. Pleopods of males similar to those of females. Appendix masculina on male pleopod 2 arising basally, long and slender, tapering evenly, extending beyond apex of exopod.

Remarks.—*Aega francoisae* fits Brusca's (1983) diagnosis of the subgenus *Rhamphion*: antennular articles 1 and 2 are not inflated or dilated, the antennae extend to the posterior margin of pereonite 2, pereopods 1–3 lack distal lobes on the propodi, and the uropodal endopods are subtriangular in outline. *Aega francoisae* differs slightly from Brusca's diagnosis of *Rhamphion* in that the distal maxillipedal palp article bears ctenate rather than simple setae in males.

Brusca (1983) noted that oostegite-bear-

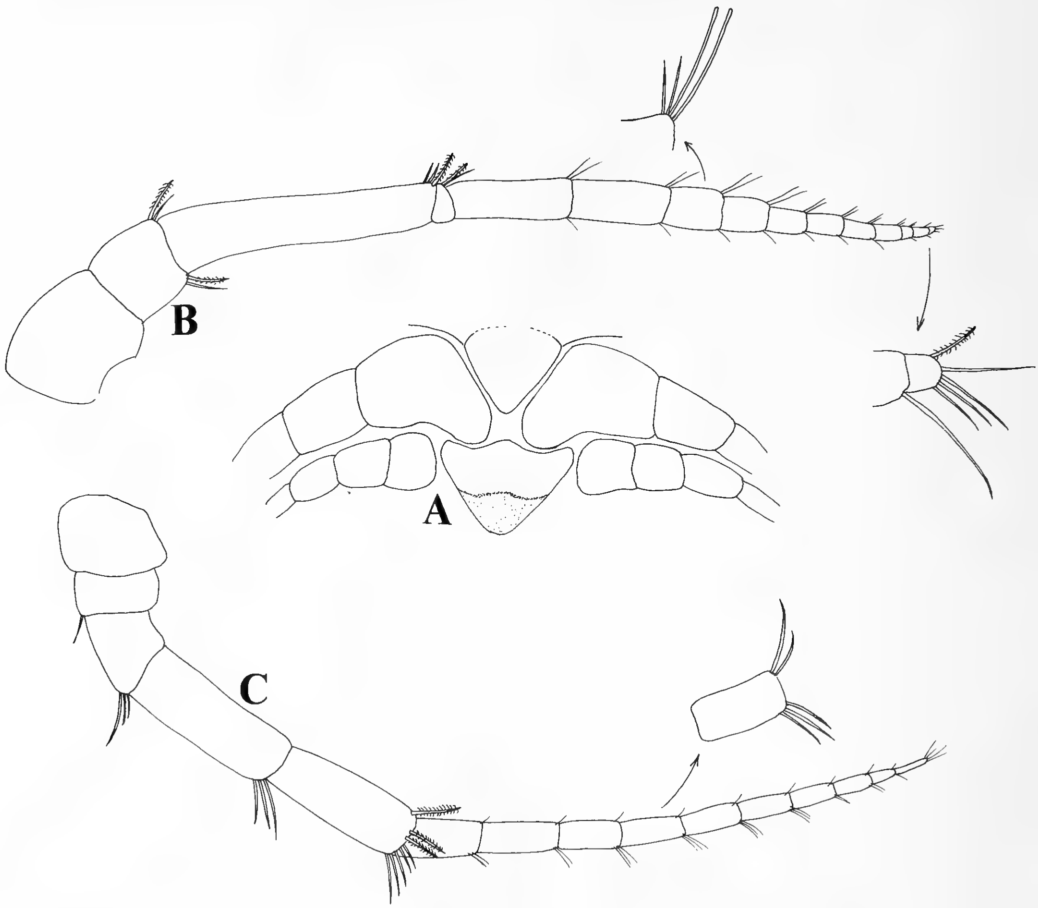


Fig. 2. *Aega francoisae* n. sp. A, frontal lamina, clypeus, labrum of female paratype (10.7 mm); B, left antennule of male paratype (9.2 mm); C, left antenna of male paratype (9.2 mm).

ing females of the families Aegidae, Corallanidae and Cymothoidae tend to replace the maxillipedal spines with PMS; *Aega francoisae* has both PMS and spines. Bruce (1988) stated that in Aegidae the mandible possesses a molar process and a 3- or 4-articulate palp. *Aega francoisae* has a molar process and a 3-articulate palp.

A review of the figures in the published literature on *Aega,* and examination of various species during this study, indicates that the morphology of the frontal lamina, clypeus and labrum can be variable and extremely valuable in distinguishing among closely related species of *Aega.* Unfortunately these structures have often not been illustrated by previous workers. In *A. francoisae* the clypeus and labrum appear to be fused into a single frontal "plate." The apparent shape of this plate varies depending upon the angle at which the specimen is viewed.

Prior to this description only three species of *Aega* had been recorded from the Galápagos Islands (Brusca 1987). *Aega acuminata* Hansen, 1897 is Panamic in distribution, occurring at depths greater than 1000 m, and Brusca (1983) assigned this species to the subgenus *Aega. Aega plebia* Hansen, 1897 and *A. longicornis* Hansen, 1897, like *A. francoisae* belong to Brusca's subgenus *Rhamphion. Aega plebia* is widespread

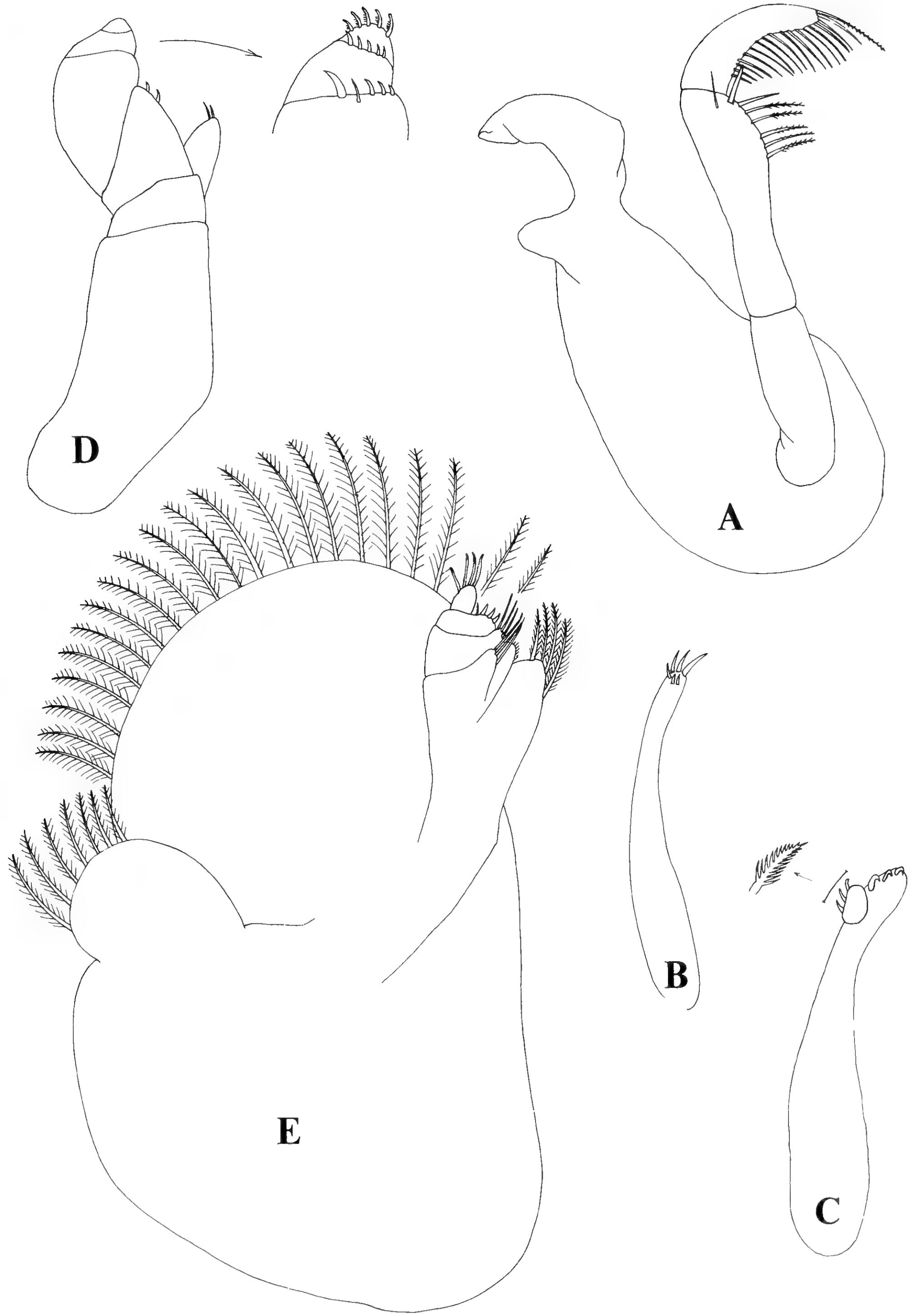


Fig. 3. *Aega francoisae* n. sp. A, left mandible of holotype; B, left maxillule of male paratype (9.2 mm); C, left maxilla of male paratype (9.2 mm); D, right maxilliped of male paratype (9.2 mm); E, right maxilliped of holotype.

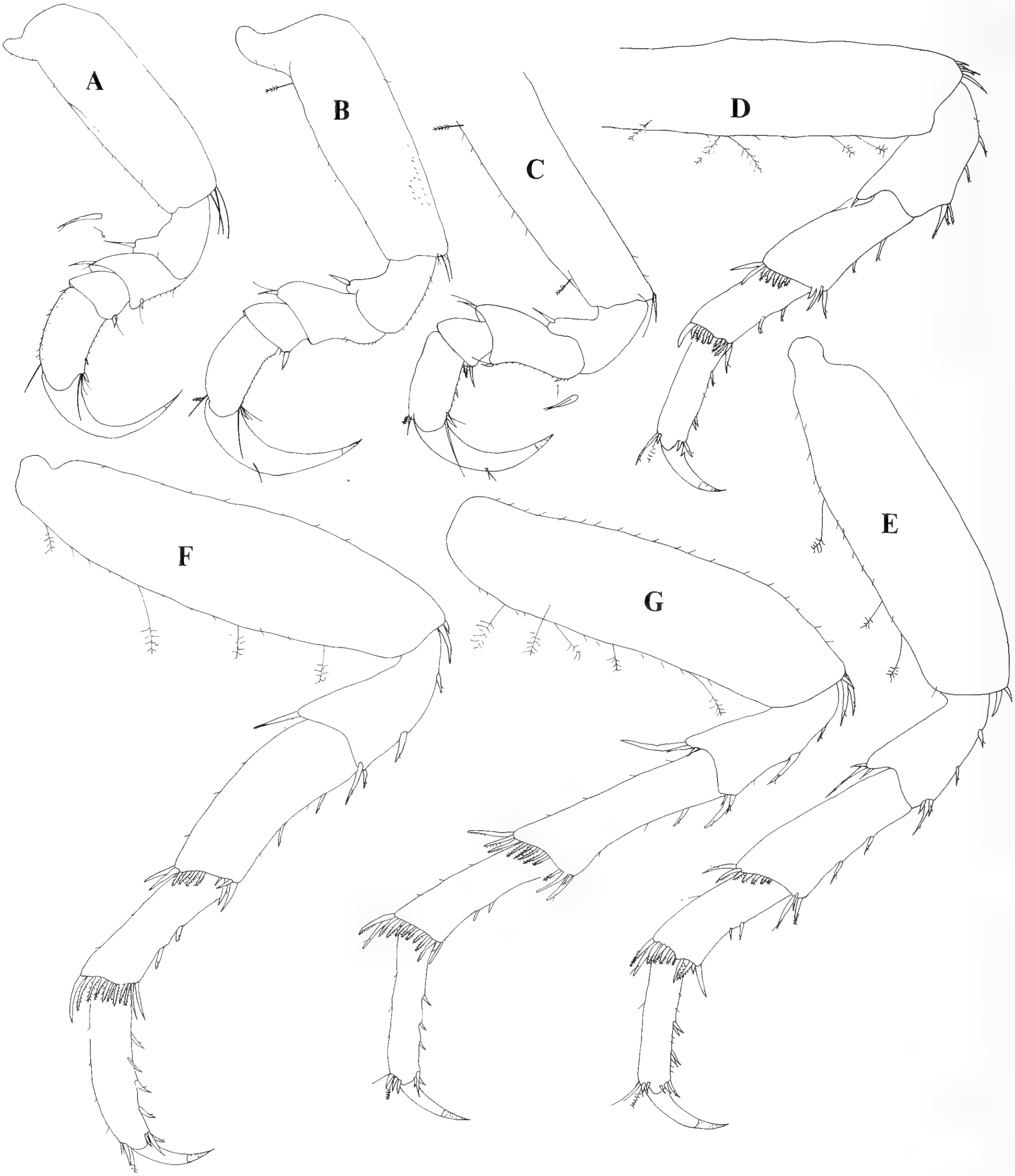


Fig. 4. *Aega francoisae* n. sp. Left pereopods of holotype (female): A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, pereopod 7.

throughout the Panamic and northwest Pacific temperate regions at depths exceeding 500 m. *Aega longicornis,* collected at *Albatross* Station 3402 (eastern Pacific Expedition) in 1891 at 0°57′30″S, 89°3′30″W at 842 m, is only known from the nonovigerous female holotype. Of these three species, *A. longicornis* most closely resembles *A. francoisae.*

Aega francoisae can be distinguished from

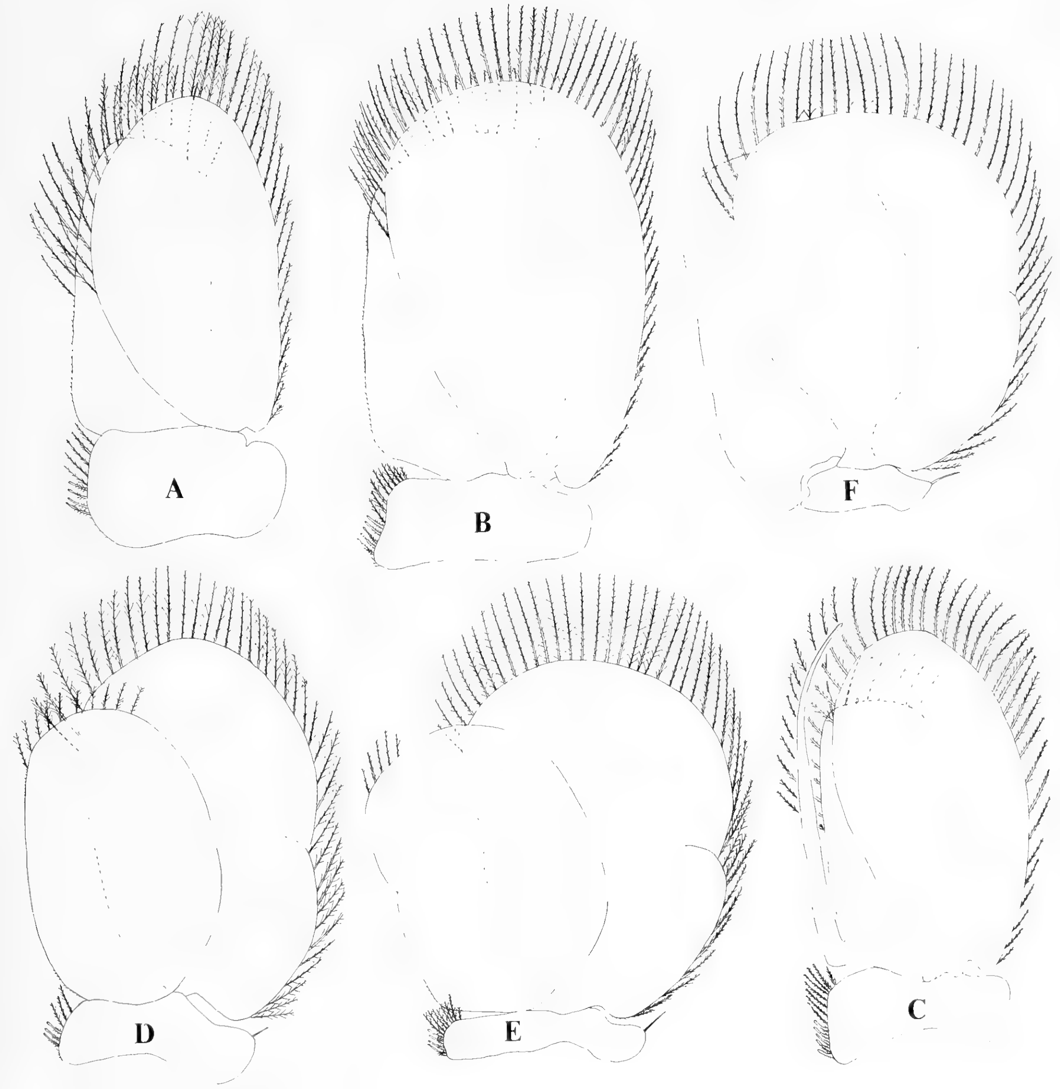


Fig. 5. *Aega francoisae* n. sp. Right pleopods: A, pleopod 1 of female paratype (10.7 mm); B, pleopod 2 of female paratype (10.7 mm); C, pleopod 2 of male paratype (9.2 mm); D, pleopod 3 of male paratype (9.2 mm); E, pleopod 4 of male paratype (9.2 mm); F, pleopod 5 of male paratype (9.2 mm).

A. longicornis by the following features: short antennae extending only to the second pereonite; incisor of mandible prominent, toothlike, not blunt; molar process present; maxillule with 3 stout apical and 3 subapical spines; uropodal exopod with one large spine apically; uropods only slightly longer than pleotelson.

None of the oostegial females had eggs or embryos in the brood pouch. However, 4 embryos were present in the sample sent to us by Dr. Monniot, suggesting that at least one of the oostegial females had been recently gravid. It is possible that the embryos were lost from the brood pouch during the ascent from 316 m depth to the surface, while in the collection basket of the *Johnson-Sea-Link*. Species of the genus *Aega* are thought to feed primarily on fish blood (Hansen 1897, Brusca 1983). Oostegite-bearing females of the type series do not appear to have recently fed, whereas all the males appear to have their guts distended with blood. F. Monniot (pers. comm.) noted no damage to the ascidian.

The ascidian *Halocynthia hispida* has been recorded from shallow waters off Sri Lanka, Tasmania, South Australia, Victoria and New South Wales (Kott 1985, Millar 1988). Monniot & Monniot (1989) describe two morphotypes for this species from the Galápagos region, a shallow-water SCUBA-collected hard form with a thick tunic, and a deep-water submersible-collected form with a soft hairy tunic. *Aega francoisae* came from the deep-water morph.

Etymology.—*Aega francoisae* is named for Dr. Françoise Monniot, Muséum National d'Histoire Naturelle, Paris, who found the isopods in the ascidian host and kindly forwarded them to R. C. Brusca.

Acknowledgments

The R/V *Seward Johnson* and *Johnson-Sea-Link* cruise was funded by Harbor Branch Oceanographic Institution, the U.S. National Cancer Institute, Natural Products Branch (contract no. N01-CM-67919), and SeaPharm Inc. The author thanks Drs. Françoise Monniot, Shirley Pomponi and Richard C. Brusca for making the specimens available, and Drs. Richard C. Brusca, Thomas E. Bowman, Gary J. Brusca and Niel L. Bruce for the many helpful suggestions from which this paper greatly benefited. The dorsum and pleotelson (Fig. 1A, C) were drawn by Ms. Jeanne Rogers.

Literature Cited

Bruce, N. L. 1983. Aegidae (Isopoda: Crustacea) from Australia with descriptions of three new species.—Journal of Natural History 17:757–788.

———. 1988. *Aega leptonica,* a new species of aegid isopod crustacean from the tropical Western Atlantic, with notes on *Rocinela oculata,* Harger and *Rocinela kapala,* new species.—Proceedings of the Biological Society of Washington 101: 95–101.

Brusca, R. C. 1983. A monograph on the isopod family Aegidae in the tropical Eastern Pacific. I. The genus *Aega.*—Allan Hancock Foundation, Monographs in Marine Biology No. 12:1–39.

———. 1987. Biogeographic relationships of Galapagos marine isopod crustaceans.—Bulletin of Marine Science 4(2):268–281.

———, & E. W. Iverson. 1985. A guide to the marine isopod Crustacea of Pacific Costa Rica.—Revista de Biologica Tropical 33(Suppl. 1):1–77.

Hansen, H. J. 1897. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross," during 1891, Lt. Commander Z. L. Tanner, U.S.N., commanding.—Bulletin of the Museum of Comparative Zoology, Harvard 31(5):95–129.

Kott, P. 1985. The Australian Ascidiacea 1, Phlebobranchiata and Stolidobranchiata. Memoirs of the Queensland Museum 23:1–440.

Millar, R. H. 1988. Ascidians collected during the South-east Pacific Biological Oceanographic Program (SEPBOP).—Journal of Natural History 22(1):225–240.

Monniot, C., & F. Monniot. 1989. Ascidians collected around the Galapagos Islands using the *Johnson-Sea-Link* Research Submersible.—Proceedings of the Biological Society of Washington 102:14–32.

San Diego Natural History Museum, Department of Marine Invertebrates, Balboa Park, San Diego, California 92101.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 663–673

SUPPLEMENTARY DESCRIPTION AND PHYLOGENETIC SIGNIFICANCE OF *ARCOSCALPELLUM CONRADI* (GABB) (CIRRIPEDIA: SCALPELLIDAE) FROM THE PALEOCENE VINCENTOWN FORMATION OF NEW JERSEY

Victor A. Zullo

Abstract.—The capitulum and peduncular armament of *Arcoscalpellum conradi* (Gabb) are described on new material from the upper Paleocene (Thanetian) Vincentown Formation in New Jersey. This species, together with the lower Paleocene (Danian) species *A. toulmini* Weisbord from Alabama and *A. elongatum* (Steenstrup) from Denmark, are derivatives of the Upper Cretaceous *A. fossula* (Darwin) group, and are representative of the ancestral stock that gave rise to eastern North American Eocene species of *Arcoscalpellum* Hoek.

The events leading to the mass extinction of invertebrate and vertebrate groups near the end of the Cretaceous (Maastrichtian Stage) also affected the cirriped fauna. As illustrated in Fig. 1, the late Cretaceous fauna was diverse and, considering the large number of holdover species, developed under relatively stable environmental conditions. Conditions responsible for the demise of the Cretaceous fauna appear to have originated with the onset of the Maastrichtian. Whereas the percentage of holdover species in Cenomanian through Campanian faunas averaged over 60%, the percentage of holdover species in the Maastrichtian dropped to 28%. After significant species diversification during the Maastrichtian, 95% of the fauna became extinct by the close of the Cretaceous, with only two species, *Zeugmatolepas cretae* (Steenstrup) and *Verruca prisca* Bosquet surviving into the early Paleocene (Danian Stage). Several genera also became extinct by the end of the Maastrichtian, including the lepadomorphs *Cretiscalpellum* Withers, *Loriculina* Dames, *Stramentum* Logan, *Titanolepas* Withers and *Virgiscalpellum* Withers, the brachylepadomorph *Brachylepas* Woodward, and the verrucomorph *Proverruca* Withers.

Only fifteen cirriped species, including seven lepadomorphs, three verrucomorphs, two brachylepadomorphs, and three balanomorphs, have been reported from Paleocene rocks (Table 1). The surviving Paleocene fauna, as currently understood, was exceedingly depauperate. How much of this record is related to a lack of Paleocene localities preserving suitable environments is unknown. Certainly Paleocene exposures are more restricted in areal extent than those of the Upper Cretaceous, but even shallow marine Paleocene deposits with well-preserved shelly invertebrates exhibit very low diversity in the cirriped component of their faunas.

The Paleocene fauna, and particularly that of the Danian, is clearly transitional between those of the Cretaceous and the Eocene (Fig. 2). With the exception of the Australasian records of *Bathylasma* Newman and Ross, *Pachylasma* Darwin, and *Eolasma* Buckeridge, all of the recorded Paleocene genera are represented in the Cretaceous, and only one genus, *Zeugmatolepas* Withers, became extinct prior to the Eocene. It is, thus, from the Paleocene survivors of the Cretaceous that the modern cirriped fauna was derived.

This study, based on new material from the Paleocene of eastern North America,

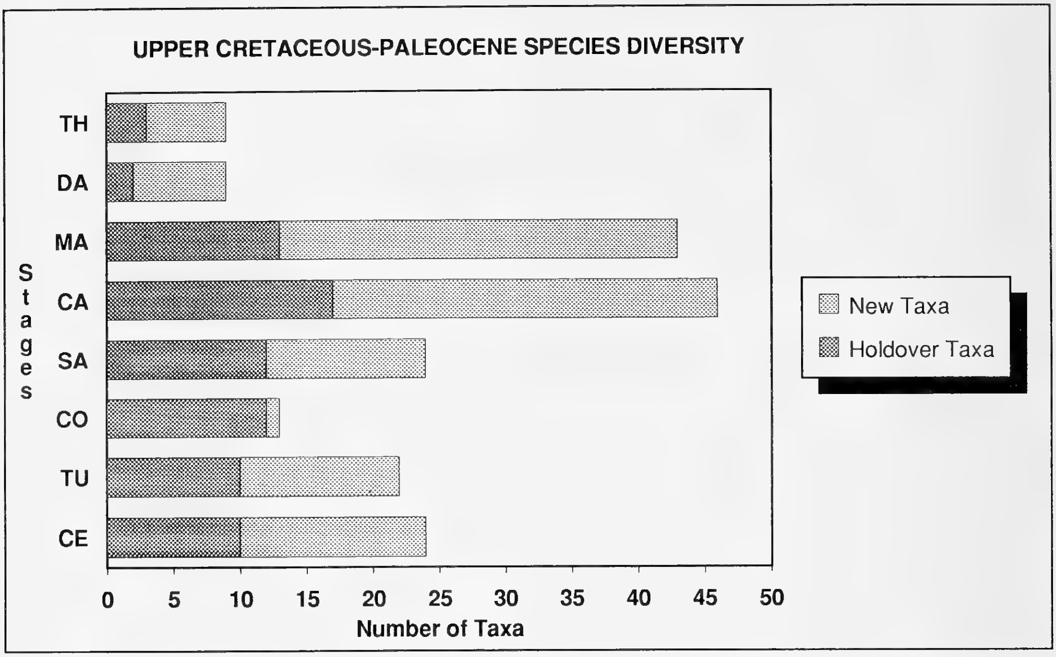


Fig. 1. Cirriped species diversity during the Late Cretaceous and Paleocene. Stage name abbreviations are, from oldest to youngest: CE, Cenomanian; TU, Turonian; CO, Coniacian; SA, Santonian; CA, Campanian; MA, Maastrichtian; DA, Danian; TH, Thanetian.

evaluates the relationship of the four known Paleocene species of *Arcoscalpellum* Hoek to the more diversified faunas of the Upper Cretaceous and Eocene (Fig. 3). Foster (1980) proposed the genus *Graviscalpellum* for species previously included in *Arcoscalpellum* that are hermaphroditic and whose lower latera are no more than one-tenth the height of the capitulum. As modified by Buckeridge (1983), Australasian fossil species of *Graviscalpellum* can be recognized by the lack of pits for complemental males on the inner surface of the scutum above the adductor muscle scar, the very low and broad rostral latus, the diminutive size of the other lower latera, and the apical umbones of the capitular plates. In all these regards, North American Paleocene and Eocene species of *Arcoscalpellum* are readily included in the genus *Graviscalpellum.* However, as noted by Foster (1980), the extant species attributed to *Graviscalpellum* range over five of the genera of extant Arcoscalpellinae described by Zevina (1978). Until the classification and nomenclature of extant arcoscalpellines can be unravelled, the North American Paleogene species will be referred to the genus *Arcoscalpellum* in the broader sense of Withers (1953).

The two species of *Arcoscalpellum* Hoek from North America are *A. toulmini* Weisbord from the Danian Porters Creek Formation in Alabama (Weisbord, 1977), and *A. conradi* (Gabb) from the Thanetian Vincentown Formation in New Jersey. Both were described from scanty material. *Arcoscalpellum toulmini* was described from two scuta and two terga, and *A. conradi* from the type lot of two fragmentary carinae and a scutum, and a questionable tergum illustrated by Weller (1907). Collections made by R. T. Perreault from the lower unnamed member and the Matthews Landing Member of the Porters Creek Formation in Wilcox County, Alabama include carinae, terga, scuta, upper latera, carinal latera, rostral

Table 1.—The Paleocene record of the cirriped order Thoracica.

Age	Taxon	Locality	Authority
Danian	*Zeugmatolepas cretae* (Steenstrup)	Denmark	Withers (1935)
	Scillaelepas dorsata (Steenstrup)	Denmark	Withers (1935)
	Arcoscalpellum elongatum (Steenstrup)	Denmark	Withers (1935)
	A. danicum (Brünnich Nielsen)	Denmark	Withers (1935)
	A. toulmini Weisbord	Alabama	Weisbord (1980)
	Verruca prisca Bosquet	Denmark	Withers (1935)
	V. rocana Steinman	Argentina	Withers (1935)
	Pycnolepas bruennichi Withers	Denmark	Withers (1935)
Thanetian	*Smilium calanticoideum* Buckeridge	New Zealand; Chatham Islands	Buckeridge (1983)
	Arcoscalpellum conradi (Gabb)	New Jersey	This paper
	Verruca rocana Steinman	North Carolina	Zullo & Baum (1979)
	Verruca tasmanica chatheca Buckeridge	Chatham Islands	Buckeridge (1983)
	Pycnolepas landenica Withers	Belgium	Withers (1953)
	Eolasma maxwelli Buckeridge	New Zealand; Chatham Islands	Buckeridge (1983)
Paleocene (undifferentiated)	*Pachylasma veteranum* Buckeridge	Chatham Islands	Buckeridge (1983)
	Bathylasma rangatira Buckeridge	Chatham Islands	Buckeridge (1983)

latera and peduncle plates. These plates are smaller than the types of *A. toulmini* and probably represent juveniles. Exhaustive sampling by H. Mendryk of three localities in the Vincentown Formation has yielded numerous well-preserved scuta, terga, carinae, upper latera, lower latera, and peduncle plates of *A. conradi.* The only plate missing for both of these species is the rostrum. The following discussion is based on a redescription of the capitular armature of *A. conradi.* The description of the Danian Porters Creek fauna, including a supplementary description of *A. toulmini,* is the subject of a forthcoming paper.

Family Scalpellidae Pilsbry, 1916
Subfamily Arcoscalpellinae Zevina, 1978
Genus *Arcoscalpellum* Hoek, 1907 (broad sense)
Arcoscalpellum conradi (Gabb, 1876)

Figs. 4, 5

Scalpellum conradi Gabb, 1876:179, pl. 5, figs. 3–4.—Johnson, 1905:28.—Weller, 1907:845, pl. 110, fig. 10.—Russell, 1967: 1546.—Richards, 1968:218.

Scalpellum (*Arcoscalpellum*) *conradi* Gabb: Withers, 1935:276, pl. 34, figs. 10a–b, 11a–b.

Arcoscalpellum conradi (Gabb): Weisbord, 1980:132, pl. 12, figs. 16–19.

Lectotype.—Basal part of carina, Academy of Natural Sciences of Philadelphia no. 4655 (designated by Withers, 1935).

Lectotype locality.—Vincentown Formation, Vincentown, Burlington County, New Jersey.

Emended diagnosis.—Intraparietes of carina very narrow, inset from parietes, extending from apex to near basal margin; tergal and lateral margins of scutum nearly equal in length; carinal segment of tergum narrow, usually less than one-fourth width of plate; occludent margin of tergum straight, about one-half length of scutal margin; umbo of upper latus apical; carinal latus triangular, broader than high, with incurved apex, apical umbo, and striated carinal segment.

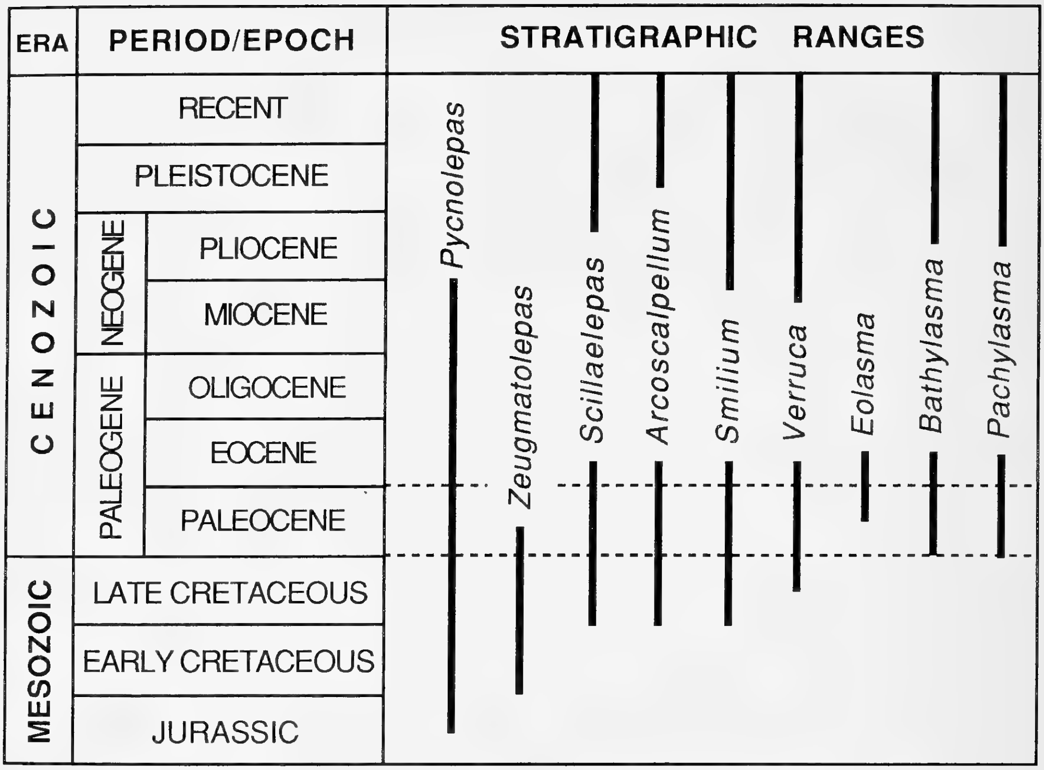


Fig. 2. Stratigraphic distribution of cirriped genera known from Paleocene strata.

Supplementary description.—Carina thin and markedly convex in side view; height averaging five and one-half times greatest width; apex narrow, acute; tectum nearly flat in apical region, but becoming gently arched in lower two-thirds, and broadening markedly toward basal margin; tectum ornamented by low, V-shaped growth increments, an indistinct median longitudinal ridge, and faint, irregularly-spaced, longitudinal striae, and bordered on both sides by narrow ridges; bordering ridges prominent in apical region, but fading toward basal margin; parietes narrow, markedly concave, offset from parietes at an angle of about 80°; intraparietes broad and thin in apical region, becoming very narrow and broadly rounded in basal region; intraparietes inset from parietes and at right angle to tectum; basal margin very thin, broadly V-shaped to gently rounded.

Scutum trapezoidal, height averaging twice width, strongly convex in cross section; gently arcuate apicobasal ridge dividing plate into subequal halves, with tergal side narrower than occludent side; apicobasal ridge distinct, broadly rounded in juvenile scuta, becoming indistinct and narrow in adults; exterior ornamented by moderately broad growth increments bearing fine, closely-spaced growth ridges, and often with a few, faint, irregularly-spaced ridges extending from apex to basal margin on either side of apicobasal ridge; apex acute, slightly curved toward tergum; tergal margin slightly concave, about equal in length to straight lateral margin; tergolateral angle obtuse, sharp to broadly rounded; basitergal angle sharp, about 90°; basal margin slightly convex; rostral angle acute, projecting slightly downward, about 90°; occludent margin convex and parallel to lateral mar-

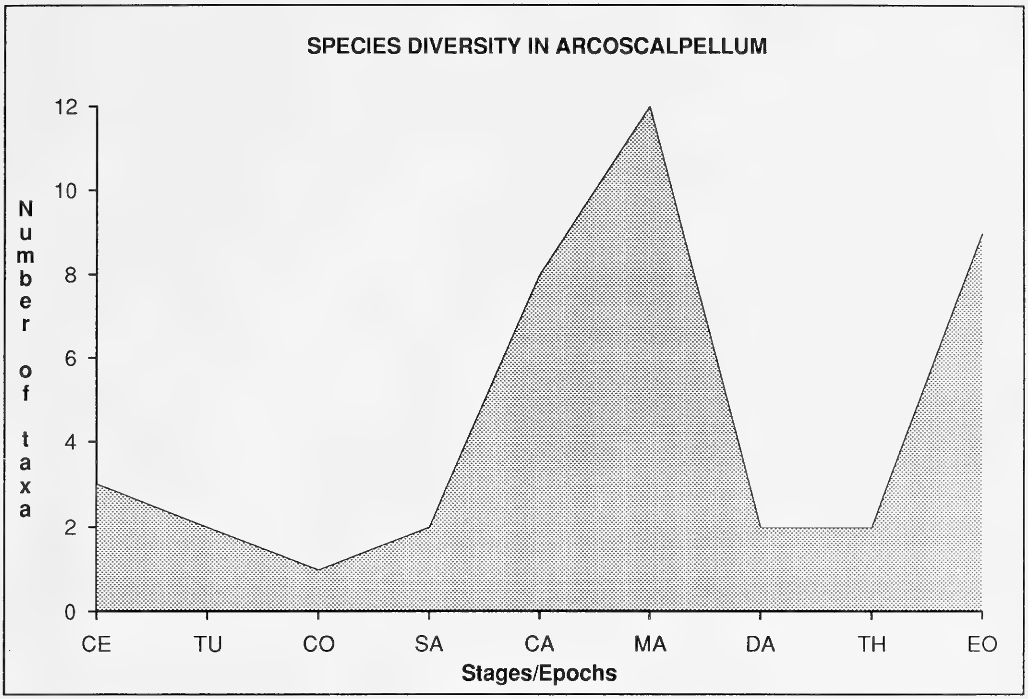


Fig. 3. Number of species ascribed to the genus *Arcoscalpellum* during the Late Cretaceous, Paleocene and Eocene (EO). Cretaceous and Paleocene stage name abbreviations as in Fig. 1.

gin; adductor muscle scar large, ovate, shallow, placed on the occludent side of the center of the plate; flattened inner surface of occludent margin narrow; thin ridge delimiting narrow, shallow, internal groove along upper part of occludent margin extends from near apex to midpoint of occludent margin; another indistinct, broadly rounded ridge roughly paralleling tergal margin extends from near apex to intersect lateral margin at point two-thirds the distance from basitergal angle to tergolateral angle; interior of apex and uppermost part of tergal margin marked by fine growth ridges.

Tergum flat, triangular, narrow, length from two to two and one-half times width, with narrow, low, nearly straight apicobasal ridge; exterior ornamented by broad growth increments bearing fine, closely-spaced growth ridges; central third of plate exterior on scutal side of apicobasal ridge often marked by narrow, regularly-spaced radial striae; apex acute, not arched toward carinal side; carinal segment of plate narrow, usually less than one-fourth width of plate, rarely up to one-third width of plate, not well-differentiated into upper and lower halves; carinal margin broadly convex; scutal margin very slightly convex, often marked at midpoint by slight angulation and change in direction of growth ridges; scutal margin nearly twice length of straight occludent margin; basal angle narrowly V-shaped; interior of tergum smooth, except for reflection of growth increments, narrow groove marking position of apicobasal ridge, and a few, short, thin, vertical ridges immediately below apical shelf; apical shelf narrow, delimited from interior of tergum by prominent narrow ridge extending from apex along occludent and upper carinal margins, and marked by fine growth ridges.

Upper latus flat, except for narrow, shallow sulcation along scutal margin, higher than wide, hexagonal in juvenile specimens, becoming quadrangular in adults, and slightly bowed toward scutum; umbo apical; exterior ornamented by growth ridges crossed by irregularly-spaced, indistinct radial striae; scutal and tergal margins straight; scutal margin bordered by prominent narrow ridge; tergal margin about eight-tenths length of scutal margin; basal margin of juvenile specimens divided into three or four unequal segments bounded by low, narrow apicobasal ridges; scutal segment of basal margin narrow, straight, upturned, about four-tenths length of broadly convex to angulate central segment; carinal segment slightly shorter than central segment, nearly straight, markedly upturned, and parallel to scutal margin; marked angulation between scutal and central segments of basal margin lost in adults; interior flat, smooth, except for beveled carina and scutal margins in adult specimens.

Carinal latus triangular, one and one-half times wider than high, with incurved apex and apical umbo; exterior ornamented by prominent growth ridges crossed by regularly-spaced radial striae on carinal side; broad, low, slightly arcuate, apicobasal ridge bordering striate surface of plate intersects basal margin to the scutal side of midpoint of basal margin; upper margin concave, marked by narrow ridge bearing upturned growth lines, and bearing thin, broad shelf inflected about 90° to plate; carinal margin gently convex; basal margin slightly concave, except slightly convex near intersection with upper margin.

Inframedian latus triangular, leaning toward scutum, low and broad, with width averaging twice height; rostral margin concave, slightly more than one-half length of nearly straight carinal margin; basal margin gently concave; umbo apical or slightly removed from apex; apex produced, forming acute point; exterior ornamented by closely-spaced, flat growth increments.

Rostral latus arcuate, very low and broad, with width about five times height; prominent, narrow, upwardly convex ridge extends from umbo across plate to lower part of rounded inframedian lateral margin; upper margin strongly convex; basal margin strongly concave; rostral margin truncate; inner surface divided into two equal halves by sharp, narrow ridges extending the breadth of the plate.

Rostrum unknown. Peduncular plates low and broad, with convex upper margin shorter than concave to straight lower margin.

Discussion.—The carinae and upper latera from the Vincentown Formation first appeared to represent two distinct species of *Arcoscalpellum,* but on further examination were recognized as growth stages of the same species. The juvenile carina has broad, very thin intraparietes developed for a short distance below the apex. In some instances, the upward growth of the intraparietes slightly offset the umbo from the apex plate. The juvenile tectum is relatively flat and bordered by prominent ribs. With growth, the tectum widens considerably, the bordering ribs become narrow and rather indistinct, and the intraparietes narrow and thicken appreciably. The broad, delicate intraparietes of the apical region are missing in adult carinae, being lost through abrasion during the life of the individual, or as a result of the fossilization process. The juvenile upper latus is sharply pentagonal to hexagonal as the result of the tripartite to quadripartite division of the basal margin. As is shown by the progression of growth increments, adult upper latera gradually lose the angulation between the scutal and central segments of the basal margin and become quadrilateral.

Arcoscalpellum conradi differs primarily from *A. toulmini* in plate proportions. The tergum of *A. conradi* is narrower, and has a much narrower carinal segment, but in other respects is very similar to that of *A. toulmini.* The scuta of the two species are also quite similar, differing primarily in the length of the tergal margin, which is considerably longer in *A. conradi.* New collections of *A. toulmini* plates made by R. T. Perreault from the Porters Creek Formation

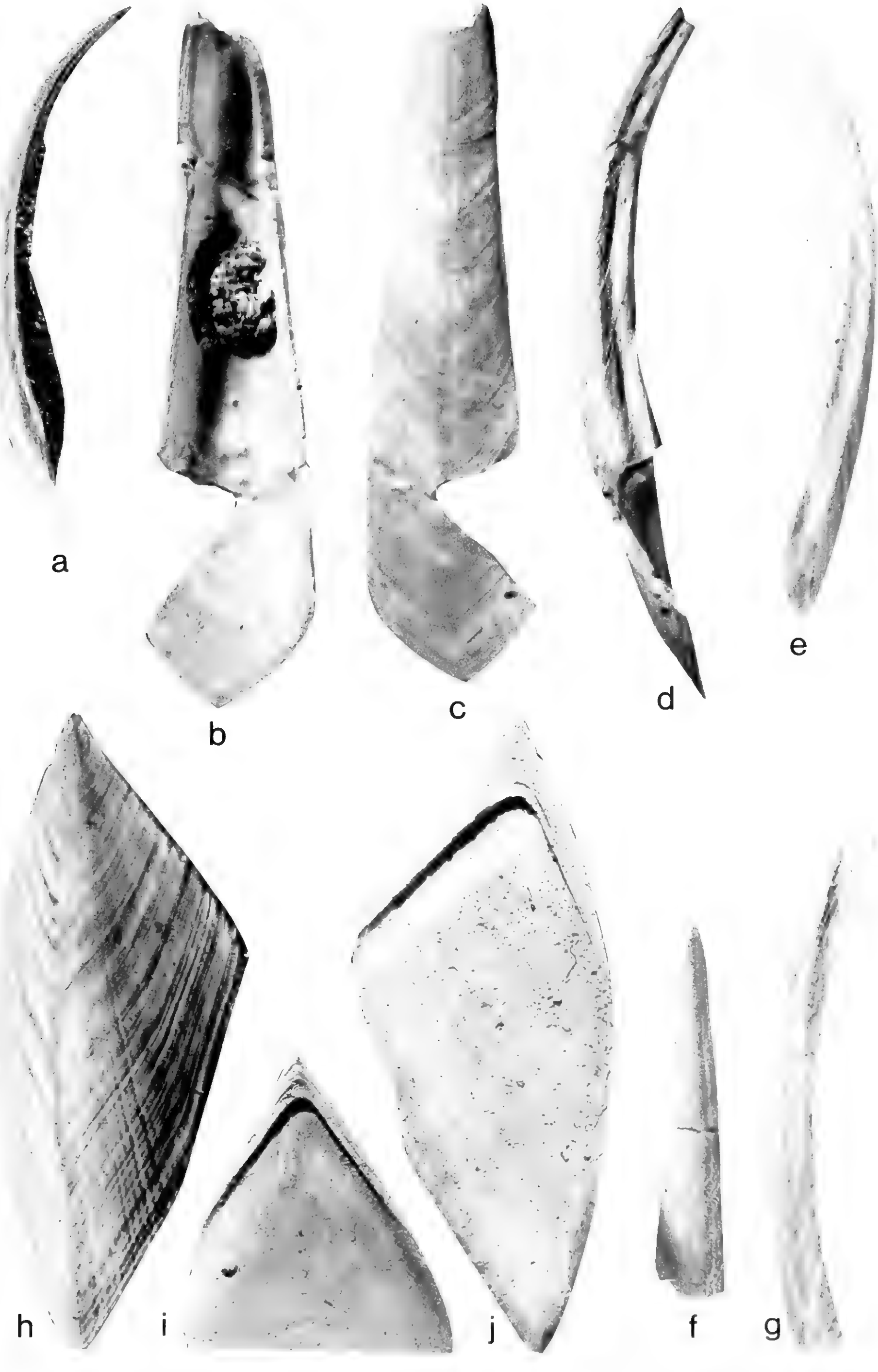


Fig. 4. Carinae and terga of *Arcoscalpellum conradi* (Gabb): a, side view of carina, hypotype USNM 444307; b–d, inner tectal and side views of carina, hypotype USNM 444308; e, side view of juvenile carina, hypotype USNM 444309; f, tectal view of juvenile carina, hypotype USNM 444310; g, side view of juvenile carina with umbo removed from apex, hypotype USNM 444311; h and j, exterior and interior view of tergum, hypotype USNM 444312; i, interior of apex of tergum showing vertical ridging, hypotype USNM 444313; a–d, h–j, ×4; e–g, ×10.

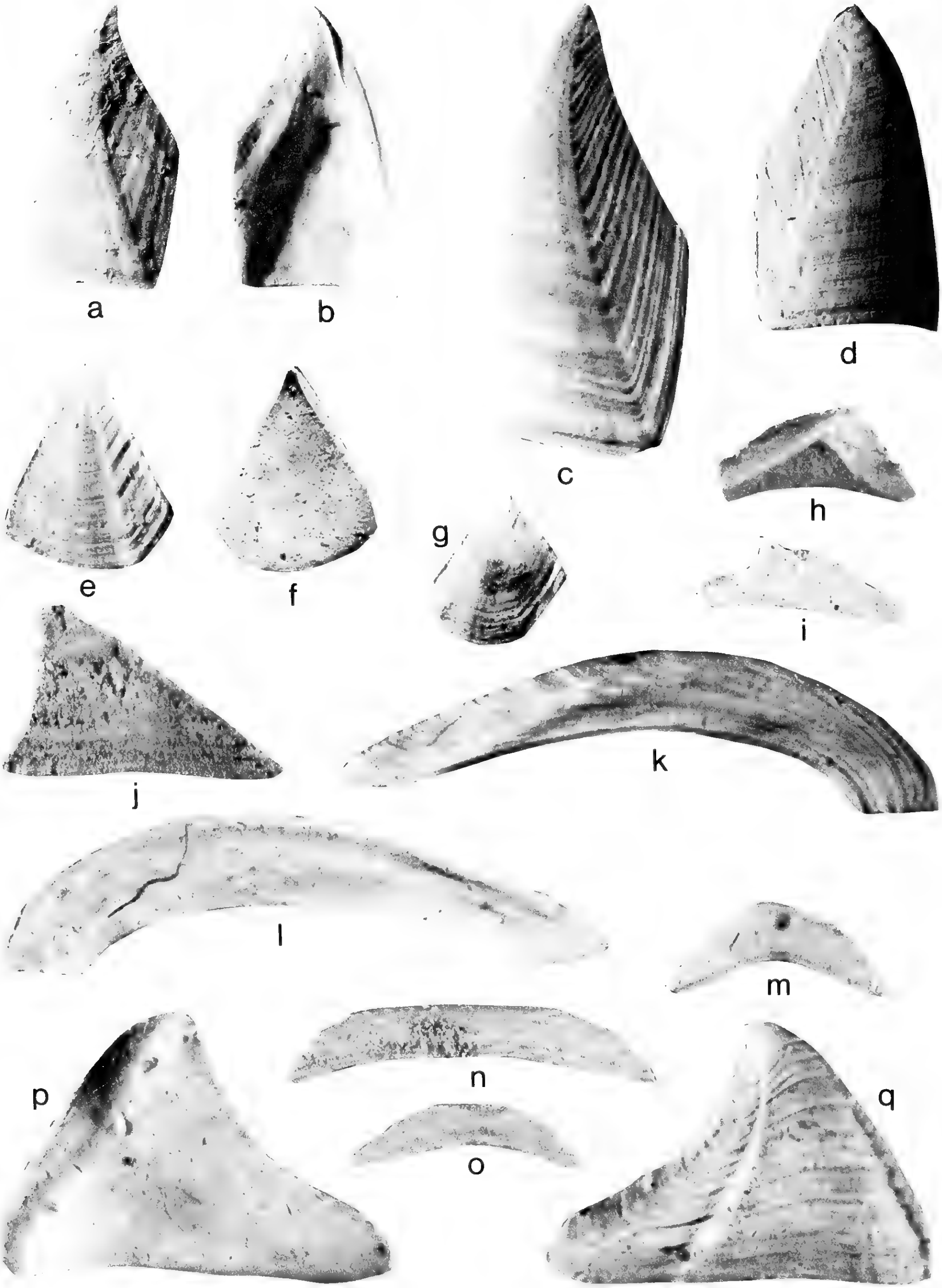


Fig. 5. Scuta, upper and lower latera, and peduncle plates of *Arcoscalpellum conradi* (Gabb): a–b, interior and exterior of scutum with well-developed apicobasal ridge, hypotype USNM 444314; c, exterior of scutum with moderately-developed apicobasal ridge, hypotype USNM 444315; d, exterior of scutum with typical apicobasal ridge, hypotype USNM 444316; e–f, exterior and interior of quadrilateral upper latus, hypotype USNM

in Alabama include carinae, terga, scuta, upper latera, carinal latera, rostral latera and peduncle plates. These plates are smaller than the types of *A. toulmini* and probably represent juveniles. The carina is similar to that of juvenile *A. conradi,* but lacks both a median and bordering longitudinal ridges. The carinal latus is similar, but is higher than wide and the basilateral angle is not produced. The rostral latus lacks the prominent external ridge diagonally traversing the breadth of the plate.

The Danish Danian species *A. danicum* is known only from a broken tergum, which resembles that of *A. conradi* in the narrowness of its carinal segment, but differs in the much greater overall width of the plate, the apparently longer scutal margin, and the markedly more arcuate apicobasal ridge. The scutum of the other Danian species from Denmark, *A. elongatum,* is remarkably similar to that of *A. conradi,* but the other plates differ substantially. The tergum of *A. elongatum* and its carinal segment are much broader, and the angle between the upper and lower carinal margins is better delimited. The upper latus is much narrower, the carinal latus lacks longitudinal striation on the carinal side, and the tectum of the carina is subcarinate.

Occurrence.—Upper Paleocene (Thanetian), Vincentown Formation, New Jersey. Previous records: lectotype locality, basal half of carina (lectotype), scutum (Gabb, 1876); Timber Creek, apical half of carina (Gabb, 1876); Hurfville, Gloucester County, ?tergum (Weller, 1907). New records: locality 1, over 200 carinae, over 300 scuta, over 300 terga, over 100 upper latera, over 100 carinal latera, 11 inframedian latera, 33 rostral latera, and over 100 peduncle plates; locality 2, nine partial carinae, six partial scuta, four partial terga, two upper latera, eight carinal latera, two partial rostral latera, nine peduncle plates; locality 3, five partial carinae, three scuta, three terga, one upper latus, one carinal latus.

Repository.—Hypotypes USNM 444307 through 444326, and hypotype lots USNM 444327 through 444329 are in the Department of Paleobiology, National Museum of Natural History, Washington, D.C.

Phylogenetic Considerations

Withers (1935) described three informal groups for the majority of Cretaceous species of *Arcoscalpellum*: the group of *A. arcuatum* (Darwin); the group of *A. fossula* (Darwin); and the group of *A. maximum* (J. de C. Sowerby). Although Withers did not provide diagnoses for these groups, they are readily distinguished by their carinae. The tectum in the *A. arcuatum* group is arched, broadens rapidly toward the base, has a median longitudinal ridge and prominent bordering ridges, and intraparietes that are bent inward at nearly right angles to the parietes. The carina in the *A. maximum* group is distinguished by its narrow apex and broad base, wide intraparietes at nearly right angles to the tectum, and longitudinal ridges separating the narrow parietes from the intraparietes. The tectum in the *A. maximum* group is arched, and bears median longitudinal and bordering ridges, but these are less prominent than the tectal ridges in the *A. arcuatum* group. The median ridge on the tectum in the *A. fossula* group is either greatly reduced or absent, the tectum is flat, and the plate is narrow throughout its length. Although prominent, the intraparietes are

---

←
444317; g, exterior of juvenile hexagonal upper latus, hypotype USNM 444318; h, interior of inframedian latus, hypotype USNM 444319; i, interior of inframedian latus, hypotype USNM 444320; j, exterior of inframedian latus, hypotype USNM 444321; k–l, exterior and interior of rostral latus, hypotype USNM 444322; m–o, exterior of peduncle plates, hypotypes USNM 444323, 444324 and 444325, respectively; p–q, interior and exterior of carinal latus, hypotype USNM 444326; a–f, ×4; h–q, ×10.

considerably less developed than those in the *A. maximum* group. Older Cretaceous species of the *A. fossula* group bear prominent ridges separating the tectum from the parietes, but in the Maastrichtian species *A. gracile* (Bosquet) these ridges are greatly reduced.

Representatives of the *A. maximum* and *A. fossula* groups are present in the Upper Cretaceous of eastern North America (Collins 1973, Zullo 1987). The *A. maximum* group is represented by *A. hubrichti* Collins from the lower Campanian of Mississippi and Alabama and *A. bakeri* Collins from the lower Maastrichtian of Mississippi and Delaware. *Arcoscalpellum campus* Collins from the Maastrichtian of Mississippi and *A. withersi* Collins from the Maastrichtian of Mississippi, Alabama, and Delaware represent the *A. fossula* group.

Based on carinal morphology, the Paleocene species of *Arcoscalpellum* appear to have been derived from the *A. fossula* group. All have flat or gently arched tecta, the median ridge is either lacking or subdued, and the bordering ridges are reduced in prominence. The carina is relatively narrow throughout its length, and the intraparietes are greatly reduced in width. As noted previously by Withers (1935) for *A. conradi,* the general form of the capitular plates of the North American Paleocene species compares favorably with that of *A. fossula* and *A. gracile,* differing primarily from the former in lacking prominent external radial ornament. The *A. fossula* facies is continued in the eastern North American Eocene species, *A. subquadratum* (Meyer and Aldrich) from the Calibornian and *A. jacksonense* Withers from the Jacksonian, with additional reduction in: 1) overall carinal width; 2) prominence of the ridges bordering the tectum; and 3) width of the parietes and intraparietes.

Vincentown Formation Locality Descriptions

1. Outer side of large meander on South Branch of Rancocas Creek, 0.75 km north of intersection of Church and Red Lion Roads at Vincentown, Mt. Holly 7.5′ quadrangle, Burlington County, New Jersey.
2. Outer side of meander on South Branch of Rancocas Creek, 0.5 km southwest of gaging station and 1.25 km north-northwest of intersection of Church and Red Lion Roads at Vincentown, Mt. Holly 7.5′ quadrangle, Burlington County, New Jersey.
3. Tributary to South Branch of Rancocas Creek, approximately 1.5 km south-southwest of Golden Pheasant Country Club, Mt. Holly 7.5′ quadrangle, Burlington County, New Jersey.

Acknowledgments

I thank Harry Mendryk of Harrison, New Jersey for the generous donation of his collection of *A. conradi,* and for information on the stratigraphy and geography of barnacle-bearing localities in the Vincentown Formation. I thank R. T. Perreault of Jarreau, Louisiana for the additional collections of *A. toulmini* from the Porters Creek Formation in Alabama. Acknowledgment is made to the Donors of the Petroleum Research Fund, administered by the American Chemical Society, for the support of this research.

Literature Cited

Buckeridge, J. S. 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia.—New Zealand Geological Survey Paleontological Bulletin 50:1–151.

Collins, J. S. H. 1973. Cirripedia from the Upper Cretaceous of Alabama and Mississippi, eastern Gulf region, U.S.A. I. Palaeontology.—Bulletin of the British Museum (Natural History), Geology 23(6):352–388.

Foster, B. A. 1980. Further records and classification of scalpellid barnacles (Cirripedia: Thoracica) from New Zealand.—New Zealand Journal of Zoology 7:523–531.

Gabb, W. A. 1876. Note on a discovery of representatives of three orders of fossils new to the Cretaceous Formation of North America.—Proceedings of the Academy of Natural Sciences of Philadelphia 28:178–179.

Hoek, P. P. C. 1907. The Cirripedia of the *Siboga-Expedition,* A. Cirripedia Pedunculata.—*Siboga-Expeditie,* Uitkomsten 18(31A):1–127.

Johnson, C. W. 1905. Annotated list of the types of invertebrate Cretaceous fossils in the collections of the Academy of Natural Sciences of Philadelphia.—Proceedings of the Academy of Natural Sciences of Philadelphia 57:4–28.

Pilsbry, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species.—United States National Museum Bulletin 93:i–xi, 1–366.

Richards, H. G. 1968. Catalogue of invertebrate fossil types at the Academy of Natural Sciences of Philadelphia.—Academy of Natural Sciences of Philadelphia Special Publication 8:1–222.

Russell, L. S. 1967. A pedunculate cirripede from Upper Cretaceous rocks of Saskatchewan.—Journal of Paleontology 41(6):1554–1557.

Weisbord, N. E. 1977. Some Paleocene and Eocene barnacles (Cirripedia) of Alabama.—Bulletins of American Paleontology 72(297):143–166.

———. 1980. Fossil lepadomorph, brachylepadomorph and verrucomorph barnacles (Cirripedia) of the Americas.—Bulletins of American Paleontology 78(311):117–212.

Weller, S. 1907. A report on the Cretaceous paleontology of New Jersey. Based upon stratigraphic studies of George N. Knapp.—New Jersey Geological Survey, Paleontological Series 4:i–ix, 1–871.

Withers, T. H. 1935. Catalogue of fossil Cirripedia in the Department of Geology, Vol. II. Cretaceous.—British Museum (Natural History), London, pp. i–xiii, 1–534.

———. 1953. Catalogue of fossil Cirripedia in the Department of Geology, Vol. III. Tertiary. British Museum (Natural History), London, pp. i–xv, 1–396.

Zevina, G. B. 1978. A new classification of the family Scalpellidae Pilsbry (Cirripedia, Thoracica). Part 2. Subfamilies Arcoscalpellinae and Meroscalpellinae.—Zoologichesky Zhurnal Akademiia Nauk SSSR 57(9):1343–1352 (in Russian).

Zullo, V. A. 1987. Scalpellid and brachylepadomorph barnacles (Cirripedia, Thoracica) from the Upper Cretaceous Mt. Laurel Sand, Delaware.—Journal of Paleontology 61(2):333–345.

———, & G. R. Baum. 1979. Paleogene barnacles from the Coastal Plain of North Carolina.—Southeastern Geology 20:229–246.

Department of Earth Sciences, University of North Carolina at Wilmington, Wilmington, North Carolina 28403.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 674–680

METACYCLOPS LEPTOPUS TOTAENSIS, NEW SUBSPECIES (CRUSTACEA: COPEPODA) FROM LAGO DE TOTA, COLOMBIA

Janet W. Reid, Javier A. Molina Arevalo, and Manuel M. Fukushima

Abstract.—*Metacyclops leptopus totaensis,* a new subspecies of cyclopoid copepod from the plankton of Lago de Tota, a high-altitude Andean lake in Colombia, differs from other members of the *leptopus*-complex in the ornamentation of the leg 1 coupler, and in the proportions of the appendages of the free article of leg 5.

Two planktonic species of copepods (Crustacea) inhabit Lago de Tota, Colombia. Lago de Tota is among the northernmost known habitats of the calanoid *Boeckella gracilis* (Daday), which is distributed through the Andes southwards to Tierra del Fuego, and in the Argentine Pampas; Gaviria (1989) supplied several new records from Colombia, and described the morphology of Colombian populations of this species. The other planktonic copepod in Lago de Tota is a previously undescribed subspecies of the *Metacyclops leptopus*-complex (Cyclopoida). Since no member of this group has yet been completely described, we furnish detailed figures to facilitate future evaluation of members of this complex.

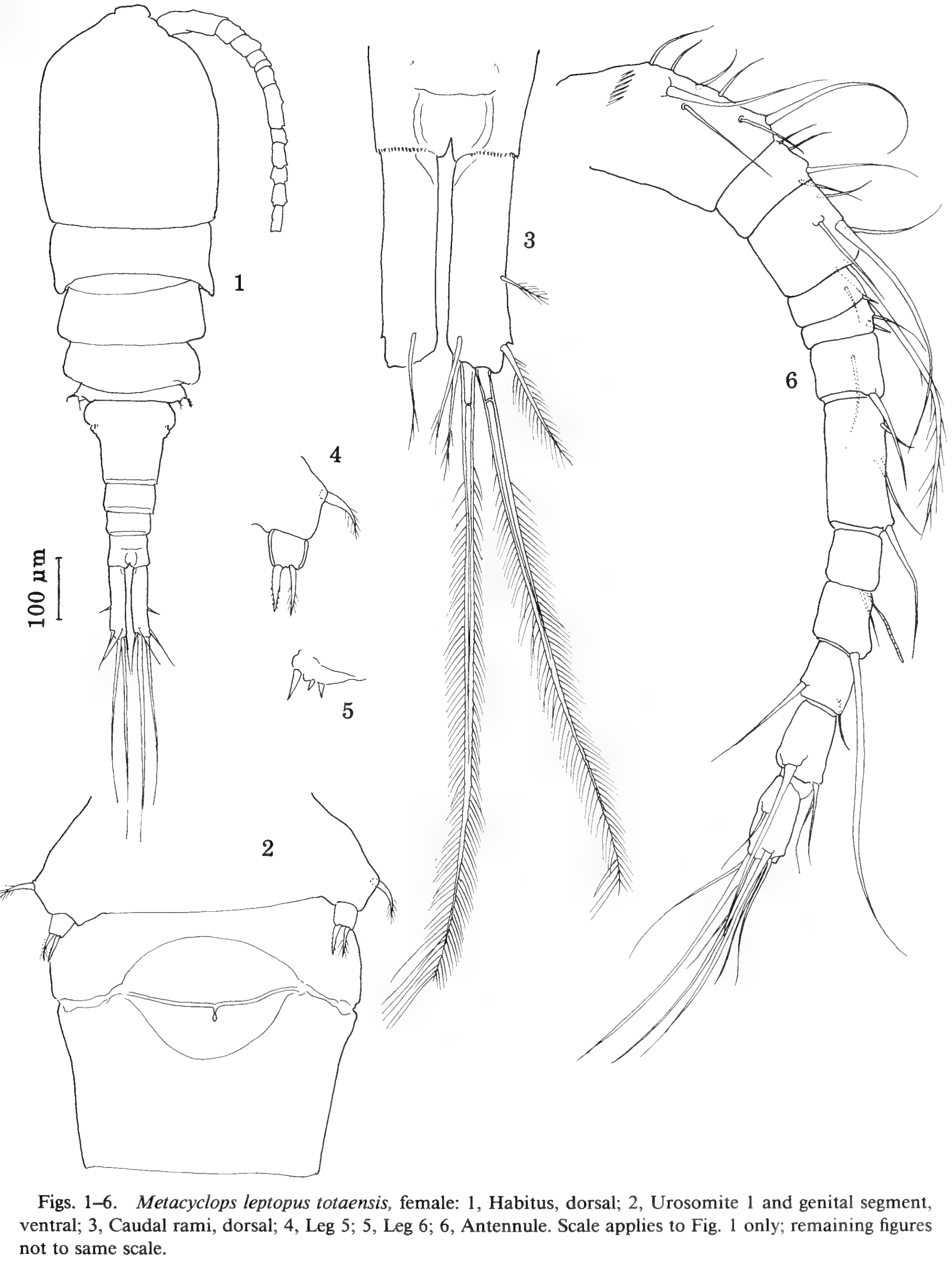
Lago de Tota is situated in the páramo region of the Colombian Andes, at 5°30′S, 72°50′W; its elevation is 3015 m, area about 56 km^2, mean depth 34 m and maximum depth 67 m. Annual ambient temperatures range from 0°–20°C, conductivity 70–90 μS, and pH values 7–9.4. Except for its large size, physical and chemical characteristics of Lago de Tota are typical of waters in the páramo region (Gaviria 1989).

Samples of zooplankton were fixed in formalin and transferred to a solution of 70% ethanol for long-term storage. Specimens were slowly evaporated to glycerin and examined in this medium, or in commercial polyvinyl lactophenol with chlorazol black E added. Drawings were made with the aid of a camera lucida at magnifications of 400× or 600×; details were confirmed under oil immersion at 1000×.

Cyclopidae Sars, 1913
Metacyclops Kiefer, 1927, sensu Lindberg, 1961
Metacyclops leptopus totaensis, new subspecies
Figs. 1–22

Material.—Holotype ♀, USNM 242365; allotype ♂, USNM 242367; paratypes: 3 ♀ and 1 ♂, dissected on slides, and 20 ♀ and 10 ♂, undissected, USNM 242366; all from Lago de Tota, col. 1985 by JAMA. All undissected specimens alcohol-preserved. Additional paratype material in personal collection of JAMA.

Female.—Length of holotype, excluding caudal setae 1.03 mm; lengths of 10 paratypes 0.90–1.08 mm (median 1.02 mm). Egg-bearing females with 1 or 2 eggs each side. Body widest at prosomite 1 in dorsal view (Fig. 1). Outer margins of posterior 2 prosomites slightly crenulate. Genital segment (Fig. 2) expanded anteriorly, length slightly less than breadth; seminal receptacle ovoid, lateral canals almost horizontal. Caudal rami (Fig. 3) 4 times longer than broad; lateral seta inserted slightly distal to midlength. Lengths of caudal setae of ho-



Figs. 1–6. *Metacyclops leptopus totaensis,* female: 1, Habitus, dorsal; 2, Urosomite 1 and genital segment, ventral; 3, Caudal rami, dorsal; 4, Leg 5; 5, Leg 6; 6, Antennule. Scale applies to Fig. 1 only; remaining figures not to same scale.

lotype (in μm): lateral 21, dorsal 60, inner to outer terminal 60, 315, 270, 60. Caudal setae finely plumose, 2 middle terminal setae each with several long medially-directed setules near tip.

Antennule (Figs. 1, 6) when reflexed reaching end of prosomite 2 (not shown completely reflexed in Fig. 1); of 12 articles, proximalmost to distalmost articles with 8, 4, 5, 1, 1, 2, 3, 1, 1, 2, 2, and 8 setae respectively; articles 4 and 5 also each with spine; articles 8 and 11 also each with slender esthetasc, each esthetasc reaching beyond distal margin of succeeding article; 2 outermost terminal setae of article 12 fused at base. Antenna (Figs. 7–9) of 4 articles; article 1 with only 2 setae, rows of setules on each surface, and small papilla near distal margin of caudal surface. Labrum (Fig. 10) with rounded protrusions at outer corners and about 10 blunt teeth; double row of long slender spinules on dorsal surface (not figured). Mandible, maxillule, maxilla and maxilliped as in Figs. 11–14, respectively.

Swimming legs 1–4 (Figs. 15–20) with rami each of 2 articles; leg 2 similar to leg 3. Spine formula 3,4,4,3. Outer spines of leg 1 exopod each with row of spinules on dorsal (anterior) margin well separated, set nearly at right angles to axis of spine; spinules on ventral (posterior) margin of each spine few, small, closely appressed to spine. Outer spines of exopods of legs 2–4 each with spinules set at approximately 45° angle to axis of spine, spinules on each margin of spine similar in size and number. Anterior surfaces of couplers of legs 1–3 and posterior surface of coupler of leg 1 ornamented with irregular rows of long and short hairs or slender spinules; ornamentation of anterior surface of coupler of leg 2 similar to that of leg 3; posterior surfaces of couplers of legs 2 and 3 without ornament. Anterior surface and distal margin of leg 4 coupler without ornament; posterior surface with 3 rows of irregularly spaced slender spinules, spinules of proximal row shorter than spinules of distal rows. Leg 4 endopod 2, 2.9 times longer than broad; lateral terminal spine slightly less than ½ length of medial terminal spine.

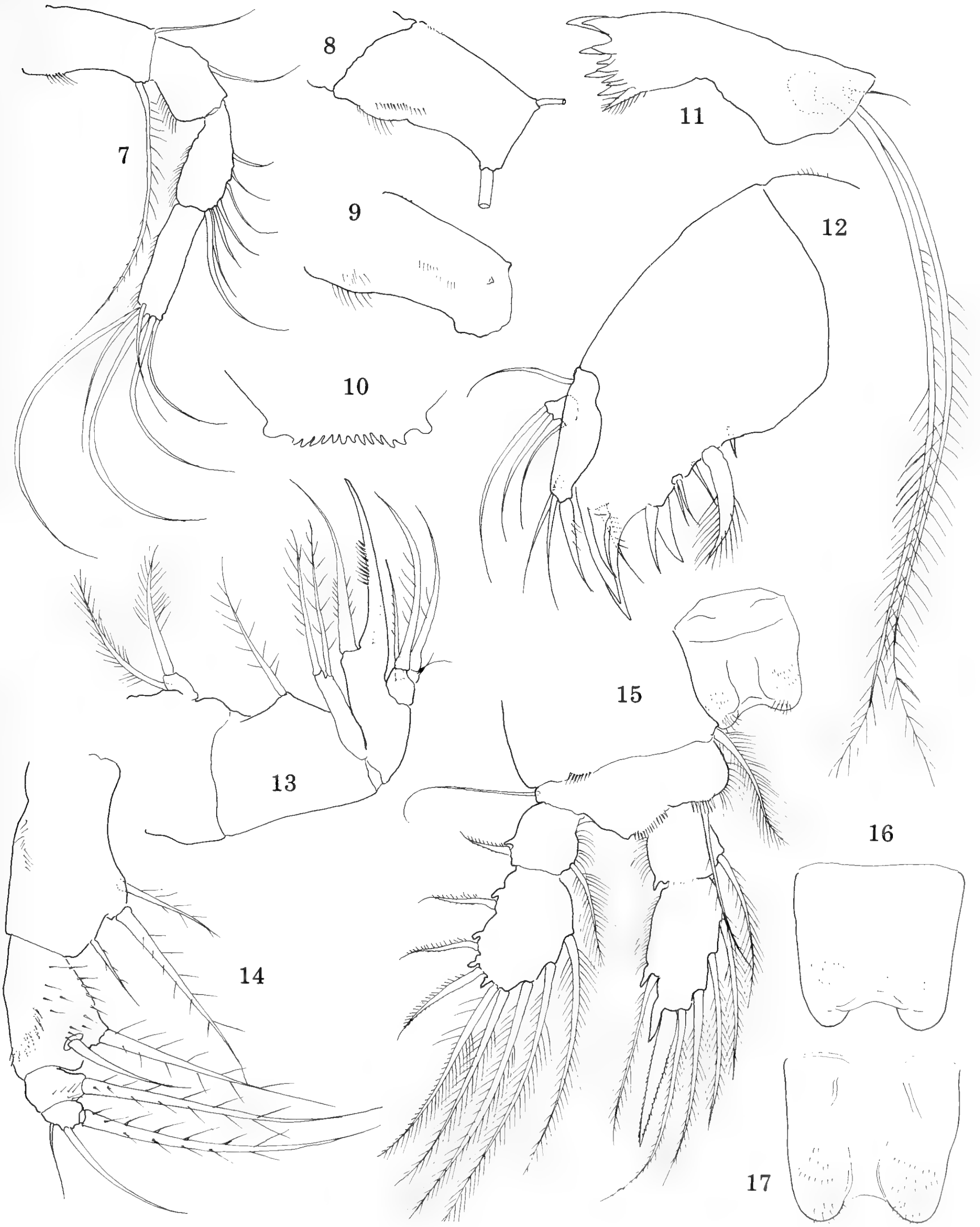
Leg 5 (Fig. 4) of 1 fused and 1 free article; free article quadrate. Medial spine and lateral seta of free article subequal in length, slightly longer than free article; medial spine slightly broader than lateral seta; medial spine with small spinules, lateral seta finely plumed. Leg 6 (Fig. 5) consisting of small prominence with 3 spines of unequal lengths, dorsalmost spine longest.

Male.—Length of allotype 0.80 mm; of 10 paratypes 0.76–0.85 mm (median 0.82 mm). Proportions of body and of caudal setae much as in female. Antennule (Fig. 21) geniculate, with 4 small esthetascs on article 1, 1 on article 9.

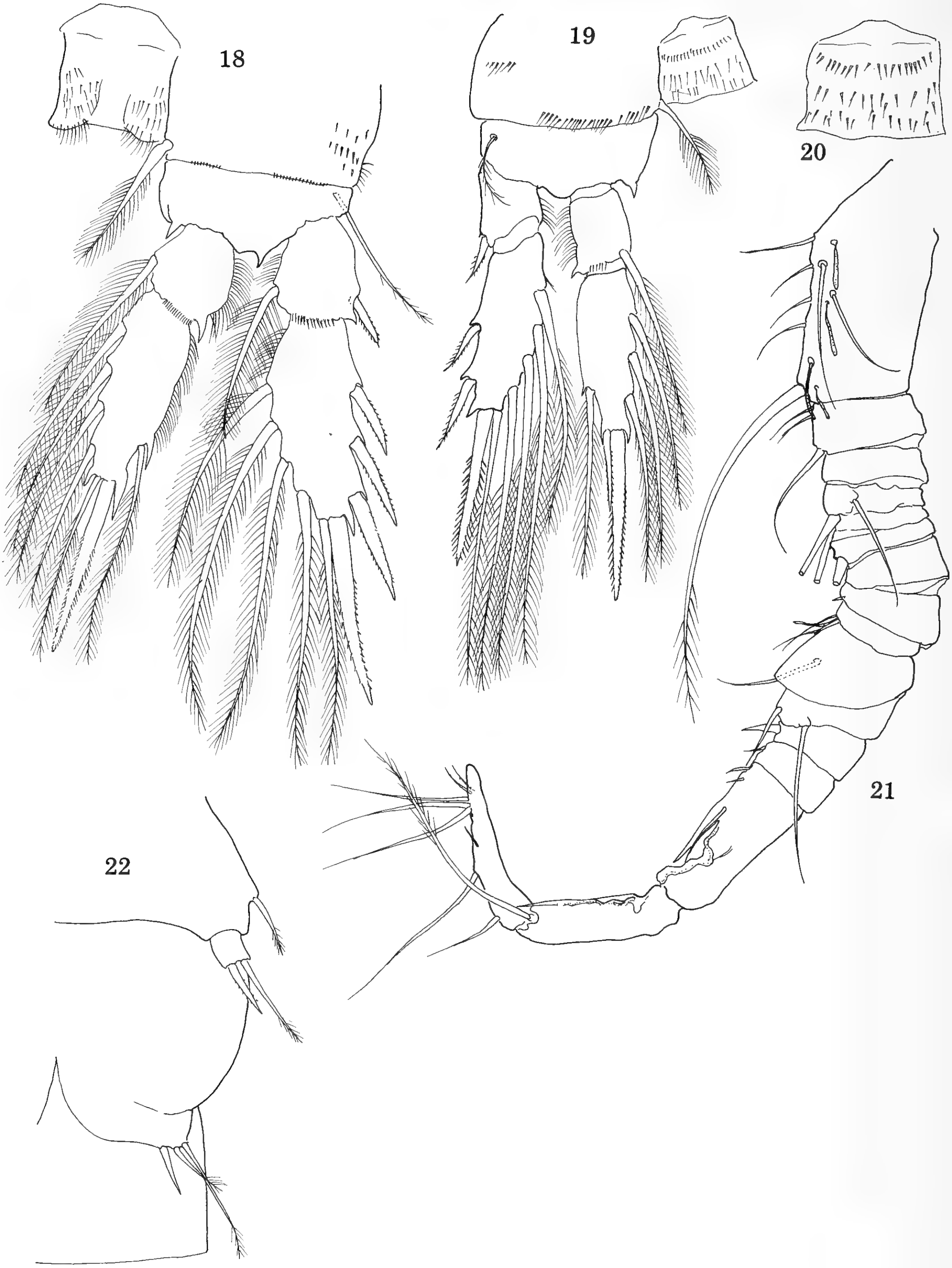
Leg 5 (Fig. 22) similar to female, except medial spine almost twice length of free article, and lateral seta about 3 times length of free article. Lengths of medial spine and middle and lateral setae of leg 6, 16, 17 and 36 μm, respectively; lateral seta reaching posterior margin of succeeding somite.

Variation.—Variation between individuals occurred in the distribution of the fine hairs on the couplers of the swimming legs (cf. Figs. 15, 17, 19, 20). Otherwise, the relative lengths of the appendages of leg 5 of both sexes were essentially constant. Variation of less than 10% was measured in the proportion of length to breadth of the leg 4 endopod. All specimens examined shared the long setules near the tips of the middle terminal caudal setae.

Discussion.—Within the *Metacyclops leptopus* species-complex, three subspecies are currently defined: *M. leptopus* s. st. (Kiefer, 1927), and *M. l. mucabajiensis* and *M. l. venezolanus* Kiefer, 1956. The nominate species has been recorded from large Andean lakes in Peru, Bolivia, and possibly Venezuela; *M. l. mucubajiensis* is known only from Laguna Mucubaji in the Venezuelan Andes; and *M. l. venezolanus* only from Mariposa Reservoir, Caracas; these



Figs. 7–17. *Metacyclops leptopus totaensis,* female: 7, Antenna (setules of most setae not drawn); 8, Antenna article 1, frontal surface, enlarged; 9, Antenna article 1, caudal surface, enlarged; 10, Labrum, ventral surface; 11, Mandible; 12, Maxillule; 13, Maxilla; 14, Maxilliped; 15, Leg 1, anterior; 16, Leg 1 coupler, posterior, enlarged; 17, Leg 1 coupler of another specimen, anterior, enlarged. Figures not to same scale.



Figs. 18–22. *Metacyclops leptopus totaensis.* Figs. 18–20, female: 18, Leg 3, anterior; 19, Leg 4, posterior; 20, Leg 4 coupler of another specimen, posterior, enlarged. Figs. 21–22, male: 21, Antennule; 22, Legs 5 and 6. Figures not to same scale.

records were summarized by Reid (1985, 1987).

Kiefer (1956) based the two subspecies from Mucubaji and Mariposa on differences in the proportions of the free article and appendages of leg 5, and in the ornamentation of the leg 1 coupler; although he later (Kiefer 1957) amplified his original description of *M. leptopus* s. st. with figures of specimens from Lake Titicaca, he never supplied extensive morphological comparisons of any of these forms. Since the specimens from Lago de Tota show remarkable constancy in the structure of leg 5 and in the ornamentation of the couplers of the swimming legs, we have chosen to follow Kiefer's lead in naming a fourth subspecies. According to Kiefer's criteria, the subspecies are discriminated as follows:

Key to Females of the Subspecies of *Metacyclops leptopus*

1. Leg 5, lateral seta 1.5–2× longer than free article; Leg 1, coupler naked or with hairs or few spinules on margin 2
– Leg 5, lateral seta 3–4× longer than free article; Leg 1, coupler with numerous posteriorly curved spinules on margin .... *leptopus* s. st.
2. Leg 5, medial spine less broad or only slightly broader than lateral seta; Leg 1, margin of coupler with hairs or few spinules 3
– Leg 5, medial spine more than twice as broad as lateral seta; Leg 1, margin of coupler naked ... *mucubajiensis*
3. Leg 5, medial spine shorter and less broad than lateral seta; Leg 1, margin of coupler with 4 spinules on each rounded protrusion . *venezolanus*
– Leg 5, medial spine slightly broader than lateral seta, spine and seta subequal in length; Leg 1, anterior surface of coupler with fine hairs on and near margin and rows of smaller hairs proximally; posterior surface with tiny spinules .... *totaensis*

Morphological variation among and within populations of this species-complex has not yet been satisfactorily evaluated. Lindberg (1955, 1957) supplied measurements and a few figures of some specimens of the *M. leptopus*-complex from lakes in the Peruvian Andes; however, his descriptions, lacking many details, do not allow determination of which subspecies he may have had. Dussart (1984) briefly redescribed *M. l. mucubajiensis* from the type locality, giving increased detail of the seminal receptacle of the female, but otherwise not extending Kiefer's original description.

There has been much confusion between *M. leptopus* and a similar species, *M. mendocinus* (Wierzejski, 1892), which has been recorded from nearly every country in South America, as well as from Central America and the Antilles (Reid 1985); for discussion of this confusion see Löffler (1963) and Petkovski (1988). A principal difference between the species lies in the proportions of their caudal setae: in *M. mendocinus,* the middle terminal caudal setae are subequal in length, the longest terminal caudal seta being less than twice the length of the caudal ramus. The corresponding setae in *M. leptopus* are unequal in length, the next innermost seta being distinctly longer than the next outermost seta, and the longest terminal seta being 2.6 or more times longer than the ramus. Löffler (1963) gave measurements of specimens from Ecuador and Chile which he ascribed to *M. mendocinus.* He unfortunately increased the confusion by emphasizing the proportions of the leg 4 endopod 3 rather than the proportions of the caudal setae as a species discriminator, although the measurements of caudal setae presented show that most of his specimens had relatively long, unequal caudal setae, similar to members of the *M. leptopus*-complex. Löffler furnished no figures, nor did he label his measurements as to the populations from which they were derived. As Dussart (1984) noted, Löffler's (1963) suggestion that *leptopus* is the pelagic form of *mendocinus* is insupportable, since both species are pelagic. Dussart (1984), however, suggested that *M. leptopus venezolanus* should be considered a form of *M. mendocinus,* without explaining his reasoning. Petkovski (1988) followed this synonymy. In spite of probable confusion in the records, the two species appear to be ecologically distinct: *M. mendocinus,* an eurytopic species, often attains dense populations in saline or highly eutrophic waters (Ringuelet 1958; Sendacz & Kubo 1982), while members of the *M. leptopus*-complex seem to inhabit relatively pristine, mostly high-altitude lakes. The conclusion of both Löffler (1963) and Dussart (1984), that it is necessary to re-evaluate both species and their forms, starting from examination of type material and encompassing representative populations from the entire range of each, is inescapable.

Literature Cited

Dussart, B. H. 1984. Some Crustacea Copepoda from Venezuela.—Hydrobiologia 113:25–67.

Gaviria, S. 1989. The calanoid fauna (Crustacea, Copepoda) of the Cordillera Oriental of the Colombian Andes.—Hydrobiologia 178:113–134.

Kiefer, F. 1927. Beiträge zur Copepodenkunde (VI). 12. Über einige südamerikanischen Cyclopiden.—Zoologischer Anzeiger 74:116–121.

———. 1956. Freilebende Ruderfusskrebse (Crustacea Copepoda). I. Calanoida und Cyclopoida.—Ergebnisse der Deutschen Limnologischen Venezuela-Expedition 1952, 1:233–268 + 2 tabs.

———. 1957. Freilebende Ruderfusskrebse (Crustacea Copepoda) des Titicacasees.—Veröffentlichungen der Zoologischen Staatssammlung München 4:125–150.

Lindberg, K. 1955. Cyclopides (crustacés copépodes) récoltés au Pérou par le Dr Hernando de Macedo.—Folia Biologica Andina, Pars II, Zoologica 1:1–18.

———. 1957. Cyclopides (crustacés copépodes) récoltés au Pérou par le Dr Hernando de Macedo (Deuxième partie).—Folia Biologica Andina, Pars II, Zoologica 1:39–52.

Löffler, H. 1963. Zur Ostrakoden- und Copepodenfauna Ekuadors.—Archiv für Hydrobiologie 59: 196–234.

Petkovski, T. K. 1988. Zur Cyclopidenfauna Kolumbiens.—Acta Musei Macedonici Scientiarum Naturalium 19(2/155):39–64.

Reid, J. W. 1985. Chave de identificação e lista de referências bibliográficas para as espécies continentais sulamericanas de vida livre da ordem Cyclopoida (Crustacea, Copepoda).—Boletim de Zoologia, São Paulo 9:17–143.

———. 1987. The cyclopoid copepods of a wet campo marsh in central Brazil.—Hydrobiologia 153: 121–138.

Ringuelet, R. A. 1958. Primeros datos ecológicos sobre Copépodos Dulciacuícolas de la República Argentina.—Physis, Buenos Aires 21:14–31.

Sendacz, S., & E. Kubo. 1982. Copepoda (Calanoida e Cyclopoida) de reservatórios do Estado de São Paulo.—Boletim do Instituto de Pesca 9:51–89.

(JWR) Department of Invertebrate Zoology, NHB-163, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (JAMA) Departamento de Zoologia, Universidad Distrital "Francisco José de Caldas," DD 30590, Bogotá, Colombia; (MMF) Universidad Nacional de Trujillo, Atahualpa 312, Trujillo, Perú.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 681–686

A NEW GENUS AND SPECIES OF POLYCHAETA COMMENSAL WITH A DEEP-SEA THYASIRID CLAM

James A. Blake

Abstract.—A new commensal species of polychaete has been discovered living between the gills of the deep-sea thyasirid clam, *Thyasira insignis.* The collections come from dense faunal communities recently discovered on the Laurentian Fan off Newfoundland and Nova Scotia. The species is named *Petrecca thyasira* new genus, new species, and is referred to the recently described family Nautilinidae, that was previously known for a single species associated with clams from the Japan Trench. Only one pair of antennae and a single tentacular segment are present. The subbiramous parapodia are well developed, but setae are reduced to one or two large hooked neuropodial spines. Nomenclatural problems that call into question the validity of the genus name *Nautilina* and the family name Nautilinidae are discussed.

During dives of the DSRV *Alvin* on the Laurentian Fan to explore the nature of the deposit of the 1929 Grand Banks earthquake and turbidity current, dense communities of living vesicomyid and thyasirid clams, gastropods, and other epifaunal taxa similar to those found in hydrothermal vent and cold seep environments were discovered (Mayer et al. 1988). The communities are at 3800–3900 m near the crests of gravel waves that were deposited by the turbidity current in 1929. Mayer et al. (1988) speculate that the communities were established subsequent to the 1929 earthquake and are sustained by chemosynthesis that is fueled by compounds derived from older organic-rich sediments that were exposed by the 1929 event.

During the course of exploring these communities, several specimens of the thyasirid clams were collected. Examination of the thyasirids revealed the presence of an unusual polychaete associated with the gills. The species has been determined to represent a new genus and species and is referred to the family Nautilinidae that was recently reported from calyptogenid clams collected from the Japan Trench. The types are deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Family Nautilinidae Miura & Laubier

Diagnosis.—Prostomium with 1–2 pairs of short antennae; a single poorly developed tentacular segment present bearing an aciculum and ventral cirrus, or tentacular segment entirely lacking; parapodia subbiramous, with notopodia and neuropodia well developed, notopodia with or without dorsal cirrus and notosetae; neuropodium with simple, hooked neuropodial spines. Proboscis soft, weakly muscular, partially eversible; without jaws or teeth.

Petrecca, new genus

Type species.—*Petrecca thyasira,* new species. Gender feminine.

Etymology.—This genus is named for Ms. Rosemarie Petrecca, marine biologist, who discovered this unique polychaete.

Diagnosis.—Body oval in cross section. Prostomium rounded, with 1 pair of antennae; eyes lacking. Pharynx weakly muscular, partially eversible. Peristomium reduced to small segment pressed near mouth, bearing ventral cirrus. Parapodia subbiramous with ventral cirrus and no distinct dorsal cirrus; notopodium elongate, with single aciculum; neuropodium with single aciculum and 1–2 simple hooked spines. Pygidium simple, lacking cirri.

Remarks.—The combination of a single pair of antennae, reduced tentacular segment with an aciculum, lack of palps, subbiramous parapodia, and simple hooked neuropodial spines is entirely unique in the Polychaeta. In a search for possible free-living or parasitic families to which this animal could be referred, the Lacydoniidae, Hesionidae, and Pilargidae were initially considered. In the genus *Lacydonia,* the dorsal aspect of the anterior end bears a superficial resemblance to that of *Petrecca.* In *Lacydonia,* there are two pairs of antennae visible and a single reduced tentacular segment clearly visible posterior to the prostomium, while in *Petrecca,* there is only a single pair of antennae and the tentacular segment is not visible dorsally, but compressed ventrally near the oral opening. Further, *Lacydonia* has well developed parapodia with spreading fascicles of noto- and compound neurosetae, while in *Petrecca,* the parapodia are subbiramous and the setae are reduced to 1–2 simple neuropodial hooked spines. Among the Hesionidae, some genera are known which lack palps and have only a single pair of antennae. All of these genera, however, have four or more tentacular segments and all hesionids have compound neurosetae. The Pilargidae have genera that share some characters with *Petrecca.* Some genera have two antennae and all have simple setae. Several genera are known with large hooked spines reminiscent to those of *Petrecca.* However, pilargids have palps and the modified spines are notopodial instead of neuropodial. Further, no pilargids are known to be commensal or parasitic and to have the reduced setal compliment present in *Petrecca.*

The recent paper by Miura & Laubier (1989) describes *Nautilina calyptogenicola* from calyptogenid clams from the Japan Trench, an animal that is subtly similar to *Petrecca thyasira.* These authors referred their species to a new family, the Nautilinidae. A careful comparison of *P. thyasira* with *N. calyptogenicola* indicates that they are closely related. Both species have a similar subbiramous parapodial structure that includes a reduced notopodium bearing only an internal aciculum and a neuropodium with simple hooked spines. Both species have a small ventral cirrus. *Nautilina* has a dorsal cirrus, while in *Petrecca* the notopodium is elongated and the dorsal cirrus is lost although the digitiform tip seen on the notopodium may represent a remnant of a dorsal cirrus. Miura & Laubier (1989) indicate that *Nautilina* has two pairs of antennae and no tentacular segment at all, whereas *Petrecca* has a single pair of antennae and a very reduced segment located near the mouth that bears a ventral cirrus. For *Petrecca,* this cirrus is seen in dorsal view and superficially resembles a second pair of antennae. Both genera have a muscular pharyngeal structure. Miura & Laubier (1989) called it a proventriculus and suggested a close relationship to the Syllidae. The same structure in *Petrecca* is not considered a proventriculus because it appears to be soft and less well-developed than the syllid structure.

Both *N. calyptogenicola* and *P. thyasira* are found in deep-sea clams and clearly belong to different, yet closely related genera. The collection of two species in this new family in similar habitats on opposite sides of the globe within two years of one another is remarkable, yet indicative of the intense scientific interest to study the ecology of organisms found in vent, seep, and related communities. With the collection of additional species and more extensive morphological analysis we will hopefully be able to more fully interpret the relationships of the Nautilinidae with other polychaetes.

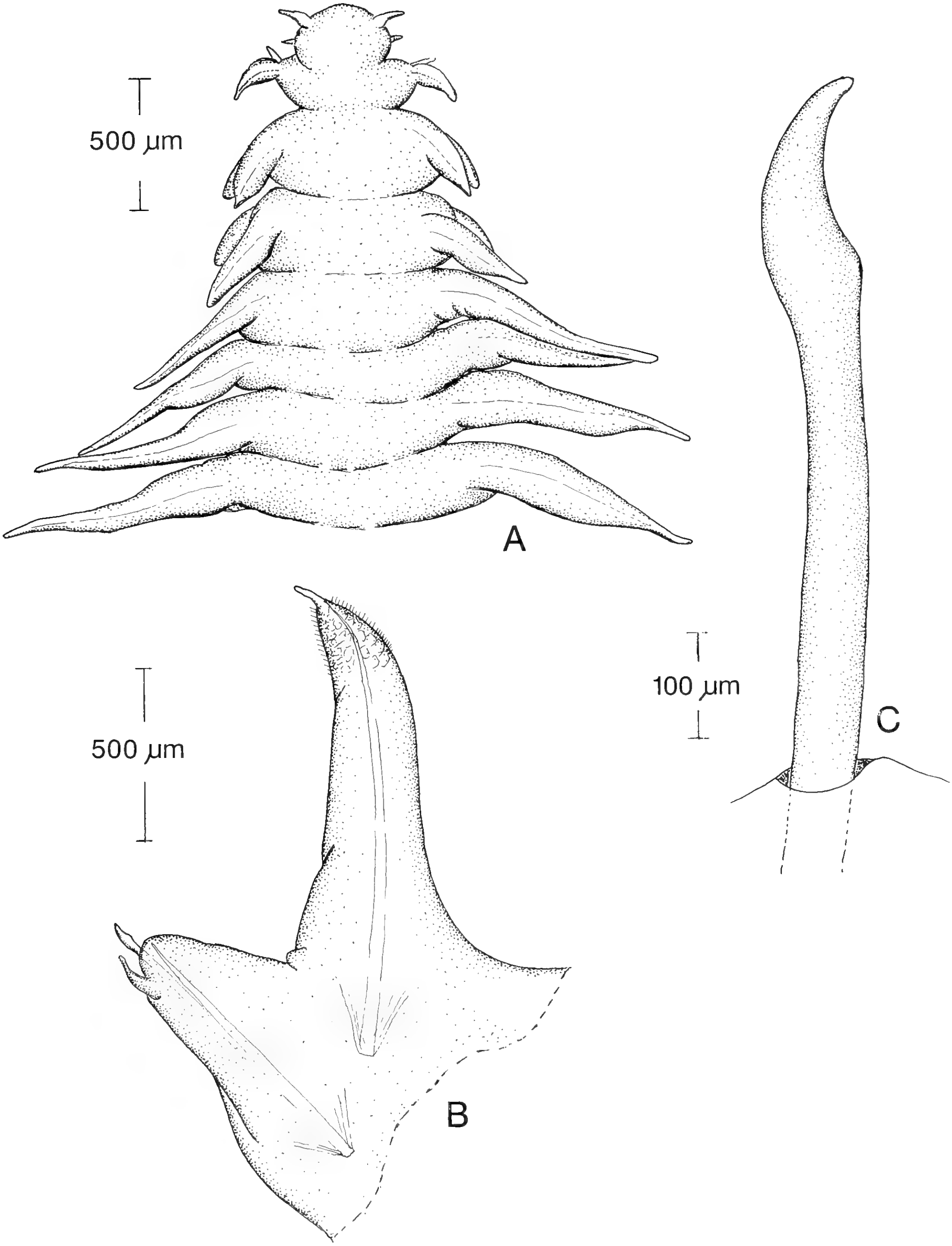


Fig. 1. *Petrecca thyasira* (USNM 126075). A, Anterior end and 7 segments in dorsal view; B, Middle parapodium; C, Neuroseta.

Petrecca thyasira, new species
Figs. 1, 2

Material examined.—Western North Atlantic, Laurentian Fan, R/V *Hudson,* Cruise 87-003, Sta. 13, 9 April 1987, 43°34.46′N, 55°38.35′W to 43°35.32′N, 55°38.23′W, 3718–3720 m, specimens found between layers of gill filaments of the thyasirid clam, *Thyasira insignis,* holotype (USNM 126074) and 4 paratypes (USNM 126075).

Description.—A moderate sized species. Holotype 16 mm long, 3 mm wide, including parapodia, with 51 setigerous segments. Four paratypes ranging from 4.4 to 12.5 mm long, 2 to 4 mm wide with 25 to 48 setigers. Color in alcohol light tan. Body narrower anteriorly, expanding in middle region due to elongated notopodia, and narrowing again posteriorly.

Prostomium rounded, as wide as long, with two digitiform antennae; without palps, eyes, or nuchal organs (Fig. 1A). Proboscis soft, eversible, with weak musculature. First or tentacular segment reduced, pressed tightly against sides of mouth opening (Fig. 2A); tentacular segment with reduced ventral lobe bearing aciculum and ventral cirrus, the latter sometimes visible dorsally (Figs. 1A, 2B).

Parapodia similar in structure, with elongated notopodium and more-or-less conical neuropodium, both supported by single internal aciculum. Notopodium of segment 2 subequal in length to neuropodium (Figs. 1A, 2B). Notopodium increasing in length over following segments becoming twice length of neuropodium (Figs. 1A, B, 2A). Notopodium tapering apically, with apex ciliated, glandular, terminating in digitiform tip. Neuropodium stubby, broadly rounded, bearing a short, digitiform ventral cirrus (Fig. 1B). Neuropodium with 1–2, large, hooked neuropodial spines (Fig. 1C).

Body terminating in narrow pygidium lacking cirri.

Etymology.—The species name refers to the generic name of the host animal, *Thyasira insignis.*

Remarks.—Of the ten specimens of *T. insignis,* collected at Station 13, five were found to harbor a single specimen of *Petrecca thyasira.* One clam examined from Station 16 did not contain a polychaete. The clams are relatively small, ranging from 29 × 30 cm to 37 × 43 cm in width × length. Thus, the presence of worms up to 16 mm long in the clams is significant. Whether these polychaetes have a commensal or parasitic relationship with the clams has yet to be determined. According to Ms. Petrecca, the worms were found lying between layers of gill filaments. The long notopodia with glandular ciliated tips would appear to be a functional adaptation to living in the proximity of long gill filaments having similar shapes.

Among the many unusual polychaetes thus far described from hydrothermal vents and methane seep communities are polynoids that are commensal in the mantle cavities of large mytilid mussels (Pettibone 1984, 1986). The presence of a non-polynoid commensal in a deep-sea clam from faunal communities that resemble vent and seep faunas is thus of considerable interest. No specimens of *Petrecca thyasira,* however, have been collected outside of their molluscan hosts. Indeed the degree of reduction of the setae to a single ventral neuropodial hook would suggest that *P. thyasira* is highly adapted to a commensal habit. The same statements would hold for *Nautilina calyptogenicola,* that comes from calyptogenid clams in the Japan Trench.

Other polychaetes reported from the mantle cavities of clams include: a hesionid, *Parasyllidea humesi,* that was described by Pettibone (1961) from an intertidal estuarine clam in West Africa; and an unusual pilargid-like polychaete, *Antonbrunnia viridis,* that was described by Hartman & Boss (1966) from 68–82 m off Madagascar.

Comments on the Validity of the Names *Nautilina* and Nautilinidae

I would like to point out a nomenclatural problem with the names *Nautilina* and Nautilinidae proposed by Miura and Lau-

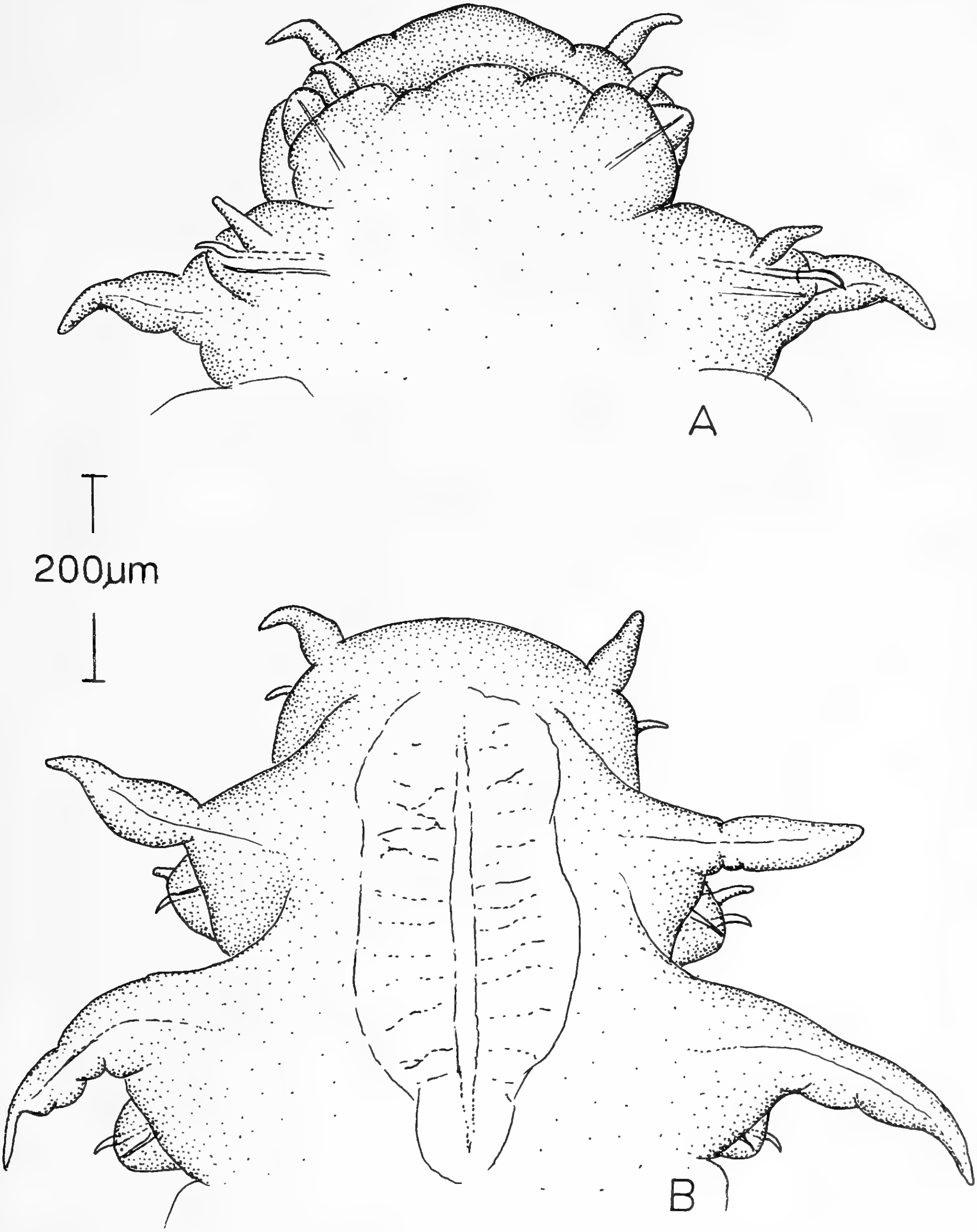


Fig. 2. *Petrecca thyasira.* A, Anterior end of paratype (USNM 126075) in ventral view; B, Anterior end of holotype (USNM 126074) in dorsal view.

bier (1989). The genus name, *Nautilina,* is preoccupied in the Mollusca, Cephalopoda, by the suborder name Nautilina, that was established by Shimanskii (1957). Although this designation was dropped by Kummel et al. (1964) in their classification of the Nautiloidea, the molluscan suborder name and the polychaete generic name nevertheless represent senior and junior homonyms, respectively, and the latter must be renamed. It is my understanding that Dr. Miura will deal with that formality himself in a future paper. The family name Nautilinidae does not appear to have been used previously. However, because the rules of nomenclature clearly state that the generic name upon which the family-group taxon is based must be valid for a genus contained in that family, it is probable that the name Nautilinidae will also need to be replaced (ICZN 1985: Article 11 (f)).

Acknowledgments

This species was collected during a cruise on the R/V *Hudson* to the Laurentian Fan. Ms. Rosemarie Petrecca collected the thyasirid clams, removed the polychaetes, and initially recognized their unique morphology. Dr. Ruth Turner confirmed the identity of the clams. The manuscript benefitted from a careful review by Dr. Marian H. Pettibone. The collection of these materials was supported in part by NSF Grant OCE 83-11021 to Dr. J. Frederick Grassle.

Literature Cited

Hartman, O., & K. J. Boss. 1966. *Antonbruunia viridis,* a new inquiline annelid with dwarf males, inhabiting a new species of pelecypod, *Lucina fosteri,* in the Mozambique Channel.—Annals & Magazine of Natural History, ser. 13, 8:177–186.

International Code of Zoological Nomenclature. 1985. Third Edition. Adapted by the XX General Assembly of the International Union of Biological Sciences. University of California Press, Berkeley and Los Angeles, xx + 338 pp.

Kummel, B., W. M. Furnish, & B. F. Glenister. 1964. Nautiloidea-Nautilida, pp. K383–K457. *In* R. C. Moore, ed., Treatise on invertebrate paleontology, Part K. Mollusca 3. Cephalopoda, general features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea. U.S. Geological Society of America and the University of Kansas Press.

Mayer, L. A., A. N. Shor, J. H. Clarke, & D. J. W. Piper. 1988. Dense biological communities at 3850 m on the Laurentian Fan and their relationship to the deposits of the 1929 Grand Banks earthquake.—Deep-Sea Research 35:1235–1246.

Miura, T., & L. Laubier. 1989. *Nautilina calyptogenicola,* a new genus and species of parasitic polychaete on a vesicomyid bivalve from the Japan Trench, representative of a new family Nautilinidae.—Zoological Science 6:387–390.

Pettibone, M. H. 1961. New species of polychaete worms from the Atlantic Ocean, with a revision of the Dorvilleidae.—Proceedings of the Biological Society of Washington, 74:167–186.

———. 1984. A new scale-worm commensal with deep-sea mussels on the Galapagos hydrothermal vent (Polychaeta: Polynoidae).—Proceedings of the Biological Society of Washington 97: 226–239.

———. 1986. 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: Branchipolynoidae).—Proceedings of the Biological Society of Washington 99:444–451.

Shimanskii, V. N. 1957. Systematics and phylogeny of the Order Nautilida.—Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, otdel geologicheskii 32(4):105–120. [In Russian.]

Note Added in Proof: A new publication by Miura & Laubier (1990) designates the genus *Nautiliniella* and the family Nautiliniellidae to replace the homonyms *Nautilina* and Nautilinidae. In addition, these authors describe two new nautiliniellid genera and two species from the mantle cavities of bivalves from the deep-sea Hatsushima cold-seep site off Sagami Bay, Japan. The new taxa include *Shinkai sagamiensis* from *Calyptogena soyoae* and *Natsushima bifurcata* from *Solemya* sp. *Petrecca* differs from these new genera by having greatly elongated noto- and neuropodia, an achaetous peristomial segment, and in details of the setae. An as yet undescribed species from mussels at the cold-seep site on the Florida Escarpment is referable to *Natsushima.*

Miura, T. & L. Laubier. 1990. Nautiliniellid polychaetes collected from the Hatsushima cold-seep site in Sagami Bay, with descriptions of new genera and species.—Zoological Science 7(2): 319–325.

Science Applications International Corporation, 89 Water Street, Woods Hole, Massachusetts 02543.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 687–690

EXOGONE ACERATA (EXOGONINAE: SYLLIDAE: POLYCHAETA), A NEW SPECIES WITHOUT ANTENNAE FROM THE MEDITERRANEAN SEA

Guillermo San Martín and Julio Parapar

Abstract.—*Exogone acerata,* a new species of Exogoninae (Syllidae, Polychaeta) from sandy bottoms off Ceuta (Spain), North Africa, in the Mediterranean Sea, is described. The new species is characterized by lacking antennae and by having long spines on the shaft heads of spinigers.

The polychaetous annelids from the Strait of Gibraltar area have been studied by Fauvel (1936), Amoureux (1972, 1976) and Sardá (1984, 1985a, 1985b, 1987). However, there is no information on the polychaetes from the litoral area of Ceuta. Therefore, during the summer of 1986, four samples of sublitoral sand were collected by scuba diving in an expedition carried out by the Musée d'Histoire Naturelle de Paris (Ceuta-86). The polychaetes from these samples are being examined; provisionally, about 88 species have been identified. Among them is the new species of *Exogone* described in this report.

Material and methods, and descriptions of collecting sites were presented in Besteiro, Urgorri & Troncoso (1990).

The type series is mounted in microscopical preparations made with glycerine jelly. Observations and measurements were made by means of a microscope with interferential contrast optics (Nomarsky). Drawings were made by means of a camera lucida drawing tube. Measurements were taken excluding appendages and setae. The type material is deposited in the Museo de Historia Natural Luis Iglesias de la Universidad de Santiago, Spain.

Family Syllidae Grube, 1850
Subfamily Exogoninae Rioja, 1925
Genus *Exogone* Örsted, 1845
Exogone acerata, new species

Material examined.—Playa Benítez (Ceuta, Spain) (36°54′15″N, 5°19′54″W); sand; 23 m depth; 9 paratypes. El Pineo (Ceuta, Spain) (36°52′36″N, 5°19′46″W); sand; 11 m depth; holotype and two paratypes. All the type series has catalogue number MHNS-1-Pol.

Etymology.—The name of the species derives from the Greek, and it means "without antennae."

Description.—Body moderately long, slender, filiform, without color marking; holotype, a complete, mature female carrying eggs, is 4 mm long, 0.2 mm wide at proventricular level, and has 40 setigers. Prostomium ovate to pentagonal, approximately three times wider than long. Four eyes in trapezoidal arrangement. Without antennae. Palps broad, longer than prostomium, completely fused all along their length, leaving a small, terminal notch (Fig. 1a). Peristomium well defined, covering dorsally posterior end of prostomium. Ten-

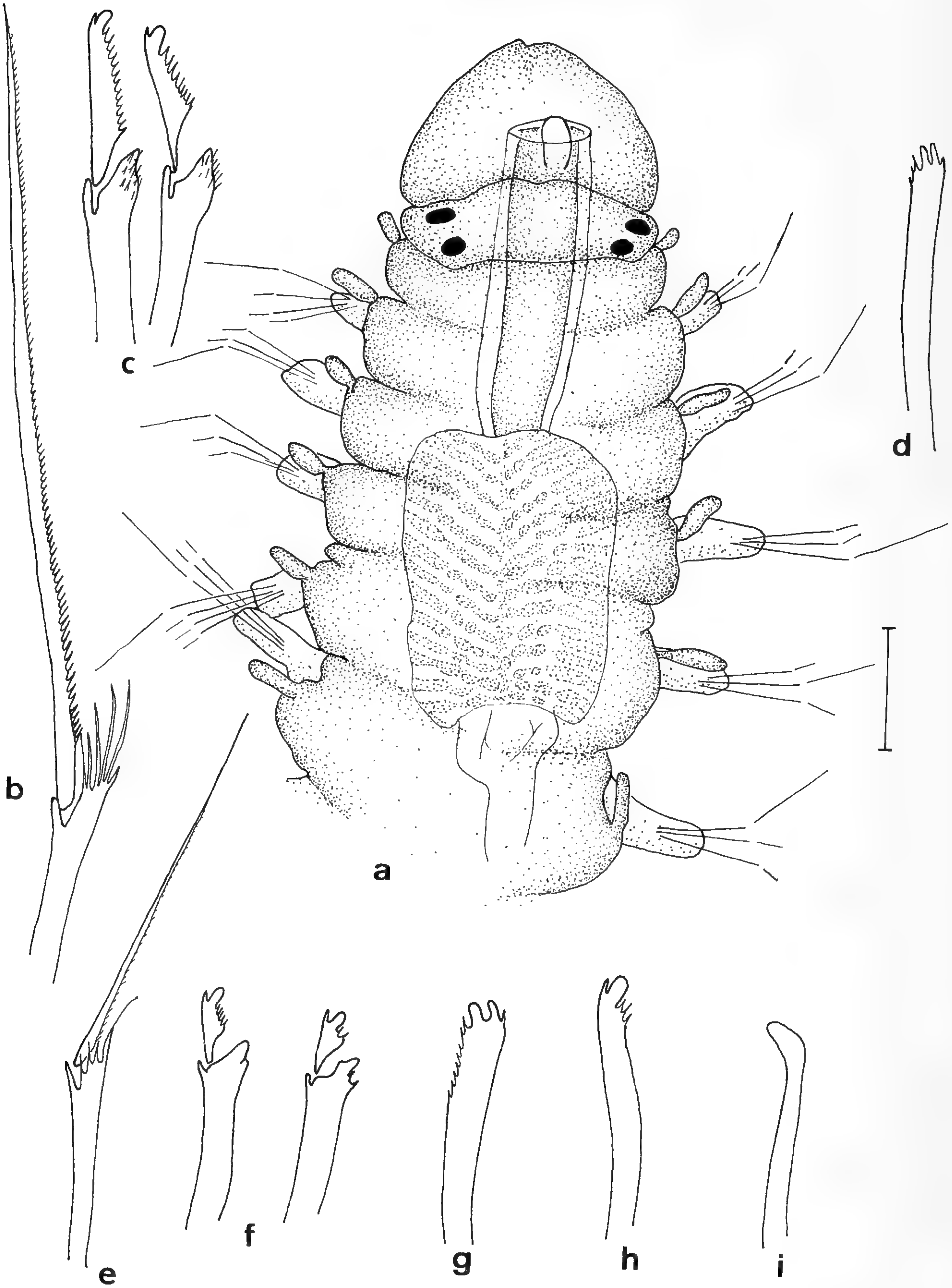


Fig. 1. *Exogone acerata,* n. sp. a, Anterior end, dorsal view of a paratype. Anterior parapodia; b, Spiniger; c, Falcigers; d, Dorsal simple seta. Middle-posterior parapodia; e, Spiniger; f, Falcigers; g, Dorsal simple seta; h, Ventral simple seta; i, Aciculum. Scale: a, 64 μm. b, c, d, e, f, g, h, i: 10 μm.

tacular cirri small, shorter than dorsal cirri. Dorsal cirri on all setigers, ovate to digitiform, shorter than parapodia (Fig. 1a). Ventral cirri similar but shorter. Compound setae including on each parapodium one spiniger with long, fine spines distally on shaft heads, and several falcigers with proximal tooth longer and wider than distal one. Anterior parapodia each with one spiniger provided with about 4 or 5 very long spines on the shaft head, blade slender, unidentate, with short spines on the cutting margin, about 62 μm long (Fig. 1b), and about 4 or 5 relatively long falcigers, without marked dorsoventral gradation in length or shape, about 20 μm long (Fig. 1c). Marked anteroposterior gradation of falcigers and spinigers, both in length and shape. Spinigers acquiring progressively shorter and thinner spines on shafts-heads, and shorter and smoother blades. Falcigers with shorter blades and thicker shafts. In a medium parapodium, a blade of spiniger (Fig. 1e) is about 40 μm long and a blade of falciger about 10 μm (Fig. 1f). Solitary dorsal seta (Fig. 1d) from first setiger, provided with two distal teeth and one distal spine and short spinulation on ventral margin, thicker and more strongly bidentate posteriorly (Fig. 1g). Solitary ventral simple setae on far posterior setigers S-shaped, bidentate, with proximal tooth larger than distal one and few, short spines on ventral side (Fig. 1h). Anterior parapodia each with two slender acicula, only one aciculum posteriorly, thicker, with tip curved and rounded (Fig. 1i). Pharynx narrow, through about 3 or 4 segments; pharyngeal tooth thick, rounded, placed on anterior margin. Proventriculus small, barrel-shaped, through about 2 or 3 segments, with about 12–14 muscle cell rows (Fig. 1a). Pygidium rounded, with two relatively short anal cirri. Epidermal granules on all surfaces of body, most abundant anteriorly.

Remarks.—Exogone acerata is the only species of the genus lacking antennae and provided with very long spines on the spiniger shaft-heads. The general shape of the body and the shape of the setae of *E. acerata* are typical of a group of species, as *E. dispar* (Webster, 1879), *E. verugera* Claparède, 1868, *E. naidina* Örsted, 1845, and many others. The lack of antennae, although contrary to the diagnosis of the genus *Exogone,* does not justify erecting a new genus. Amoureux (1986) reported an *Exogone* sp. from Atlantic areas close to the Iberian Peninsula, and from the short description, these specimens also lack antennae. Hartman & Fauchald (1971) described the genus *Exogonita,* very close to *Exogone,* but without antennae and provided with two pairs of tentacular cirri rather than one pair. The first author of this paper examined all the type series of *Exogonita oculata* and, indeed, it lacks antennae, but all the specimens have only one pair of tentacular cirri rather than two pairs as it was described. So, *Exogonita oculata* is very similar to *E. acerata,* but lacks the long spines on the shafts of spinigers.

Acknowledgments

We wish to express our gratitude to Leslie Harris, Allan Hancock Foundation, California, U.S.A., for allowing the first author to examine the type series of *Exogonita oculata.*

Literature Cited

Amoureux, L. 1972. Annélides Polychètes du Maroc.—Bulletin de la Societé des Sciences Naturelles et Physiques du Maroc 52:47–72.

———. 1976. Annélides Polychètes recoltés par J. Stirn en 1969, sur les côtes marocaines du detroit de Gibraltar.—Cuadernos de Ciencias Biológicas 5:5–33.

———. 1986. Annélides Polychètes abyssaux de la Campagne Abyplaine au large de Madère.—Bulletin du Musee national d'Histoire naturelle de Paris, 4 sér., 8(A, 3):591–615.

Besteiro, C., V. Urgorri, & J. S. Troncoso. 1990. Presence and distribution of the interstitial fauna in the coast of Ceuta (N. Africa).—Marine Biology (in press).

Fauvel, P. 1936. Contribution a la faune des Annélides Polychètes du Maroc. — Mémoires de la Société des Sciences Naturelles du Maroc 43:1–143.

Hartman, O., & K. Fauchald. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Part 2. — Allan Hancock Monographs on Marine Biology 6:1–327.

Sardá, R. 1984. La subfamilia Exogoninae (Polychaeta: Syllidae) de Gibraltar, con la descripción de *Pseudobrania euritmica,* n. sp. — Publicaciones del Departamento de Zoología de la Universidad de Barcelona 10:7–13.

———. 1985a. Estudio de la fauna de Anélidos Poliquetos de las zonas mediolitoral e infralitoral, en la región del Estrecho de Gibraltar. Resumen de la Tesis Doctoral. — Edicions de la Universitat de Barcelona 1–49.

———. 1985b. Anélidos Poliquetos del Estrecho de Gibraltar. I. Amphinomida, Spintherida y Phyllodocida. — Miscellània Zoologica 9:65–78.

———. 1987. Sphaerodoridae (Annelida, Polychaeta) from the region of Gibraltar Strait with description of *Euritmia hamulisetosa,* gen. et sp. n.–Zoologica Scripta 16(1):47–50.

(GSM) Departamento de Biología, Unidad de Zoología, Facultad de Ciencias, Universidad Autónoma de Madrid, Canto Blanco, 28049 Madrid, Spain; (JP) Departamento de Bioloxía Animal, Facultade de Bioloxía, Universidade de Santiago de Compostela, La Coruña, Spain.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 691–730

A REVISION OF THE SUBGENUS *PHASCOLOSOMA* (SIPUNCULA: *PHASCOLOSOMA*)

Norma J. Cutler and Edward B. Cutler

Abstract.—The 54 putative species of the nominate sipunculan subgenus *Phascolosoma* (*Phascolosoma*) and the morphological characters used to differentiate them are critically reviewed. The monograph of Stephen & Edmonds (1972) is used as a starting place and all changes made in the intervening years are reiterated here. Available type material was studied and new collections of Hawaiian and Caribbean worms are used to analyze within-deme variation. Twenty chromosomes of gradually differing sizes are present. Four characters are broadly useful at the species level (number of hook rings, secondary tooth of hook, pigment on introvert, and pre-anal papillae). Eight characters can be used in a more restricted manner for subsets or special cases (hook size, angle of hook-tip, internal clear areas, basal elaborations, nephridial length, trunk papillae shape, papillae platelets, and retractor origins). Six appear to be of no value to the taxonomist (hook presence, introvert length, number of longitudinal muscle bands, nephridiopore/anus relationship, rectal caecum, and contractile vessel). A key to, and a discussion of, the 16 remaining species (plus two reduced to subspecies) with newly designated synonyms are presented. A brief statement of the distribution of each species is given. An overall summary of the zoogeography and habitat shows the border area between the Indian and Pacific Oceans to be the most diverse with respect to *Phascolosoma* (81% of known species). Nineteen percent (three species) live in the Caribbean. With a few exceptions this genus lives in warm, shallow waters and hard substrates.

This work concludes our reexamination of the sipunculan genera (Cutler & Jurczak 1975; Cutler & Murina 1977; Cutler 1979, 1986; Cutler & Cutler 1982, 1983, 1985a, 1985b, 1986, 1987a, 1988, 1989; Cutler et al. 1983; Gibbs et al. 1983). The monograph of Stephen & Edmonds (1972) is the starting place for this work (40 species names). The five species erected and the nine species transferred into this genus since that time are also included (Table 1).

The genus *Phascolosoma* was erected by Leuckart in 1828, placed in the family, Phascolosomatidae by Stephen & Edmonds (1972), and in the order Phascolosomatiformes by Cutler & Gibbs (1985). The general name *Phascolosoma* went through an unfortunate period when it was incorrectly used to replace *Golfingia* for seventy years (1880 to 1950). During this time the names *Phymosoma* and *Physcosoma* replaced *Phascolosoma*. In 1950 Fisher reestablished the correct usage of these names, but the non-specialist literature and biological supply houses continued using the incorrect names for another 30 years.

Four subgenera of *Phascolosoma* were proposed by Stephen & Edmonds (1972: 270). Three of these (*Antillesoma, Rueppellisoma,* and *Satonus*) were reviewed by Cutler & Cutler (1983) resulting in the elimination of all but one *Antillesoma* (elevated to generic status) and one *P.* (*Satonus*) species. This action was reviewed in Gibbs & Cutler (1987) where the subgenus *Satonus* was redefined and replaced by the name *Ed-*

Table 1.—Species considered and proposed taxonomic changes.

Present name	Proposed name
Phascolosoma abyssorum (Southern, 1913)	*Apionsoma capitatum*
Phascolosoma agassizii Keferstein, 1867	no change
Phascolosoma albolineatum Baird, 1868	no change
Phascolosoma ambonense (Fischer, 1896)	*Phascolosoma arcuatum*
Phascolosoma andamanensis Johnson, 1971	*Phascolosoma albolineatum*
Phascolosoma annulatum Hutton, 1879	no change
Phascolosoma arcuatum Gray, 1828	no change
Phascolosoma corallicolum (ten Broeke, 1925)	incertae sedis
Phascolosoma deani (Ikeda, 1905a)	*Phascolosoma arcuatum*
Phascolosoma diaphanes (Sluiter, 1886)	*Phascolosoma nigrescens*
Phascolosoma dunwichi Edmonds, 1956	*Phascolosoma scolops*
Phascolosoma duplicigranulatum (Sluiter, 1886)	*Phascolosoma nigrescens*
Phascolosoma esculentum (Chen & Yeh, 1958)	*Phascolosoma arcuatum*
Phascolosoma evisceratum (Lanchester, 1905a)	*Phascolosoma nigrescens*
Phascolosoma extortum (Sluiter, 1902)	*Phascolosoma nigrescens*
Phascolosoma formosense (Satô, 1939)	*Phascolosoma agassizii*
Phascolosoma funafutiense (Fischer, 1914)	*Phascolosoma glabrum*
Phascolosoma glabrum (Sluiter, 1902)	no change
Phascolosoma glaucum (Satô, 1930)	*Phascolosoma agassizii*
Phascolosoma granulatum Leuckart, 1828	no change
Phascolosoma heronis Edmonds, 1956	*Phascolosoma stephensoni*
Phascolosoma horsti (ten Broeke, 1925)	*Phascolosoma nigrescens*
Phascolosoma japonicum Grübe, 1877	*Phascolosoma agassizii*
Phascolosoma kapalum Edmonds, 1985	*Phascolosoma turnerae*
Phascolosoma kurilense (Satô, 1937a)	*Phascolosoma agassizii kurilense*
Phascolosoma lacteum (Sluiter, 1886)	*Phascolosoma nigrescens*
Phascolosoma maculatum (Sluiter, 1886)	no change
Phascolosoma meteori (Hérubel, 1904a)	no change
Phascolosoma microdentigerum (ten Broeke, 1925)	*Phascolosoma perlucens*
Phascolosoma microdontoton (Sluiter, 1886)	*Phascolosoma albolineatum*
Phascolosoma minutum (ten Broeke, 1925)	*Phascolosoma nigrescens*
Phascolosoma multiannulatum Wesenberg-Lund, 1954b	*Phascolosoma glabrum multiannulatum*
Phascolosoma nahaense (Ikeda, 1904)	*Phascolosoma scolops*
Phascolosoma nigrescens Keferstein, 1865a	no change
Phascolosoma nigritorquatum (Sluiter, 1881)	incertae sedis
Phascolosoma noduliferum Stimpson, 1855	no change
Phascolosoma pacificum Keferstein, 1866	no change
Phascolosoma perlucens Baird, 1868	no change
Phascolosoma psaron (Sluiter, 1886)	*Phascolosoma scolops*
Phascolosoma puntarenae Grübe, 1858	*Phascolosoma nigrescens*
Phascolosoma riukiuensis Murina, 1975	*Phascolosoma scolops*
Phascolosoma rottnesti Edmonds, 1956	*Phascolosoma scolops*
Phascolosoma saprophagicum Gibbs, 1987	no change
Phascolosoma scolops (Selenka, de Man & Bülow 1883)	no change
Phascolosoma socium (Lanchester, 1905b)	*Phascolosoma scolops*
Phascolosoma spengeli (Sluiter, 1886)	*Phascolosoma nigrescens*
Phascolosoma spinosum Johnson, 1971	*Phascolosoma perlucens*
Phascolosoma spongicolum (Sluiter, 1902)	*Phascolosoma scolops*
Phascolosoma stephensoni (Stephen, 1942)	no change
Phascolosoma thomense (Augener, 1903)	*Phascolosoma perlucens*
Phascolosoma turnerae Rice, 1985	no change
Phascolosoma varians Keferstein, 1865	*Phascolosoma nigrescens*
Phascolosoma vermiculus (de Quatrefages, 1865)	*Phascolosoma perlucens*
Phascolosoma yezoense (Ikeda, 1924)	*Phascolosoma agassizii*
Aspidosiphon insularis Lanchester, 1905	*Phascolosoma perlucens*

mondsius with its single species *P. pectinatum* Keferstein. This uncommon, circumtropical species has bilobed nephridia, a spindle muscle not attached to the posterior end of the trunk, and introvert hooks with basal spinelets.

Whenever possible, type material has been obtained to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to better evaluate the traditionally used morphological characters. Recent collecting trips to Hawaii, Curaçao and Venezuela (Cumaná and Islas de Los Roques) have greatly facilitated this effort. The opportunity to observe living material is invaluable.

The order of this paper is: an analysis of the morphological characters that have been used by previous authors in their species descriptions in light of our recent analyses; a discussion of those taxa clearly not belonging to the genus; a key to the newly validated species; a discussion of each species including a synonymy, comments on newly added junior synonyms, and known distribution; and a short zoogeographical summary of the genus.

The following abbreviations are used in the text for the museums from which we borrowed material: Australian Museum, South Sydney (AMSS), British Museum (Natural History), London (BMNH); Museum of Comparative Zoology, Harvard, Cambridge, MA (MCZH), Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Humboldt-Universitat zu Berlin (MNHU); Naturhistoriska Riksmuseet, Stockholm (NHRS); Royal Scottish Museum, Edinburgh (RSME); National Museum of Natural History, Washington (USNM); Wroclaw University Museum, Poland (UWMP); University Museum of Zoology, Cambridge, England (UZMC), Zoologisk Museum, Copenhagen (UZMK); Zoölogisch Museum Universiteit van Amsterdam (ZMUA); Zoologisches Museum Universität Hamburg (ZMUH); Zoology Museum, University of Tokyo (ZMUT).

Morphological Characters

While Stephen & Edmonds (1972) were able to construct a key to all other genera, they could only construct a table with comparative morphological data for *Phascolosoma* (p. 291). We include those characters and add additional ones.

1. Introvert hooks.—A. Presence: All *Phascolosoma* bear laterally compressed, posteriorly directed hooks arranged in rings around the distal portion of the introvert. Historically, one exception has been *P. meteori,* but small pale hooks are present in type material we examined (see below). Other accounts of hookless *Phascolosoma* species are also erroneous.

B. Number of rings: Although many authors describe the number of rings of hooks present, only a few have attempted to analyze the information. Our work shows that new hooks are produced at the distal tip of the introvert (see also Cutler 1979). What we do not know is whether this production of hooks continues throughout the life of a worm or if there is some species specific upper limit to the number. Proximal rings often are partially (especially on the ventral surface) or completely missing in some specimens. We presume this is caused by abrasion against the surrounding substrate. While new ones are produced at the distal end, old hooks may be lost elsewhere. Nevertheless, a pattern does emerge wherein about half the species have fewer than 50 hook rings (commonly 15–25) while the remainder have over 50 (often over 100). In a few species (e.g., *P. nigrescens*) areas of scattered hooks are present proximal to the rings.

C. Size: When hooks are measured they should be flat; otherwise distortions occur both in size and shape. Measured from the posterior base straight to the tip *Phascolosoma* hooks commonly measure 30–70 μm

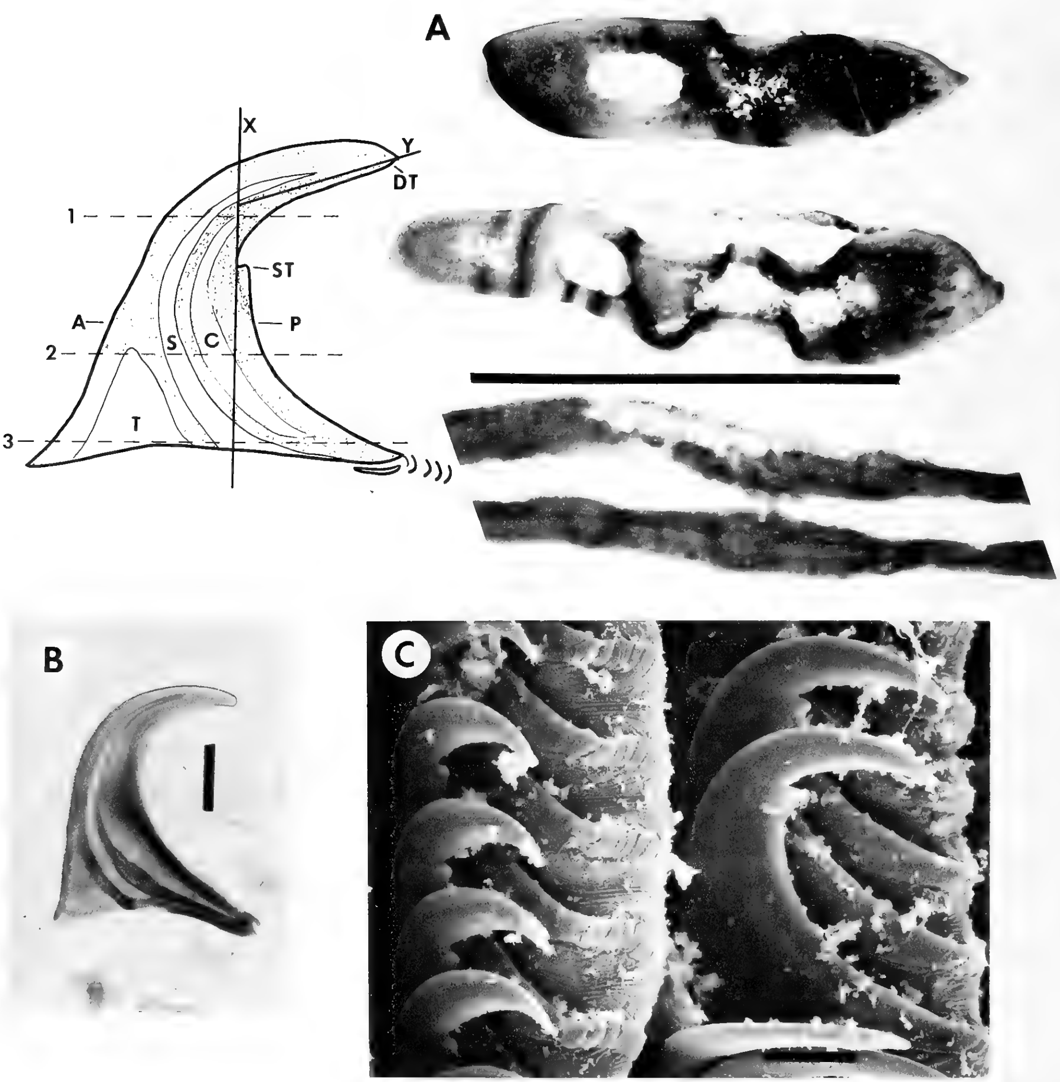


Fig. 1. Introvert hook of *P. stephensoni.* A. Generalized hook showing: anterior (A), posterior (P), distal tip (DT), and secondary tooth (ST), plus the interior clear streak (S), crescent (C), and triangle (T). The lines numbered 1, 2, 3, indicate where the three adjacent Transmission Electron photomicrographs were taken. The upper angle formed between X and Y is used when referring to tip angle. B. Light microscope view. C. Scanning electron photomicrograph of two rings of hooks. Scale lines = 20 μm. Tissue for TEM embedded in Spurr's medium, sectioned 2000 Å thick, and photographed on a Zeiss 902.

(Fig. 1A). Exceptions to this include *P. pacificum* (90–125 μm), *P. meteori* and *P. saprophagicum* (15–30 μm). Three species (*P. arcuatum, P. nigrescens,* and *P. stephensoni*) are reported to have hooks in the 50–80 μm range, but we have measured hooks up to 120 μm in the latter. Small worms tend to have smaller hooks than larger members of the same population (see Appendix). Therefore, while this character state is not diagnostic for most species it can be helpful for a few at the two ends of this continuum.

D. Shape (secondary tooth and tip): Introvert hooks differ in shape but how to describe the differences has often proved difficult. Consequently the same hook is not always consistently described. A "secondary" or "accessory" tooth or "keel" is commonly present on the posterior edge (concave side) of most species of *Phascolosoma* (Figs. 1, 2). It ranges from being small, fragile, and sharp to being large, hump-like and blunt. The tooth is constant within a species (except for *P. nigrescens*) and has taxonomic importance.

The distal tip may also vary from an acute point to a rounded, blunt apex. While there is a generally consistent pattern within a species, one does find worn and rounded hooks on an individual with normally pointed hooks, consequently more than a few hooks per worm must be examined. The tip of the hook bends at an angle to the perpendicular and this angle varies within (and among) populations. We have measured this angle as shown in Fig. 1A. Line X is drawn perpendicular to the base through the most anterior part of the concave side and Y is drawn from the tip to intersect X in the middle of the point. Some species have angles less than 90°, and others in the 90–115° range. This second group includes those species commonly described as having hooks bent at a right angle (e.g., *P. albolineatum* and *P. glabrum*). The variation in angle within a deme shows no correlation to hook size or whether the hook came from a proximal or distal ring.

E. Internal clear streak (apical canal) and triangle: When viewed by transmitted light one sees zones of differing opacity. Transmission electron micrographs show the paler, lighter regions are where there is little or no organic material (Fig. 1A). The hooks are open basally so that a hollow space (clear streak) extends along the basal edge. This may not always be apparent when the hooks are removed from the tissue. The clear streak (hollow space) extends upward from the base to near the apex. There may also be a triangular clear area in the anterio-basal corner that may or may not be separated from the slender clear streak. Additionally, *P. stephensoni* has a pale "crescent" posterior to the clear streak (Fig. 1A, B).

The width of the streak, whether it has a sharp or gradual bend near the midpoint, and the presence of swellings along its length have been used in species diagnoses. Using TEM, SEM, and light microscopy together with a comparison of the internal architecture of newly formed hooks (from very small worms or from the first two rings) to older, more mature hooks (Fig. 7G, H), it becomes clear that *Phascolosoma* hooks begin with an open internal space into which partitions of reinforcing material are secreted eventually. The resulting subdivisions into triangles, streaks, or crescents must be at least partially genetically determined. Our examination of the literature and many hooks from within demes suggests that there are some species with distinctive morphs (e.g., *P. nigrescens* and *P. stephensoni*), but the degree of variation in many populations is great. One must accept the fact that within some species-complexes (e.g., *P. scolops/agassizii*) there is overlap and a degree of variation that can be confusing. Therefore, one must use caution when looking at internal hook-structure despite its potential usefulness.

F. Posterior basal elaborations: Separate, small units of diverse shape are associated with the posterior basal edge of most hooks in *Phascolosoma* (only *P. arcuatum* has no basal ornamentation). The units are separated from the main body of the hook and each other, but they really form a single structure which is considered part of the hook. Scanning electron micrographs illustrate three variations: like *P. stephensoni* most species are warty (Fig. 3A). In *P. saprophagicum* and *P. turnerae* these basal processes (rootlets) are taller and thinner (Rice 1985, fig. 1e; Gibbs 1987, fig. 1) while in *P. glabrum* an elaborate series of toes to the side of the hook and differing in the two subspecies (Fig. 3B, C) is present. Therefore,

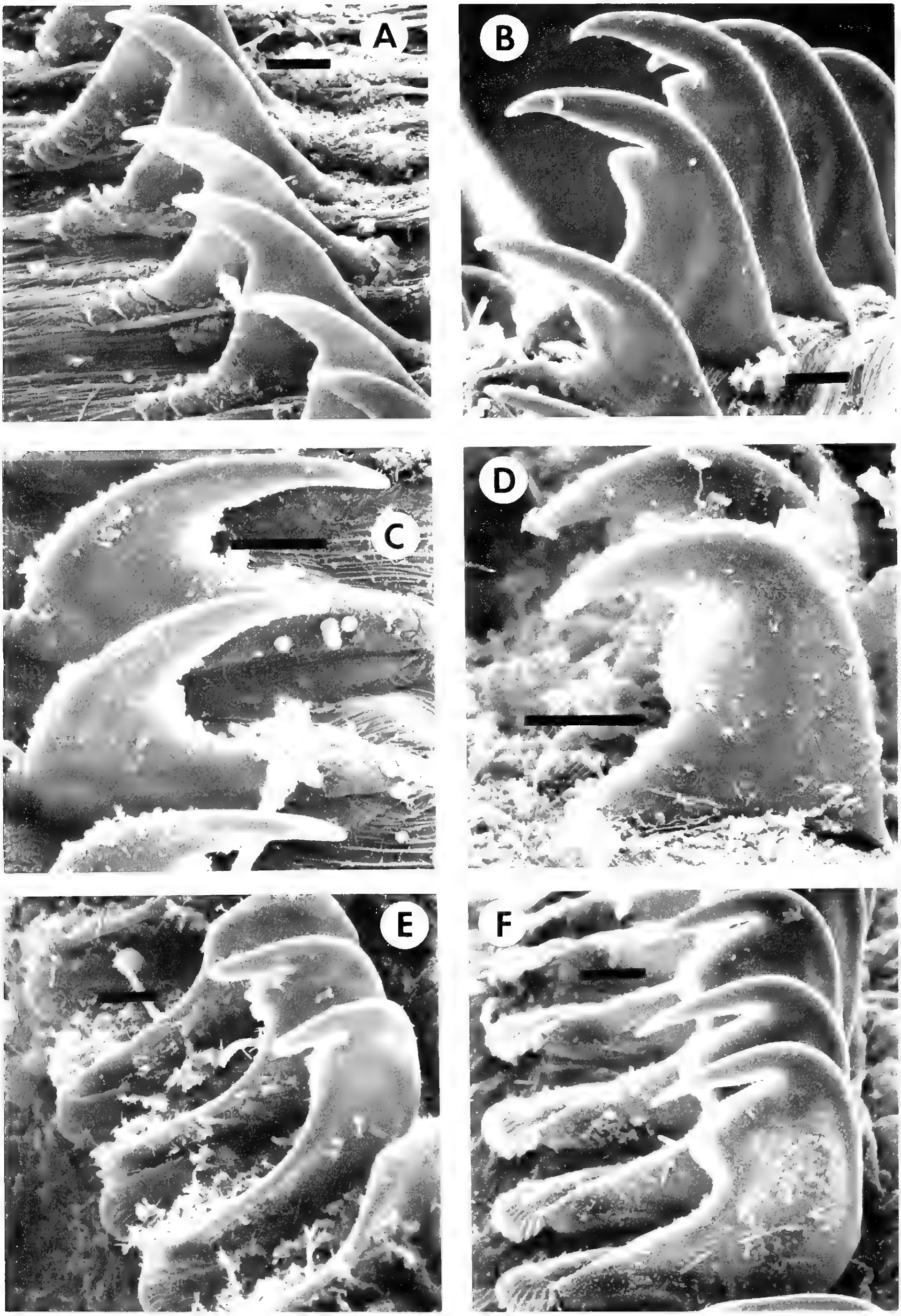


Fig. 2. SEM photographs of hooks from several *Phascolosoma*: A. *P. granulatum*; B. *P. perlucens*; C. *P. scolops*; D. *P. albolineatum*; E. *P. glabrum glabrum*; F. *P. glabrum multiannulatum*. Scale lines equal 10 μm.

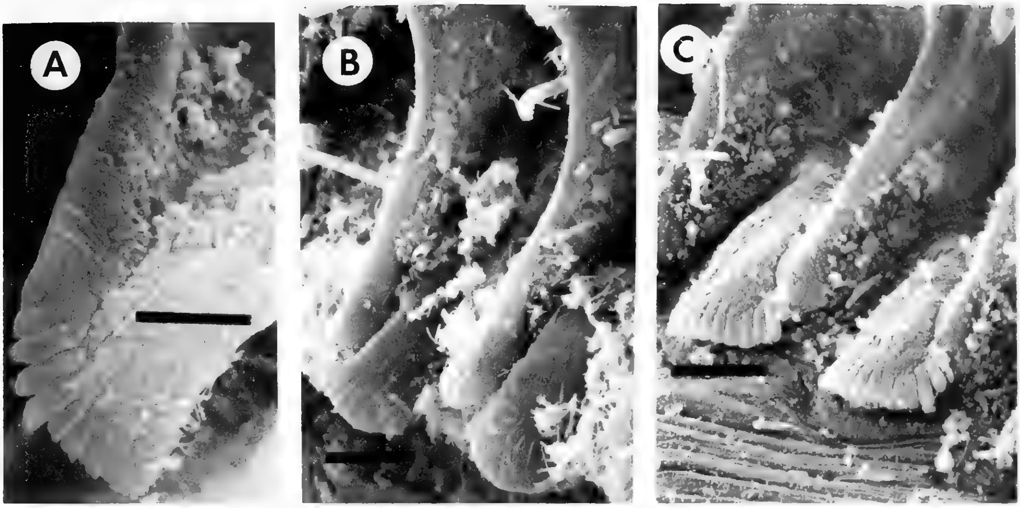


Fig. 3. SEM photographs of basal elaborations: A. Warts of *P. stephensoni*; B. Toes of *P. glabrum glabrum*; C. Toes of *P. glabrum multiannulatum*. Scale lines equal 10 μm.

for these latter species basal elaborations are taxonomically useful.

2. Pigmented introvert bands/stripes.—The dorsal side of the introvert is darker than the ventral side in many species. When present, this reddish-brown color is distributed in patches of varying size, from large and almost continuous in *P. perlucens,* to the more common pattern of irregular, narrow bands as in *P. scolops* and *P. agassizii.* With the exception of *P. nigrescens* the presence or absence of pigmented bands is consistent within a species and, therefore, of systematic value.

3. Introvert length.—The difficulty in using the relative length of the introvert lies in the elastic nature of this body region, easily observed in living worms. Additionally, as demonstrated in other genera, the trunk grows faster than the introvert so that the introvert becomes a smaller part of the whole in larger worms (allometric growth). The slope of the linear regression is always negative (Fig. 4). Depending on whether or not the introvert was extended and, if so, how well narcotized the worm was when preserved, the same introvert may appear to be from 75% to 125% of the trunk length. Within one population such a range is common in preserved material (see Appendix). Despite the fact that some populations have introverts averaging less than 90% of the trunk and others average over 125%, the overlapping ranges around these means preclude use of these data to identify an individual worm (Fig. 4 insert).

4. Number of longitudinal muscle bands.—The longitudinal muscle layer on the inside of the body wall is divided into a variable number of bundles or bands. In almost every species there are 18–24, occasionally as few as 15 in smaller or as many as 30 in larger worms (*P. pacificum* has 30–40). The bands anastomose occasionally and generally are more numerous towards the posterior end (see Appendix). This anterior/posterior difference can range from 0 to 10, and the order of magnitude of this difference is larger for some species than others. The number of bands is not as absolute or constant as stated in Stephen & Edmonds (1972:291), and appears to have no systematic value in the genus.

5. Nephridiopore/anus relationship.—These openings almost always occur at the same anterior/posterior level. If there is a

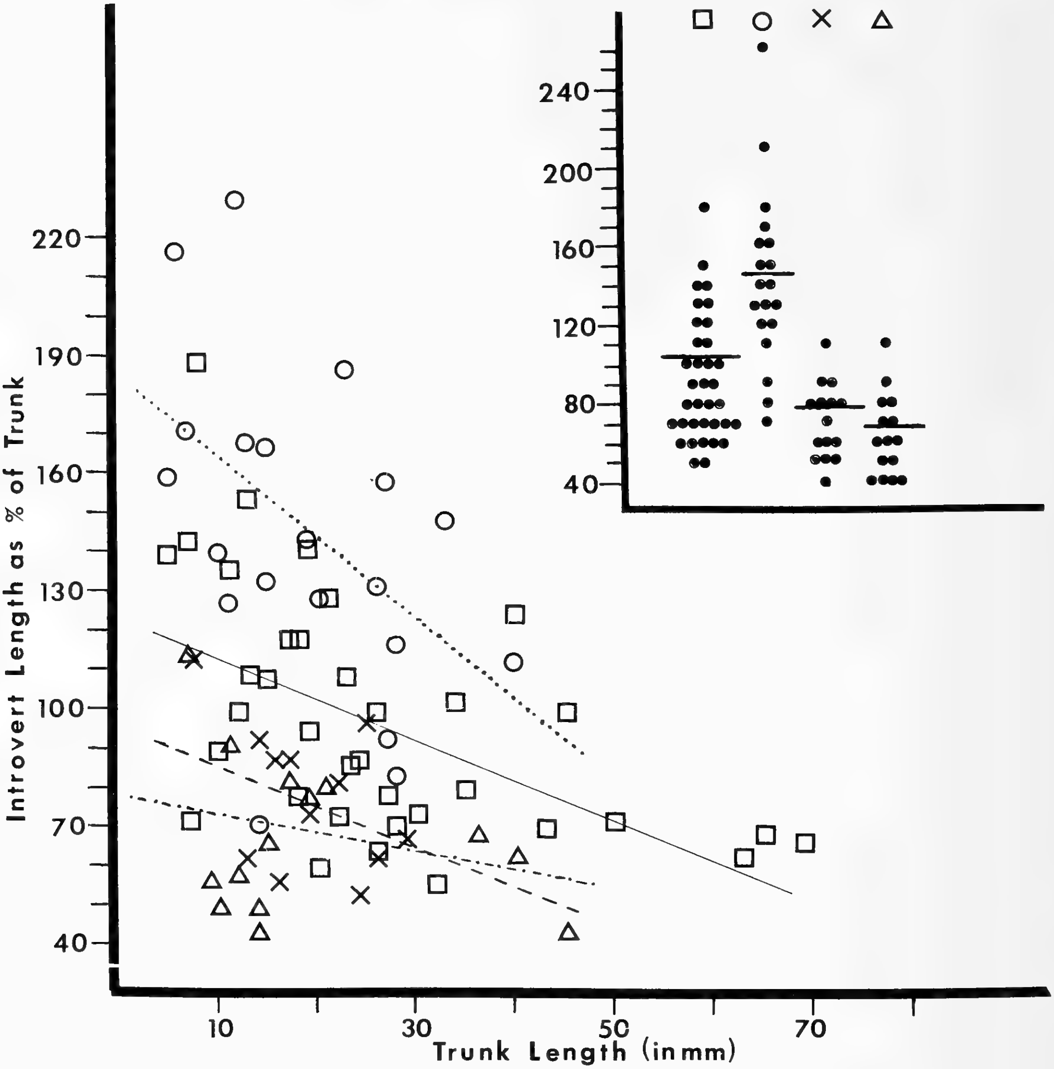


Fig. 4. Relationship between trunk length and introvert length of four *Phascolosoma* species; lines are linear regressions (y = a + bx): Squares = *P. agassizii,* b = −1.01; Circles = *P. nigrescens,* b = −2.06; X's = *P. perlucens,* b = −1.04; Triangles = *P. albolineatum,* b = −0.47. Insert shows introvert length of same four species to illustrate overlapping ranges despite significantly different means. Each dot represents one extended worm; the horizontal lines are the mean length for each species.

difference, the nephridiopores shift anterior (occasionally) or posterior (rarely) to the anus. When a shift occurs, the distance is on the order of 0.5 mm. To use this character in a taxonomic context for this genus would be a mistake.

6. *Nephridia length and attachment.*—The nephridia are a pair of tubular organs extending towards the posterior end of the trunk. In a few species (e.g., *P. pacificum* and *P. glabrum*) they are quite long, 95–100% of the trunk, and in a few species (e.g., *P. perlucens*) they are short (25–45%). In most species they are 40–65% of the trunk length (see Appendix).

Between the body wall and the nephridia there are thin connective tissue strands and most authors have noted the extent of their attachment. While in most species the value averages around 50%, the range within any population can be 30–70% of the nephridia length with no clear correlation to size of nephridia or trunk. Because of the delicate nature of this attachment it can be easily torn during dissection. In a few species this organ is attached along almost its entire length (e.g., *P. pacificum*). These nephridial features are taxonomically helpful for only a few special cases. Most species are similar, i.e., in the broad mid-range and variable.

7. Rectal caecum.—Located near the beginning of the rectum there may be a small digitiform or bulbous caecum. The presence or absence of this structure has been assumed to be consistent within a species. In Stephen & Edmonds' table (1972:291) they list 10 species with a caecum, 12 without, and 14 unknown. In our analysis (see Appendix) we find from 11–57% of the individuals in a population have a caecum. Sometimes it is clearly visible on the straight part of the gut, but at other times it is covered by the coiled portion and more difficult to find. It is hard to understand how this degree of polymorphism can exist if this structure might have some physiological function. Nevertheless, based on these data, we conclude that this character cannot be used for taxonomic purposes.

8. Papillae (shape/platelets/size).—Descriptions of the glandular epidermal structures known as papillae are varied, but not always precise or helpful. The careful drawings and measurements provided by many early workers are an expression of a typological species concept that overlooks the variations present within demes. These structures do differ but in less precise ways.

Three general shapes occur: domelike, mammillate, and conical. Many worms exhibit at least two types in various regions of the same animal. The papillae around the base of the introvert (pre-anal) are of particular interest because they help to differentiate species (Fig. 5).

When observed by transmitted light the papillae appear to have granular platelets of different sizes arranged in diverse patterns around a central pore. The pattern, however, seems to be consistent and unique only in *P. noduliferum*. When viewed with the SEM the papillae surface appears smooth. This observation suggests that the platelets are sub-cuticular. Additionally, the cuticle over the pre-anal papillae of a few species (e.g., *P. stephensoni* and *P. perlucens*) has a smooth hardened appearance (not granular in transmitted light).

Size measurements (height, basal diameter) have been presented, but the possible range of the measurements over the surface of a single worm is great, usually being smaller in the mid-trunk and larger towards the ends. In a general manner one can speak of large or small papillae, but this is a subjective, overall impression and larger worms tend to have larger papillae.

9. Contractile vessel villi.—Along the dorsal side of the esophagus runs a tubular contractile vessel. In some genera the vessel possesses digitiform extensions or villi, but *Phascolosoma* species do not. Stephen & Edmonds (1972:315) repeat ten Broeke's (1925) assertion that *P. nigrescens* has villi, but our examination of her material shows only a bulbous vessel with vesicular pouches, not villi.

10. Retractor muscle origins.—In most species the pair of dorsal retractor muscles has its origins from the body wall about 45% of the distance towards the posterior end of the trunk (the range may be as wide as 30–60% in a given population). The ventral pair originates at about 65% but may range from 50–75% within a population (see Appendix). Only *P. saprophagicum* has the ventral retractors in the posterior quarter of the trunk. In this species and *P. arcuatum,* both pairs of muscles originate at about the same distance from the ventral nerve cord so that the terms dorsal and ventral lose their meaning. Except for these two species, retractor origins cannot be used as an aid in identifying specimens.

11. Karyotypes.—While karyology may eventually be useful to systematists, our

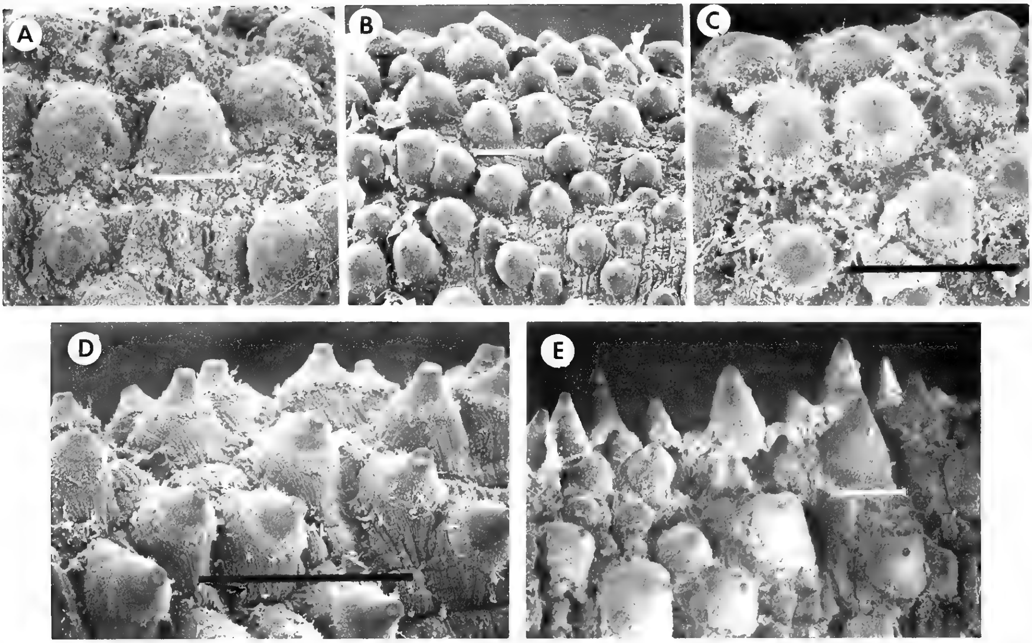


Fig. 5. SEM photographs of different shaped pre-anal papillae from several *Phascolosoma*: A. *P. granulatum* (dome); B. *P. scolops* (mammilate); C. *P. albolineatum* (dome); D. *P. perlucens* (cone); E. *P. stephensoni* (cone). Scale lines = 0.2 mm.

present data base is too small to be of value at the species level. Through the efforts of J. Silverstein (pers. comm.) we have information on the chromosomal morphology of *Phascolosoma scolops, P. pacificum, P. perlucens,* and *P. agassizii.* All have 2N = 20 with a common tendency toward asymmetry of chromosome arm length, e.g., 70–100% of the chromosomes are subtelocentric or telocentric. They all show a gradual reduction in chromosome length from pair one to pair 10 rather than a bimodal pattern of distinctly large and small chromosomes as is seen in other sipunculan genera.

Summary.—Four character states are determined to be consistent and broadly useful to the taxonomist at the species level. These are the number of hook rings, nature of the secondary tooth of the hook, pigment bands on introvert, and shape/size/texture of the pre-anal papillae. Eight characters can be used in a more restricted manner for smaller subsets or special cases. These include hook size, tip angle, internal clear streak/triangle/crescent, basal elaborations (warts/toes), nephridial length, trunk papillae shape, arrangement of papillae platelets, and the position of the retractor muscle origins. Six previously used attributes are of no value to the taxonomist, because of the within-deme variability. These are the presence/absence of hooks, introvert length, the number of longitudinal muscle bands, nephridiopore/anus relationship, the presence of a rectal caecum, and the nature of the contractile vessel.

Systematic Section

Genus *Phascolosoma* Leuckart, 1828

Phascolosoma Leuckart, 1828:22, fig. 5.—Keferstein, 1863:39 (part); 1865a:422 (part).—Baird, 1868:91.—Fisher, 1950: 551; 1952:422.—Stephen & Edmonds, 1972:270–271.—Gibbs & Cutler, 1987: 54.

Phascolosomum Diesing, 1851:63 (part); 1859:758 (part).
Phymosomum de Quatrefages, 1865:621.
Phymosoma Selenka et al., 1883:54 (emendation of *Phymosomum*).
Physcosoma Selenka, 1897:460.—Spengel, 1898:50.

Diagnosis.—Introvert of variable length often equal to trunk with numerous rings of recurved hooks. Body wall with longitudinal muscle layer gathered into bands. Tentacles (less than 30) in crescent around nuchal organ (peripheral tentacles lacking). Contractile vessel without true villi. Four introvert retractor muscles, lateral pairs sometimes partially, rarely completely, fused. Spindle muscle may or may not be attached posteriorly. Two nephridia.

Type species.—*Phascolosoma granulatum* Leuckart, 1828.

Subgenus *Phascolosoma* Leuckart, 1828

Phascolosoma (*Phascolosoma*) Stephen & Edmonds, 1972:289–291.—Gibbs & Cutler, 1987:54.

Diagnosis.—Spindle muscle attached posteriorly. Introvert hooks without accessory spinelets.

The following three taxa are not considered valid members of this genus and are discussed first. After the key, the remaining species are alphabetically arranged.

Phascolosoma corallicola
(ten Broeke, 1925)

Physcosoma corallicola ten Broeke, 1925: 90, text fig. 12 (not *Sipunculus corallicolus* Pourtalès, 1851:41).
Phascolosoma (*Phascolosoma*) *corallicolum.*—Stephen & Edmonds, 1972:298–299.

Discussion.—In the bottle at ZMUA labeled as type (V.Si. 96) is one piece of coral and three anthozoans but no sipunculans. There are unresolvable peculiarities in ten Broeke's description of a damaged, hookless worm of unspecified size. She did say it had 12 tentacles despite Stephen & Edmonds (1972) statement that they were absent. Extensive collections in the type locality in recent decades by ourselves and others have failed to yield any worms like this. For these reasons it seems most prudent to place this name on the list of incertae sedis.

Phascolosoma longicolle
Rüppell & Leuckart, 1828

Phascolosoma longicolle Rüppell & Leuckart, 1828:6, fig. 1. Grübe, 1840:47; 1868: 644.—Diesing, 1851:64; 1859:762.—Baird, 1868:95.—Stephen & Edmonds, 1972:339.—Saiz Salinas, 1989:208.

Material examined.—MNHU, Grübe's Red Sea specimen (3171).

Discussion.—The recent analysis by Saiz Salinas shows this name (considered incertae sedis by Stephen & Edmonds, 1972) to be associated with worms that belong to the species *Golfingia vulgaris.* Grübe's specimen in Berlin is a *P. scolops.*

Phascolosoma nigritorquatum
(Sluiter, 1881)

Phymosoma nigritorquatum Sluiter, 1881: 151–152, pl. 1, figs. 3, 8, 11; 1891:117.—Selenka et al., 1883:68–69.
Physcosoma nigritorquatum.—Sluiter, 1902: 13.—Fischer, 1919:280; 1921:4–5; 1927: 416.
Phascolosoma (*Satonus*) *nigritorquatum.*—Stephen & Edmonds, 1972:286–287.—Edmonds, 1980:61–62.—Cutler & Cutler, 1983:186.

Material examined.—ZMUA, type (V.Si. 80); ZMUH, Fischer's 1921 material (V8916).

Discussion.—We reaffirm our position taken in Cutler & Cutler (1983) that these worms belong in this subgenus, but the quality of the material precludes a meaningful definition of this species and the status of incertae sedis is appropriate including Fischer's material.

Phascolosoma abyssorum
(Southern, 1913)

Physcosoma abyssorum Southern, 1913:12–14, pl. 1, fig. 1, pl. 2, fig. 1.—Fischer, 1916:6; 1922b:6; (not *Phascolosoma abyssorum* Koren & Danielssen, 1877 = *Golfingia abyssora*).

Phascolosoma (*Phascolosoma*) *abyssorum*.—Stephen & Edmonds, 1972:292.

Discussion.—We concur with Gibbs (1986), who showed Southern's species to be conspecific with, and a junior synonym to, *Apionsoma capitatum*.

Key to *Phascolosoma* Species

This is based on the characters of mature hooks taken from complete rings (not distal 2 or 3 or posterior worn and scattered ones).

1. More than 50 rings (complete and/or incomplete) of hooks 2
– Less than 50 rings (complete and/or incomplete) of hooks 9
2. Most hooks over 100 μm tall, nephridia as long as trunk (Fig. 6A) .... *P. pacificum*
– Hooks less than 100 μm tall 3
3. Concave side of hook with large rounded hump, toes present but not warts (2 subspecies, Fig. 6B) .... *P. glabrum*
– Concave side of hook is smoothly tapered or with small secondary tooth 4
4. Hooks with long, thin basal processes (Fig. 3C) .... *P. turnerae*
– Basal processes, if present, as normal warts 5
5. Hooks without basal warts (Fig. 6D) .... *P. arcuatum*
– Hooks with basal warts 6
6. Clear streak of hook with swelling in middle of vertical and horizontal portion (Fig. 6E) ... *P. nigrescens*
– Clear streak without abrupt swellings 7
7. Hooks with posterior crescent, many over 75 μm tall, pre-anal papillae smooth cones, pigment bands on introvert (Fig. 1) .... *P. stephensoni*
– Hooks without crescents, most less than 75 μm tall, no pigment bands on introvert 8
8. Hooks with granular triangle (Fig. 6F), close-set, randomly distributed papillae platelets ... *P. granulatum*
– Hooks without triangle, posterior hooks more triangular shape and narrower clear streak (Fig. 7D, E), papillae platelets around pore small and close-set then abruptly more wide-spread .... *P. noduliferum*
9. Hooks less than 25 μm tall 10
– Hooks over 25 μm tall 11
10. Fewer than 10 rings of inconspicuous hooks. (Fig. 6G) .... *P. meteori*
– More than 15 hook rings (Fig. 6H) .... *P. saprophagicum*
11. Angle of hook tip greater than 90° (Fig. 6I) .... *P. albolineatum*
– Angle of hook tip 90° or less 12
12. Large rounded hump on concave side of hook, pre-anal papillae smooth, posteriorly directed, cone-shaped (Fig. 7A) .... *P. perlucens*
– Concave side smooth or with small tooth 13
13. Hooks with separate anterior basal triangle 14
– Hooks without triangles (Fig. 7B) .... *P. maculatum*
14. Trunk papillae platelets extending onto inter-papillae surfaces (Fig. 7C) .... *P. annulatum*
– Papillae platelets restricted to papillae surfaces 15
15. Hook with distinct triangle, narrow band of red cone-shaped pre-

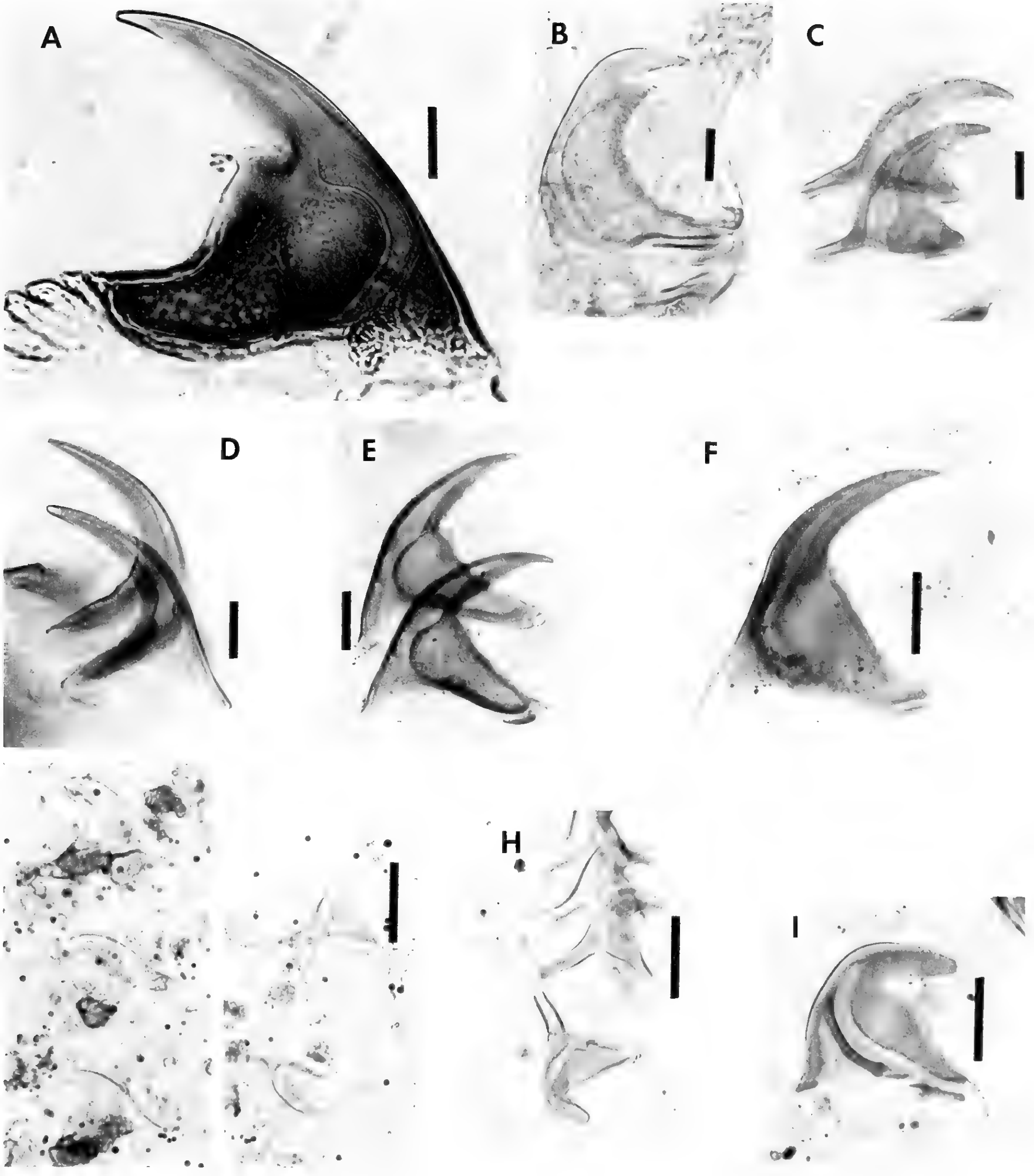


Fig. 6. Light microscope photographs of *Phascolosoma* introvert hooks arranged as in the Key. Scale lines = 20 μm: A. *P. pacificum*; B. *P. glabrum*; C. *P. turnerae*; D. *P. arcuatum*; E. *P. nigrescens*; F. *P. granulatum*; G. *P. meteori*; H. *P. saprophagicum*; I. *P. albolineatum*.

anal papillae (Fig. 7F) . . . *P. scolops*

– Hook triangle indistinct or absent, pre-anal papillae not distinct from dome-shaped trunk papillae (Fig. 7G, H) . . *P. agassizii*

Phascolosoma agassizii
Keferstein, 1866

Phascolosoma agassizii Keferstein, 1866: 218–219; 1867:46.—Baird, 1868:92;

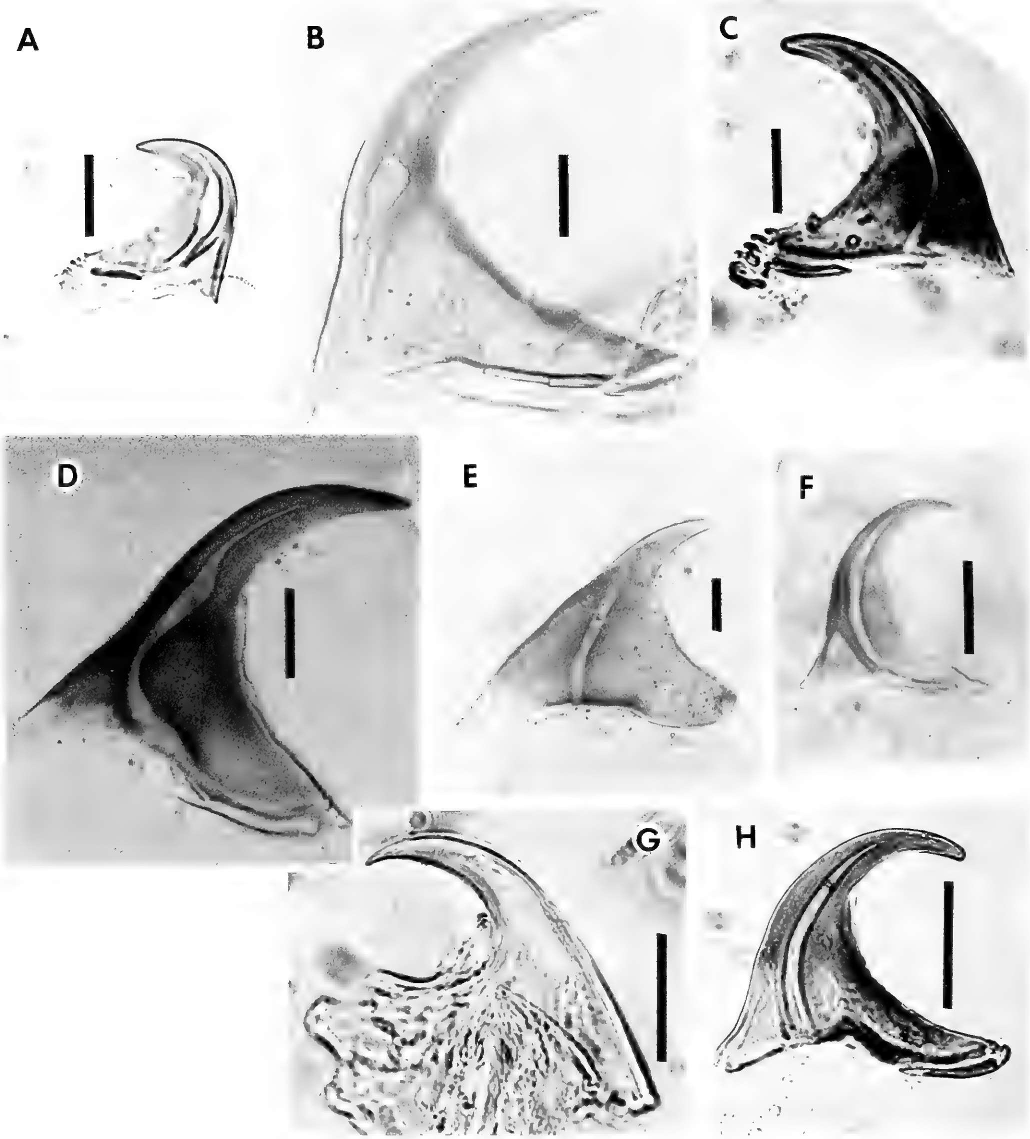


Fig. 7. As for Fig. 6: A. *P. perlucens*; B. *P. maculatum*; C. *P. annulatum*; D & E. *P. noduliferum* (anterior & posterior); F. *P. scolops*; G & H. *P. agassizii* from most distal ring, not completely erupted (G) & middle ring (H).

Fisher, 1952:424–430.—Wesenberg-Lund, 1954a:8–9; 1957a:3; 1959b:210; 1963:126.—Stephen, 1960:516–517; 1966:147–148.—Rice, 1967:143–171; 1973:1–51.—Stephen & Cutler, 1969:115; Johnson, 1971:599–600.

Phymosoma agassizii.—Selenka et al., 1883: 78–79. *Physcosoma agassizii.*—Fischer, 1895:10; 1914a:6; 1914b:67–68; 1923:23; 1927:200.—Shipley, 1891:123; 1899a: 155; 1902:133; 1903:174.—Chamberlin, 1920a:30; 1920b:5D.—Leroy, 1936:424 (not Fischer, 1919:280; 1922a:7–9).

Phascolosoma (*Phascolosoma*) *agassizii.*—Stephen & Edmonds, 1972:292–293.—Dybas, 1976:67–75.—Cutler & Cutler, 1979a:982–983.—Rice, 1980:492.—Frank, 1983:23–24.—Saiz Salinas, 1986: 52–55.

Phymosoma lordi Baird, 1868:92.—Rice & Stephen, 1970:62.

Phascolosoma japonicum Grübe, 1877: 73.—Fisher, 1952:429.—Wesenberg-Lund, 1963:116–119.—Stephen & Cutler, 1969:115.—Cutler 1977b:154–155.—Cutler et al., 1984:293–296.

Phymosoma japonicum.—Selenka et al., 1883:76–78.—Ikeda, 1904:22–23.

Physcosoma japonicum.—Selenka, 1888: 220.—Shipley, 1891:122.—Fischer, 1895: 12; 1914a:5–6; 1916:15; 1922a:13–14; 1923:3.—Chamberlin, 1920b:5D.—Ostroumov, 1909:321–322.—Satô, 1930:9–11; 1937b:149–150; 1939:383–386.—Stephen, 1942:247–248; 1948:220 (vide *P. noduliferum*).—Leroy, 1936:424 (not Selenka, 1885:21.—Fischer, 1922b:7–8).

Phascolosoma (*Phascolosoma*) *japonicum.*—Stephen & Edmonds, 1972:309–310.

Physcosoma yezoense Ikeda, 1924:32–34, pl. 1, figs. 3–6.

Phascolosoma (*Phascolosoma*) *yezoense.*—Stephen & Edmonds, 1972:328–329.—Cutler & Cutler, 1981:91–92.

Physcosoma glaucum Satô, 1930:15–17, pl. 1, fig. 6, fl. 2, figs. 7–8, text fig. 4 (not *Phascolosoma glaucum* Lanchester, 1905a:32 = *Golfingia glauca*).

Phascolosoma (*Phascolosoma*) *glaucum.*—Stephen & Edmonds, 1972:306.—Cutler & Cutler, 1981:89–90.

Physcosoma formosense Satô, 1939:398–401, pl. 20, fig. 15, text figs. 36–41.

Phascolosoma (*Phascolosoma*) *formosense.*—Stephen & Edmonds, 1972:304.—Cutler & Cutler, 1981:89.

Phascolosoma (*Rueppellisoma*) *golikovi* Murina, 1975:54–55, fig. 1.—Cutler & Cutler, 1983:180.

Material examined.—MCZH, type material (186, 439); our recent California collections; *P. japonicum,* MNHU, type (1024) plus 979 & 1025, and Fischer's 1922 Port Elizabeth specimens (6087); NHRS, Fischer's 1922 Eugenie material (162, 164); recent Japanese collections (Cutler et al. 1984).

Discussion.—Considerable lack of clarity about this taxon has existed. Our decision to combine these names comes after protracted analysis of numerous specimens. As presently defined *P. agassizii* has fewer than 30 rings of hooks that are 30–70 μm tall, each having a variable clear streak, a triangle that is usually indistinct, and if a secondary tooth is present, it is small (Fig. 7G, H, and Fisher 1952, plates 37–38 for variety). When others have reported this species as having more than 30 rings of hooks they were probably looking at a different species. The introvert has irregular pigment bands and is about as long as the trunk. The trunk is covered with papillae that exhibit much variety in color (generally darker than the skin). Papillae platelets are variable in size (3–9 μm) and with a random distribution. Published illustrations overlook the variation present, even on a single worm.

Previous decisions to reduce some taxa to junior synonyms of *P. japonicum* are reaffirmed here with the subsequent move into synonymy with *P. agassizii.* These are *P. glaucum* and *P. yezoense* (Cutler & Cutler 1981), plus *P. golikovi* (Cutler & Cutler 1983).

In the description of *P. formosense,* Satô (1939) seems inconsistent. He stated that the hooks are scattered but later wrote about the number of rings. His figure shows three hooks in a line as if part of a ring. As suggested in Cutler & Cutler (1981) Satô probably had two worms with few hook rings that were partially covered by a fold of skin. The hook and papillae shape fit within our concept of *P. agassizii.*

Distribution.—Common on both sides of the north Pacific Ocean (Mexico to Alaska on the eastern side and Japanese waters in the west), plus scattered records from cooler Indian Ocean waters. Several records from south and west Africa exist, and while these may include some misidentified *P. granu-*

latum, others are correct. Australian and other warm water Indian and Pacific Ocean records (including Keferstein's Panama material) are considered to be other *Phascolosoma* species.

Phascolosoma agassizii kurilense (Satô, 1937)

Physcosoma kurilense Satô, 1937a:117–120, text fig. 14.
Phascolosoma (*Phascolosoma*) *kurilense.*—Stephen & Edmonds, 1972:310–311.—Cutler & Cutler, 1981:91.

Material examined.—None.

Discussion.—The earlier decision (Cutler & Cutler 1981) to reduce the northern *P. kurilense* to a subspecies of *P. japonicum* is reaffirmed here. However, *P. japonicum* is now a junior synynym of *P. agassizii.* The one morphological difference is the presence of a small secondary lobe on the nephridia of mature worms.

Distribution.—Kurile Islands.

Phascolosoma albolineatum (Baird, 1868)

Phascolosoma albolineatum Baird, 1868:91–92.—Wesenberg-Lund, 1963:128.—Stephen, 1967:45.—Rice & Stephen, 1970: 59.—Edmonds, 1980:56–57.—Murina, 1981:13.—Cutler et al., 1984:292–293.
Phymosoma albolineatum.—Selenka et al., 1883:71–72.—Augener, 1903:301–302.
Physcosoma albolineatum.—Fischer, 1913: 99; 1914a:6; 1922a:9.—Ikeda, 1924:32.—Leroy, 1942:6–9.—Satô, 1935:312; 1939: 395–396.—Tokioka, 1953:140.
Phascolosoma (*Phascolosoma*) *albolineatum.*—Stephen & Edmonds, 1972:293–295.—Cutler & Cutler, 1979a:983.
Phymosoma microdontoton Sluiter, 1886: 506, pl. 4, fig. 9; 1891:118; 1902:13.
Phascolosoma (*Phascolosoma*) *microdontoton.*—Stephen & Edmonds, 1972:312–313.
Phascolosoma multiannulata Wesenberg-Lund, 1954b:378–383, text figs. 2–6 (part).
Phascolosoma andamanensis Johnson, 1971:603–604, pl. 1, figs. 1–7.—Haldar, 1976:3–4.

Material examined.—BMNH, type; Indian Ocean and Japanese material (Cutler & Cutler 1979a, Cutler et al. 1984); *P. multiannulatum,* UZMK, type material, (cataloged as *Golfingia multiannulata*); *P. microdontoton,* ZMUA, type (V.Si. 77).

Discussion.—This taxon is characterized by the tip of the hooks being bent at an angle of more than 90°. Superficially it strongly resembles pale specimens of *P. scolops,* and unless hooks are examined the two species could be misidentified. On the concave side the hooks have a large bulge but no secondary tooth, giving the base a less triangular form. The clear streak often does not extend beyond the mid-point (Fig. 6I). The hooks are from 25–65 μm tall and arranged in less than 40 rings. The introvert is shorter than the trunk, and the nephridia are usually less than one-half the trunk length. In some specimens only two or three retractor muscles are present owing to some degree of fusion (Cutler & Cutler 1979a:983, Cutler et al. 1984:292).

Phascolosoma microdontoton (Sluiter, 1886) is considered a junior synonym. The original illustration of a hook is misleading. The internal structure and the external shape match *P. albolineatum* except that the tips of some hooks are worn down. The band of pre-anal papillae are also comparable.

When Wesenberg-Lund (1954b) described *P. multiannulatum* she reported 500 specimens, of which only 20 can now be located. Of these, 16 are clearly *P. albolineatum,* with pale trunks 8–25 mm long. Her description was a combination of characters and we have redefined her taxon below.

The name *P. andamanensis* was introduced by Johnson (1971) and used by Halder in 1976 for a population that was like *P. albolineatum* except that the hooks had basal bar and warts (see discussion in Morphological Section). Haldar (1988), after collecting many specimens in the Andaman

Islands, placed the name in synonymy with *P. albolineatum* and we concur.

Distribution.—Wide spread but not common in Indo-West Pacific tropical shallow waters.

Phascolosoma annulatum (Hutton, 1879)

Phascolosoma annulatum Hutton, 1879: 278.—Benham, 1903:174.—Edmonds, 1960:160–162.
Phascolosoma (*Phascolosoma*) *annulatum.*—Stephen & Edmonds, 1972:296–297.—Cutler, 1977a:151–152.—Edmonds, 1980:57–58.
Physcosoma scolops var. *mossambiciense.*—Augener, 1903:339.
Physcosoma scolops tasmaniense Fischer, 1914a:3–4.
Physcosoma scolops.—Wheeler, 1938:346.
Phascolosoma tasmaniense Edmonds, 1956: 285–286.

Material examined.—BMNH, type; two worms identified by Edmonds from New Zealand and Australia.

Discussion.—This species has been recorded up to 50 mm long with introverts 1–2 times the trunk bearing up to 30 tentacles. The hooks in this species are very similar to *P. scolops,* 45–60 μm tall, in up to 25 complete rings. The separate triangle is less distinct (Fig. 7C). Proximal, incomplete, dorsal rings of smaller (30–35 μm), more triangular hooks are partially obscured by the papillae and pigment. The bases of the trunk papillae appear polygonal (not oval) and are covered by dark polygonal platelets. These platelets spread out over the skin in the interpapillae spaces in a distinctive manner.

Distribution.—Southern Australia, New Zealand, and Campbell Island in cooler water.

Phascolosoma arcuatum (Gray, 1828)

Siphunculus arcuatus Gray, 1828:8.—Baird, 1868:88.—Rice & Stephen, 1970:50–51.
Phascolosoma (*Phascolosoma*) *arcuatum arcuatum.*—Stephen & Edmonds, 1972: 297–298.—Edmonds, 1980:58–59.
Phymosoma lurco Selenka et al., 1883:61–63.
Physcosoma lurco.—Fischer, 1895:12; 1914a:4–5; 1922a:15.—Sluiter, 1902: 12.—Lanchester, 1905b:37.—Leroy, 1936:424.
Phascolosoma lurco.—Edmonds, 1956:290–291.
Phymosoma lurco malaccensis Selenka et al., 1883:63.
Physcosoma lurco malaccensis.—Sluiter, 1902:12.
Phascolosoma arcuatum malaccense.—Stephen & Edmonds, 1972:298.
Phascolosoma rhizophora Sluiter, 1891:119–121; 1902:13.
Physcosoma ambonense Fischer, 1896:337–338, text figs. 1–3.
Phascolosoma (*Phascolosoma*) *ambonense.*—Stephen & Edmonds, 1972:295–296.
Phymosoma deani Ikeda, 1905:171–172, pl. 8, figs. 5–8.
Phascolosoma (*Phascolosoma*) *deani.*—Stephen & Edmonds, 1972:299.—Cutler & Cutler, 1981:88–89.
Physcosoma esculenta Chen & Yeh, 1958: 273–274, text figs. 1–2.
Phascolosoma esculenta.—Murina, 1964: 263.
Phascolosoma (*Phascolosoma*) *esculentum.*—Stephen & Edmonds, 1972:301.

Material examined.—*P. deani,* ZMUT, type; *P. esculenta,* material identified by Murina; *P. lurco,* MNHU, type (488, 971); UZMC, Lanchester's material; *P. rhizophora,* ZMUA, type (V.Si. 84).

Discussion.—This species has very dark, large papillae with sharp borders against a light yellow-brown skin. The introvert may be twice the trunk length and bears over 100 complete and incomplete rings of hooks. The hooks are 40–70 μm tall, without secondary teeth, warts, or toes. Internally the hooks are simple, with the clear streak greatly expanded basally. The retractor muscles are unique in that the origins of the broad posterior pair have shifted dorsally (to longitudinal muscle bands 2–3) and the origins of the thinner anterior pair have shifted ventrally (to muscle band 1). Also, the entire retractor complex may appear as a single fused unit with four roots when contracted. The circular muscle layer is divided into anastomosing bands thereby creating "coelomic sacs" where gas exchange between the environment and the coelomic fluid can occur more readily as in many Sipunculidae.

In 1970 Rice & Stephen concluded that *P. arcuatum* and *P. lurco* were conspecific and in 1972 Stephen & Edmonds added *P. rhizophora.* In 1981 Cutler & Cutler continued this process by adding *P. deani* and *P. esculenta* to the list of junior synonyms.

The justification for retaining *P. arcuatum malaccense* as a valid subspecies is weak. "The papillae on the middle of the trunk are formed of many concentric plates instead of being arranged irregularly" (Stephen & Edmonds 1972:298). Later they state ". . . figure of . . . nominate form shows only a partial concentric arrangement of the plates." Selenka et al. (1883) did not provide any illustrations of their subspecies, and we conclude that this taxon does not merit separate status.

The type material of *P. ambonense* Fischer, 1896, is not located in those museums where Fischer deposited other specimens, and there are no other records of this taxon. The similarities of this to *P. arcuatum,* a species common in Indonesia, have been noted by earlier writers and include: the retractor muscles (ventral pair anterior to dorsal), the weakly developed and few longitudinal muscle bands (only 16 in a 140 mm worm (total length and not 14 mm as in Stephen & Edmonds 1972:285)), and hook shape. Our inability to verify this information is not helpful. Rather than add this name on the list of species inquirendum, pending future clarification, we place it in the present synonymy.

Distribution.—Northeast India, Andaman Islands, southern China, Vietnam, Philippines, Malaysia, Indonesia, and northern Australia. Tolerates extended periods out of the water and in brackish water, e.g., in mangrove estuaries.

Phascolosoma glabrum glabrum
(Sluiter, 1902)

Physcosoma glabrum Sluiter, 1902:14–15, pl. 1, figs. 7–8.

Phascolosoma (*Phascolosoma*) *glabrum.*—Stephen & Edmonds, 1972:305.

Phymosoma microdontoton.—Shipley, 1898:471; 1899b:56.

Physcosoma funafutiense Fischer, 1914a:6–8, pl. 1, fig. 8; 1922a:11–13.

Phascolosoma (*Phascolosoma*) *funafutiense.*—Stephen & Edmonds, 1972:304–305; Cutler & Cutler, 1979a:983–984.

Material examined.—ZMUA, type (V.Si. 128/5); *P. funafutiense,* ZMUH, 4 worms collected in West Java by Beneden and determined by Augener but never published (V10983); NHRS, Fischer's 1922 material; Pacific and Indian Ocean specimens (Cutler & Cutler 1979a). *P. microdontoton,* UZMC, Shipley's 1898 worms.

Discussion.—In several ways (nephridia 75–100% of trunk, trunk papillae evenly distributed and of uniform size all over, a large number of hook rings) *P. glabrum* is similar to *P. pacificum,* but is distinguished by having somewhat smaller hooks (60–85 μm) with a different shape and internal structure (Fig. 6B). The hooks have a large hump on the posterior edge, the clear streak has an apical expansion, and they are the only hooks that have basal toes (Fig. 3B). In addition, the skin has a smoother texture because of smaller dome-shaped papillae (vs. tall cones). The differences between the two subspecies are described in the following section.

When Fischer (1914a) described *P. funafutiense* he made no reference to *P. glabrum.*

Sluiter's illustration does not show any basal toes while Fischer's material has them. Sluiter overlooked them, although they are present on the type. Cutler & Cutler (1979a) focused on the hook structure and used Fischer's name. It is now clear that these two species are conspecific.

Fischer (1914a) maintained that Shipley's (1898, 1899b) *P. microdontoton* actually was synonymous with his new species. Our analysis confirms that conclusion, and, thus, Shipley's reports are included here.

Distribution.—Scattered records from Indo-West Pacific (Diego Garcia, Indonesia, Eniwetok, Funafuti, Rotuma, and Christmas Island).

Phascolosoma glabrum multiannulatum
(Wesenberg-Lund, 1954)

Phascolosoma multiannulata Wesenberg-Lund, 1954b:378–383, text figs. 2–6 (part).

Phascolosoma (*Phascolosoma*) *multiannulatum.*—Stephen & Edmonds, 1972:313–314.

Material examined.—UZMK, type material, (cataloged as *Golfingia multiannulata*).

Discussion.—In the museum collections there are 20 specimens from Wesenberg-Lund's type material; only four of which have hooks that fit her description. The other 16 worms are *P. albolineatum.* We do not know what happened to the other 480 worms in the original collection and suspect that Wesenberg-Lund's description is an amalgamation of features of both populations. Her description and drawings of the hooks (her figs. 3–5) are of *P. g. multiannulatum.* Her comments about the papillae and her drawings of these and the internal anatomy (her figs. 2 and 6) fit the *P. albolineatum* morph.

The differences between these four specimens and the nominate form are subtle. Our present action allows for future workers, having access to a larger sample size, to treat this population as conspecific or reestablish it as a species. The hooks are smaller (up to 60 μm), the clear streak is without an apical expansion, and there are 12 toes on the left instead of 10 toes on the right side (Fig. 3C). The hook rings are farther apart, the trunk papillae are larger domes, and sometimes lie in rectangles formed by folds of skin.

Distribution.—Type locality at Hikueru, Tahiti. This is at the eastern edge of the species' range.

Phascolosoma granulatum
Leuckart, 1828

Phascolosoma granulatum Leuckart, 1828: 22, text fig. 5. (For references between 1828 and 1969 see Stephen & Edmonds, 1972:306–307 and Saiz Salinas, 1984b: 203–205.)

Phascolosoma (*Phascolosoma*) *granulatum.*—Stephen & Edmonds, 1972:306–309.—Walter, 1973:487.—Haldar, 1975: 59.—Zavodnik, 1975:99.—Zavodnik & Murina, 1975:127; 1976:83.—Gibbs, 1977:28–29.—Saiz et al., 1979:209–210.—Saiz Salinas & Rallo Gruss, 1980: 114.—Saiz Salinas, 1984a:185–186; 1984b:203–205; 1986:55–62; 1988b: 11.—Ocharan, 1980:115–116.—Murina, 1977:160–162; 1981:13–14 (not Cutler & Cutler, 1979b:109; 1987b:71).

Physcosoma lanzarotae Harms, 1921:307 (part).

Physcosoma japonicum.—Fischer, 1922b: 7–8.

Material examined.—UZMK, Wesenberg-Lund's 1959a material from Cape Verde and Canary Islands; Saiz Salinas' 1986 material from Spain; Brazil and Cape Verde material (Cutler & Cutler 1979b); *P. japonicum,* MNHU, Fischer's 1922b Port Elizabeth material (6087); *P. laeve,* MNHU, Keferstein's 1865a worms (6990); *P. loveni,* UZMK, Wesenberg-Lund's 1930 material.

Discussion.—There has been a lack of

clarity about the distinction between this species and *P. stephensoni.* Some of the earlier reports of *P. granulatum* are really *P. stephensoni.* Their ranges overlap. It is also probable that some descriptions have been based on a mixture of the two species. The papillae of *P. granulatum* are granular and dome-shaped, occasionally darker than the body wall, without the taller, smoother, cone-shaped pre-anal papillae that characterize *P. stephensoni.* The introvert is without any dark pigmented bands. The hooks are arranged in over 50 rings, some incomplete. The hooks are 35–70 μm tall, have a narrow clear streak with an indistinct granular triangle, and ill-defined or no secondary tooth (Fig. 6F). The number of longitudinal muscle bands varies considerably between the anterior and posterior in a given worm, averaging 18 and 26 respectively. In general, there is a lack of diagnostic apomorphic characters suggesting that this may represent an evolutionarily significant morphology—closest to the ancestral stock.

The material described by Wesenberg-Lund (1930) as *P. loveni* is clearly *Apionsoma capitatum.* Satô's two reports (1935, 1939) cannot be verified, but based on his comments, and upon zoogeographical considerations, we propose that his worms were probably *P. scolops.*

Collin (1892), Wesenberg-Lund (1959c), and Murina (1981) have reported *P. granulatum* from the Indian Ocean. We have not been able to examine these collections, the descriptions are brief with no figures, and we suggest that the worms belong to one of the tropical *Phascolosoma* species. Reexamination of the material from Brazil and Cape Verde (Cutler & Cutler 1979b), as well as Wesenberg-Lund's (1959a) from the Canary Islands, show them to be what we now consider *P. stephensoni.*

Distribution.—Common in the northeastern Atlantic Ocean from southern Norway along the coasts of Europe and the British Isles to northern Africa out to the Azores and Cape Verde Islands. It extends into the Mediterranean and Adriatic Seas. The Brazilian record was an error and we suspect that the Indian Ocean records are not this species either.

Phascolosoma maculatum (Sluiter, 1886)

Phymosoma maculatum Sluiter, 1886:511–512, pl. 4, fig. 4; 1891:118–119.—Augener, 1903:308–310.

Physcosoma maculatum.—Sluiter, 1902:11.

Phascolosoma (*Satonus*) *maculatum.*—Stephen & Edmonds, 1972:285.—Cutler & Cutler, 1983:185.

Material examined.—ZMUA, type (V.Si. 76).

Discussion.—Although based on only three individuals whose differences from other species are not clear, *P. maculatum* is retained as a species. The hooks are distinctive: 90–95 μm tall, slender, with the clear streak reaching one-half to two-thirds the distance towards the tip and usually expanding into a broad basal triangle (Fig. 7B). Only some of the hooks have a secondary tooth and up to 12 basal warts are present. The posterior trunk papillae are tall cone-shaped while the anterior papillae are mammiform.

The decision by Cutler & Cutler (1983) to move this from the subgenus *Satonus* was based on our observation that a posteriorly attached spindle muscle was present.

Distribution.—Indonesia.

Phascolosoma meteori (Hérubel, 1904)

Phymosoma meteori Hérubel, 1904a:477–478, figs. 2–3; 1904b:563; 1907:123–128.

Physcosoma meteori.—Stephen, 1941:405.

Phascolosoma meteori.—Wesenberg-Lund, 1957b:12.

Phascolosoma (*Phascolosoma*) *meteori.*—Stephen & Edmonds, 1972:312.

Material examined.—MNHN, type material (V-22).

Discussion.—These are grayish worms with introvert shorter than the trunk. The trunk papillae are small domes and the preanal papillae are not randomly arranged but in clusters of 2–5. We found up to ten incomplete rings of pale hooks (15–30 μm) with a bent clear streak and anterior triangle only on the ventral surface. These were overlooked by Hérubel.

This species is well founded on well preserved specimens and, except for an assumed lack of hooks, is very similar to the other members of this genus. Hérbuel's three papers are all based on the same material, the second 1904 paper is simply a listing of the stations while in 1907 he gave a more detailed morphological description. However, not all of the museum material is this species (the six Djibouti worms are a mixture of *P. nigrescens* and *P. scolops*).

Some of the animals were surrounded by a mud coating that must have been formed by mucus secretions much like that of *Phascolion lutense.* One had a commensal polychaete sharing the shelter as do some *Phascolion* species. The contractile vessel is large and folded with vesicular swellings, and not villi (even in those specimens with the introvert completely extended.) The many tentacles and enlarged contractile vessel are probably adaptations to increase the surface area for gas exchange, a feature seen in other sipunculans from this region (*Sipunculus, Phascolion*).

Distribution.—Red Sea and Gulf of Aden, 18–38 m.

Phascolosoma nigrescens
(Keferstein, 1865)

Phascolosoma nigrescens Keferstein, 1865a: 424, pl. 31, fig. 2, pl. 32, figs. 14–15; 1865b:198–199. (For references between 1865 and 1965 see Stephen & Edmonds, 1972:315.).—Murina, 1964:263–265; 1967:43–44; 1968:422; 1970:68; 1971: 83.—Stephen, 1965:82; 1967:46.—Cutler & Kirsteuer, 1968:353.—Edmonds, 1971:148–149.—Amor, 1975:22–23.—Haldar, 1975:59–60; 1976:4–5.—Saiz Salinas, 1988a:165; 1988b:12.

Phascolosoma (*Phascolosoma*) *nigrescens.*—Stephen & Edmonds, 1972:315–316.—Cutler, 1977a:152.—Cutler & Cutler, 1979a:984–985; 1979b:108.—Edmonds, 1980:59–61.—Murina, 1981:14; Cutler et al., 1984:296.—Saiz Salinas, 1984b:208–210.

Phascolosoma puntarenae Grübe & Öersted, 1858:13.—Diesing, 1859:761.—Keferstein, 1863:40.—Fisher, 1952:430–432 (not Wesenberg-Lund, 1959a:191–193).

Sipunculus (*Phymosomum*) *puntarenae.*—de Quatrefages, 1865:624.

Phascolosoma (*Phascolosoma*) *puntarenae.*—Stephen & Edmonds, 1972:319–320.

Phascolosoma varians Keferstein, 1865a: 424–426, pl. 32, fig. 22; 1865b:199–200; 1867:48–49.—de Quatrefages, 1865: 623.—Wesenberg-Lund, 1954a:7–8.—Rice, 1975:35–49.

Phymosoma varians.—Selenka et al., 1883: 69–70.—Shipley, 1890:1–24.—Augener, 1903:340.

Physcosoma varians.—Shipley, 1898:468–473.—Gerould, 1913:419–420.—Fischer, 1922a:16.—ten Broeke, 1925:5.—Satô, 1939:391–394.—Leroy, 1936:424.

Phascolosoma (*Phascolosoma*) *varians.*—Stephen & Edmonds, 1972:327–328.—Cutler, 1977a:153.—Rice & MacIntyre, 1979:314.

Phascolosoma agassizii Keferstein, 1867:46 (part).

Physcosoma agassizii var. *puntarenae.*—Selenka et al., 1883:79.

Phascolosoma planispinosum Baird, 1868: 93.—Rice & Stephen, 1970:65.

Phymosoma spengeli Sluiter, 1886:498–499, pl. 3, fig. 3, pl. 4, fig. 7; 1891:117.

Physcosoma spengeli.—Shipley, 1899a:156.

Phascolosoma (*Phascolosoma*) *spengeli.*—Stephen & Edmonds, 1972:325.

Phymosoma duplicigranulatum Sluiter,

1886:501–502; 1891:118.—Augener, 1903:307–308.

Physcosoma duplicigranulatum.—Shipley, 1899a:155.—Sluiter, 1902:13.

Phascolosoma (*Satonus*) *duplicigranulatum.*—Stephen & Edmonds, 1972:283–284.—Cutler & Cutler, 1983:185.

Phymosoma lacteum Sluiter, 1886:507–508, pl. 4, figs. 1, 10, 12; 1891:118.

Physcosoma lacteum.—Sluiter, 1902:13.—Shipley, 1899a:155; 1902:134.

Phascolosoma (*Phascolosoma*) *lacteum.*—Stephen & Edmonds, 1972:311–312.

Phymosoma diaphanes Sluiter, 1886:509–510, pl. 4, figs. 2, 11; 1891:118.

Phascolosoma (*Phascolosoma*) *diaphanes.*—Stephen & Edmonds, 1972:299–300.

Physcosoma extortum Sluiter, 1902:15–16, pl. 1, figs. 9–10.

Phascolosoma (*Phascolosoma*) *extortum.*—Stephen & Edmonds, 1972:303–304.

Physcosoma evisceratum Lanchester, 1905a: 31, pl. 1, fig. 1.—Stephen & Robertson, 1952:437.

Phascolosoma (*Phascolosoma*) *evisceratum.*—Stephen & Edmonds, 1972:301–303.

Physcosoma minutum ten Broeke, 1925:87–88, text figs. 6–7 (not *Phascolosoma minutum* Keferstein, 1863:40 = *Golfingia minuta* (Kef.)).

Phascolosoma (*Antillesoma*) *minutum.*—Stephen & Edmonds, 1972:281.—Cutler & Cutler, 1983:179.

Physcosoma horsti ten Broeke, 1925:89, text fig. 11.

Phascolosoma (*Antillesoma*) *horsti.*—Stephen & Edmonds, 1972:280.—Cutler & Cutler, 1983:178.

Material examined.—MNHU, type (6976) plus Keferstein's from Nordwachter (6998); UWMP, listed as type; RSME, Stephen's from Senegal (1960.48.10); Indian Ocean material (Cutler & Cutler 1979a); Japanese material (Cutler et al. 1984); our 1988 Caribbean material; *P. diaphanes,* ZMUA, type (V.Si. 101); *P. duplicigranulatum,* BMNH, ZMUA (V.Si. 102), co-types; UZMC, Shipley's 1899a material; *P. evisceratum,* BMNH, type (1924.3.1.163); RSME, Stephen & Robertson's 1952 material (1958.23.66 & 67); *P. extortum,* ZMUA, type (V.Si. 128/6); *P. horsti,* ZMUA, type (V.Si. 108); *P. lacteum,* ZMUA, type (V.Si. 75); *P. minutum,* ZMUA, type (V.Si. 117); *P. puntarenae,* MNHU, type (1023); UZMK, from Grübe's original collections; USNM, identified by W. K. Fisher from Bay of Panama (21463) and from Mexico (24732); *P. spengeli,* ZMUA, type (V.Si. 128); UZMC, Shipley's material; *P. varians,* MCZH, type material (423, 428, 1604).

Discussion.—The character that most easily distinguishes this species is the clear streak in the hook that has an expansion near the mid-point of both the vertical and the horizontal portion (Fig. 6E). The angle of the point is usually less (as low as 65°) but may be slightly more than 90°, and within one deme the secondary tooth may be large or absent, but is usually small. Hooks are arranged in over 100 mostly incomplete rings and measure 35–90 μm tall. The trunk and the uniform dome-shaped papillae are commonly brown. The introvert is longer than the trunk and may have pigmented bands. The contractile vessel may be enlarged with vesicular swellings but not true villi.

As earlier authors, including Edmonds (1980:60) have pointed out, "It is difficult to find a satisfactory character which can be used to distinguish *P. nigrescens* from *P. puntarenae* Grübe. If they are the same, *P. puntarenae* Grübe, 1859 [sic] has priority." We agree with this but have been reluctant to submerge the more familiar name. The type material of *P. puntarenae* is in poor condition, lacks the introvert, and is of no value as a voucher specimen. In Copenhagen there are two specimens that appear to be part of Grübe's original material. These had never been dissected nor had any hooks been removed. Our examination showed them to be *Nephasoma* and probably *N. pellucidum.* So while there is a very poor foundation for the name *P. puntarenae, P. nigrescens* is represented by the type plus 13 other bottles of worms in Berlin. The single *P. nigrescens* in Poland, labeled as type, is completely dried out and had not been dissected. The older name has been used only twice in the past 125 years. Fisher (1952) used it for five worms from Panama and Mexico but commented on its similarity to *P. nigrescens,* the difference stated as the bend in the hook. Wesenberg-Lund (1959a) used this name for four worms collected off the Cape Verde Islands. Her comments about the hooks (distinct triangle, absence of swelling on clear streak in many), nephridia (longer than the trunk), and the cool water habitat cast doubt on her record. Saiz Salinas (pers. comm.), having looked at her material, concludes that it is *P. thomense* that we consider conspecific with *P. perlucens.*

The name *P. puntarenae,* based on a shaky foundation, has been avoided by most biologists for over a century, while *P. nigrescens* has been used over 60 times during that same period. Therefore, while we consider these taxa to be conspecific, we shall continue the past practice of using the familiar junior synonym to preserve nomenclatural stability and avoid confusion.

We reaffirm Cutler & Cutler's (1983) conclusion that three names, previously in other subgenera, are conspecific with this species: *P. duplicigranulatum, P. horsti,* and *P. minutum.*

The name *P. varians* (Keferstein, 1865a) has been used by several biologists for Caribbean worms (3 from the Pacific) with hooks having the internal structure of *P. nigrescens,* but with the tip being more bent. Most of these hooks also have a blunt secondary tooth on the concave border. Shipley (1890) made a detailed micro and macro anatomical study of *P. varians.* Many features he studied are common to all *Phascolosoma,* and they cannot be used to differentiate *P. varians* from *P. nigrescens.* We could find no consistent differences between the two species. When one compares hooks from different populations, a continuum of curvature and secondary tooth development can be observed (Fig. 8). One possible hypothesis is that hook morphology is determined by more than one pair of genes and that allelic frequencies vary from place to place. The alleles for sharp angle and large secondary tooth occur at a high frequency in the Caribbean and a low frequency in the Indo-West Pacific. It is our conclusion that the species are conspecific and that *P. varians* is the junior name because it was described later on the page.

The reason Sluiter (1886) named one worm *P. diaphanes* seems to be the peculiar arrangement of the retractor muscles. The two ventral muscles are partially split into several strands (not uncommon in this genus), the right dorsal retractor is absent, and the left dorsal retractor has its origin atypically close to the ventral nerve cord. Such fusion and splitting of retractor muscles has been observed elsewhere (Gibbs 1973). This species (individual) with anomalous retractors is a junior synonym of *P. nigrescens.*

In the same paper Sluiter (1886) erected *P. lacteum* on the basis of one worm, with no differential diagnosis. The distal hooks are up to 90 μm tall with long points like some *P. nigrescens* from Madagascar (Fig. 8). Sluiter evidently measured the smaller (55 μm) proximal hooks. In all ways this worm fits the *P. nigrescens* morph, and we find no reason to retain it as a separate taxon.

When Sluiter (1886) erected *P. spengeli,* on the basis of two worms, he offered no differential diagnosis so it is not clear how he thought it differed from *P. nigrescens.* He counted only 22 rings of hooks, and we presume he found differences in hook and papillae morphology. Part of the introvert of the dissected worm is missing and some rings have only a few remaining hooks. A large part of each hook is hidden by folds in the

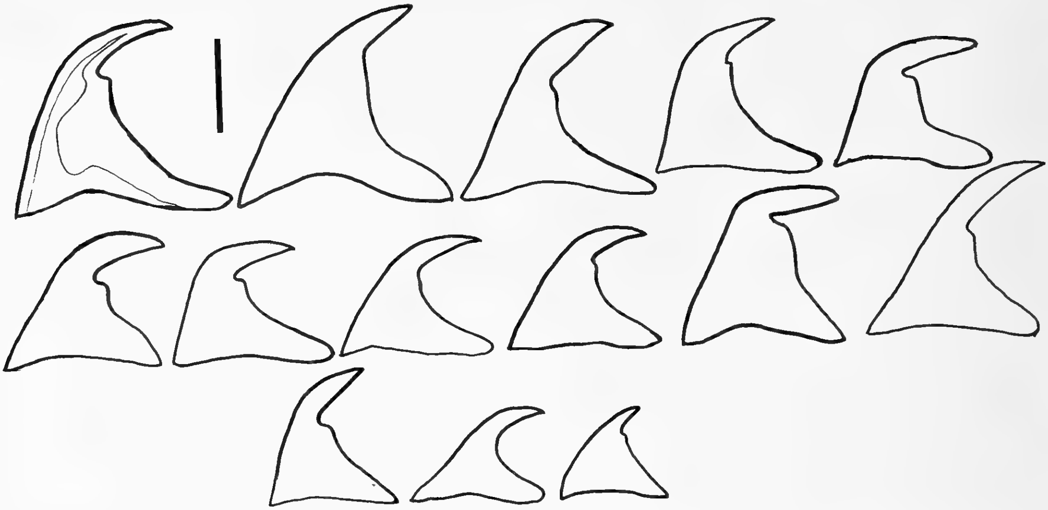


Fig. 8. Composite drawing of *P. nigrescens* hooks from different populations (internal structure same for all but only shown in first): Row one from single Japanese deme, last three from a single worm. Row two from left to right: Keferstein's type (first two), *P. puntarenae* of Fisher, type of *P. extortum* (same as Cutlers' Hawaii *P. nigrescens),* type of *P. varians,* type of *P. lacteum* (same as Cutler's Madagascar *P. nigrescens*). Row 3; types of *P. horsti, P. spengeli, P. minutum.* (Scale line = 50 μm.)

tissue of the retracted introvert and consequently easily overlooked. The second worm has at least 50 rings of hooks. The papillae in the mid-trunk are smaller and less dense than in most worms, but overall these animals fall within the range of variation described above and *P. spengeli* becomes a junior synonym. Of the five worms Shipley (1899a) thus described, two are a species of *Themiste,* and the remaining three are *P. nigrescens.*

The putative differences used by Sluiter (1902) to differentiate *P. extortum* from *P. nigrescens* were the loosely wound gut coil and the hook morphology. Sluiter's figure of the hook matches that of *P. nigrescens* very well. The looseness of the gut coil in this single worm is not significant, and there is no reason to retain *P. extortum* as a valid specific name.

Lanchester (1905a) named *P. evisceratum* on the basis of hooks and papillae of one specimen that consisted of the epidermis only. The hook that is illustrated is clearly one from the most posterior part of the introvert. Stephen & Robertson (1952) used this name for two complete worms but without removing any hooks. Our examination of their material convinced us that it is *P. nigrescens.*

Distribution.—The most wide spread, circum-tropical species in the genus; generally between 30°N and S in shallow water of all oceans.

Phascolosoma noduliferum
Stimpson, 1855

Phascolosoma noduliferum Stimpson, 1855: 390.—Keferstein, 1865a:423; 1865b: 198.—Baird, 1868:92.—Edmonds, 1956: 286–288; 1966:176.

Phascolosoma (*Phascolosoma*) *noduliferum.*—Stephen & Edmonds, 1972:316–317.—Cutler, 1977a:152.—Murina, 1978: 121.—Edmonds, 1980:62.

Siphunculus tuberculatus Gray, 1828:8 (part).—Rice & Stephen, 1970:52–53.

Sipunculus (*Phymosomum*) *nodulosus* de Quatrefages, 1865:621–622.

Sipunculus (*Phymosomum*) *javanensis* de Quatrefages, 1865:622 (part); Stephen &

Edmonds, 1972:339 (incertae sedis).—Saiz Salinas, 1984b:144–148.

Phascolosoma javenense.—Baird, 1968:94 (part).

Sipunculus (*Phymosomum*) *noduliferus* de Quatrefages, 1865:624.

Phascolosoma grayi Baird, 1868:88.—Rice & Stephen, 1970:52.

Phymosoma japonicum Selenka et al., 1883: 76–78 (part).

Physcosoma japonicum.—Stephen, 1948: 220.

Material examined.—MNHU, specimen listed as type but appears to be one of Keferstein's worms; S. Edmonds' specimen from Victoria, Australia.

Discussion.—The similarities to *P. agassizii* are marked, but the differences seem real and lie in the papillae and hooks. The introvert lacks pigment bands, and the papillae are of uniform size, more crowded posteriorly. The uniqueness of the papillae lies in the arrangement of platelets, i.e., around the central pore there is a narrow ring of closely set units that abruptly become much more dispersed, but do not extend onto the interpapillae skin. In *P. agassizii* the platelets are more uniformly distributed over the papillae surface. Illustrations of the hooks in the literature appear to be of the posterior hooks (from incomplete rings or scattered). The more anterior hooks are much more like *P. agassizii* (Fig. 7D, E). In general, these hooks have a more narrow clear streak, lack a triangle, are 60–90 μm tall, usually in more than 50 rings, and have no secondary tooth.

Distribution.—Southern Australia and Tasmania plus deep water records from Philippines, New Guinea, and New Zealand (Cutler 1977a).

Phascolosoma pacificum Keferstein, 1866

Phascolosoma pacificum Keferstein, 1866: 8–9; 1867:49–50.—Baird, 1868:96.—Edmonds, 1956:291–292; 1971:146–148.—Wesenberg-Lund, 1957b:6–7; 1959c:62–63.—Stephen, 1967:46.—Haldar, 1976:5–6.—Cutler et al., 1984:296–297.

Phymosoma pacificum.—Selenka et al., 1883:63–65.—Fischer, 1895:12; 1896: 337.—Augener, 1903:310–311.

Physcosoma pacificum.—Shipley, 1898:470; 1899a:156; 1902:134.—Sluiter, 1902: 11.—Ikeda, 1904:25–26; 1905:169.—Fischer, 1914a:6; 1922b:8; 1926:108.—Leroy, 1942:23.—Monro, 1931:34.—Satô, 1935:310; 1939:390–391.—Stephen & Robertson, 1952:436.—Stephen, 1952:182.

Phascolosoma (*Phascolosoma*) *pacificum.*—Stephen & Edmonds, 1972:317–318.—Cutler & Cutler, 1979a:965–986.—Edmonds, 1980:62–63.—Saiz Salinas, 1984b:210–211.

Sipunculus (*Phymosomum*) *javanensis* de Quatrefages, 1865:622 (part).—Stephen & Edmonds, 1972:339 (incertae sedis).—Saiz Salinas, 1984b:148–155.

Phascolosoma javanense.—Baird, 1868:94.

Phascolosoma asperum Grübe, 1868:642–643.

Phymosoma asperum.—Selenka et al., 1883: 61.

Material examined.—MNHU, labeled type (6969) but only contains eggs; seven additional bottles in this collection, at least two named by Keferstein; MCZH, dried out but appear to be part of the original collection and co-types (500).

Discussion.—The uniformly distributed, tall, cone-shaped papillae give this species a rough, sand-paper texture. It is one of the largest species, commonly being up to 80 μm (occasionally 125 mm), and is uniformly colored. The hooks resemble those of *P. perlucens,* have a broad base, are 70–125 mm tall, arranged in 80–200 rings, the secondary tooth is hump-like, and an irregular clear streak with a separate triangle is present (Fig. 6A). The nephridia are long (range from 75–125% of the trunk length) and attached for most of their length. Up to 40 anastomosing longitudinal muscle bands have been recorded.

Distribution.—From the Red Sea, throughout the Indian Ocean, and the western Pacific Ocean from southern Japan to northern Australia including Indonesia and numerous tropical islands at depths less than 3 m.

Phascolosoma perlucens Baird, 1868

Phascolosoma perlucens Baird, 1868:90–91, pl. 10, fig. 2.—Rice & Stephen, 1970:63–64.—Rice, 1975:35–48.—Rice & MacIntyre, 1979:314.—Edmonds, 1980:63–64.—Cutler et al., 1984:297.

Phascolosoma (*Phascolosoma*) *perlucens.*—Stephen & Edmonds, 1972:318–319.—Cutler, 1977a:151.—Cutler & Cutler, 1979a:987.

Sipunculus (*Phascolosomum*) *vermiculus* de Quatrefages, 1865:621.

Phascolosoma vermiculum.—Baird, 1868:85.

Sipunculus vermiculus.—Stephen & Edmonds, 1972:339 (incertae sedis).

Phascolosoma (*Phascolosoma*) *vermiculus.*—Saiz Salinas, 1984b:90–97, 203.

Phymosoma dentigerum Selenka et al., 1883:67–68.—Sluiter, 1886:500.

Physcosoma dentigerum.—Sluiter, 1891:118; 1902:11–12.—Shipley, 1898:474; 1902:134.—Augener, 1903:304–305.—Fischer, 1922a:10–11; 1922b:7.—Monro, 1931:34.

Phascolosoma dentigerum.—Fisher, 1952:432–434.—Murina, 1964:262.—Cutler, 1965:58.—Cutler & Kirsteuer, 1968:354.—Murina, 1972:306–307.

Physcosoma thomense Augener, 1903:343–344, text fig. 19.

Phascolosoma thomense.—Murina, 1967:44–45; 1968:422.

Phascolosoma (*Phascolosoma*) *thomense.*—Stephen & Edmonds, 1972:327.

Aspidosiphon insularis Lanchester, 1905b:40, pl. 2, fig. 4.—Gibbs & Cutler, 1987:56.

Paraspidosiphon insularis.—Stephen & Edmonds, 1972:247.

Physcosoma microdentigerum ten Broeke, 1925:88–89, text figs. 8–10.—Stephen, 1960:517–518.

Phascolosoma (*Antillesoma*) *microdentigerum.*—Stephen & Edmonds, 1972:280–281.—Cutler & Cutler, 1983:178.

Physcosoma scolops.—ten Broeke, 1925:86.

Phascolosoma puntarenae.—Wesenberg-Lund, 1959a:191–193.

Phascolosoma spinosum Johnson, 1971; 601–602, pl. 2, figs. 1–9.

Material examined.—BMNH, 3 type specimens; our 1988 Caribbean collections; *P. dentigerum,* MNHU, 2 type specimens (976); *P. microdentigerum,* ZMUA, type (V.Si. 111) plus additional specimens; *A. insularis,* BMNH, type (1924.3.1.80); *P. thomense,* MNHU, type (7010); specimen from Cuba identified by Murina.

Discussion.—In 1970 Rice & Stephen redescribed Baird's material and reduced the more familiar *P. dentigerum* to a junior synonym. The assertion that this is the most common rock boring sipunculan in the Caribbean (Rice & MacIntyre 1979) is confirmed by our recent observations. The reddish, conical, posteriorly directed, pre-anal papillae on the dorsal base of the introvert characterize this species. The hooks are 30–60 μm tall, in 15–25 rings (8–10 in a 5 mm worm), and have a large rounded secondary tooth. The internal triangle is separate from the clear streak similar to that in *P. scolops.* The trunk is commonly up to 35 mm long (a few at 45–50 mm), and the introvert is not longer than the trunk, usually with patches of reddish pigment on the dorsal surface.

In 1984b Saiz Salinas reintroduced the name *P. vermiculus* de Quatrefages, 1865. He considered this a senior synonym of *P. thomense.* While we do not disagree with this, we conclude that both names are synonymous with *P. perlucens.* While strict application of the ICZN rules would allow using this older name (not used for over 120 years) we will continue applying the more familiar name to avoid confusion and preserve nomenclatural stability.

The name proposed by Augener (1903) for two worms from St. Thomas, *P. thomense,* was used twice by Murina (1967, 1968) for some Cuban material. Neither author used the name *P. perlucens* and our analysis of their specimens, especially the hook morphology, makes it clear that these two names are conspecific.

In 1983 Cutler & Cutler examined ten Broeke's *P. microdentigerum* and concluded that it is conspecific with *P. perlucens.* We reaffirm that decision. The contractile vessel exhibits only vesicular swellings, not true villi. The only record of this taxon from the eastern Atlantic is Stephen (1960) with no description or illustrations. Many specimens of *P. stephensoni* (a species also having enlarged, reddish, pre-anal papillae) have been collected there. The latter may be what Stephen saw, but we cannot confirm this since his specimens cannot be located.

Gibbs & Cutler (1987) observed that *Aspidosiphon insularis* was a *Phascolosoma* species and probably *P. perlucens.* This information was repeated in Cutler & Cutler (1989), and is reaffirmed here.

Haldar (1988) compared his Indian material to Johnson's (1971) description of *P. spinosum* and concluded that they were conspecific, and we agree.

Distribution.—Common in the Caribbean (Venezuela to southern Florida), and the western Pacific (Queensland to central Japan). Also recorded from several Indian Ocean locations and in the eastern Pacific off Panama and northern Mexico. The two eastern Atlantic records complete this circum-tropical but patchy distribution.

Phascolosoma saprophagicum Gibbs, 1987

Phascolosoma saprophagicum Gibbs, 1987: 135–137, fig. 1.

Material examined.—Several worms identified by P. Gibbs from type collection.

Discussion.—The single known population was collected from a decaying whale skull. The worms have small (20–25 μm) bluntly rounded hooks with a simple narrow internal clear streak (Fig. 6H) and small inconspicuous papillae. The nephridiopores are anterior to the anus by up to 10% of the trunk length, and the ventral retractor muscles originate in the posterior quarter of the trunk.

Distribution.—Chatham Island, New Zealand, 880 m.

Phascolosoma scolops
(Selenka, de Man & Bülow, 1883)

Phymosoma scolops Selenka et al., 1883: 75–76, pl. 2, fig. 17, pl. 10, figs. 138–144. (For synonymy between 1883 and 1965 see Stephen & Edmonds, 1972:321 and Saiz Salinas, 1984b:206–208.) (Not *Physcosoma scolops* ten Broeke, 1925:86.)

Phascolosoma scolops.—Stephen, 1965:83; 1966:148; 1967:46–47.—Cutler, 1965: 57.—Stephen & Cutler, 1969:116.—Murina, 1971:83.—Haldar, 1975:61; 1976: 6–7.—Edmonds, 1980:55–60.

Phascolosoma (*Phascolosoma*) *scolops.*—Cutler, 1977a:152–153.—Murina, 1978: 121.—Cutler & Cutler, 1979a:987–988; 1979b:108–109.—Cutler et al., 1984:298–299.—Saiz Salinas, 1984b:206–208; 1986: 62–63.

Phascolosoma (*Phascolosoma*) *scolops scolops.*—Stephen & Edmonds, 1972:321–323.

Phymosoma scolops var. *mossambiciense* Selenka et al., 1883:76, pl. 10, fig. 144.

Physcosoma scolops var. *mossambiciense.*—Sluiter, 1898:444.—Leroy, 1936: 424.—Stephen, 1942:249.—Edmonds, 1956:285 (not Augener, 1903:339).

Phascolosoma (*Phascolosoma*) *scolops mossambiciense.*—Stephen & Edmonds, 1972:324.

Phascolosoma carneum Rüppell & Leuckart, 1828:7.—Diesing, 1859:764.—Baird, 1868:85.—Stephen & Edmonds, 1972: 321.—Saiz Salinas, 1989:210–211.

Phascolosoma longicolle.—Grübe, 1840:47.

Phymosoma psaron Sluiter, 1886:505; 1891: 118.

Physcosoma psaron.—Sluiter, 1902:13.

Phascolosoma (*Phascolosoma*) *psaron.*—Stephen & Edmonds, 1972:319.

Physcosoma spongicola Sluiter, 1902:16–17, pl. 1, figs. 11–12.

Phascolosoma (*Phascolosoma*) *spongicolum.*—Stephen & Edmonds, 1972:325–326.

Physcosoma scolops var. *adenticulatum* Hérubel, 1904b:563.

Phascolosoma (*Phascolosoma*) *scolops adenticulatum.*—Stephen & Edmonds, 1972:323–324.

Phymosoma nahaense Ikeda, 1904:29–31, figs. 8, 59–62.

Phascolosoma (*Rueppellisoma*) *nahaense.*—Stephen & Edmonds, 1972:274.—Cutler & Cutler, 1981:85–86; 1983:180.

Physcosoma socium Lanchester, 1905b:37–38, pl. 2, fig. 1 (not *Phascolosoma socium* Lanchester, 1908:1 = *Golfingia socia* (Lanchester) = *Golfingia margaritacea* (Sars)).

Phascolosoma (*Phascolosoma*) *socium.*—Stephen & Edmonds, 1972:324–325.

Physcosoma agassizii.—Fischer, 1919:280; 1922a:7–9 (part).

Phascolosoma rottnesti Edmonds, 1956:282–284, text figs. 1–4.

Phascolosoma (*Phascolosoma*) *rottnesti.*—Stephen & Edmonds, 1972:320–321.—Edmonds, 1980:64–65.

Phascolosoma dunwichi Edmonds, 1956:292–293, text figs. 12–13; 1980:65–66.

Phascolosoma (*Phascolosoma*) *dunwichi.*—Stephen & Edmonds, 1972:300–301.

Phascolosoma riukiuensis Murina, 1975:55–57, fig. 2.

Phascolosoma (*Antillesoma*) *pelmum.*—Cutler, 1977a:150.

Material examined.—MNHU, Selenka's material (960, 977, 978); ZMUA, ten Broeke's 1925 material (V.Si. 119); our Indian, Pacific, Atlantic Ocean material (Cutler 1965, 1977a, Cutler & Cutler 1979a, 1979b); *P. scolops mossambiciense,* MNHU, type material (956, 958); *P. scolops tasmaniense,* ZMUH, type (V5407); *P. psaron,* ZMUA (V.Si. 83); *P. rottnesti,* AMSS, type (W3598); *P. socium,* BMNH, type; *P. spongicolum,* ZMUA, type (V.Si. 128–7).

Discussion.—These are usually pale worms with reddish-brown mammiform to dome-shaped pre-anal papillae. While the mid-trunk papillae are small and widely scattered, their size, color, and density increases towards the posterior end. The introvert is commonly shorter than the trunk and exhibits pigmented bands. The hooks are arrayed in less than 25 rings, are 20–60 μm tall, and if a secondary tooth is present it is small (Fig. 7F). The clear streak is separate from the distinct triangle.

Apart from hook morphology there are two minor internal differences from the similar *P. albolineatum*: the rectal caecum is present in more than half the worms (vs. 10%), and the retractor origins are closer to the posterior end of the trunk by about 10% (ventral retractors around 60% vs. 50%).

Previous action by Cutler & Cutler (1981) reduced *P. nahaense* to a junior synonym of *P. scolops,* and we reaffirm that decision.

The two subspecies in Stephen & Edmonds (1972) have characters well within the range we observe in the nominate form and are here considered to have no distinct status. In 1980 Edmonds reduced his *P. dunwichi* to a junior synonym of *P. scolops* and we concur.

When Sluiter (1886) described *P. psaron* he asserted that it lacked hooks and had only fine spines. Our examination revealed rows of normal hooks and papillae of the *P. scolops* type. Thus we place this name in synonymy.

The single 25 mm worm Sluiter (1902) described as *P. spongicolum* had unusually puffy, thickened skin, but over time this must have changed because it now appears rather normal. The papillae are mammiform to cone-shaped and while large, not outside the *P. scolops* range. Figure 33Q in Stephen & Edmonds (1972), presented as

Sluiter's *P. spongicolum* hook, is really Sluiter's fig. 14 of an *Aspidosiphon cylindricus* conical hook. Sluiter did illustrate these hooks as fig. 11, which do not show a separate clear steak and triangle. Our observations show the hooks to have the *P. scolops* attributes, and these are considered conspecific taxa.

Lanchester (1905b) described *P. socium* as lacking hooks. Of the three specimens, two lack introverts while the third has rings of *P. scolops* hooks. He compared this to *P. psaron,* but we can find nothing to distinguish this from *P. scolops.*

Examination of *P. rottnesti* material convinced us that Edmonds' (1956) distinctions (papillae platelets and presence of caecum) overlooks the variation within *P. scolops.* While some authors contend that *P. scolops* lacks a caecum, we observed one in 57% of those we examined.

Another hookless worm was given the name *P. riukiuensis* by Murina (1975). The distal end of the introvert is hookless, but it is also white and gives the impression of a regenerating body part. On the basis of other attributes, we conclude that this is an anomalous individual *P. scolops* and not a distinct species.

Saiz Salinas (1989) reexamined *P. carneum* that Stephen & Edmonds (1972) placed in incertae sedis. He concluded that it is conspecific with *P. scolops* and is the most senior available name. However, because the name has been unused for over 120 years, we would again appeal to the logic of ICZN article 79b to preserve nomenclatural stability and conserve the very often used junior synonym in this case.

Distribution.—Common throughout the Indo-West Pacific area including the Red Sea, up to northern Japan, down to northern Australia, and out to Hawaii. The several records from west Africa (Gulf of Guinea and south) cannot all be verified, but we suspect that some of these are *P. stephensoni* as well as the one Bermuda record (Rice 1986). The single Caribbean worm (ten Broeke 1925) is *P. perlucens.*

Phascolosoma stephensoni
(Stephen, 1942)

Physcosoma stephensoni Stephen, 1942:250, pl. 11, figs. 3–5.

Phascolosoma stephensoni.—Wesenberg-Lund, 1963:121–126.

Phascolosoma (*Phascolosoma*) *stephensoni.*—Stephen & Edmonds, 1972:326–327.—Cutler, 1977a:153.—Edmonds, 1980:67–68; 1987:197.—Saiz Salinas, 1982:197–199; 1984b:205–206; 1986:63–70; 1988a:166.—Haldar, 1988:127–130.

Phascolosoma laeve.—Keferstein, 1863:38–39 (part).

Sipunculus (*Phymosomum*) *spinicauda* de Quatrefages, 1865:621.

Phascolosoma spinicauda, Baird, 1868:93.

Physcosoma lanzarotae Harms, 1921:307 (part).

Physcosoma agassizii.—Fischer, 1922a:7 (part).

Physcosoma scolops.—Monro, 1931:35.

Phascolosoma heronis Edmonds, 1956:293–295, text fig. 14.

Phascolosoma (*Phascolosoma*) *heronis.*—Stephen & Edmonds, 1972:309.

Phascolosoma granulatum.—Wesenberg-Lund, 1959a:193–194 (part); Cutler & Cutler, 1979b:108.

Material examined.—RSME, type material (1958:23:17); recent east Atlantic material (Saiz Salinas 1982 and as *P. granulatum,* Cutler & Cutler 1987a); *P. laeve,* MNHU, Keferstein's 1863 worms (6991).

Discussion.—The large smooth cone-like pre-anal and posterior papillae distinguish *P. stephensoni* from the similar *P. granulatum* that shares part of its range. When viewed under the microscope these papillae show none of the platelets typical of this genus. The smaller papillae in the mid-trunk exhibit only very small, uniform size granules, not platelets. The introvert has irregular pigmented bands and over 40 rings of hooks, 60–110 μm tall. There may be only 10–20 complete rings, the remainder represented by dorsal patches only. Internally, the clear streak is smooth, the triangular space is clear, and posterior to the clear streak is a distinct crescentic clear area (Fig. 1). This figure shows that the clear areas are hollow spaces within a more solid matrix. The shape of the hooks varies from distal to proximal, the latter are more scattered, blunter, smaller (30–45 μm), more triangular, and the crescentic clear area is not often present. In most hooks the secondary tooth is present and distinct.

Edmonds (1980) synonymized *P. heronis* and Fischer's (1922a) Port Jackson *P. agassizii* under *P. stephensoni,* and we concur. For many years *P. laeve* Keferstein, and *P. spinicauda* de Quatrefages, have been considered synonyms of *P. granulatum.* Keferstein's (1863) material is a mixture, some from Sicily is *P. stephensoni* while another portion from the Adriatic is *P. granulatum.* Saiz Salinas has reexamined de Quatrefages single worm and transfers it here, and we concur. As noted above, other biologists have confused these two species (see also Saiz Salinas 1986). An example of this is Harms (1921). Based on his figures *P. lanzarotae* is clearly a mixture of these.

Distribution.—Mediterranean Sea (Sicily and southern Spain), east Atlantic (Azores, Canaries, Gulf of Guinea to South Africa), Indian Ocean (Durban, Mozambique, southwest India), and western Pacific (northern Australia, Solomon Islands, and Hawaii).

Phascolosoma turnerae Rice, 1985

Phascolosoma turnerae Rice, 1985:54–60, figs. 1–4.

Phascolosoma (*Phascolosoma*) *kapalum* Edmonds, 1985:43–44, 2 figs.

Material examined.—USNM, type (96687). Six worms from Gyre cruise 87-G-2, sta. EJ-87-127, in cluster of vestimentiferans, 600 m, Bush Hill, off Louisiana, two deposited at USNM (118769).

Discussion.—The sharply bent hooks (45–80 μm tall) have up to 10 long, posterior, basal processes/rootlets (Rice 1985, fig. 2). In light microscope preparations these appear as warts (Fig. 6C). The anterior base is drawn out into a thin prong-like extension. The clear streak is close to the anterior side and often narrows towards the base. The papillae are large and mammillate with "prominent apical protuberances."

The Bush Hill material differed from Rice's in minor ways: the papillae in the middle of the trunk are almost as large as those at the extremities, and the nephridia are slightly anterior to the anus (not at the same level) and only 50% attached vs. 75%. The introvert is 1.7 (vs. up to 1.4) times the trunk length in a 19 mm worm with an extended introvert.

Edmonds' (1985) *P. kapalum* while geographically separated is also from deep water and the putative differences can be explained by the larger size (hook size) and retracted introverts (shorter than trunk). Edmonds (pers. comm.), after looking at specimens of *P. turnerae,* agrees with this synonymy.

Distribution.—Two of the records are from the Gulf of Mexico; off Florida and Alabama at 366–1184 m in wood, and off Louisiana at 600 m near a cold water seep. In both cases these were in close association with Pogonophora. The third record, from 710 m off New South Wales does not include comparable ecological data.

Zoogeographical Summary

Four of the 16 *Phascolosoma* species appear to have very restricted ranges, three in specialized habitats: *P. meteori* from the Red and Arabian Seas (warm, high salinity, low oxygen tension), *P. turnerae* from the Gulf of Mexico and off Australia (deep cold water in wood or near cold-water seeps), and *P. saprophagicum* from New Zealand (deep cold water from rotting whale skull). *Phascolosoma maculatum* is from more typical habitat off Indonesia.

The most striking feature of the remaining 12 species is that 11 of these occur in the waters between the Indian and Pacific Oceans (Australia/Indonesia/Philippines). Adding the two local endemic species and *P. turnerae* means that 88% live here. This species richness is unparalleled by other sipunculan genera. Eight of these (50% of species in the genus) are widespread throughout the Indo-West Pacific (IWP). Only *P. granulatum* (from cooler waters of the northeastern Atlantic Ocean and the Mediterranean Sea) and *P. meteori* are not found in this part of the world.

A second noteworthy feature is that only three species live in the Caribbean basin (the circum-tropical *P. perlucens,* and *P. nigrescens,* plus the restricted *P. turnerae*). This situation contrasts sharply with that found in *Aspidosiphon,* the other burrowers in hard substrata, and this suggests a different evolutionary history.

In the eastern Pacific one finds the two shallow water Caribbean species just mentioned, plus *P. agassizii* (cool water), and *P. scolops* (warm water); these four also are found throughout the IWP. *Phascolosoma stephensoni* extends eastward only as far as Hawaii, but also westward to the Mediterranean and the eastern Atlantic. Four species do not extend outside the IWP (*P. albolineatum, P. arcuatum, P. glabrum,* and *P. pacificum*), while *P. noduliferum* and *P. annulatum* are restricted to the boundary between the Indian and western Pacific Oceans.

Acknowledgments

An open exchange of information, ideas, and specimens with J. Saiz Salinas, Bilbao, were most important to several stages of this work, especially in resolving the *P. granulatum/stephensoni* complex. The continued encouragement and exchange of specimens with S. J. Edmonds, Adelaide, has helped us complete this work. We are indebted to B. P. Haldar, Calcutta, for the opportunity to read an unpublished manuscript. The field work in Curaçao was dependent on the cooperation of W. Bakhuis, Carmabi Foundation. In Cumaná J. Perez at the Universidad de Oriente assisted us in many ways. The visit to the Fundación Cientifica Los Roques was made possible by the cooperation of B. Alverez and her associates. Lynn Cutler, Mountain View, and J. Silverstein, Seattle, provided invaluable assistance in the field and lab, the former also provided the transmission electron micrographs. Correct spelling of species' names was kindly verified by G. Steyskal, Washington, and K. Bart, Clinton, New York, assisted with the scanning electron microscope. Partial financial support was provided by the National Science Foundation (BSR 86-15315) and part by our respective institutions.

The cooperation of the following persons and institutions in the loan of reference material and/or providing access to their collections was essential to the completion of this project and greatly appreciated: P. Berents (AMSS); E. Easton (BMNH); H. Levi (MCZH); J-L. Justine, (MNHN); G. Hartwich (MNHU); R. Olerod (NHRS); S. Chambers (RSME); M. Rice (USNM); J. Wiktor (UWMP); R. C. Preece (UZMC); J. Kirkegaard (UZMK); A. Pierrot-Bults (ZMUA); M. Dzwillo (ZMUH); University of Tokyo (ZMUT).

Literature Cited

Amor, A. 1975. Notas sobre Sipuncula de la Argentina, Brasil y Peru.—Physis 34(88):113–120.

Augener, H. 1903. Beiträge zur Kenntnis der Gephyreen nach Untersuchung der im Göttinger zoologischen Museum befindlichen Sipunculiden und Echiuriden.—Archiv für Naturgeschichte 69:297–371.

Baird, W. 1868. Monograph on the species of worms belonging to the subclass Gephyreae.—Proceedings of the Zoological Society of London 1868: 77–114.

Benham, W. B. 1903. The sipunculids of New Zealand.—Transactions of the Royal Society of New Zealand 36:172–189.

Chamberlin, R. V. 1920a. Notes on the sipunculids of Laguna Beach.—Journal of Entomology and Zoology 12:30–31.

———. 1920b. Gephyrea.—Report of the Canadian Arctic Expedition 1913–18 9(D):3–7.

Chen, Y., & C. C. Yeh. 1958. Notes on some gephyrea of China with descriptions of four new species.—Acta Zoologica Sinica 10:265–278.

Collin, A. 1892. Gephyreen gesammelt von Herrn Stabsarzt Dr. Sander auf der Reise S.M.S. "Prinz Adalbert."—Archiv für Naturgeschichte 58(1): 177–182.

Cutler, E. B. 1965. Sipunculids of Madagascar.—Extrait des cahiers ORSTOM-Océanographie 3(4): 51–63.

———. 1977a. The bathyal and abyssal Sipuncula.—Galathea Report 14:135–156.

———. 1977b. Shallow water sipunculans collected by the Galathea Expedition (Sipuncula).—Steenstrupia 4:151–155.

———. 1979. A reconsideration of the *Golfingia* subgenera *Fisherana* Stephen, *Mitosiphon* Fisher, and *Apionsoma* Sluiter (Sipuncula).—Zoological Journal of the Linnean Society 65:367–384.

———. 1986. The family Sipunculidae (Sipuncula): body wall structure and phylogenetic relationships.—Bulletin of Marine Science 38(3):488–497.

———, & N. J. Cutler. 1979a. Madagascar and Indian Ocean Sipuncula.—Bulletin du Muséum National d'Histoire Naturelle, Paris 4e(1):941–990.

———, & ———. 1979b. Campagnes de la Calypso au large des côtes Atlantiques Africaines (1956 et 1959) et Sud-Américaines (1960–1961). 23. Sipuncula.—Campagnes de la Calypso XI: 103–109.

———, & ———. 1981. A reconsideration of Sipuncula named by I. Ikeda and H. Sâto.—Publications of the Seto Marine Biological Laboratory 26:51–93.

———, & ———. 1982. A revision of the genus *Siphonosoma* (Sipuncula).—Proceedings of the Biological Society of Washington 95(4):748–762.

———, & ———. 1983. An examination of the *Phascolosoma* subgenera *Antillesoma, Rueppellisoma,* and *Satonus* (Sipuncula).—Zoological Journal of the Linnean Society 77:175–187.

———, & ———. 1985a. A revision of the genera *Phascolion* Theél and *Onchnesoma* Koren and Danielssen (Sipuncula).—Proceedings of the Biological Society of Washington 98(4):809–850.

———, & ———. 1985b. A revision of the genera *Sipunculus* and *Xenosiphon* (Sipuncula).—Zoological Journal of the Linnean Society 85:219–246.

———, & ———. 1987a. A revision of the genus *Golfingia* (Sipuncula: Golfingiidae).—Proceedings of the Biological Society of Washington 100(4):735–761.

———, & ———. 1987b. Deep-water Sipuncula from the eastern Atlantic Ocean.—Sarsia 72:71–89.

———, & ———. 1988. A revision of the genus *Themiste* (Sipuncula).—Proceedings of the Biological Society of Washington 101(4):741–766.

———, & ———. 1989. A revision of the genus *Aspidosiphon* (Sipuncula).—Proceedings of the Biological Society of Washington 102:826–865.

———, ———, & P. E. Gibbs. 1983. A reconsideration of the *Golfingia* subgenera *Golfingiella* and *Siphonoides* (Sipuncula).—Proceedings of the Biological Society of Washington 96(4):669–694.

———, ———, & T. Nishikawa. 1984. The Sipuncula of Japan: their systematics and distribution.—Publications of the Seto Marine Biological Laboratory 29(4/6):249–322.

———, & P. E. Gibbs. 1985. A phylogenetic analysis of higher taxa in the phylum Sipuncula.—Systematic Zoology 34:162–173.

———, & E. Jurczak. 1975. The sipunculan genus *Lithacrosiphon* Shipley, a taxonomic review.—Zoological Journal of the Linnean Society 56(3);235–248.

———, & E. Kirsteuer. 1968. Additional notes on some sipuncula from Madagascar. Results of Australian Indo-West Pacific Expedition, 1959–60. Part 12.—Zoologischer Anzeiger 180:352–356.

———, & V. V. Murina. 1977. On the sipunculan genus *Golfingia* Lankester, 1885.—Zoological Journal of the Linnean Society 60:173–189.

Cutler, N. J., & E. B. Cutler. 1986. A revision of the genus *Nephasoma* (Sipuncula, Golfingiidae).—Proceedings of the Biological Society of Washington 99(4):547–573.

Diesing, K. M. 1851. Systema Helminthum. Braumiller, Vindobonae, 558 pp.

———. M. 1859. Revision der Rhyngodeen.—Sitzungsberichte de mathematisch-naturwissenschaftliche Klasse, Akademie der Wissenschaften in Wien 37:719–782.

Ditadi, A. S. F. 1976. *Sipunculus marcusi* spec. nov. (Sipuncula) from southern Brazil.—Boletim de Zoologia, Universidade de São Paulo 1:81–84.

Dybas, L. 1976. A light and electron microscopic study of the ciliated urn of *Phascolosoma agassizii* (Sipunculida).—Cell and Tissue Research 169:67–75.

Edmonds, S. J. 1956. Australian Sipuncoloidea II. The genera *Phascolosoma, Dendrostomum, Golfingia, Aspidosiphon,* and *Cloeosiphon.*—Australian Journal of Marine and Freshwater Research 7(2):281–315.

———. 1960. Sipunculids from New Zealand and the Chatham Islands.—New Zealand Department of Scientific and Industrial Research Bulletin 139(4):159–167.

———. 1966. Port Phillip Survey 1957–1963. Sipunculoidea and Echiuroidea.—Memoirs of the National Museum of Victoria 1966:175–178.

———. 1971. Some sipunculans and echiurans, chiefly from Guam (Sipuncula and Echiura).—Micronesica 7(1–2):137–151.

———. 1980. A revision of the systematics of Australian sipunculans (Sipuncula).—Records of the South Australian Museum (Adelaide) 18(1):1–74.

———. 1985. A new species of *Phascolosoma* (Sipuncula) from Australia.—Transactions of the Royal Society of South Australia 109(2):43–44.

———. 1987. Phyla Sipuncula and Echiura. Pp. 185–212 *in* D. M. Devaney and L. G. Eldredge, eds., Reef and shore fauna of Hawaii. Bishop Museum Press, Honolulu.

Fischer, W. 1895. Die Gephyreen des Naturhistorischen Museums zu Hamburg.—Abhandlungen aus dem Gebiet der Naturwissenschaften, Hamburg 13:1–24.

———. 1896. In: Semon, Zoologische Forschungsreisen in Australien und Malayischen Archipel.—Medizinischnaturwissenschaftliche Gesellschaft zu Jena, Denkschriften 8:337–339.

———. 1913. Über einige Sipunculiden des Naturhistorischen Museums zu Hamburg.—Jahrbuch der Hamburgischen wissenschaftlichen Anstalten 30 2:93–101.

———. 1914a. Weitere Mitteilungen über die Gephyreen des Naturhistorischen (Zoologischen) Museums zu Hamburg.—Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 31:1–28.

———. 1914b. Gephyrea. Beiträge zur Kenntnis der Meeresfauna Westafrikas.—Beiträge zur Kenntnis der Meeresfauna Westafrikas 1:57–84.

———. 1916. Die Gephyreensausbeute der deutschen Tiefsee Expedition (1898–1899) vorlaufige Mitteilung.—Zoologischer Anzeiger 48:14–20.

———. 1919. Gephyreen der Süd-westküste Australiens.—Zoologischer Anzeiger 50:277–285.

———. 1921. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia. 1910–1913. 27. Gephyreen.—Kungliga Svenska Vetenskaps-Akademiens Handlingar 61(8):1–39.

———. 1922a. Gephyreen des Reichsmuseums zu Stockholm.—Arkiv für Zoologi 14(19):1–39.

———. 1922b. Gephyreen der deutschen Tiefsee-Expedition, auf des Dampfer "Valdivia" 1898–1899.—Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition, Valdivia 22(1):1–26.

———. 1923. Gephyreen des Golfes von Siam.—Videnskabelige Meddelelser Dansk fra Naturhistorisk Forening 76:21–27.

———. 1926. Sipunculiden und Echiuriden der Hamburger Sudsee-Expedition 1908–1909.—Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg 42:104–117.

———. 1927. Sipunculoidea und Echiuroidea. Pp. 199–216 *in* W. Michaelsen and R. Hartmeyer, eds., Die Fauna Sudwest Australiens, volume 5. G. Fischer, Jena.

Fisher, W. K. 1950. The sipunculid genus *Phascolosoma.*—Annals and Magazine of Natural History (12)3:547–552.

———. 1952. The sipunculid worms of California and Baja California.—Proceedings of the United States National Museum 102:371–450.

Frank, P. G. 1983. A checklist and bibliography of the Sipuncula from Canadian and adjacent waters.—Syllogeus 46:1–47.

Gerould, J. H. 1913. The sipunculids of the eastern coast of North America.—Proceedings of the United States National Museum 44:373–437.

Gibbs, P. E. 1973. On the genus *Golfingia* (Sipuncula) in the Plymouth area with a description of a new species.—Journal of the Marine Biological Association of the United Kingdom 53:73–86.

———. 1977. British sipunculans.—Synopses of the British Fauna (new series) 12:1–35.

———. 1986. The taxonomy of some little-known Sipuncula from the north-east Atlantic region including new records.—Journal of the Marine Biological Association of the United Kingdom 66:335–341.

———. 1987. A new species of *Phascolosoma* (Sipuncula) associated with a decaying whale's skull trawled at 880 m depth in the south-west Pacific.—New Zealand Journal of Zoology 14:135–137.

———, & E. B. Cutler. 1987. A classification of the phylum Sipuncula.—Bulletin of the British Museum Natural History (Zoology) 52(1):43–58.

———, ———, & N. J. Cutler. 1983. A review of the genus *Thysanocardia* Fisher (Sipuncula).—Zoologica Scripta 12(4);295–304.

Gray, J. E. 1828. Spicilegia Zoologica. Treuttel Wurtz and Company, London, 12 pp.

Grübe, E. 1840. Actinien, Echinodermen und Wurmer des Adriatischen- und Mittelmeers nach einigen Sammlungen beschriben von . . . J. H. Bon, Konisberg, 92 pp.

———. 1868. Beschreibungen einiger von Georg Ritter von Frauenfeld gesammeltr Anneliden und Gephyreen des rothen Meeres.—Zoologisch-Botanische Gesellschaft in Wien. Verhandlungen der kaiserlich-khoniglichen zoologischbotanischen Gesellschaft in Wien 18:629–650.

———. 1877. Vierundfunfzigster Jahresbericht der Schles.—Gesellschaft für vaterlandische Cultur, Breslau 1877:73.

———, & A. S. Öersted. 1858. Annulata Öerstediana.—Videnskabelige Meddelelser Dansk fra naturhistorisk Forening i Kjobenhavn: 105–120.

Haldar, B. P. 1975. Sipuncula of the Indian Ocean in the collection of the Zoological Survey of India. Pp. 51–92 *in* M. E. Rice and M. Todorović, eds., Proceedings of the International Symposium of Sipuncula and Echiura, volume 1. Naučno Delo Press, Belgrade.

———. 1976. Sipuncula from the Andaman and Nicobar Islands.—Records of the Zoological Survey of India 70:109.

———. 1988. Sipuncula of the Indian coast. Unpublished Ph.D. dissertation, Calcutta University, India, 250 pp.

Harms, W. 1921. Morphologische und kausal-analytische Untersuchungen uber das Internephridialorgan von *Physcosoma lanzarotae.*—Archiv für Entwicklungsmechanik 47:307–374.

Hérubel, M. A. 1904a. Sur les Sipunculides nouveaux rapportés de la mer Rouge, par M. Ch. Gravier (note préliminaire).—Bulletin du Muséum National d'Histoire Naturelle, Paris 10:476–480.

———. 1904b. Liste des Sipunculides et des Échiurides rapportés par M. Ch. Gravier du Golfe de Tadjourah (mer Rouge).—Bulletin du Muséum National d'Histoire Naturelle, Paris 10:562–565.

———. 1907. Recherches sur les Sipunculides.—Memoires de la Societé de France 20:107–418.

Hutton, W. K. 1879. Additions to the list of New Zealand worms.—Transactions of the Royal Society of New Zealand 12:277–278.

Ikeda, I. 1904. The Gephyrea of Japan.—Journal of the College of Science, Imperial University of Tokyo 20(4);1–87.

———. 1905. Gephyreans collected by Professor Dean at Manjuyodi, Southern Negros (Philippine Islands).—Annotationes Zoologicae Japonenses 5:169–174.

———. 1924. Further notes on the Gephyrea of Japan, with descriptions of some new species from the Marshall, Caroline, and Palau Islands.—Japanese Journal of Zoology 1:23–44.

Johnson, P. 1971. Sipunculids from Indian waters.—Journal of the Bombay Natural History Society 68(3):596–608.

Keferstein, W. 1863. Beiträge sur Kenntnis der Gattung *Phascolosoma* F. S. Leuck. Untersuchungen über niedere Seethiere.—Zeitschrift für Wissenschaftliche Zoologie 12:35–51.

———. 1865a. Beiträge zur anatomischen und systematischen Kenntniss der Sipunculiden.—Zeitschrift für Wissenschaftliche Zoologie 15: 404–445.

———. 1865b. Beiträge zur anatomischen und systematischen Kenntnis der Sipunculiden.—Nachrichten von der Königl. Geselschaft der Wissenschaften und der Georg-Augusts-Universitat zu Göttingen, Göttingen 1865:189–209.

———. 1866. Untersuchungen über einige amerikanische Sipunculiden.—Nachrichten von der Königl. Geselschaft der Wissenschaften und der Georg-Augusts-Universitat zu Göttingen, Göttingen 1866(14):215–228.

———. 1867. Untersuchungen über einige amerikanische Sipunculiden.—Zeitschrift für Wissenschaftliche Zoologie 17:44–55.

Koren, J., & D. C. Danielssen. 1877. The natural history of the Norwegian gephyreae. Pp. 111–156 *in* M. Sars, ed., Fauna Littoralis Norvegiae, Druck und Verlag von Johann Dahl, Christiania.

Lanchester, W. F. 1905a. Gephyrea in the marine fauna of Zanzibar and British East Africa from the collections made by C. Crossland in 1901–1902.—Proceedings of the Zoological Society of London 1:28–35.

———. 1905b. On the sipunculids and echiurids collected during the "Skeat" Expedition to the Malay Peninsula.—Proceedings of the Zoological Society of London 1:35–41.

———. 1908. Sipunculoidea of the National Antarctic Expedition 1901–1904.—Natural History 4: 1–6.

Leroy, P. 1936. Les sipunculiens du Muséum d'Histoire Naturelle de Paris.—Bulletin du Muséum National d'Histoire Naturelle, Paris Serie 2, 8: 423–426.

———. 1942. Sipunculiens d'Indochine.—40e Note Institut Océanographique de l'Indochine 40:1–51.

Leuckart, F. S. 1828. Breves animalium quorundam maxima ex parte marinorum descriptiones. Heidelbergae, A. Osswaldi, 24 pp.

Monro, C. A. 1931. Polychaeta, Oligochaeta, Echiuroidea and Sipunculoidea.—Scientific Report of the Barrier Reef Expedition 4:1037.

Murina, V. V. 1964. Report on the sipunculid worms from the coast of South Chinese Sea.—Trudy Instituta Okeanologii Akademii Nauk SSSR 69: 254–270.

———. 1967. On the sipunculid fauna of the littoral of Cuba.—Zoologicheskii Zhurnal 46:35–47.

———. 1968. On the distribution of new sipunculid fauna from Cuba and Gulf of Mexico.—Revue Roumaine de Biologie-Zoologie 13(6):421–423.

———. 1970. Contributions to the fauna of sipunculid worms from the Aden Gulf.—Vestnik Zoologii 2:65–71.

———. 1971. On the species composition and ecology of sipunculids of the Red Sea. Pp. 76–88 *in*

A. O. Kovalevski, ed., Shelf benthos of the Red Sea. Academii Nauk SSSR, Moscow.

———. 1972. Contribution of the sipunculid fauna of the Southern Hemisphere.—Zoologii Instituta Akademii Nauk SSSR 11(19):294–314.

———. 1975. New species of genus *Phascolosoma* (Sipuncula).—Vestnik Zoologii 197:54–59.

———. 1977. Marine worms of the Arctic and boreal waters of Europe. Works on the fauna of the USSR. Academy of Science USSR, Leningrad, 283 pp.

———. 1978. On the sipunculids and priapulids fauna of the southern Pacific.—Trudy Instituta Okeanologii Academii Nauk SSSR 113:120–131.

———. 1981. First report of the sea worms Sipuncula and Echiura from littoral Somali.—Vestnik Zoologii 1:11–18.

Ocharan, F. J. 1980. Primeros datos sobre los sipunculides del litoral N.Y. N.W. de España (Santander, Asturias y Galicia).—Boletín de Ciencias de la Naturaleza I 26:111–119.

Ostroumov, A. 1909. Sur les gephyriens du nord de la mer du Japan.—Ezhegodnik Zoologischeskiî Muzeî 14:319–321.

Pourtalès, L. F. de. 1851. On the Gephyrea of the Atlantic coast of the United States.—Proceedings of the American Association for the Advancement of Science, 5th meeting 5:39–42.

Quatrefages, M. A. de. 1865. Géphyriens Inermes.—Histoire naturelle des Annelés marins et d'eau douce, Paris 2:599–632.

Rice, M. E. 1967. A comparative study of the development of *Phascolosoma agassizii, Golfingia pugettensis,* and *Themiste pyroides* with a discussion of developmental patterns in the Sipuncula.—Ophelia 4:143–171.

———. 1973. Morphology, behavior and histogenesis of the pelagosphera larva of *Phascolosoma agassizii* (Sipuncula).—Smithsonian Contributions to Zoology 132:1–51.

———. 1975. Survey of the Sipuncula of the coral and beach rock communities of the Caribbean Sea. Pp. 35–49 *in* M. E. Rice and M. Todorović, eds., Proceedings of the International Symposium of Sipuncula and Echiura. Naučno Delo Press, Belgrade.

———. 1980. Sipuncula and Echiura. Pp. 490–498 *in* R. H. Morris, D. P. Abbott, & E. C. Haderlie, eds., Intertidal invertebrates of California, chapter 19. Stanford University Press, Palo Alto.

———. 1985. Description of a wood dwelling sipunculan, *Phascolosoma turnerae,* new species.—Proceedings of the Biological Society of Washington 98:54–60.

———. 1986. Phylum Sipuncula (Peanut worms). Pp. 224–228 *in* W. Sterrer, ed., Marine fauna and flora of Bermuda. John Wiley & Sons, Inc., New York.

———, & I. G. MacIntyre. 1979. Distribution of Sipuncula in the coral reef community, Carrie Bow Cay, Belize.—Smithsonian Contributions to Marine Sciences 12:311–320.

———, & A. C. Stephen. 1970. The type specimens of Sipuncula and Echiura described by J. E. Gray and W. Baird in the collections of the British Museum of Natural History.—Bulletin of the British Museum of Natural History 20(2):49–72.

Rüppell, E., & F. S. Leuckart. 1828. Neue wirbellose Thiere des rothen Meers. P. 50 *in* E. Rüppell, ed. Atlas zu der Reise im nordlichen Afrika; 1. Zoologie. Senckenbergische Naturforschung Gesellschaft, Frankfurt.

Saiz, J. I., A. Rallo, F. Rodríguez, & E. Gutiérrez. 1979. Sipuncula y Echiura de la costa Viacaina.—Actas del Primer Simposio Ibérico de Estudios del Bentos Marino 1:207–221.

Saiz Salinas, J. I. 1982. Nuevos datos sobre los sipunculidos de costas españolas y de mares adyacentes.—Actas del Primer Simposio Ibérico de Estudios del Bentos Marino 3:193–201.

———. 1984a. Gusanos sipunculidos (Sipuncula) de varias localidades de la costa de Portugal. Pp. 177–188 *in* V. Monteiro-Marques, ed., Actas do 4th Símposio Ibérico de Estudos do Benthos Marinho. Associacão des Estudantes da Faculdade Ciências de Lisboa, Lisboa.

———. 1984b. Los tipos de sipunculidos de Quatrefages del Museo de Paris. Bilbao, Universidad del Pais Vasco, 258 pp.

———. 1986. Los gusanos sipunculidos (Sipuncula) de los fondos litorales y circalitorales de las costas de la peninsula Ibérica, Islas Baleares, Canarias y mares adyacentes.—Monografias Instituto Español de Oceanográfia, Madrid 1–84.

———. 1988a. Sipunculid worms from several locations off the southwestern coast of Africa (Sipuncula).—Monográfias de Zoologia Marina 3:159–176.

———. 1988b. Sipunculiden (Sipuncula) des ostlichen Nordatlantik, gesammelt wahrend der Fahrten des FS "Meteor."—Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 85:7–23.

———. 1989. Die Typen und Typoide des Natur-Museums Senckenberg, 80 Sipuncula. Die von Rüppell & Leuckart 1828 beschribenen Arten.—Senckenbergiana biologica 689(1/3):207–212.

———, & A. Rallo Gruss. 1980. Sipunculidos litorales de costas ibericas. Primera cita de *Golfingia* (*Nephasoma*) *rimicola* Gibbs, 1973, fuera de su localidad-tipo en el sudoeste de Inglaterra.—Boletin de la Real Sociedad Española de Historia Natural Seccion Biologica 78:113–120.

Satô, H. 1930. Report on the biological survey of

Mutsu Bay. 15. Sipunculoidea.—Science Reports. Series 4 Biology 5:1–40.

———. 1935. Sipunculoidea and Echiuroidea of the West Caroline Islands.—Tohoku Daigaku, Sendai, Japan. Science Reports, series 4, 10:299–329.

———. 1937a. Note on a new sipunculid, *Physcosoma kurilense* n. sp. found in Shumshir Island.—Annotationes Zoologicae Japonenses 16:117–120.

———. 1937b. Echiuroidea, Sipunculoidea, and Priapulaidea obtained in northeast Honshu, Japan.—Saito Ho-on Kai Museum, Research Bulletin 12:137–176.

———. 1939. Studies on the Echiuridea, Sipunculids, and Priapulids of Japan.—Science Reports of Tohoku Imperial University 14(4):339–459.

Selenka, E. 1885. Report on the Gephyrea collected by H. M. S. Challenger during 1873–76.—Report of the Scientific Results of the Voyage of Challenger Zoology 13(36):1–25.

———. 1888. On the Gephyrea of the Mergui Archipelago collected for the Trustees of the Indian Museum.—Journal of the Linnean Society of London, Zoology 21:220–222.

———. 1897. Die Sipunculiden-Gattung *Phymosoma.*—Zoologischer Anzeiger 20:460.

———, J. G. de Man, & C. Bülow. 1883. Die Sipunculiden, eine systematische Monographie.—Semper Reisen in Archipel Phillippinen 2, 4:1–131.

Shipley, A. E. 1890. On *Phymosoma varians.*—Quarterly Journal of Microscopical Science 31:1–27.

———. 1891. On a new species of *Phymosoma,* with a synopsis of the genus and some account of its geographical distribution.—Quarterly Journal of Microscopical Science 32:111–126.

———. 1898. Report on the Gephyrean worms collected by Mr. J. Stanley Gardiner at Rotuma and Funafuti.—Journal of Zoology 1898:468–473.

———. 1899a. A report on the Sipunculoidea collected by Dr. Willey at the Loyalty Islands and in New Britain. Pp. 151–160 *in* A. Willey, ed., Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere collected 1885–1897 by A. Willey. University Press, Cambridge.

———. 1899b. On Gephyrean worms from Christmas Island.—Proceedings of the Zoological Society of London 22:54–57.

———. 1902. Sipunculoidea, with an account of a new genus *Lithacrosiphon.* Pp. 131–140 *in* J. S. Gardiner, ed., Fauna and geography of the Maldive and Laccadive Archipelagoes. University Press, Cambridge.

———. 1903. Report on the Gephyrea collected by Prof. Herdman at Ceylon in 1902.—Ceylon Pearl Oyster Fisheries Supplementary Reports 3:169–176.

Sluiter, C. P. 1881. Beiträge zu der Kenntnis der Gephyreën aus dem Malayischen Archipel. Zweite Mittheilung.—Natuurkundig Tijdschrift voor Nederlandsich-Indie 41:148–171.

———. 1886. Beiträge zu der Kenntnis der Gephyreën aus dem Malayischen Archipel.—Natuurkundig Tijdschrift voor Nederlandisch-Indie 45:472–517.

———. 1891. Die Evertebraten aus der Sammlung des Königlichen naturwissenschaftlichen Vereins in Nederländisch-Indien in Batavia.—Natuurkundig Tijdschrift voor Nederländisch-Indie 50:102–123.

———. 1898. Gephyreen von Süd Africa.—Zoologische Jahrbücher Abteilung für Systematik 11:442–450.

———. 1902. Die Sipunculiden und Echiuriden der "Siboga" Expedition, nebst Zusammenstellung der Überdies aus den indischen Archipel bekannten Arten.—Siboga-Expeditie, Monographie 25:1–53.

Southern, R. 1913. Gephyrea of the coasts of Ireland.—Scientific Investigations of the Fisheries Branch, Department of Agriculture for Ireland 3:1–46.

Spengel, J. W. 1898. Der Name *Physcosoma.*—Zoologischer Anzeiger 21:50.

Stephen, A. C. 1941. Sipunculids and Echiurids of the John Murray Expedition to the Red Sea and Indian Ocean 1933–34.—Scientific Reports of the John Murray Expedition 7:401–409.

———. 1942. The South African intertidal zone and its relation to ocean currents. Notes on the intertidal sipunculids of Cape Province and Natal.—Annals of the Natal Museum 10(2):245–256.

———. 1948. Sipunculids.—B.A.N.Z.A.R.E. Reports, Series B 5(4):213–220.

———. 1952. Gephyrea. The "Manihine" Expedition to the Gulf of Aqaba.—Bulletin of the British Museum (Natural History) 1:181–182.

———. 1960. Echiuroidea and Sipunculoidea from Senegal, West Africa.—Bulletin de l'Institut Francais d'Afrique Noire 22a(2):512–520.

———. 1965. Echiura and Sipuncula from the Israel South Red Sea Expedition.—Sea Fisheries Research Station Haifa Bulletin 40:79–83.

———. 1966. A collection of Sipuncula taken on the summit of the Vema Sea-mount, South Atlantic Ocean.—Annals and Magazine of Natural History 9(13):145–148.

———. 1967. Sipuncula and Echiura from Nouvelle-Caledonie.—Cahiers du Pacifique 10:44–50.

———, & E. B. Cutler. 1969. On a collection of Sipuncula, Echiura, and Priapulida from South African waters.—Transactions of the Royal Society of South Africa 38(2):111–121.

———, & S. J. Edmonds. 1972. The phyla Sipuncula and Echiura. Trustees British Museum (Natural History), London, 528 pp.

———, & J. D. Robertson. 1952. A preliminary report on the Echiuridae and Sipunculidae of Zanzibar.—Proceedings of the Royal Society of Edinburgh 64(4):426–444.

Stimpson, W. 1855. Description of some new marine invertebrates.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:390–391.

ten Broeke, A. 1925. Westindische Sipunculiden und Echuiriden.—Bijdragen tot de Dierkunde 24:81–96.

Tokioka, T. 1953. Invertebrate fauna of the intertidal zone of the Tokara Islands. iii. Echiuroidea and Sipunculoidea.—Publications of the Seto Marine Biological Laboratory 3(2):140.

Walter, M. D. 1973. Fressverhalten und Darminhaltsuntersuchungen bei Sipunculiden.—Helgoländer Wissenschaftliche Meeresuntersuchungen 25:486–494.

Wesenberg-Lund, E. 1930. Priapulidae and Sipunculidae.—The Danish "Ingolf" Expedition 4(7).

———. 1954a. Priapuloidea, Sipunculoidea and Echiuroidea.—Bulletin Institut royal des Sciences naturelles de Belgique 30(16):1–18.

———. 1954b. Sipunculids and Echiurids collected by Mr. G. Ranson in Oceania in 1952.—Bulletin du Muséum National d'Histoire Naturelle, Paris 26:376–384.

———. 1957a. Sipunculoidea and Echiuroidea from West Africa together with a bibliography on Gephyrea after 1920.—Bulletin Institut royal des Sciences naturelles de Belgique 33(42):1–24.

———. 1957b. Sipunculoidea and Echiuroidea from the Red Sea.—Contributions to the Knowledge of the Red Sea No. 3, The Sea Fisheries Research Station, Haifa Bulletin 14:1–15.

———. 1959a. Sipunculoidea and Echiuroidea from tropical West Africa.—Atlantide Report 5:177–210.

———. 1959b. Campagne de la "Calypso": Golfe de Guinée 7. Sipunculoidea and Echiuroidea.—Résultats Scientifiques des Campagnes de la "Calypso" 4:207–217.

———. 1959c. Sipunculoidea and Echiuroidea from Mauritius.—Videnskabelige Meddelelser Dansk fra Naturhistorisk Forening 121:53–73.

———. 1963. South African sipunculids and echiuroids from coastal waters.—Videnskabelige Meddelelser Dansk fra Naturhistorisk Forening 125:101–146.

Wheeler, M. B. 1938. The Sir Joseph Banks Islands. Reports of the expedition of the McCoy Society for field investigations and research.—Proceedings of the Royal Society, Victoria 50(1):345.

Zavodnik, D. 1975. Contribution to the ecology and zoogeography of North Adriatic sipunculans. Pp. 93–102 *in* M.E. Rice and M. Todorović, eds., Proceedings of the International Symposium of Sipuncula and Echiura, volume 1. Naučno Delo Press, Belgrade.

———, & V. G. Murina. 1975. Contribution to Sipuncula of North Adriatic insular region.—Rapports et procès-verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer-Méditerranée 23(2):127–128.

———, & ———. 1976. Sipuncula of the region of Rovinj (North Adriatic Sea).—Biosistematika 2(1):79–89.

(NJC) Biology Department, Hamilton College, Clinton, New York 13323; (EBC) Biology Department, Utica College of Syracuse University, Utica, New York 13502.

Appendix.—Comparative morphological data.

Trunk length in mm.	Introvert length as % trunk	Number of hook rings	Longitudinal muscle bands		Retractor origins as % of trunk		Nephridia length & % attached		Rectal caecum
			anter.	post.	dorsal :	ventral			
P. agassizii—California									
8	188	20	14	20	50	62	75	83	N
10	300	18	17	22	50	70	40	75	N
10	90	14	14	18	50	60	50	60	Y
13	154	14	99	21	46	69	46	50	Y
13	108	16	22	24	54	69	53	57	N
15	107	23	18	21	40	60	40	67	N
18	78	18	17	20	44	67	44	50	Y
19	142	24	26	30	47	68	37	43	N
20	60	18	23	24	55	75	50	50	N
23	109	19	21	25	52	65	57	77	Y
26	100	19	17	18	50	58	69	72	N
26	65	12	22	22	54	69	46	67	Y
27	78	24	22	22	44	63	37	70	Y
28	71	20	20	21	54	71	48	?	Y
32	56	22	22	21	47	69	47	73	N
34	103	24	25	28	59	74	47	63	N
35	80	20	20	23	43	57	37	?	N
40	125	?	23	24	45	62	45	72	N
43	70	20	19	22	53	70	47	70	N
45	100	18	18	24	49	60	67	67	N
50	72	22	21	19	52	68	44	77	N
63	63	23	20	25	48	63	51	69	N
65	69	20	22	23	63	78	57	59	N
69	67	22	20	25	54	68	41	71	Y
P. agassizii—Japan									
5	140	16	20	21	50	70	100	80	N
7	143	10	16	18	57	64	71	60	N
7	71	12	20	20	57	71	71	40	N
11	136	37	24	26	55	73	45	40	Y
12	100	16	21	24	42	58	75	50	Y
17	118	15	18	26	47	71	41	57	N
18	117	54	21	24	50	72	44	50	N
19	95	16	24	26	53	63	37	86	N
21	129	16	20	25	62	71	33	57	N
22	73	56	22	22	45	64	45	?	N
23	87	18	20	25	43	57	57	38	N
24	88	27	26	28	46	67	29	71	N
30	73	20	17	99	53	67	50	67	Y
P. albolineatum—West Pacific									
7	114	17	22	22	43	57	57	50	N
9	56	18	16	16	56	67	33	67	N
10	50	16	18	20	50	60	40	75	N
11	91	18	16	18	27	45	36	50	N
12	58	16	16	18	42	50	33	75	N
14	43	18	20	18	50	64	29	75	N
14	50	18	18	20	43	57	50	71	N
15	67	18	20	14	33	47	20	67	N
17	82	20	20	22	29	41	41	43	Y

Appendix.—Continued.

Trunk length in mm.	Introvert length as % trunk	Number of hook rings	Longitudinal muscle bands anter. post.		Retractor origins as % of trunk dorsal : ventral		Nephridia length & % attached		Rectal caecum
P. granulatum—Spain									
18	122	35	18	23	61	72	56	50	N
24	133	74	20	28	46	67	62	40	N
28	86	44	15	24	43	61	46	54	Y
31	113	68	19	30	48	58	39	67	Y
P. nigrescens—I.W.P.									
12	267	150	20	26	58	75	67	50	N
14	71	?	?	26	36	57	50	71	N
15	167	125	24	30	47	60	40	50	Y
21	129	100	22	26	33	52	48	?	?
23	187	200	26	28	39	52	?	?	N
26	131	100	28	24	42	54	54	57	N
27	159	125	20	28	30	44	44	50	N
27	93	100	24	30	33	56	33	?	N
30	117	125	26	28	40	63	60	56	N
30	83	70	30	32	37	53	40	42	N
33	148	200	20	26	30	45	67	55	Y
40	112	150	26	32	40	55	55	68	N
P. nigrescens—Caribbean									
5	160	45	?	?	40	60	30	67	N
6	217	60	20	28	33	67	50	33	N
7	171	150	18	?	29	43	71	?	N
10	140	150	16	22	50	70	70	57	N
11	127	70	?	24	45	64	45	60	N
13	169	133	26	36	31	46	46	50	N
15	133	50	16	24	47	67	47	57	N
19	142	150	22	32	37	74	47	56	N
P. perlucens—Caribbean									
7	114	14	20	18	43	57	57	75	N
10	90	17	18	18	40	50	40	50	Y
12	58	16	19	21	42	58	25	67	N
13	62	18	18	23	46	62	38	40	N
14	93	14	18	20	50	57	43	50	N
16	56	18	20	18	44	56	38	83	N
16	88	19	18	20	44	50	44	29	N
17	88	18	18	23	35	41	35	50	N
19	74	18	16	18	37	53	26	60	N
22	82	22	18	20	41	50	36	?	N
24	54	20	18	22	38	50	25	67	N
25	96	16	17	23	36	48	40	70	N
26	65	24	19	23	35	42	23	33	Y
29	66	20	16	19	41	52	38	73	N
54	43	16	20	20	44	56	37	55	Y
P. scolops—I.W.P.									
5	100	10	16	20	60	80	40	50	Y
6	67	10	16	18	50	67	50	67	N
7	57	14	16	18	57	86	29	50	Y
7	57	10	18	18	29	43	29	50	N

Appendix.—Continued.

Trunk length in mm.	Introvert length as % trunk	Number of hook rings	Longitudinal muscle bands anter. post.		Retractor origins as % of trunk dorsal : ventral		Nephridia length & % attached		Rectal caecum
8	88	10	16	18	50	62	75	67	Y
9	89	12	20	20	56	67	56	80	Y
10	100	12	18	18	50	60	50	60	N
11	82	12	18	20	55	64	27	67	Y
24	67	15	19	22	38	50	33	88	Y
27	93	14	19	21	52	59	37	60	Y
P. stephensoni—Hawaii									
11	91	16	20	24	36	45	45	80	N
19	105	20	20	22	63	74	53	70	N
21	62	20	22	26	57	71	57	83	N
22	114	18	18	26	59	41	64	71	Y
27	96	18	22	20	48	63	48	54	N

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 731–745

CORRECTION OF IJIMA'S (1927) LIST OF RECENT HEXACTINELLID SPONGES (PORIFERA)

Henry M. Reiswig

Abstract.—Errors in the final species list of Ijima's posthumously published *Siboga* Monograph on the Hexactinellida (Porifera) have been the cause of misallocations of species in later publications and disorder of museum collections. The text of the entire monograph has been reviewed in detail in an attempt to provide a faithful reflection of Ijima's opinions and a corrected list of species as understood by him at the time of his death. A total of 421 forms are recognized, consisting of 381 species and 40 additional subspecies. The taxonomic actions attributable to Ijima in this monograph are summarized in an action list.

Isao Ijima's (1927) monograph, "The Hexactinellida of the *Siboga* Expedition," is still regarded by specialists as the most important authority for present taxonomic arrangement of this class of Porifera. It does, however, contain significant, unrecognized hazards for both casual and serious research users. Its prominence is attributable both to its major reorganization of higher taxa, which has served as the basis for later reviews (de Laubenfels 1936) and modifications (e.g., Reid 1957, 1963), and to its inclusion of a revised list of all extant hexactinellids—the last such attempt. The monograph's appended "List of Recognizably Known Recent Hexactinellids Arranged Systematically," pp. 364–377 (hereafter referred to as the "Final List" or "FL"), has served as reference for subsequent hexactinellid collection reports (e.g., Burton 1954) and as the basic guide for systematic arrangement of specimen collections of most major museums throughout the world. Unfortunately, the Final List is extensively flawed at lower taxonomic levels due to editorial actions in the preparation of the final publication.

As noted in Kaburaki's preface and the introduction to the monograph, Ijima inherited responsibility for the *Siboga* hexactinellid collection in 1907 after ill health incapacitated F. E. Schulze. Ijima spent the final ten years of his life preparing the report, but died in 1921 before completing his revision of the second half of the material—basically the Lyssacinosa. Responsibility for final preparation fell upon Y. Okada, Ijima's assistant, and Max Weber, the editor of the *Siboga* Series. While the main text is accepted here as a faithful reflection of Ijima's taxonomic opinions, the Final List, presumably assembled by Okada and/or Weber, contradicts Ijima's text conclusions on many points.

The Final List, with its unappreciated errors, continues to be the most widely used portion of the monograph due to omission of an index of scientific names in this work. Even Burton (1928), in his careful taxonomic review for the Zoological Record, failed to detect several new genera erected by Ijima. These errors continue to be perpetuated in modern literature (e.g., Hartman 1982, Koltun 1967, Reiswig 1979, Tuzet 1973), hence correction of the list is urgently needed. Ijima, a major figure in hexactinellid systematics, ranking second only to F. E. Schulze in terms of total contributions to the field, deserves better recognition for his last major accomplishment than appearing to be the source of taxonomic confusion. Museum collection managers likewise need an accurate scheme for arranging specimens without the necessity of scrutinizing the fragmented literature of this class. A corrected version of the Final List is also required for eventual development of a current list of the recent hexactinellids and, ultimately, inclusion of fossil groupings into a single classification.

Because of the numerous contradictions to Ijima's text, the details presented in the Final List of the *Siboga* Monograph cannot be attributed to Ijima. The transfers and synonomies implied by that list should be ignored where these conflict with statements or implications of Ijima's text. In preparation of the corrected list, my primary aim has been to reflect Ijima's concepts as faithfully as possible. Simple errors of spelling and statements of authority as presented in the text have been corrected where these have been detected. Names for typical subspecies have been added where Ijima's recognition of atypic subspecies requires formal recognition of the reference taxon. Clear statements of uncertainty by Ijima on allocation of specific taxa are indicated by symbol. Text contradictions or absence of clear statement of allocation by Ijima were resolved by reviewing his previous publications and, occasionally, by educated guess. These points are clearly identified in the annotations. Species which Ijima either did not mention, or mentioned only in trivial context (lacking any implication of recognition), are identified by symbol. All transfers and synonomies attributed to Ijima in this work are included in an Action List, with the cautionary note that several of these may have been previously suggested, but without conviction of formal intent. A complete index of generic, specific and subspecific names contained in the *Siboga* Monograph is available from the author upon request. Publication date of the *Siboga* Monograph is often erroneously cited as 1926; the publisher, E. J. Brill, Leiden, has advised me that their booklet advertising the *Siboga* Series clearly states the date of availability as January, 1927 (H. Reerink, pers. comm.).

Corrected version of Ijima's 1927 "LIST OF RECOGNIZABLY KNOWN RECENT HEXACTINELLIDS ARRANGED SYSTEMATICALLY."

Ijima's overall systematic arrangement is retained, but in the absence of data on phylogenetic relationships at lower levels, species are listed alphabetically under genera and subgenera. All page numbers refer to Ijima, 1927. An asterisk (*) before the species number identifies species or subspecies either not mentioned or, if mentioned, not clearly allocated in the text; Ijima's concept of the status of these names, at the time of his death in 1921, cannot be assessed. Taxa for which Ijima explicitly or implicitly expressed uncertainty in recognition or allocation are indicated by a question mark after the species number. Brackets identify nominate subspecies which are implied but not formed in the text. They are required by recognition of non-nominate subspecies by Ijima, and, although formed here by HMR, their status is implied by Ijima. Annotations following the list are indicated by parentheses.

Suborder I AMPHIDISCOPHORA Schulze, 1899

Fam. I PHERONEMATIDAE Gray, 1870 (emended)

Gen. 1 *Pheronema* Leidy, 1868; p. 7, 9

*1	*annae* Leidy, 1868
*2	*carpenteri* (Thomson, 1869)
3	*echinatum* Ijima, 1927; p. 9, 21
4	*giganteum* Schulze, 1886; p. 9, 10
5	?*gigas* (Schulze, 1886); p. 9, (a)
6	*globosum* Schulze, 1886; p. 21
*7	*grayi* Kent, 1869
*8	*hemisphaericum* Gray, 1873; p. 8
9	*raphanus* Schulze, 1894; p. 21
10	*weberi* Ijima, 1927; p. 9, 17

Gen. 2 *Poliopogon* Thomson, 1873; p. 7, 9

1 *amadou* Thomson 1873; p. 9

Gen. 3. *Sericolophus* Ijima, (1894) 1901; p. 9, 25, (b)

1 *reflexus* (Ijima, 1894); p. 25, 26

Gen. 4 *Semperella* Gray, 1868; p. 9, 28

1 *cucumis* Schulze, 1895; p. 28
2 *schultzei* (Semper, 1868); p. 28
3 *similis* Ijima, 1927; p. 28
4 *spicifera* Schulze, 1904; p. 28
5 *stomata* Ijima, 1896; p. 28

Gen. 5 *Platylistrum* Schulze, 1904; p. 7, 9

1 *platessa* Schulze, 1904; p. 25

Fam. II MONORHAPHIDIDAE Ijima, 1927
Gen. 1 *Monorhaphis* Schulze, 1904; p. 36, 37

1 *chuni* Schulze, 1904; p. 37
2 *dives* Schulze, 1904; p. 37
3 ?*fruticosa* (Schulze, 1893); p. 37, (c)

Fam. III HYALONEMATIDAE Gray, 1857, emend.
Gen. 1 *Chalaronema* Ijima, 1927; p. 41, 43

1 *sibogae* Ijima, 1927; p. 43

Gen. 2 *Hyalonema* Gray, 1832; p. 43, 49
Subgen. 1 *Euhyalonema* Ijima, 1927; p. 50

1 *intermedium* Ijima, 1927; p. 50, 55
2 *keianum* Ijima, 1927; p. 50, 58
3 *pellucidum* (Ijima, 1894); p. 50, 52
4 *proximum* (Schulze, 1904); p. 50
5 *sieboldi* (Gray, 1835); p. 50

Subgen. 2. *Pteronema* Ijima, 1927; p. 50

1 *aculeatum* (Schulze, 1894); p. 50
2 *cebuense* (Higgin, 1875); p. 50
3 *globus* (Schulze, 1886); p. 50
4 *heideri* (Schulze, 1894); p. 50
5 *polycaulum* (Lendenfeld, 1915); p. 50, (c)
6 *topsenti* Ijima, 1927; p. 50, 61

Subgen. 3 *Coscinonema* Ijima, 1927; p. 50

1 *conus* (Schulze, 1886); p. 51
2 ?*elegans* (Schulze, 1886); p. 51
3 ?*gracile* (Schulze, 1886); p. 51
4 *heymonsi* Schulze, 1895; p. 51, (d)
5 *indicum andamanense* (Schulze, 1895); p. 51, (e)
6 *indicum laccadivense* (Schulze, 1895); p. 51, (e)
7 *kenti* (Schmidt, 1880); p. 51
8 *kirkpatricki* Ijima, 1927; p. 51, 68
9 *lamella* (Schulze, 1900); p. 51
10 *pateriferum* (Wilson, 1904); p. 51, 52
11 *schmidti* (Schulze, 1899); p. 51
12 *toxeres* (Thomson, 1877); p. 51, (c)

Subgen. 4 *Cyliconema* Ijima, 1927; p. 50, 51

1 *apertum apertum* (Schulze, 1886); p. 51, (f)
2 *apertum maehrenthali* (Schulze, 1895); p. 51, 72, (b, g)
3 *coniforme* (Schulze, 1904); p. 51
4 *drygalskii* (Schulze, 1910); p. 51
5 *globiferum* (Schulze, 1904); p. 51
6 *infundibulum* (Topsent, 1896); p. 51
7 *keiense* Ijima, 1927; p. 51, 90
8 *martabanense* (Schulze, 1900); p. 51, (h)
9 *molle* (Schulze, 1904); p. 51
10 *nicobaricum* (Schulze, 1904); p. 51, (i)
11 *ovatum* (Ijima, 1895); p. 51
12 *pirum* (Schulze, 1895); p. 51
13 *rapa* (Schulze, 1900); p. 51, (b)
14 *simile* (Schulze, 1904); p. 51
15 *somalicum* (Schulze, 1904); p. 51, (i)
16 *tenerum* (Schulze, 1886); p. 51
17 *thomsonis* (Marshall, 1875); p. 51, (c)
18 *timorense* Ijima, 1927; p. 51, 88
19 *tulipa* (Schulze, 1904); p. 51
20 *valdiviae* (Schulze, 1904); p. 51

Subgen. 5 *Paradisconema* Ijima, 1927; p. 50, 52

1 *alcocki* (Schulze, 1895); p. 52

2 *investigatoris* (Schulze, 1900); p. 52
3 *vosmaeri* Ijima, 1927; p. 52, 93

Subgen. 6 *Leptonema* Lendenfeld, 1915; p. 50, 52

1 *acuferum* (Schulze, 1893); p. 52
2 *campanula* Lendenfeld, 1915; p. 52
3 *divergens* (Schulze, 1886); p. 52
4 *flagelliferum* Ijima, 1927; p. 52, 97
5 *lusitanicum* (B. d. Bocage, 1864); p. 52
6 *ovuliferum* (Schulze, 1899); p. 52
7 *solutum* (Schulze, 1904); p. 52
8 *urna* (Schulze, 1904); p. 52

Subgen. 7 *Thamnonema* Ijima, 1927; p. 50, 52

1 *thamnophorum* Ijima, 1927; p. 52, 99

Subgen. 8 *Phialonema* Lendenfeld, 1915; p. 50, 52

1 *brevancora* Lendenfeld, 1915; p. 52

Subgen. 9 *Prionema* Lendenfeld, 1915; p. 50, 52

1 *agujanum* Lendenfeld, 1915; p. 52, 53
2 *azuerone* Lendenfeld, 1915; p. 53
3 *crassum* Lendenfeld, 1915; p. 53
4 *fimbriatum* Lendenfeld, 1915; p. 53
5 *pinulifusum* Lendenfeld, 1915; p. 53
6 *poculum* (Schulze, 1886); p. 53
7 *spinosum* Lendenfeld, 1915; p. 53
8 *validum* (Schulze, 1904); p. 53

Subgen. 10 *Corynonema* Ijima, 1927; p. 50, 53

1 *calix* (Schulze, 1904); p. 53
2 *clathratum* (Ijima, 1895); p. 53
3 *clavigerum* (Schulze, 1886); p. 53
4 ?*cupressiferum* (Schulze, 1893); p. 53, (h)
5 ?*depressum* (Schulze, 1886); p. 53
6 *grandancora* (Lendenfeld, 1915); p. 53
7 *hercules* (Schulze, 1899); p. 53
8 *masoni* (Schulze, 1895); p. 53
9 *owstoni* (Ijima, 1894); p. 53
10 *placuna* (Lendenfeld, 1915); p. 53
11 *populiferum* (Schulze, 1899); p. 53
12 *rotundum* Ijima, 1927; p. 53, 102
13 *tenuifusum* (Lendenfeld, 1915); p. 53
14 *tylostylum* (Lendenfeld, 1915); p. 53
15 *weltneri* (Schulze, 1895); p. 53

Subgen. 11 *Onconema* Ijima, 1927; p. 50, 53

1 *agassizi* (Lendenfeld, 1915); p. 53
2 *obtusum gracile* (Lendenfeld, 1915); p. 53, (h,i)
3 *obtusum robustum* (Lendenfeld, 1915); p. 53, (h,i)

Subgen. 12 *Oonema* Lendenfeld, 1915 (emended); p. 50, 53

1 *aequatoriale* (Lendenfeld, 1915); p. 54, (k)
2 *bianchoratum* (Wilson, 1904); p. 53, 54
3 *crassipinulum* Lendenfeld, 1915; p. 54
4 *densum* Lendenfeld, 1915; p. 54
5 *geminatum* (Lendenfeld, 1915); p. 54, (k)
6 *henshawi* Lendenfeld, 1915; p. 54
7 *pedunculatum* (Wilson, 1904); p. 54
8 *robustum* (Schulze, 1886); p. 54
9 *sequoia* Lendenfeld, 1915; p. 54
10 *umbraculum* (Lendenfeld, 1915); p. 54, (k)

Gen. 3. *Compsocalyx* Schulze, 1904; p. 41, 43

*1 *gibberosa* Schulze, 1904

Gen. 4 *Lophophysema* Schulze, 1900; p. 41, 43

*1 *inflatum* Schulze, 1900

Suborder II HEXASTEROPHORA Schulze, 1899
Tribe A HEXACTINOSA Schrammen, 1910–1912
Subtribe a CLAVULARIA Schulze, 1886
Fam. I FARREIDAE Schulze, 1886
Gen. 1 *Farrea* Bowerbank, 1862; p. 130

1 *aculeata* Schulze, 1899; p. 131
2 *convolvulus* Schulze, 1899; p. 131, 158
3 *hanitschi* Ijima, 1927; p. 151
4 *lendenfeldi* Ijima, 1927; p. 159
5 *mexicana* Wilson, 1904; p. 160
6 *nodulosa* Ijima, 1927; p. 154
7 *occa claviformis* Wilson, 1904; p. 132, 140
8 *occa clavigera* (Schulze, 1887); p. 131, 137
9 *occa cuspidata* Ijima, 1927; p. 145
10 *occa erecta* Ijima, 1927; p. 132
11 *occa foliascens* Topsent, 1906; p. 162
*12 *occa laminaris* Topsent, 1904
13 *occa mammillata* Ijima, 1927; p. 142
14 *occa occa* Bowerbank, 1862, Carter, 1885; p. 131, (b)
15 *occa ouwensi* Ijima, 1927; p. 148
*16 *occa scutella* Lendenfeld, 1915
17 *occa subclavigera* Ijima, 1927; p. 140
18 *sollasi* Schulze, 1886; p. 153
19 *spirifera* Ijima, 1927; p. 156
20 *vosmaeri* Schulze, 1886; p. 131, 154
21 *weltneri* Topsent, 1901; p. 153

Gen. 2 *Lonchiphora* Ijima, 1927; p. 130, (1)

1 *inversa* Ijima, 1927; p. 162, (1)

Gen. 3 *Claviscopulia* Schulze, 1899; p. 126, 130, (h)

*1 *intermedia* Schulze, 1899

Gen. 4 *Sarostegia* Topsent, 1904; p. 130

*1 *oculata* Topsent, 1904; p. 124

Subtribe b. SCOPULARIA Schulze, 1886
Fam. I EURETIDAE Schulze, 1886
Gen. 1 *Eurete* Semper, 1868; p. 165, 166, (b, m)

1 *bowerbanki* Schulze, 1886; p. 165, 166
2 *freelandi* Ijima, 1927; p. 167, 176
3 *marshalli* Schulze, 1886; p. 166, 167
4 *schmidti kampeni* Ijima, 1927; p. 173
5 *schmidti schmidti* Schulze, 1886, Ijima, 1927; p. 166, 171, (f)
6 *schmidti treubi* Ijima, 1927; p. 170
7 *simplicissimum* Semper, 1868; p. 166
8 *spinosum* Lendenfeld, 1915; p. 166
9 *trachydocus* Ijima, 1927; p. 168

Gen. 2 *Pararete* Ijima, 1927; p. 165, 178

1 *baliense* Ijima, 1927; p. 178, 187, (n)
2 *carteri* (Schulze, 1886); p. 166, 178
3 *farreopsis farreopsis* (Carter, 1877) Ijima, 1927; p. 166, 178
4 *farreopsis fragiferum* Ijima, 1927; p. 182
5 *farreopsis jakosalemi* Ijima, 1927; p. 178, 185
6 *farreopsis subglobosum* Ijima, 1927; p. 178, 183
7 *freeri* Ijima, 1927; p. 178, 190
8 *gerlachei* (Topsent, 1901); p. 166, 178
9 *kangeanganum* Ijima, 1927; p. 178, 189, (n)
10 *semperi* (Schulze, 1886); p. 178, 193

Gen. 3 *Pleurochorium* Schrammen, 1910–1912; p. 165, 195

1 *annandalei* (Kirkpatrick, 1908); p. 166, 196, (h)
2 *cornutum* Ijima, 1927; p. 196, 197

Gen. 4 *Periphragella* Marshall, 1875; p. 165, 203

1 *challengeri* Ijima, 1927; p. 204
2 *elisae* [*elisae*] Marshall, 1875; p. 165, 204, (o)
3 *elisae japonica* Ijima, 1927; p. 204, (p)
4 *irregularis* Ijima, 1927; p. 205, 208
5 *lusitanica* Topsent, 1890; p. 205
6 *parva* Ijima, 1927; p. 205

Gen. 5 *Lefroyella* Thomson, 1877; p. 165, 210

1 *ceramensis* Ijima, 1927; p. 210
2 *decora* Thomson, 1877; p. 165, 210

Gen. 6 *Myliusia* Gray, 1859; p. 165, 213

1 *callocyathus* Gray, 1859; p. 165, 215
2 *conica* (Schmidt, 1880); p. 214
3 ?*subglobosa* (Gray, 1867); p. 214, (b)
4 *verrucosa* Ijima, 1927; p. 214, 217

Gen. 7 *Margaritella* Schmidt, 1880; p. 113, 165, (h)

1 *coeloptychioides* Schmidt, 1880; p. 165

Gen. 8 *Chonelasma* Schulze, 1886; p. 118, 165, (q)

*1 *ijimai* Topsent, 1901
2 *lamella* [*lamella*] Schulze, 1886; p. 165, (o)
*3 *lamella choanoides* Schulze & Kirkpatrick, 1910

Gen. 9 *Ptychodesia* Schrammen, 1910–1912; p. 165

1 *doederleini* (Schulze, 1886); p. 165

Gen. 10 *Bathyxiphus* Schulze, 1899; p. 165

1 *subtilis* Schulze, 1899; p. 165

Gen. 11 *Heterorete* Dendy, 1916; p. 165

1 *pulchrum* Dendy, 1916; p. 165, (h)

Gen. 12 *Dactylocalyx* Stutchbury, 1841; p. 114, 166, (r)

1 *ingalli* (Bowerbank, 1869); p. 214
2 ?*patella* Schulze, 1887; p. 231
*3 *potatorum* Schmidt, 1880
4 *pumiceus* Stutchbury, 1841; p. 166, 214

Gen. 13 *Iphiteon* Bowerbank, 1869; p. 166, (h)

1 *panicea* Bowerbank, 1869; p. 166

Gen. 14 *Conorete* Ijima, 1927; p. 165, 166, (f, m)

1 *erectum erectum* (Schulze, 1899); p. 165, 166
*2 *erectum tubuliferum* (Wilson, 1904)
*3 *erectum gracile* (Wilson, 1904)
*4 *erectum* forma D (Lendenfeld, 1915)
*5 *mucronatum* (Wilson, 1904)

Gen. 15 *Gymnorete* Ijima, 1927; p. 165, 166, (f, m, s)

1 *alicei* (Topsent, 1901); p. 165, 166

Fam. II TRETODICTYIDAE Schulze, 1886 1886

Gen. 1 *Tretodictyum* (Schulze, 1886); p. 219, 220, (u)

1 ?*labyrinthicum* (Wilson, 1904); p. 231, (t)
2 *pumicosum* Ijima, 1927; p. 220, 229
3 *schrammeni* Ijima, 1927; p. 220, 224
4 *tubulosum* (Schulze, 1886); p. 220, 221

Gen. 2 *Hexactinella* Carter, 1885; p. 219, 231

1 *grimaldii* Topsent, 1890; p. 231, 234
2 *lata* (Schulze, 1886); p. 231, 235
3 *lingua* Ijima, 1927; p. 231, 242
4 *rugosa* Ijima, 1927; p. 231, 237
5 ?*spongiosa* Ijima, 1927; p. 231, 246, (u)
6 *ventilabrum* Carter, 1885; p. 231, 232
7 *vermiculosa* Ijima, 1927; p. 231, 239

Gen. 3 *Auloplax* Schulze, 1904; p. 219, 231

1 *auricularis* Schulze, 1904; p. 219, 231
2 ?*filholi* (Topsent, 1904); p. 231, 244, (v)

Gen. 4 *Cyrtaulon* Schulze, 1887; p. 219

1 *sigsbeei* (Schmidt, 1880); p. 6
2 *solutus* Schulze, 1886; p. 219

Gen. 5 *Tretocalyx* Schulze, 1900; p. 219

1 *monticularis* (Lendenfeld, 1915); p. 231
2 *polae* Schulze, 1900; p. 219

Gen. 6 *Sclerothamnopsis* Wilson,1904; p. 219, 248

1 *compressa* Wilson, 1904, p. 219, 248
2 *schulzei* Ijima, 1927; p. 248, 249

Gen. 7 *Sclerothamnus* Marshall, 1875; p. 219, 253

1 *clausi* Marshall, 1875; p. 219, 253

Gen. 8 *Psilocalyx* Ijima, 1927; p. 219, 265

1 *wilsoni* Ijima, 1927; p. 219, 265

Gen. 9 *Anomochone* Ijima, 1927; p. 219, 268

1 *expansa* Ijima, 1927; p. 219, 269
2 *globosa* Ijima, 1927; p. 272

Fam. III AULOCALYCIDAE Ijima, 1927
Gen. 1 *Aulocalyx* Schulze, 1886; p. 274, 276

1 *irregularis* Schulze, 1886; p. 274
2 *serialis* Dendy, 1916; p. 274

Gen. 2 *Rhabdodictyum* (Schmidt, 1880); p. 274, 276

1 *delicatum* (Schmidt, 1880); p. 274, 277
2 *kurense* Ijima, 1927; p. 274, 277

Gen. 3 *Euryplegma* Schulze, 1886; p. 274, 276

1 *auriculare* Schulze, 1886; p. 274

Gen. 4 *Fieldingia* Kent, 1870; p. 274, 276

1 *lagettoides* Kent, 1870; p. 274

Gen. 5 *Tretopleura* Ijima, 1927; p. 276, 280

1 *candelabrum* Ijima, 1927; p. 274, 280

Fam. IV CRATICULARIDAE Rauff, 1893
Gen. 1 *Tretorete* Ijima, 1927; p. 298

1 *incertum* Ijima, 1927; p. 298

Fam. V APHROCALLISTIDAE Gray, 1867
Gen. 1 *Aphrocallistes* Gray, 1858; p. 284, 286, (w)

1 *beatrix beatrix* Gray, 1858, Ijima, 1916; p. 286, 297
2 *beatrix orientalis* Ijima, 1916; p. 287, 288
3 *vastus* Schulze, 1886; p. 286, 287

Gen. 2. *Heterochone* Ijima, 1927; p. 284, 285, (f, q)

1 *calyx* (Schulze, 1886); p. 118, 284
2 ?*hamata* (Schulze, 1886); p. 284, (h)
3 *tenera* (Schulze, 1899); p. 284, (h)

Tribe B LYCHNISCOSA Schrammen, 1903
Fam. I AULOCYSTIDAE Schulze, 1886, (b)
Gen. 1 *Aulocystis* Schulze, 1886; p. 302

1 *grayi grayi* (Bowerbank, 1869); p. 302, 304
2 *grayi polae* Ijima, 1927; p. 303, 304
3 *zitteli sibogae* Ijima, 1927; p. 304, 305
4 *zitteli zitteli* (Marshall & Meyer, 1877) Ijima, 1927; p. 302, 304

Incertae Sedis (Aulocystidae)

1 ?*superstes* Schmidt, 1880, (*Cystispongia*); p. 302, (f)
2 ?*mixtum* Schmidt, 1880, (*Diplacodium*); p. 302, (f)
3 ?*lanterna* Schmidt, 1880, (*Scleroplegma*); p. 214, 302, (f)

Fam. II DIAPLEURIDAE Ijima, 1927
Gen. 1 *Diapleura* Ijima, 1927; p. 314

1 *maasi* Ijima, 1927; p. 314

Tribe C LYSSACINOSA Ijima, 1927
Fam. I LEUCOPSACADIDAE Ijima, 1903, (h)
Gen. 1 *Leucopsacas* Ijima, (1898) 1903; p. 320

1 *orthodocus* Ijima, 1898; p. 321
2 *scoliodocus* [*scoliodocus*] Ijima, 1898; p. 320, 321, (o)
3 *scoliodocus retroscissa* Topsent, 1904; p. 321, (f)

Gen. 2 *Placopegma* Schulze, 1896; p. 320

*1 *solutum* Schulze, 1896; p. 105, 319

Gen. 3 *Caulocalyx* Schulze, 1886; p. 320

*1 *tenera* Schulze, 1886, (h)

Gen. 4 *Chaunangium* Schulze, 1904; p. 320

*1 *crater* Schulze, 1904

Gen. 5 *Chaunoplectella* Ijima, (1896) 1903; p. 320, 323

1 *cavernosa* Ijima, 1896; p. 323, 324

2 *spinifera* Ijima, 1903; p. 323
3 *stelleta* Ijima, 1927; p. 320, 323

Fam. II EUPLECTELLIDAE (Gray, 1867) Ijima, 1903, (b)
Subfam. a Euplectellinae Ijima, 1903
Gen. 1 *Euplectella* Owen, 1841; p. 327

*1 *aspera* Schulze, 1895
2 *aspergillum* Owen, 1841; p. 106, 329
*3 *crassistellata* Schulze, 1886
*4 *cucumer* Owen, 1857
*5 *curvistellata* Ijima, 1901
6 *imperialis* Ijima, 1894; p. 105, 327
*7 *jovis* Schmidt, 1880
8 *marshalli* Ijima, 1895; p. 328, 334
*9 *nobilis* Schulze, 1904
*10 *nodosa* Schulze, 1886
*11 *oweni* Herklots & Marshall, 1868
12 *regalis* Schulze, 1900; p. 327, 334
*13 *simplex* Schulze, 1895
*14 *suberea* Thomson, 1876
15 *timorensis* Ijima, 1927; p. 327

Gen. 2 *Holascus* Schulze, 1886; p. 327

*1 *edwardsi* Lendenfeld, 1915
*2 *fibulatus* Schulze, 1886
*3 *obesus* Schulze, 1904
*4 *polejaevi* Schulze, 1886
*5 *ridleyi* Schulze, 1886
*6 *robustus* Schulze, 1895
*7 *stellatus* Schulze, 1887
*8 *tener* Schulze, 1895
*9 *tenuis* Schulze, 1904
*10 *undulatus* Schulze, 1899

Gen. 3. *Malacosaccus* Schulze, 1886; p. 327

*1 *coatsi* Topsent, 1910; p. 105
*2 *floricomatus* Topsent, 1901
*3 *pedunculatus* Topsent, 1910
*4 *unguiculatus* Schulze, 1886
*5 *vastus* Schulze, 1886

Gen. 4 *Docosaccus* Topsent, 1910; p. 327

*1 *ancoratus* Topsent, 1910; p. 105

Gen. 5. *Acoelocalyx* Topsent, 1910; p. 327

*1 *brucei* Topsent, 1910; p. 105

Gen. 6 *Holascella* Lendenfeld, 1915; p. 327

*1 *ancorata* Lendenfeld, 1915
*2 *euonyx* Lendenfeld, 1915
*3 *taraxacum* Lendenfeld, 1915

Subfam. b Corbitellinae Ijima, 1903
Gen. 1 *Regadrella* Schmidt, 1880; p. 334, 335

1 *cylindrica* Ijima, 1927; p. 335
2 *decora* Schulze, 1900; p. 335
3 *delicata* Wilson, 1904; p. 337
4 *komeyamai* Ijima, 1901; p. 337
5 *okinoseana* Ijima, 1896; p. 335
6 *phoenix* Schmidt, 1880; p. 337

Gen. 2 *Corbitella* Gray, 1867; p. 344

*1 *elegans* (Marshall, 1875)
*2 *pulchra* (Schulze, 1887)
*3 *speciosa* (Quoy & Gaimard, 1833); p. 106

Gen. 3 *Heterotella* Gray, 1867; p. 344

*1 *corbicula* (Bowerbank, 1858)

Gen. 4 *Walteria* Schulze, 1886; p. 343

1 *flemmingi* Schulze, 1886; p. 343
2 *leuckarti* Ijima, 1896; p. 343

Gen. 5 *Dictyaulus* Schulze, 1895

*1 *elegans* Schulze, 1895

Gen. 6 *Dictyocalyx* Schulze, 1886

*1 *gracilis* Schulze, 1886; p. 277

Gen. 7 *Hertwigia* Schmidt, 1880

*1 *falcifera* Schmidt, 1880

Gen. 8 *Trachycaulus* Schulze, 1886

*1 *gurlitti* Schulze, 1886

Gen. 9 *Saccocalyx* Schulze, 1895; p. 276

*1 *pedunculata* Schulze, 1895; p. 279, (h)

Gen. 10 *Rhabdopectella* Schmidt, 1880; p. 276

*1 *tintinnus* Schmidt, 1880; p. 279

Gen. 11 *Hyalostylus* Schulze, 1886

*1 *dives* Schulze, 1886

Gen. 12 *Bolosoma* (Ijima, 1903) Schulze, 1904; p. 334, 340, (b)

1 *cavum* Ijima, 1927; p. 340
2 *paradictyum* (Ijima, 1903); p. 341

Fam. III CAULOPHACIDAE Ijima, 1903
Gen. 1 *Caulophacus* Schulze, 1886, p. 345, 346

*1 *agassizi* Schulze, 1899
*2 *antarcticus* Schulze & Kirkpatrick, 1910
*3 *arcticus* (Hansen, 1885)
*4 *elegans* Schulze, 1886
*5 *instabilis* Topsent, 1910
*6 *latus* Schulze, 1886
7 *oviformis* (Schulze, 1886); p. 345
*8 *pipetta* (Schulze, 1886)
*9 *schulzei* Wilson, 1904
*10 *scotiae* Topsent, 1910
*11 *valdiviae* Schulze, 1904; p. 106

Gen. 2. *Caulophacella* Lendenfeld, 1915; p. 345, 346

*1 *tenuis* Lendenfeld, 1915

Gen. 3 *Sympagella* Schmidt, 1870; p. 345, 346, (h)

*1 *anomala* Ijima, 1903
*2 *cantharellus helix* Lendenfeld, 1915; p. 345, (x)
*3 *cantharellus megonychia* Lendenfeld, 1915; p. 345, (x)
*4 *cantharellus simplex* Lendenfeld, 1915; p. 345, (x)
5 *gracilis* (Schulze, 1903); p. 345
*6 *johnstoni* (Schulze, 1903)
7 *nux* Schmidt, 1870; p. 106

Gen. 4 *Caulodiscus* Ijima, 1927; p. 345, 346, (f)

1 *lotifolium* (Ijima, 1903); p. 345, (f)

Fam. IV ROSSELLIDAE (Schulze, 1886), Ijima, 1903; (b)
Subfam. a Lanuginellinae Schulze, 1897

Gen. 1 *Lanuginella* Schmidt, 1869; p. 352

1 *pupa* Schmidt, 1870; p. 352

Gen. 2 *Lanugonychia* Lendenfeld, 1915; p. 347

1 *flabellum* Lendenfeld, 1915; p. 347

Gen. 3 *Calycosoma* Schulze, 1899; p. 345

1 *validum* Schulze, 1896; p. 345

Gen. 4 *Mellonympha* Schulze, 1897; p. 105, 319

*1 *velata* (Thomson, 1873)

Gen. 5 *Lophocalyx* Schulze, 1887; p. 348

1 *philippinensis* (Gray, 1872); p. 348, 352
2 *spinosa* Schulze, 1900; p. 352
3 *suluana* Ijima, 1927; p. 348, 352, (h)

Subfam. b Rossellinae Schulze, 1897
Gen. 1 *Rossella* Carter, 1872; p. 105, 319

*1 *antarctica antarctica* Carter, 1872; p. 105
*2 *antarctica gaussi* Schulze & Kirkpatrick, 1910
*3 *anarctica solida* Kirkpatrick, 1907
*4 *dubia* (Schulze, 1886)
*5 *fibulata* Schulze & Kirkpatrick, 1910
*6 *gaussi* Schulze & Kirkpatrick, 1910
*7 *lychnophora* Schulze & Kirkpatrick, 1910
*8 *mixta* Schulze & Kirkpatrick, 1910
*9 *nodastrella* Topsent, 1915
*10 *podagrosa* Kirkpatrick, 1907
*11 *racovitzae hexactinophila* Kirkpatrick, 1910
*12 *racovitzae microdiscina* Topsent, 1916
*13 *racovitzae minuta* Schulze & Kirkpatrick, 1910
*14 *racovitzae* [*racovitzae*] Topsent, 1901; (o, y)
*15 *racovitzae racovitzae* Schulze & Kirkpatrick, 1910; (b, y)

Gen. 2 *Aulorossella* Kirkpatrick, 1907; p. 353

*1 *aperta* Topsent, 1916
*2 *gaini* Topsent, 1916
*3 *laevis* Kirkpatrick, 1907
*4 *longstaffi* Kirkpatrick, 1907
*5 *pilosa* Kirkpatrick, 1907
*6 *vanhoeffeni armata* Schulze & Kirkpatrick, 1910
*7 *vanhoeffeni* [*vanhoeffeni*] Schulze & Kirkpatrick, 1910; (o)

Gen. 3 *Gymnorossella* Topsent, 1916; p. 353

*1 *inermis* Topsent, 1916
*2 *nuda* (Topsent, 1901)

Gen. 4 *Scyphidium* Schulze, 1900

*1 *chilense* Ijima, 1904, 1927; (b)
*2 *longispina* (Ijima, 1896)
*3 *namiyei* (Ijima, 1898)
*4 *septentrionale* Schulze, 1900

Gen. 5 *Vitrollula* Ijima, 1898

*1 *fertilis* Ijima, 1898

Gen. 6 *Schaudinnia* Schulze, 1900; p. 105, 319

*1 *arctica* Schulze, 1900; p. 105

Gen. 7 *Crateromorpha* Gray, 1872

*1 *corrugata* Ijima, 1898
*2 *meyeri* [*meyeri*] Gray, 1872
*3 *meyeri rugosa* Ijima, 1898
*4 *meyeri tuberosa* Ijima, 1898
*5 *pachyactina* Ijima, 1898
*6 *thierfelderi* Schulze, 1886
*7 *tumida* Schulze, 1886

Gen. 8 *Hyalascus* Ijima, 1896

*1 *giganteus* Ijima, 1898
*2 *hodgsoni* Kirkpatrick, 1907
*3 *sagamiensis* Ijima, 1896
*4 *similis* Ijima, 1904

Gen. 9 *Anaulosoma* Kirkpatrick, 1907; p. 353

*1 *schulzei* Kirkpatrick, 1907

Gen. 10 *Aulochone* Schulze, 1886

*1 *cylindrica* Schulze, 1886
*2 *lankesteri* (Kirkpatrick, 1902)
*3 *lilium* Schulze, 1886

Gen. 11 *Aulosaccus* Ijima, 1896

*1 *ijimae* (Schulze, 1899)
*2 *misukurii* Ijima, 1898
*3 *schulzei* Ijima, 1896

Gen. 12 *Asconema* Kent, 1870

*1 *setubalense* Kent, 1870

Gen. 13 *Trichasterina* Schulze, 1900; p. 105, 319

1 *borealis* Schulze, 1900; p. 105
*2 *sagittaria* Topsent, 1913

Gen. 14 *Aphorme* Schulze, 1899

*1 *horrida* Schulze, 1899

Gen. 15 *Bathydorus* Schulze, 1886; p. 353

1 *baculifer* Schulze, 1886; p. 355
2 *fimbriatus* Schulze, 1886; p. 355
3 *laevis* [*laevis*] Schulze, 1895; p. 355
*4 *laevis ciliatus* Topsent, 1910
*5 *laevis spinosus* Wilson, 1904
6 *pedunculatus* Ijima, 1927; p. 353
*7 *spinosissimus* Lendenfeld, 1915
8 *spinosus* Schulze, 1886; p. 355
9 *stellatus* Schulze, 1886; p. 355
10 *uncifer* Schulze, 1899; p. 355

Gen. 16 *Anoxycalyx* Kirkpatrick, 1907; p. 353

*1 *ijimai* Kirkpatrick, 1907

Gen. 17 *Scolymastra* Topsent, 1916; p. 353

*1 *joubini* Topsent, 1916

Subfam. c. Acanthascinae Schulze, 1897; (b)
Gen. 1 *Acanthascus* Schulze, 1886; p. 355

*1 *alani* Ijima, 1898
*2 *cactus* Schulze, 1886
*3 *platei* Schulze, 1899

Gen. 2 *Staurocalyptus* Ijima, 1897; p. 355

1 *affinis* Ijima, 1904; p. 357
2 *celebesianus* Ijima 1927; p. 355, (h)
3 *dowlingi* (Lambe, 1893); p. 357

*4 *entacanthus* Ijima, 1904
*5 *fasciculatus* Schulze, 1899
6 *glaber* Ijima, 1897; p. 357
*7 *hamatus* Lendenfeld, 1915
8 *heteractinus* Ijima, 1897; p. 357
9 *microchetus* Ijima, 1898; p. 357
*10 *pleorhaphides* Ijima, 1897
*11 *roeperi* (Schulze, 1886)
*12 *solidus* Schulze, 1899
*13 *tubulosus* Ijima, 1904

Gen. 3 *Rhabdocalyptus* Schulze, 1886; p. 355

*1 *asper* Schulze, 1899
*2 *australis* Topsent, 1901
*3 *baculifer* Schulze, 1904
*4 *capillatus* Ijima, 1897
*5 *dawsoni* (Lambe, 1892); (h)
6 *mirabilis* Schulze, 1899; p. 107, 108
*7 *mollis* Schulze, 1886
*8 *nodulosus* Schulze, 1899
*9 *plumodigitatus* Kirkpatrick, 1901
*10 *tener* Schulze, 1899
*11 *tenuis* (Schulze, 1899)
*12 *unguiculatus* Ijima, 1904
13 *victor* Ijima, 1897; p. 325

Annotations

(a) Ijima suggested transfer of *Poliopogon gigas* to *Pheronema* or to a new unnamed genus.

(b) Authority corrected—name(s), date or punctuation.

(c) Suffix differs from FL or text; form chosen to conform either to text usage or original spelling where recent ICZN rule ammendment permits.

(d) Erroneously treated in FL as a synonym of *H. indicum* and misspelled as "*heymousi.*"

(e) Ijima makes no mention of the two subspecies *H.* (*C.*) *indicum andamanense* (Schulze, 1895) and *H.* (*C.*) *indicum laccadivense* (Schulze, 1895); the species and the two subspecies are erroneously given separate (duplicate) entries in the FL. Distinction of the two subspecies is retained as common for the period.

(f) Name (genus, species or subspecies) was erroneously omitted from FL.

(g) Indication as n. ssp. on p. 55 is erroneous.

(h) Misspelling of FL or text is corrected.

(i) FL entry of subspecies *nicobaricum* and *somalicum* does not agree with text; Ijima may have been "doubtful" that these are specifically distinct (p. 51) but he listed them as recognized species. FL also contradicts Schulze (1904) who, with doubt, recognized *somalicum* as a species but did not mention *nicobaricum.* Both are included here in conformity with Ijima's text list.

(j) FL erroneously contains separate entries for *H.* (*Onconema*) *obtusum* as well as the two constituent varieties: *gracilis* and *robusta*; since Ijima's concept of the varieties (subspecies here) is not stated, they are accepted as for the period.

(k) Ijima clearly dropped the subgenera *Skianema* Lendenfeld, 1915, and *Thallonema* Lendenfeld, 1915, to synonomy with *Oonema* Lendenfeld, 1915, in the text. Their retention in FL, and the position of their contained species, are erroneous.

(l) Ijima did not intend his terse descriptions of *Lonchiphora* and *L. inversa* provided here to constitute formal diagnoses; strict reflection of his opinion would require deletion of these from the corrected FL. However, his intent to provide a more detailed report at a later date was never realized. The information given by Ijima has been accepted by Reid, 1958 and 1963, and by the author as adequate indications for both. The relation of Ijima's "*L.* sp." to *L. inversa* needs reevaluation.

(m) Species and subspecies entries of FL under *Eurete* are particularly troublesome. Text statements clearly indicate Ijima's movement of *E. erectum erectum, E. erectum tubuliferum* and *E. erectum gracile* to *Conorete. E. alicei* Topsent, 1901, is also clearly transferred to *Gym-*

norete alicei (Topsent, 1901). The allocation of *E. erectum* forma D Lendenfeld, 1915, and *E. mucronatum* Wilson, 1904, are not indicated in the text, but symbols on FL are interpreted to reflect Ijima's text implication to transfer these to *Conorete.*

(n) Placement in FL as a subspecies is erroneous; it is a newly described species.

(o) The required nominate subspecies name is inserted by HMR.

(p) FL entry as a full species is erroneous; *japonica* is clearly described as a subspecies of *P. elisae* in the text. There is no earlier use of *P. japonica.*

(q) Ijima's transfer of *C. calyx* Schulze, 1886, and *C. tenerum* Schulze, 1899, and suggested transfer of *H. hamatum* Schulze, 1886, to *Heterochone* are accepted. He made no mention of *H. lamella* subspecies, but they are included with indication of their uncertain status.

(r) Ijima's (p. 210) recognition of *D. crispus* Schmidt, 1870, as a questionable synonym of *Lefroyella decora* Thomson, 1877, is accepted as intent; retention of *D. crispus* in FL is considered erroneous.

(s) The undescribed species, *Gymnorete variolosum* mentioned on p. 120, 166, was a nomen nudem as of 1927. Reference to the ms form *Gymnodictyum variolosum* (p. 164) is taken as a mistaken reference to that species.

(t) Ijima's intent to transfer *Hexactinella labyrinthica* to *Tretodictyum* is ambiguous but accepted.

(u) Ijima's occasional use of "*Tretodictyum spongiosum*" in the text, e.g., p. 209, 236, is nowhere stated to imply taxonomic validity of that combination; these are interpreted to be errors in reference to *Hexactinella spongiosa* Ijima.

(v) Text statements concerning distinction between *A. auricularis* and *filholi* are contradictory; the final text remark is adopted.

(w) Here (p. 297) and in his last (1916) publication, Ijima clearly rejects formal recognition of many historic names for varieties and subspecies of *A. beatrix* (e.g., *bocagei, ramosus* and *azoricus*) and forms of *A. vastus* (*vastus* and *whiteavesianus*). He does, however, maintain distinction of *A. beatrix orientalis* which necessitates acceptance of a named nominate subspecies, *A. beatrix beatrix* Gray, but it is understood to include all of the other poorly known forms not included in *A. beatrix orientalis.* The species status accorded to *A. bocagei, ramosus,* and *whiteavesianus* in FL is contrary to Ijima's concepts.

(x) FL erroneously retains *Calycosilva* Lendenfeld, 1915, and the single species consisting of 3 varieties (here subspecies); the move to *Sympagella* is clearly indicated on p. 345.

(y) Schulze and Kirkpatrick, 1910, employed the nominate trinomial, *Rossella racovitzae racovitzae,* for a form clearly not assignable to Topsent's type; it requires a new subspecific name.

Action List

Taxonomic actions, at and below generic level, which are attributable to Ijima, 1927, are arranged alphabetically within subclass. Newly erected taxa may be indentified by authority on the preceeding Corrected List. Transfer is represented by "origin → final"; synonymy by "junior ⇒ senior"; "?" indicates that Ijima expressed lack of strong conviction for the action or inconsistency in his statements.

AMPHIDISCOPHORA:

aculeatum (Schulze, 1894), p. 50 (*Hyalonema*) → (*Pteronema*).

aequatoriale Lendenfeld, 1915, p. 54 (*Skianema*) → (*Oonema*).

agassizi (Lendenfeld, 1915), p. 53 (*Hyalonema*) → (*Onconema*).

alcocki (Shulze, 1895), p. 52 (*Hyalonema*) → (*Paradisconema*).

apertum apertum (Schulze, 1886), p. 51 (*Hyalonema*) → (*Cyliconema*).

apertum maehrenthali (Schulze, 1895), p. 51 (*Hyalonema*) reinstated and → (*Cyliconema*).

calix (Schulze, 1904), p. 53 (*Hyalonema*) → (*Corynonema*).

cebuense (Higgin, 1875), p. 50 (*Hyalonema*) → (*Pteronema*).

clathratum (Ijima, 1895), p. 53 (*Hyalonema*) → (*Corynonema*).

clavigerum (Schulze, 1886), p. 53 (*Hyalonema*) → (*Corynonema*).

coniforme (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

conus (Schulze, 1886), p. 51 (*Hyalonema*) → (*Coscinonema*).

cupresiferum (Schulze, 1893), p. 53 (*Prionema*) ?→ (*Corynonema*).

depressum (Schulze, 1886), p. 53 (*Leptonema*) ?→ (*Corynonema*).

drygalskii (Schulze, 1910), p. 51 (*Hyalonema*) → (*Cyliconema*).

elegans (Schulze, 1886), p. 51 (*Hyalonema*) ?→ (*Coscinonema*).

fruticosum Schulze, 1893, p. 37 *Hyalonema* ?→ *Monorhaphis*.

geminatum Lendenfeld, 1915, p. 54 (*Thallonema*) → (*Oonema*).

gigas Schulze, 1902, p. 9, *Poliopogon* ?→ *Pheronema*.

globiferum (Schulze, 1904), p. 51 (*Oonema*) → (*Cyliconema*).

globus (Schulze, 1886), p. 50 (*Hyalonema*) → (*Pteronema*).

gracile (Schulze, 1886), p. 51 (*Hyalonema*) ?→ (*Coscinonema*).

grandancora (Lendenfeld, 1915), p. 53 (*Hyalonema*) → (*Corynonema*).

heideri (Schulze, 1894), p. 50 (*Hyalonema*) → (*Pteronema*).

hercules (Schulze, 1899), p. 53 (*Hyalonema*) → (*Corynonema*).

heymonsi Schulze, 1895, p. 51 (*Hyalonema*) → (*Coscinonema*).

(*Hyalonema*) s. restr. Lendenfeld, 1915, p. 49, 50 subdivided to 7 new subgenera: (*Euhyalonema*), (*Pteronema*), (*Coscinonema*), (*Cyliconema*), (*Paradisconema*), (*Corynonema*), (*Onconema*).

indicum (Schulze, 1895) p. 51 (*Hyalonema*) with 2 ssp. → (*Coscinonema*).

infundibulum (Topsent, 1896), p. 51 (*Hyalonema*) → (*Cyliconema*).

investigatoris (Schulze, 1900), p. 52 (*Hyalonema*) → (*Paradisconema*).

kenti (Schmidt, 1880), p. 51 (*Hyalonema*) → (*Coscinonema*).

lamella (Schulze, 1900), p. 51 (*Hyalonema*) → (*Coscinonema*).

lusitanicum (B. d. Bocage, 1864), p. 52 (*Prionema*) → (*Leptonema*).

martabanense (Schulze, 1900), p. 51 (*Hyalonema*) → (*Cyliconema*).

masoni (Schulze, 1895), p. 53 (*Hyalonema*) → (*Corynonema*).

molle (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

nicobaricum (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

obtusum (Lendenfeld, 1915), p. 53 (*Hyalonema*) with 2 ssp. → (*Onconema*).

ovatum (Ijima, 1895), p. 51 (*Hyalonema*) → (*Cyliconema*).

ovuliferum (Schulze, 1899), p. 52 (*Oonema*) → (*Leptonema*).

owstoni (Ijima, 1894), p. 53 (*Hyalonema*) → (*Corynonema*).

pateriferum (Wilson, 1904), p. 51 (*Phialonema*) → (*Coscinonema*).

pellucidum (Ijima, 1894), p. 50 (*Phialonema*) → (*Euhyalonema*).

pirum (Schulze, 1895), p. 51 (*Hyalonema*) → (*Cyliconema*).

placuna (Lendenfeld, 1915), p. 53 (*Hyalonema*) → (*Corynonema*).

polycaulum (Lendenfeld, 1915), p. 50 (*Hyalonema*) → (*Pteronema*).

populiferum (Schulze, 1899), p. 53 (*Hyalonema*) → (*Corynonema*).

proximum (Schulze, 1904), p. 50 (*Hyalonema*) → (*Euhyalonema*).

rapa (Schulze, 1900), p. 51 (*Hyalonema*) → (*Cyliconema*).

schmidti (Schulze, 1899), p. 51 (*Hyalonema*) → (*Coscinonema*).

sieboldi (Gray, 1835), p. 28, 50 (*Hyalonema*) → (*Euhyalonema*).

simile (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

(*Skianema*) Lendenfeld, 1915, p. 49 ⟹ (*Oonema*) Lendenfeld, 1915.

somalicum (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

tenerum (Schulze, 1886), p. 51 (*Oonema*) → (*Cyliconema*).

tenuifusum (Lendenfeld, 1915), p. 53 (*Hyalonema*) → (*Corynonema*).

(*Thallonema*) Lendenfeld, 1915, p. 49 ⟹ (*Oonema*) Lendenfeld, 1915.

thomsonis (Marshall, 1875), p. 51 (*Hyalonema*) → (*Cyliconema*).

toxeres (Thomson, 1877), p. 51 (*Hyalonema*) → (*Coscinonema*).

tulipa (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

tylostylum (Lendenfeld, 1915), p. 53 (*Hyalonema*) → (*Corynonema*).

umbraculum Lendenfeld, 1915, p. 54 (*Skianema*) → (*Oonema*).

valdiviae (Schulze, 1904), p. 51 (*Hyalonema*) → (*Cyliconema*).

weltneri (Schulze, 1895), p. 53 (*Hyalonema*) → (*Corynonema*).

HEXASTEROPHORA:

alicei Topsent, 1901, p. 166 *Eurete* → *Gymnorete.*

annandalei Kirkpatrick, 1908, p. 166 *Eurete* → *Pleurochorium.*

Calycosilva Lendenfeld, 1915, p. 345 ⟹ *Sympagella* Schmidt, 1870.

calyx Schulze, 1886, p. 118, 284 *Chonelasma* → *Heterochone.*

cantharellus Lendenfeld, 1915, p. 345 *Calycosilva* with 3 ssp. implied → *Sympagella.*

carteri Schulze, 1886, p. 166, 178 *Eurete* → *Pararete.*

Chonelasma Schulze, 1886, p. 118, 284 part → *Heterochone* Ijima, 1927.

clavigera (Schulze, 1887) Topsent, 1904, p. 137 *Claviscopulia* → *Farrea occa clavigera* (Schulze, 1887).

conicum Schmidt, 1880, p. 214 *Scleroplegma* → *Myliusia.*

doederleini Schulze, 1886, p. 165 *Chonelasma* → *Ptychodesia.*

erectum Schulze, 1899, p. 166 *Eurete* → *Conorete.*

farreopsis Carter, 1877, p. 166, 178 *Eurete* → *Pararete farreopsis farreopsis.*

filholi Topsent, 1904, p. 112, 231, 244 *Hexactinella* ?→ *Auloplax.*

gerlachei Topsent, 1901, p. 166 *Eurete* → *Pararete.*

hamatum Schulze, 1886, p. 284 *Chonelasma* ?→ *Heterochone.*

ingalli Bowerbank, 1869, p. 214 *Iphiteon* → *Dactylocalyx.*

labyrinthica Wilson, 1904, p. 231 *Hexactinella* ?→ *Tretodictyum.*

latum Schulze, 1886, p. 220, 231 *Tretodictyum* → *Hexactinella.*

Leucopsacus Ijima, 1898, p. 320 → *Leucopsacas* (spelling correction).

lotifolium Ijima, 1903, p. 345 *Caulophacus* → *Caulodiscus.*

monticularis (Lendenfeld, 1915), p. 231 *Hexactinella* → *Tretocalyx.*

occa Bowerbank, 1862, Carter, 1885, p. 131 → *Farrea occa occa* Bowerbank, 1862, Carter, 1885.

oviformis (Schulze, 1886), p. 345 *Pleorhabdus* implied → *Caulophacus.*

Pleorhabdus (Schulze, 1887), p. 345 ⟹ *Caulophacus* Schulze, 1886.

Ramella Schulze, 1904, p. 130 ⟹ *Sarostegia* Topsent, 1904.

schmidti Schulze, 1886, p. 171 *Eurete* → *Eurete schmidti schmidti.*

schulzei Topsent, 1890, 1892, 1901, 1904, p. 205 *Chonelasma* ⟹ *Periphragella lusitanica* Topsent.

semperi (Schulze, 1886), p. 166 *Eurete* → *Pararete.*

subglobosus Gray, 1867, p. 214 *Dactylocalyx* ?→ *Myliusia.*

subglobosus of Schmidt, 1880 & Schulze, 1887, p. 214 *Dactylocalyx* ? ⟹ *Dactylocalyx ingalli* (Bowerbank).

Syringidium Schmidt, 1880, p. 210 ⟹ *Lefroyella* Thomson, 1877.

tenerum Schulze, 1899, p. 284 *Chonelasma* → *Heterochone.*

tubulosa Schulze, 1904, p. 130 *Ramella* ? ⇒ *Sarostegia oculata* Topsent, 1904.

zitteli Schmidt, 1880, p. 210 *Syringidium* ⇒ *Lefroyella decora* Thomson, 1877.

Acknowledgments

This work was supported by an operating grant from the Natural Sciences and Engineering Research Council of Canada.

Literature Cited

Burton, M. 1928. Porifera or Spongida.—The Zoological Record [1927] 64(III):1–11.

———. 1954. Sponges (*Rosaura* Expedition).—Bulletin of the British Museum (Natural History), Zoology 2:215–239, pl. 9.

Hartman, W. D. 1982. Porifera. Pp. 640–666 *in* S. P. Parker, ed., Synopsis and classification of living organisms, volume 1. McGraw Hill, New York.

Ijima, I. 1916. Notes on *Aphrocallistes beatrix* Gray, particularly with reference to the form occurring in East Asiatic Seas.—Annotationes Zoologicae Japonenses IX:173–183.

———. 1927. The Hexactinellida of the *Siboga* Expedition. *Siboga* Expedition reports, volume 6. E. J. Brill, Leiden, i–vii, 1–383, pls. 1–26.

Koltun, V. M. 1967. (Vitreous sponges of the northern and far-eastern seas of the USSR.) (In Russian).—Opredeliteli po Faune SSSR, Izdavayemyye Zoologicheskik Institutom Akademii Nauk SSSR 94:1–124.

Laubenfels, M. W. de. 1936. A discussion of the sponge fauna of the Dry Tortugas, in particular, with material for a revision of the families and orders of the Porifera.—Carnegie Institution of Washington Publication 467:1–225, pls. 1–22.

Reid, R. E. H. 1957. Notes on the hexactinellid sponges. II. *Dactylocalyx* Stutchbury and the family Dactylocalycidae Gray.—Annals and Magazine of Natural History (12)10:821–826.

———. 1958. A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part II.—Paleontographical Society of London CXII:xlvii–xlviii, 1–26, pls. I–IV.

———. 1963. Notes on a classification of the Hexactinosa.—Journal of Paleontology 37:218–231.

Reiswig, H. M. 1979. Histology of Hexactinellida (Porifera). Pp. 173–180 *in* C. Levi & N. Boury-Esnault, eds., Biologie des spongiaires. Centre National de la Recherche Scientifique, Paris.

Schulze, F. E. 1904. Hexactinellida. Wissenschafliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "*Valdivia*" 1898–1899, Band IV. Gustav Fisher, Jena, i–viii, 1–266, 52 Taf.

Schulze, F. E. & R. Kirkpatrick. 1910. Die Hexactinelliden der deutschen Südpolar-Expedition 1901–1903.—Deutsche Südpolar-Expedition 1901–1903, Band 12, Heft 1, G. Reimer, Berlin, 1–62, 10 Taf.

Tuzet, O. 1973. Hexactinellides ou Hyalosponges. Pp. 633–690 *in* P.-P. Grasse, ed., Traite de Zoologie, III Spongiaires. Masson et Cie, Paris.

Redpath Museum and Biology Department, McGill University, 859 Sherbrooke St. West, Montreal, Quebec, Canada H3A 2K6.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 746–768

TWO NEW SPECIES OF *CENTROLENELLA* (ANURA: CENTROLENIDAE) FROM NORTHWESTERN PERU

John E. Cadle and Roy W. McDiarmid

Abstract.—Two new species of *Centrolenella* are described from the Pacific versant of the Andes in northern Peru (Río Zaña, Cajamarca Department). These constitute the first records for the genus on the western slopes of the Andes in Peru. *Centrolenella euhystrix,* a large species (males to 31.3 mm, females to 33.6 mm snout–vent length), has a distinctive coloration (dark greenish black when active at night), broad digits, and large hands. Males of this species have very spinose dorsal skin and lack humeral spines. Although males of *C. euhystrix* call from rock ledges in or along cascading streams, an unusual calling site for *Centrolenella,* neither egg masses nor reproduction were observed in this species. *Centrolenella hesperia* is a smaller species (males to 27.3 mm, females to 28.8 mm snout–vent length) which lacks a typanum, is bright green when active, and has a distinctive lateral white stripe from the snout to the groin. Males of this species have spinose dorsal skin and humeral spines. The reproductive behavior, vocalizations, and larval morphology of *C. hesperia* are similar to those known for other species of *Centrolenella* except that females have an unusual behavior at the clutch and egg masses contain empty capsules. The intercalary elements in these species are mineralized; the nature of this element in the Centrolenidae and other frogs is discussed.

Resumen.—Se describen dos nuevas especies de *Centrolenella* de la vertiente pacífica de los Andes en el norte del Perú (Río Zaña, Departamento de Cajamarca). Estas especies se componen el primer registro del género en Perú occidental. *Centrolenella euhystrix* es una especie grande (los machos alcanzan a 31.3 mm de longitud corporal y las hembras a 33.6 mm) que tiene una coloración distintiva (negro verdoso oscuro durante la actividad nocturnal), los dedos anchos, y las manos grandes. Los machos de esta especie son muy espinosos y carecen de espinas humerales. Aunque los machos de *C. euhystrix* cantan desde anaqueles rocosos en torrentes, o a lo largo de los mismos, un sitio de canto poco frecuente para *Centrolenella,* ni masas de huevos ni la reproducción fueron observadas en esta especie. *Centrolenella hesperia* es una especie más pequeña (machos hasta 27.3 mm de longitud corporal, hembras hasta 28.8 mm) que carece de un tímpano, es verde brillante cuando está activa, y tiene una raya lateral blanca desde el hocico hasta la ingle. Los machos de esta especie son también espinosos y tienen espinas humerales. El comportamiento reproductivo, las vocalizaciones, y la morfología larval de *C. hesperia* son similares a aquellas conocidas de otras especies de *Centrolenella,* menos que las hembras muestran un comportamiento extraña a la nidada, y que las masas de huevos contienen cápsulas vacias. Los elementos intercalares de estas especies están mineralizados; se discute la forma de este elemento en las Centrolenidae y otras ranas.

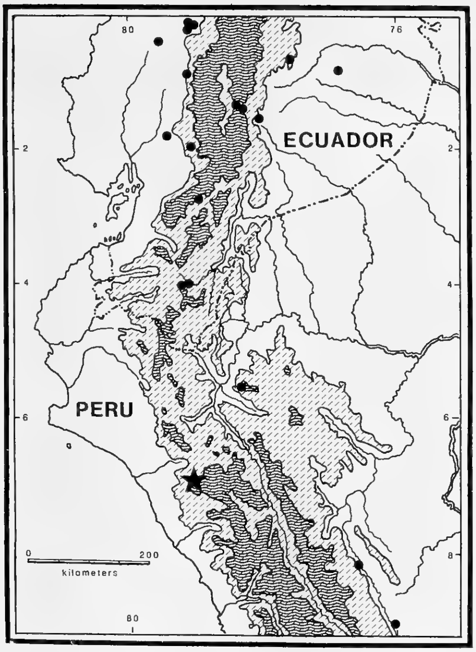


Fig. 1. Map of the central Andes of southern Ecuador and northern Peru showing the Monte Seco area (star), the type locality for *Centrolenella euhystrix* and *C. hesperia,* and all other localities (dots) at which species of *Centrolenella* are known to occur. The light hatching indicates areas between 1000 m and 3000 m; darker areas indicate those regions above 3000 m. The Huancabamba Depression of northern Peru and southern Ecuador has only a few, disjunct areas above 3000 m.

Many frogs of the genus *Centrolenella* (Centrolenidae) are known from the eastern Andean slopes of Colombia, Ecuador, and Peru (Frost 1985), and new species are being discovered at an astonishing rate (Duellman & Burrowes 1989; Flores 1985, 1987; Flores & McDiarmid 1989). Cannatella & Duellman (1982) noted 10 species in Peru (nine discovered since the mid-1970s), and indicated five undescribed species from the Amazonian slopes. Although *Centrolenella* is known from the western foothills and slopes of the Andes in Colombia and Ecuador, none has been reported from Peru's western slopes. Herein we describe two species from the Pacific versant of northern Peru about 350 km south of the nearest reported localities on the Pacific versant in Ecuador, and about 175 km southwest of the nearest reported locality (Cannatella & Duellman 1982) on the Amazonian versant of Peru (Fig. 1).

Cadle collected during the periods 1 May to 25 June, 1987 and 13 to 31 January, 1989, near Monte Seco, a coffee cooperative at 1200 m in the valley of the Río Zaña, Department of Cajamarca, Peru (Fig. 2). Although the coast and western slopes of the Peruvian Andes are generally arid and support primarily desert or dry scrub forest, local conditions sometimes permit more mesic environments, particularly in northern Peru (Koepcke 1961). The slopes north and east of Monte Seco above about 1500 m support a wet forest that receives heavy rains from January to April, and that is enveloped by dense clouds for at least the early part of the dry season (May to December). Frogs were collected near streams and waterfalls whose headwaters originate on a ridge north and east of Monte Seco. Locally, the highest mountains extend to about 3000 m elevation.

Methods and Materials

Using dial calipers, we measured to the nearest 0.1 mm as follows: snout–vent length (SVL), straight line from tip of head to vent; head length (HL), angle of the jaw to tip of the head; head width (HW), width of the head at the angle of the jaw; snout length (SL), anterior border of eye to tip of head; eye diameter (ED), measured in the horizontal plane; eye to nostril (EN), anterior border of eye to middle of the nostril; tympanum width (TW), measured in horizontal plane; tibia length (TL), measured with the limb flexed; hand length (HnL), from the proximal border of the outer palmar tubercle to tip of digit III. Webbing formula notations follow Savage & Heyer (1967), as modified by Myers & Duellman (1982). In determining webbing formulae, we used the point of intersection of the web base with a

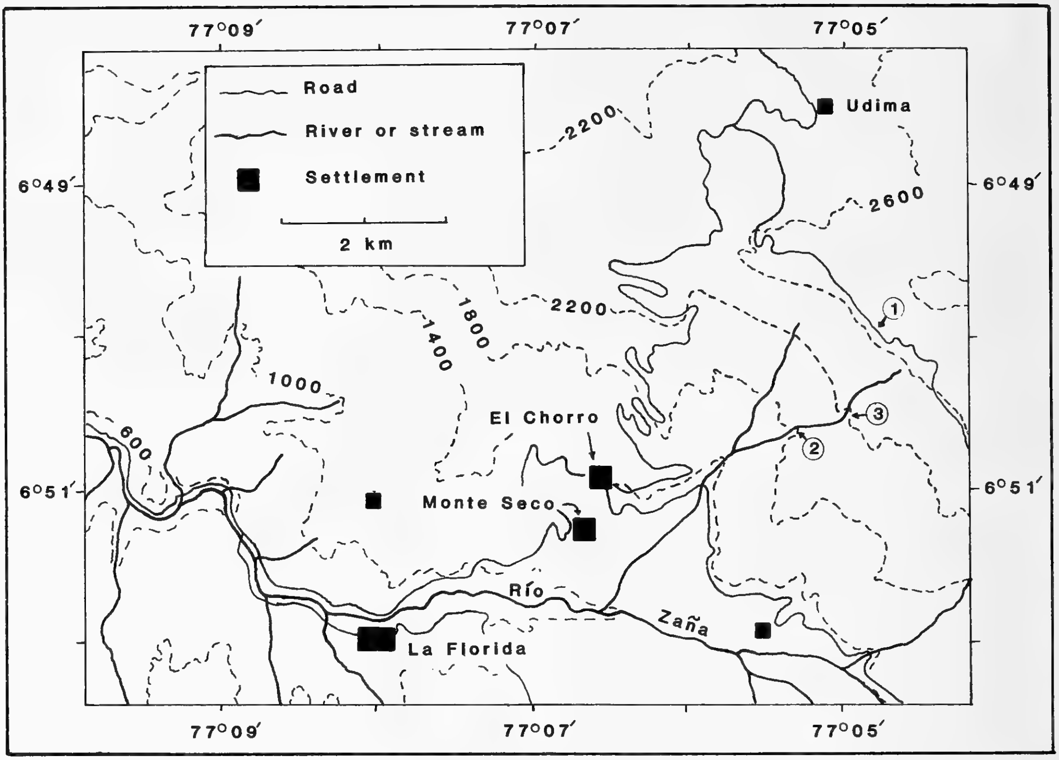


Fig. 2. Map of the Monte Seco region showing type localities and local place-names. Numbered sites refer to the following: (1) Type locality for *Centrolenella euhystrix*; (2) Type locality for *Centrolenella hesperia*; (3) "Chorro Blanco"—a waterfall and local landmark. Cadle's field camps were near site 2. Contours are in meters.

perpendicular drawn to the digit at that point. Digit lengths were determined as the relative extent of digit protrusion from the hand or foot. Nuptial pads were classified according to Flores (1985). Developmental stages follow Gosner (1960), and tadpole terminology follows Altig (1970).

We recorded calls of one species with a SONY ECM-929LT microphone and Walkman Professional® cassette tape recorder. A copy of the tape has been deposited in the tape archive, Division of Amphibians and Reptiles, National Museum of Natural History. These calls were analyzed using a Kay Digital Sona-Graph 7800 and a Multigon Uniscan II real-time analyzer. Pulse rates and call lengths were measured from waveform analyses or from wide-band audiospectrograms. Call rates were measured from the real-time analyzer screen.

Two specimens cleared and double-stained for cartilage and bone using the method of Dingerkus & Uhler (1977) were used for osteological descriptions. Museum depositories for specimens are abbreviated as in Leviton et al. (1985), except for the museum formerly known as the Museo de Historia Natural "Javier Prado" (MHNJP) in Lima, Peru. This museum, presently known as the Museo de Historia Natural de San Marcos, is abbreviated as MHNSM.

Descriptions

Centrolenella euhystrix, new species
Figs. 3–5

Holotype.—Field Museum of Natural History (FMNH) 232510 (field number J. E. Cadle 7628), an adult male, taken from the ridge above basecamp (near Chorro

Blanco), about 4–4.5 km (airline) NE of Monte Seco, Río Zaña, Department of Cajamarca, Peru, 2610 m. (Fig. 2). Collected 16 May 1987 by J. E. Cadle.

Paratypes.—Fifteen specimens with the following data: FMNH 232509 (adult male), 232511 (adult male, cleared and stained), 232513–14 (adult male and female respectively), and MHNSM 3501 (adult female), from about 4.5 km (airline) NE of Monte Seco, 2630 m, 2 June 1987; USNM 292588 (adult female) and ANSP 31574–75 (adult female and male respectively), from 4 km (airline) NE of Monte Seco, 2550–2650 m, 23–24 January 1989; FMNH 232512 (adult male collected 7 May 1987), 231763 (subadult collected 24 June 1987), 231770 (adult male collected 24 June 1987), MHNSM 3502 (adult male), 3503 (subadult male), 3504 (adult female), collected 6 May 1987, and USNM 292587 (adult male), collected 28 January 1989, all from basecamp on trail between Monte Seco and Chorro Blanco, about 2.5 km (airline) NE of Monte Seco, 1800 m.

Definition.—The following diagnostic features (Lynch & Duellman 1973, Flores 1985) distinguish *C. euhystrix* from other *Centrolenella* species: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white, visceral peritoneum clear; (4) color in life: when active at night, dark greenish black with lighter green spicules; when concealed during day, nearly black; when active during day, dark green (brownish in sunlight) with light green spicules; color in preservative: dark gray to medium gray with white spicules; (5) finger webbing (I–II(2^-)–(3.5)III(2.5)–(2^+)IV; (6) toe webbing I(1)–(2^-)II(1^-)–(2^+–2.5)III(1^-)–(2.5)IV(3^-)–(1)V; (7) head round in dorsal outline; snout truncate from above and truncate (slightly rounded in some females) in profile; (8) dorsal skin texture finely spinose with large pointed spicules in males, smoother in females; (9) ulnar and tarsal ridges absent; (10) no humeral spine; (11) tympanum two-thirds to completely visible; (12) prepollex well developed, no externally visible prepollical spine; (13) nuptial excrescences white, forming large Type I pad; (14) no lateral glands; one pair of tubercles ventral to cloacal opening.

Description.—Head distinct, wider than body, wider than long, round in outline (most easily seen from below). Snout protruding, forming anterior outline of head viewed from above, truncate (occasionally with weak point) from above and truncate to slightly rounded (females) in profile, SL about 23% of HL; canthus rostralis straight, distinct, rounded in section; loreal region shallowly concave; lips not or only slightly flared. Nostril small, slit-like to elliptical, directed laterally on protuberance; internarial area flat to slightly concave. Eye moderate, directed slightly anterior of anterolaterally (>135°). Tympanum distinct, heavily pigmented, two-thirds to completely visible, dorsomedially inclined, posterolaterally directed; usually smooth or with low spicule; annulus tympanicus indicated as elevated and unpigmented border along anteroventral third to lower two-thirds of tympanum. Supratympanic fold heavy, especially in males, sometimes covering up to one-third of tympanum. Tongue round to weakly cordate. Vomerine teeth absent. Choanae round to slightly elongate, occasionally slightly rectangular, about size of subarticular tubercle on finger III, separated by distance 5.5 times their diameter. Vocal slits paired, elongate, posterolateral to tongue.

Dorsal skin texture of males finely spinose with large, white (in preservative), pointed (often more rounded medially) spicules; spicules sparsely distributed on snout and dorsum of head and best developed dorsolaterally, above tympanum, and on upper arms (Fig. 3); dorsal surfaces of limbs spiculate; spicules present on sides of head and legs, extending onto lateral sides of foot to basal part of digit V; lateral parts of body and dorsal surface of hands smooth. Dorsal skin of females much smoother,

Fig. 3. Adult male *Centrolenella euhystrix* (SVL 31.3 mm, FMNH 232513), collected on 2 June 1987 from about 4.5 km (airline) NE of Monte Seco, 2630 m, Department of Cajamarca, Peru.

spicules absent (usually) or sparsely distributed on sides of head, dorsolateral surface of body, and on limbs. Skin on belly variable (possible preservation artifact), nearly smooth or weakly to coarsely granulose, sometimes areolate; pectoral area and throat smooth; ventral surfaces of thighs weakly granulose. Moderately to poorly developed pair of cloacal (ventral to pubis) tubercles. Cloacal opening high between thighs; covered by moderately large flap with straight or slightly incised edge; flap margin smooth to crenulate; cluster of 0–9 spicules on each side below the opening.

Hands large (HnL/HL, 1.22); digits very wide, lateral ridges along all fingers. Digit lengths of hand I < II < IV < III; webbing absent between I and II, basal between II and III, moderate between III and IV; webbing formula I–II(2^-)–(3.5)III(2.5)–(2^+)IV. Thumb tip expanded, disc I 60% width of discs III or IV; discs on fingers II–IV expanded, broader than disc I, those of III and IV about equal in width. Prepollical area enlarged, no external prepollical spine. Nuptial excrescences large, whitish, Type I. Subarticular tubercles present, that on finger IV largest. Inner metacarpal tubercle elongate; outer tubercle more elliptical, equal to or slightly smaller than inner. Small palmar tubercles at base of fingers. No fringes or tubercles along outer edge of forearm. Forearm larger than upper arm; no obvious sexual dimorphism. No humeral spine.

Digit lengths on foot I < II < III <=> V < IV. Webbing extensive, toe webbing formula I(1)–(2^-)II(1^-)–(2^+–2.5)III(1^-)–(2.5)IV(3^-)–(1)V. All toe discs expanded; tip on toe I 60% of that on toe IV; discs on toes III–V about equal in size. No tarsal fold. Subarticular tubercles moderate, rounded, about of equal size. Distinct inner metatar-

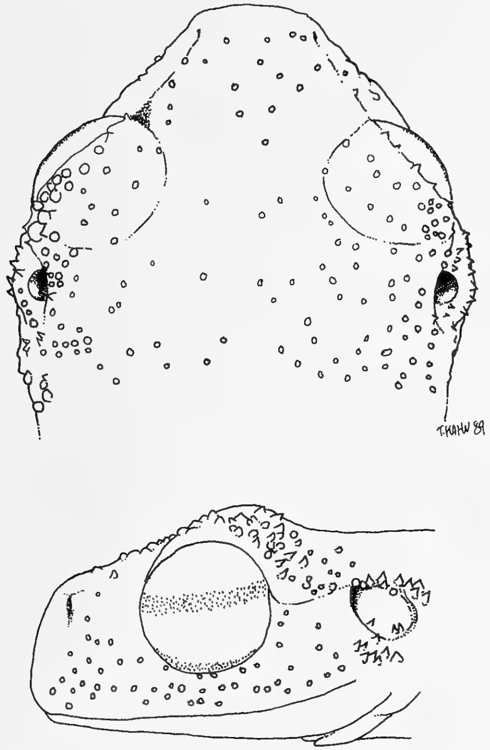


Fig. 4. Dorsal and lateral views of the head of the holotype of *Centrolenella euhystrix* (male, SVL 31.1, FMNH 232510).

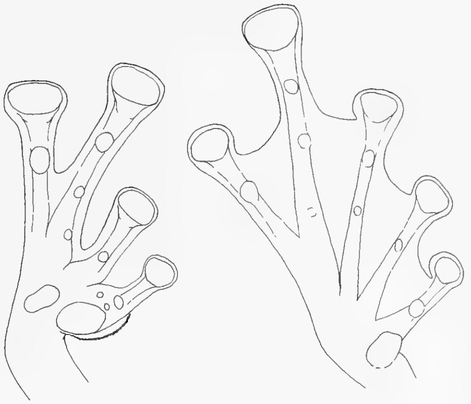


Fig. 5. Diagrammatic representations of the right hand and foot of the holotype of *Centrolenella euhystrix* (male, SVL 31.1, FMNH 232510).

sal tubercle, width about equal to tip of digit I; outer tubercle small, poorly developed.

Snout–vent lengths of adult males 28.5–31.3 mm; of adult females 31.1–33.6 mm.

Coloration.—In life the dorsum is dark greenish black in active individuals, and dark green in inactive ones. The head (especially eyelids and lips), back, and limbs of males are densely covered with large, light green spicules, lighter than dorsal ground color and giving a finely spotted appearance to dorsum. Females generally have smooth skin with few spicules on forelimbs, upper lip, and shank, and generally lack the spotted appearance. The venter is greenish with yellow wash on anterior belly region. The parietal peritoneum is white over anterior half of belly. The feet and hands are clear or greenish yellow with dull yellowish wash; the webbing is transparent yellowish. The bones are green. The irises of female (MHNSM 3504) and subadult male (MHNSN 3503) were "gray with fine black irregular reticulations" (Cadle, field notes); that of adult male (FMNH 232512) deep medium brown. In bright sunlight the dorsum changes to light greenish gray.

Centrolenella euhystrix is capable of rapid color changes from a uniform black to dull dark green. When collected, the holotype was totally black dorsally, with some yellow on the palmar and plantar surfaces, matching the black log under which it was found. After a short time in the collecting bag, this frog turned a dull dark green.

In preservative, dorsal surfaces of head, body, and limbs of males dark gray to medium gray, tubercles white; dorsal surfaces of hands, feet, and webbing pale gray; flanks gray, gradually lightening ventrally; venter creamish gray, palest on proximal parts of thighs and pectoral region; some males dark gray on chest and throat; nuptial excrescences creamish. Females pale to dark gray dorsally; creamish to gray ventrally. Nictitating membrane covered with gray melanophores except in central portion of upper half, which lacks pigment.

Measurements of holotype.—SVL—31.1;

HL—9.7; HW—11.0; ED—3.1; EN—2.2; SL—4.7; TW—0.65; TL—15.9; HnL—11.8.

Osteology.—A cleared and stained male specimen of *C. euhystrix* (SVL 31.0; FMNH 232511) has the prepollex completely enclosed within thumb base; the prepollex extends about 80% the length of metacarpal I. The tip of the prepollex is distinct, cartilaginous, with some mineralization (see Discussion for use of this term). Metacarpal III bears a medially projecting bony flange near the midpoint. Digit tips are T- to slightly Y-shaped; the intercalary elements are mineralized. The proximal flange (deltoid crest) of the humerus is about 45% the length of the bone; it lacks a projecting spine. The vomers are widely separated medially, embedded in the large cartilaginous floor of the nasal capsule, and lack teeth. The frontoparietal fontanelle is large; the anterior projections of the frontoparietals on the skull table overlap the sphenethmoid. The parasphenoid does not reach the level of the palatines. On the lateral surface of the braincase, the sphenethmoid is separated by a small cartilaginous gap from the posterior portions of the cranium. Quadratojugals are present but do not articulate with the maxilla. A cartilaginous annulus tympanicus and bony columella are present.

The hyoid of *Centrolenella euhystrix* differs from that illustrated by Eaton (1958, fig. 5) for *C. prosoblepon.* Eaton indicated only the bony posteromedial processes of the hyoid plate (Duellman & Trueb 1986, fig. 13.21), whereas the hyoid of *C. euhystrix* bears cartilaginous anterolateral and posterolateral processes as well. David C. Cannatella (pers. comm.) informed us that these processes are typical of *Centrolenella* hyoids and that Eaton's figure is erroneous in these details. In general form the hyoid of *C. euhystrix* is similar to that illustrated for *Leptodactylus ocellatus* by Duellman & Trueb (1986, fig. 13.21D). The hyoid plate is broad, about 1.5 times as wide as long. The tips of the anterolateral processes are flared distally. The posterolateral processes are slightly longer than the anterolateral processes, and tapered distally. The only bony elements of the hyoid are the posteromedial processes.

All digits have intercalary elements between the penultimate and ultimate phalanges, and in all cases these elements are mineralized (i.e., they stain red with alizarin; see Discussion for further consideration of terminology). In the hand the intercalary elements are as wide as the distal ends of the penultimate phalanges. They are proximo-distally compressed with the proximal surface slightly convex and the distal surface concave. The intercalary elements in the feet are of the same general form as on the forelimb. The epiphyses of all phalanges are well-mineralized.

Natural history notes.—At night, individuals of *Centrolenella euhystrix* were active mostly on vertical rockfaces in the splash/spray zone of waterfalls, on rock ledges (upper or lower surfaces) in or around waterfalls, and on liverwort- and moss-covered wet boulders in midstream. Most were located by eye-shine. Many individuals were observed on rock ledges in waterfalls 6–8 m high, but were too high to collect. At night their dark greenish bodies were difficult to see against the mosses and liverworts that usually cover their perches. A juvenile male (MHNSM 3503; 28.3 SVL) clung to a twig hanging from a vertical rock face 0.8 m above the water in a waterfall spray zone. Another individual was perched on a leaf over water at night. The holotype, the only individual found by day, was under a log in a pile of debris in the middle of a stream. In general, *C. euhystrix* seems to prefer microhabitats along streams close to water splashing or pouring over rocks.

Observations of the behavior of adult *C. euhystrix* are similar to those reported for *Centrolene geckoideum* in Colombia (Lynch et al. 1983). These authors reported female and calling male *Centrolene* on vertical or overhanging rock faces in the spray zones of waterfalls, and egg masses attached to the same rock faces. Given that virtually all individuals of *C. euhystrix* were associated with rock faces near or in waterfalls and that no egg masses attributable to this species were found attached to vegetation, we consider it possible that eggs of this species are attached to rocks as in *Centrolene.* Such behavior has not been reported for any species of *Centrolenella.*

Vocalization and reproductive behavior.—Males called from rock ledges or vertical faces at two sites around waterfalls at about 2600 m on 2 June. A lone male called from a large boulder 20 cm above a stream at 1800 m on 6 May. The call sites often were within the splash zone of small waterfalls and on dripping rock faces covered with mosses and liverworts. The call is a short "click" or "chirp" usually given as two notes in rapid succession; occasionally a call consisted of only a single note. Although no individuals were heard calling in January 1989, the noise from the torrential streams which are excessively swollen during the rainy season, may have precluded hearing the calls. One female (MHNSM 3504) was collected 0.3 m above the rushing stream and was difficult to see on the bryophyte-covered rock. Two frogs were found in close proximity on a vertical rock face in a spray zone of a waterfall on 23 January. The male (ANSP 31575) was above the female (ANSP 31574) but mostly lateral to her body, and the pair was not observed in amplexus. Possibly, the pair had been disturbed by the observer before they were noticed. The male rapidly ascended the rockface when a light was shone on them. No egg masses that we could attribute to this species were found.

Distribution.—*Centrolenella euhystrix* is known only from two streams at the type locality and from about 2.5 km (airline) NE of Monte Seco at 1800 m along a trail to Chorro Blanco (Fig. 2). Monte Seco is a coffee cooperative located approximately 80 km ESE of Chiclayo. The type locality is along an abandoned logging road that parallels the ridge to the northeast of Monte Seco. Chorro Blanco is a waterfall near the site of Cadle's field camp. The recorded elevational range is 1800 m to 2630 m.

Etymology.—The specific epithet "euhystrix" is derived from the Greek word "hystrix," meaning porcupine, and the prefix "eu," meaning very. We use it as a noun in apposition to refer to the very spiny, porcupine-like dorsum of males of *euhystrix,* which for a centrolenid is quite unusual.

Centrolenella hesperia, new species

Figs. 6–8

Holotype.—Field Museum of Natural History (FMNH) 236200 (field number J.E. Cadle 9260), an adult male, taken near the basecamp on trail between Monte Seco and Chorro Blanco, about 2.5 km (airline) NE of Monte Seco, Río Zaña, Department of Cajamarca, Peru, 1800 m (Fig. 2). Collected 28 Jan 1989 by J. E. Cadle.

Paratypes.—Sixty-seven specimens with the following data: FMNH 232495, 232503 (adult females), 232496–232501, 232504–232508 (adult males), 232502 (adult male, cleared and stained), and MHNSM 3505–3507 (adult males), 3508–3509 (adult females), collected between 6 and 17 May 1987; USNM 292582, 292584 (adult males), 292583 (adult female), and ANSP 31576, 31586, 31588 (adult females), 31577–85, 31587 (adult males) collected 14 Jan 1989; USNM 292585 (adult male) and ANSP 31601–06, 31608 (adult males), 31607 (adult female) collected 18 Jan 1989; USNM 292586 (adult male) and ANSP 31609–13, 31615–18 (adult males) and 31614 (adult female) collected 28 Jan 1989; all from same locality as holotype. ANSP 31589–90, 31592–94 (adult males), 31591 (adult female) from 1.5 km (airline) NE of Monte Seco on trail to Chorro Blanco, 1530 m, and ANSP 31595–98 (adult males), 31599–600 (adult females), from the same locality at 1630 m, 15 Jan 1989.

Definition.—The following diagnostic features (Lynch & Duellman 1973, Flores 1985) distinguish *C. hesperia* from other

Fig. 6. Adult male *Centrolenella hesperia* (SVL 26.0, FMNH 232501), collected on 8 May 1987 from 2.5 km (airline) NE of Monte Seco, 1800 m, Department of Cajamarca, Peru.

Centrolenella species: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white, visceral peritoneum clear; (4) color in life leaf green with green spicules, light lateral stripe, and white cloacal patch; in preservative pale lavender with irregularly placed, pigmentless spots surrounding large, white spicules, giving the appearance of light-colored dots; (5) webbing formula on fingers I–II(2^+)–(>3.5)III(3^-)–(2.5)IV; (6) webbing on toes I(2^-)–(2.5)II(1^+)–(2^-–2.5)III(1^+–1.5)–(3^-–3.5)IV(3^+)–(1.5–2^-)V; (7) head round in dorsal outline; snout weakly truncate from above, obtuse to moderately sloped in profile; (8) dorsal skin texture in males shagreen with minute spicules and scattered larger spicules, smoother in females; (9) ulnar and tarsal ridges present; (10) humeral spine present in males; (11) tympanum not visible; (12) prepollex slightly enlarged, lacking an external prepollical spine; (13) creamish nuptial excrescences, Type I pad; (14) no lateral glands; one pair of tubercles ventral to cloacal opening; skin beneath cloacal opening thickened, appearing glandular.

Description.—Head wide, 1.2 times length, only slightly wider than body, round in outline. Snout short (SL about 18% of HL), not or only slightly protruding, weakly truncate in dorsal outline, obtuse to moderately sloped in profile; canthus rostralis indistinct; loreal region weakly concave to flat, slightly obtuse; lips slightly flared. Nostrils oval to slitlike, slightly recessed, directed posterolaterally; internarial area concave to nearly flat. Eyes small, directed slightly anterior of 135°. Tympanum not differentiated externally; annulus tympanicus not obvious, tympanic region usually indicated by raised area which, when present, is most distinct anteroventrally. Supratym-

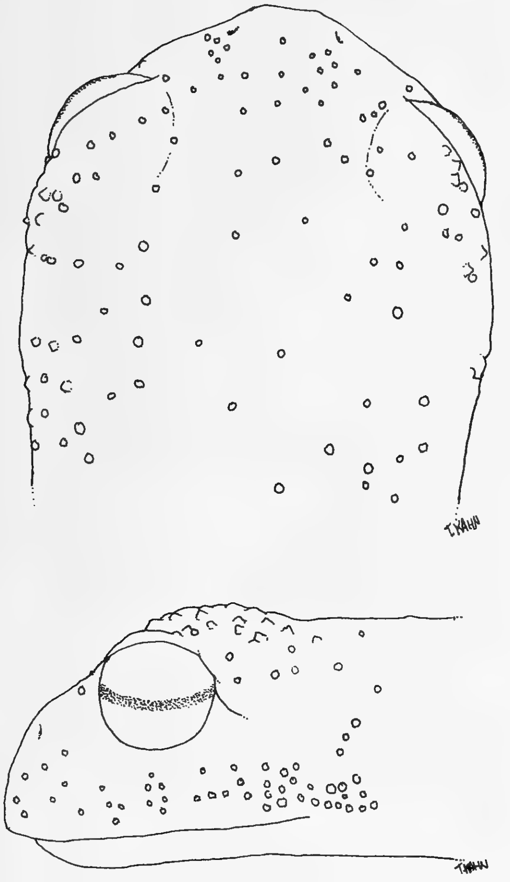


Fig. 7. Dorsal and lateral views of the head of the holotype of *Centrolenella hesperia* (male, SVL 25.5, FMNH 236200).

panic fold indistinct. Tongue round to oval, slightly broader anteriorly, occasionally slightly notched anteriorly and posteriorly. Vocal slits large, posterolaterally situated. No vomerine teeth. Choanae round, about 30–40% width of pad on finger I; separated by distance about four times their diameter.

Dorsally, skin in males shagreen with minute spicules and larger, scattered spicules with white tips; spicules smaller and densest on lip below eye and below tympanic area on head, larger and more evenly distributed on back, somewhat sparser on snout and upper surfaces of limbs; skin smooth or with few scattered spicules in females; lateral (below stripe) skin smoother, without spicules; ventral skin coarsely and uniformly granulose on belly, smooth on throat and chest, less granulose on ventral surfaces of thighs. Moderately developed pair of ventral tubercles below cloacal opening. Cloacal opening on upper quarter between limbs, subterminal (visible from above), covered by straight-edged (rarely weakly scalloped), shallow flap; area below cloacal area appears glandular.

Hands moderately large (HnL/HL, 1.19); order of finger lengths I < II < IV < III. Finger webbing absent between digits I and II, basal between fingers II and III, and slight between III and IV; formula I–II(2^+)–(>3.5)III(3^-)–(2.5)IV. Ridges along lateral edge of all digits, especially well developed on lateral margins of II and III, and on medial margin of IV. Tip of thumb slightly expanded, about 55% of disc III; disc III widest, discs II and IV about equal. Prepollical area moderately expanded, no external prepollical spine. Nuptial excrescences cream-colored but not greatly enlarged, Type I pad, relatively large cells on ventral surface of thumb base. Subarticular tubercles low, round, largest on finger IV. Metacarpal tubercles indistinct, inner elongate to kidney-shaped, outer more oval; palm tubercular. Ulnar fringe distinct, extending onto hand. Humeral spine present, not protruding externally. Forearm larger than upper arm, no obvious sexual dimorphism in arm size.

Toe lengths I < II < III < V < IV. Toe webbing smooth to granulose, of moderate extent; webbing formula I(2^-)–(2.5)II(1^+)–(2^-–2.5)III(1^+–1.5)–(3^-–3.5)IV(3^+)–(1.5–2^-)V. Thumb disc slightly expanded, 60% of width of disc IV; disc IV widest, III and V about equal. Lateral tarsal ridge extending onto base of digit V. Subarticular tubercles moderate, rounded. Inner metatarsal tubercle small, elongate, slightly larger than low outer tubercle, both weakly developed.

Snout–vent lengths of adult males 23.0–27.3 mm; of adult females 24.7–28.8 mm.

Coloration.—In life, the dorsum of *C. hesperia* is light leaf green with pale green spicules on upper surfaces of limbs, head, and body (Fig. 6). A pale cream upper labial stripe continues laterally along the body to the groin, and separates the dorsal color from the yellowish cream ventral color. The irises are grayish white with black reticulations. Ventral surfaces of throat and shank are clear green. Feet, webbing, and ventral surfaces of thighs have a yellow wash. Anterior belly region is cream to yellowish cream. Parietal peritoneum is white over most of belly. A white rump patch is present. A white line runs along the outer border (with frog in sitting position) of the limbs. The bones are green.

In preservative males are pale lavender with some scattered, irregular pigmentless spots and white spines giving the appearance of pale dots; females are uniform lavender with a few irregular pale areas. The upper lip is pale, without pigment. Eyelids also lack pigment except for a few melanophores along the upper margins and more at the bases. Under 20× magnification melanophores on some specimens are arranged in a circular pattern in the ear region. A sharply demarcated line occurs laterally between the dorsal pigmentation and the light unpigmented sides. Venter is creamy white; palmar and plantar surfaces and webbing are white. White labial, lateral, ulnar, and tarsal lines, and a white rump patch are visible in specimens preserved less than eight months but not visible in the 1987 sample. (This may reflect some difference in preservation between samples rather than fading.)

Measurements of holotype.—SVL—25.5; HL—7.8; HW—9.2; ED—2.6; EN—1.4; SL—3.4; TL—14.5; HnL—9.3

Osteology.—A cleared and stained male specimen (22.2 SVL; FMNH 232502) has a prepollex that extends about 75% of length of metacarpal I and is completely enclosed within the thumb base; a non-mineralized cartilaginous tip is distinct. Metacarpal III has a medial bony flange with cartilaginous anterior and posterior borders. The tips of the digits are T- or shallowly Y-shaped; intercalary elements are mineralized. The proximal flange (deltoid crest) of the humerus bears a distal projecting spine that extends about half the length of the flange. The vomers lack teeth and are embedded in the cartilaginous matrix of the floor of the nasal capsule. The frontoparietal fontanelle is large; anterior projections of the frontoparietals on the skull table narrowly overlap the sphenethmoid. The anterior tip of the parasphenoid nearly reaches the level of the palatines. On the lateral surface of the braincase, the sphenethmoid is separated by a large cartilaginous gap from the posterior cranial elements. The quadratojugals are present but do not articulate with the maxilla. A cartilaginous annulus tympanicus and bony columella are present.

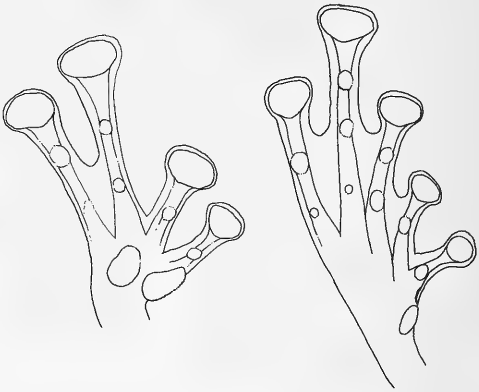


Fig. 8. Diagrammatic representations of the right hand and foot of the holotype of *Centrolenella hesperia* (male, SVL 25.5, FMNH 236200).

The hyoid structure of *Centrolenella hesperia* is similar to that described previously for *C. euhystrix* with two exceptions. The distal tips of the anterolateral processes are irregularly-shaped and not expanded as in *C. euhystrix.* In *C. hesperia* the posterolateral process on the right side is interrupted by a small non-cartilaginous gap and is less robust than on the left side, which bears a complete process. Undoubtedly, this is an individual aberration or artifact of preparation, but it may reflect a developmental source of variation in this structure for this or other species of *Centrolenella.*

Intercalary elements are present between the penultimate and ultimate phalanges of all digits. These elements are small (narrower than the distal end of the penultimate phalanx) and of the same form but not as well mineralized as those in *C. euhystrix.* In the hand only a trace of mineralization is evident in the intercalary element of digit I. The intercalary elements in the foot show a progressive increase in mineralization from that in digit I, in which no mineralization is detectable, to that in digits IV and V, which are well mineralized. A similar pattern of mineralization was observed in a preparation of *C. orientalis* (USNM 257182). The epiphyses of all phalanges are entirely cartilaginous.

Natural history notes.—At night nearly all individuals were perched on the upper surfaces of leaves over streams. One female (FMNH 232503) was found by day, apparently having been disturbed during survey work. She was hopping on the litter in low vegetation >30 m from the nearest stream. Several others were observed during the day as they rested vertically on upper leaf surfaces over streams where breeding occurred.

Breeding in this species apparently begins with the onset of rains. Males call from the upper surfaces of leaves 0.5–3 m above streams. In 1989, regular daily rains did not begin until 20 January (as inferred from degree of soil moisture and interviews with locals), and this coincided with males calling regularly each night. A search for eggs along two streams on 14 January revealed only a single mass, despite many calling individuals on that date. Within two weeks, however, egg masses along these streams were abundant. During the dry season males were calling between 6 May and 15 June, but none thereafter (Cadle left the field site on 25 June).

Although no males were individually marked, it is our impression that males are active at the same site for several nights and may attract more than one female. Multiple egg masses in different developmental stages often were seen on the same or adjacent leaves near a calling male. As many as four masses, three with eggs in different developmental stages ranging from early neurula to near-hatching, and the jelly remains of another clutch already hatched, were observed in the same bush near one male on 7 May. Males (presumably the same individuals) were observed calling from the same sites over the span of several days. Male densities often were very high, as was breeding activity (based on the number of observed egg masses in some stream sections) compared to our experience with other species of the genus. In two frequently-worked sections of stream, male densities sometimes exceeded 30 individuals along approximately 10 m. Densities apparently depend primarily on the amount of foliage available for perches.

Although only one kind of vocalization was noted, aggressive interactions occurred among males. On 7 May at 2204 hr, two males (MHNSM 3505, 23.0 mm SVL; 3506, 24.3 mm SVL) were observed fighting belly-to-belly on the petiole of an elephant-ear leaf (Araceae) in a head-to-vent position. They released their grappling holds when disturbed by the light. Grappling or similar behavior between males has been observed in other species of *Centrolenella*: *C. fleischmanni* in Mexico and *C. valerioi* in Costa Rica (McDiarmid & Adler 1974), *C. griffithsi* in Ecuador (Duellman & Savitzky 1976), *C. fleischmanni* and *C. prosoblepon* in Costa Rica (Jacobson 1985), *C. prosoblepon* in Panama (Jungfer 1988), and in Ecuador (McDiarmid, unpublished field notes), and is not unexpected in high-density situations especially among territorial males. This head-to-vent position has not been observed previously, but we are not surprised and view it as another variant of the several grappling positions reported. Males of many centrolenid species equipped with specialized morphological structures (e.g., humeral hooks or spines, prepollical spines) are territorial (McDiarmid, unpublished notes) and use them in an agressive fashion against other males during fights over calling and egg-laying sites. The outcome of the fight, not the positions assumed by the combatants during the grappling, is the more significant parameter. Taylor's suggestion (1949) that the prepollical spines in *Centrolenella spinosa* serve as a grasping organ during mating has not been supported by field observations and seems highly unlikely to us. Likewise, suggestions in the literature that the humeral spines in *Centrolene geckoideum* may have some scansorial function, perhaps enabling an individual to maintain its hold on a tree (Noble 1920), or in other species (e.g., *Centrolenella prosoblepon*) apparently functioning to insure amplexus (Noble 1924) or involved mechanically in amplexus (Eaton 1958) also are unverified and lack merit. We have seen mating pairs of several species (including *C. prosoblepon*) whose males have humeral spines, and in no instance did the males insure their grips on the females or otherwise use their spines during amplexus. We contend that humeral spines are secondary sexual traits used by males to defend their territories from other males and in this sense are analogous to horns in certain territorial mammals.

Centrolenella hesperia lays light greenish-white eggs in a single, loosely arranged layer on the upper surfaces of leaves above water, usually on the distal quarter of the leaf near its tip. Egg masses (FMNH 232713–15; ANSP 31619–21; USNM 292591) were found on ferns (*Polystichum*), a melastome, leaflets of a small palm, elephant ears (Araceae), and other understory plants along the stream margins. In two or three instances masses were attached to aerial roots of epiphytes situated on tree limbs overhanging the water.

An egg mass (FMNH 232715) taken from a leaf 1.5 m above the water at 2114 hr on 7 May contained 26 light green eggs in Gosner stage 1. These eggs measured about 2.2 mm diameter and may have been laid earlier that evening. A calling male (FMNH 232508, SVL 25.7) was collected on the same bush about 1.0 m above the water. Another egg mass (USNM 292591) collected during the day of 29 January contained 38 eggs in stages 4 and 5 that measured 2.5 to 2.7 mm diameter. A sleeping male was found on top of a leaf near this clutch. This clutch of 38 eggs was attached to the upper surface of a fern frond (*Polystichum* sp.) and had 16 empty capsules on its proximal (top) edge (Fig. 9). All egg masses examined had empty capsules on the side closest to the leaf petiole. Empty capsules have been observed in egg masses of certain other *Centrolenella* species (McDiarmid, unpublished field observations) but not with the apparent consistency of this species. Because the capsules are always positioned along the upper edge of the clutches of *Centrolenella hesperia,* we suspect that they may function to increase the adhesion of the egg mass to the leaf or, by way of their hygroscopic tendencies, retain water and serve as an additional water source for the eggs during their several days of development when they are exposed to the air.

The size of 12 "dry season" clutches (2–9 May) range from 16 to 30, $\bar{X} = 20.7 \pm 4.4$. This is significantly smaller than the size of 15 clutches laid at the beginning of the "wet season" (29 Jan), range 19–42, $\bar{X} = 33 \pm 6.9$ (t-test for difference between the means, $t = 4.096$, $P < 0.001$).

Some observations suggest that loss of egg masses due to desiccation was a problem in 1987 for those laid after mid-May. Breeding activity for this species, as indicated by the number and regularity of calling males and recent egg masses, declined rapidly after mid-May. By this time the regular rains had ceased, fogs characteristic of the site were less intense and enduring, and the humidity was lower. The last viable clutches were observed on 25 May, when three masses with

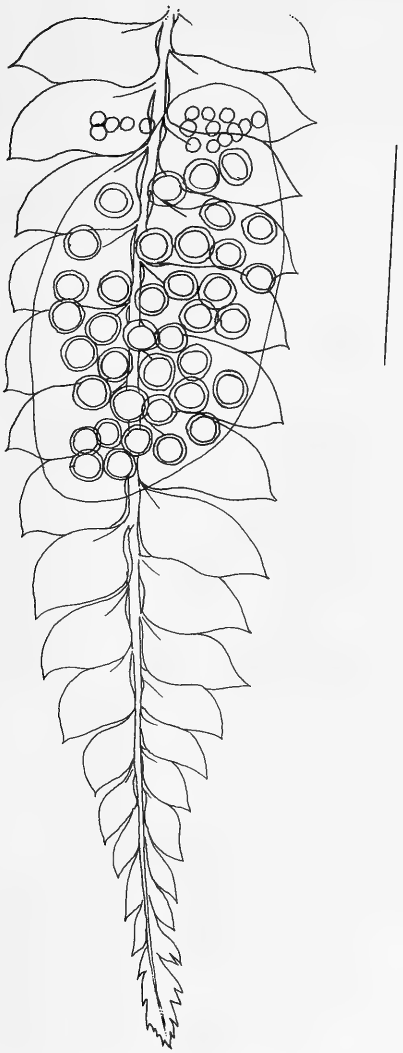


Fig. 9. Drawing of an egg mass (USNM 292591) of *Centrolenella hesperia* attached to the upper surface of a fern (*Polystichum* sp.) frond showing the position of the 38 eggs and 16 capsules. Line equals 20 mm.

advanced tadpoles were found along the stream where most of the previous breeding activity had occurred. Two desiccated clutches and no fresh egg masses were observed here on 15 June. On 26 May along another stream two desiccated clutches were found on the same palm frond where viable clutches had been seen earlier in the month.

At 2055 hr on 7 May, a male was calling about 40 cm from a female that was alone on top of an egg mass. When checked at 2248 hr the male was still calling but the female was gone; 17 eggs were in the clutch. At the time Cadle pondered the meaning of this behavior and wondered whether the female was performing some egg-laying activity in the absence of the male. More detailed observations of what appears to be the same behavior were made later at a different site on the same stream. On 10 May a female (FMNH 232495; 28.8 SVL) was found at 2116 hr next to an egg mass. When first observed, the female was flattened against the leaf in a normal sitting position with her cloacal opening oriented above the upper (proximal for the leaf) edge of the mass containing 16 recently laid eggs. After maintaining this position for several minutes, she raised the rear part of her body, and at the same time positioned her thighs perpendicular to the body axis. She held this new position for several minutes. During the next hour, the female alternated several times between this behavior and the more normal sitting position, at which time the frog was collected.

We do not understand the significance of these females' behavior. We do not think that the females were depositing eggs independently of the males, and no issuances from the cloaca were observed. Dissection of female FMNH 232495 revealed small ova in the right ovary, and small, as well as somewhat larger ova in the left ovary. No eggs were present in the body cavity or oviducts (which were enlarged). These observations suggest that she was not ready to lay eggs when collected, but the enlarged oviducts indicate that she may have recently laid eggs. We speculate that the females were: (1) wetting the egg mass (likely their own and presumably with water stored in their bladder), a behavior that has been reported for males of *C. fleischmanni* in Costa Rica (Jacobson 1985, Mark Hayes, pers. comm.); (2) depositing empty capsules in the mass presumably just after depositing the eggs (see previous discussion); or (3) pressing the eggs against the leaf surface to increase adhesion. Aichinger (1987) reported a similar behavior by female *Hyla brevifrons* that he described as brushing the eggs into a monolayer. Because rain is more likely to detach an egg mass placed on the upper surface of a leaf than one placed on the lower surface of a leaf, and because the choice of an egg deposition site apparently is species-specific, those species that place their eggs on the upper surface of leaves might be expected to have behaviors that increase egg mass adhesion. We suspect (but did not observe) that the females' behavior was associated with depositing empty egg capsules, but cannot rule out the other two explanations. Whatever the functional significance of this peculiar behavior in females might be, to our knowledge it has not been reported previously in species of *Centrolenella.*

Larvae.—A few tadpoles (FMNH 232710–232712) were reared to stage 25 (Gosner 1960) from clutches taken from leaves in the field. The largest of these measured 14.9 mm total length with a tail 10.2 mm long. The tadpole is typical of centrolenids and has a fusiform body, rounded snout, and long, narrow tail. The eyes are small, cresent-shaped and dorsally located. The nostrils are located slightly closer to the eye than to the tip of the snout. Near the midpoint of the tail, the ventral fin is slightly deeper than the dorsal fin, and each is about 20% of the tail height. The tail has a rounded tip. The spiracle is small, oval, and opens posterolaterally about three-fourths of the way back on the left side of the body below the midline. The vent tube is medial. The oral disc is anteroventral and has a uniserial row of about 22 large marginal papillae laterally and posteriorly (the anterior edge is bare). Jaw sheaths are narrow, weakly keratinized, and serrate; they appear striated. The labial tooth rows are barely visible and not completely keratinized; A–2 has a wide medial gap; the short sections are located nearly lateral to the anterior jaw sheath. The labial tooth row formula is 2(2)/3.

Vocalizations.—*Centrolenella hesperia* has a short, two-note, high-frequency call (Fig. 10). A calling male (FMNH 232499, SVL 25.4) was recorded on 8 May 1987. The only air temperature data available are maximum (26°C) and minimum (10°C) values recorded for that day. An analysis of seven calls shows the following call characteristics (means are given with ranges in parentheses). The call consists of two notes with an overall duration of 0.12 sec (0.10–0.13). The first note has either two distinct pulses (two calls) or three distinct pulses (five calls) with an overall duration of 0.04 sec (0.03–0.05). The second note, consisting of one (occasionally two) pulses, lasts 0.02 sec (0.02–0.03) and is separated from the first note by 0.05 sec (0.04–0.06). In both notes the dominant frequency of the call is in the 3300–4000 hz range (mean about 3630 hz). Calls (Fig. 10) were given at a rate of about two per second. The pulse rate calculated for the first note was 71.4 notes per second (62.5–76.9). The rise time for these pulses is very fast, averaging 0.0014 sec (0.0008–0.0025).

Distribution.—*Centrolenella hesperia* is known only from the vicinity of the type locality (Fig. 2). The recorded elevational range is 1500 m–1800 m. Although stream inaccessibility made searching extensively above 1800 m difficult, this species does not appear to occur above 2500 m where its detection would have been likely.

Etymology.—The specific epithet "hesperia" is a Latinized word derived from the Greek "hesperos" meaning western or of the evening. We use it as an adjective in reference to its being one of two species of *Centrolenella* first recorded from western Peru, and in refrence to its evening activities.

Discussion

Comparisons.—We do not understand the relationships among centrolenid frogs. In part this is due to the incredible rate at which new species have been discovered and de-

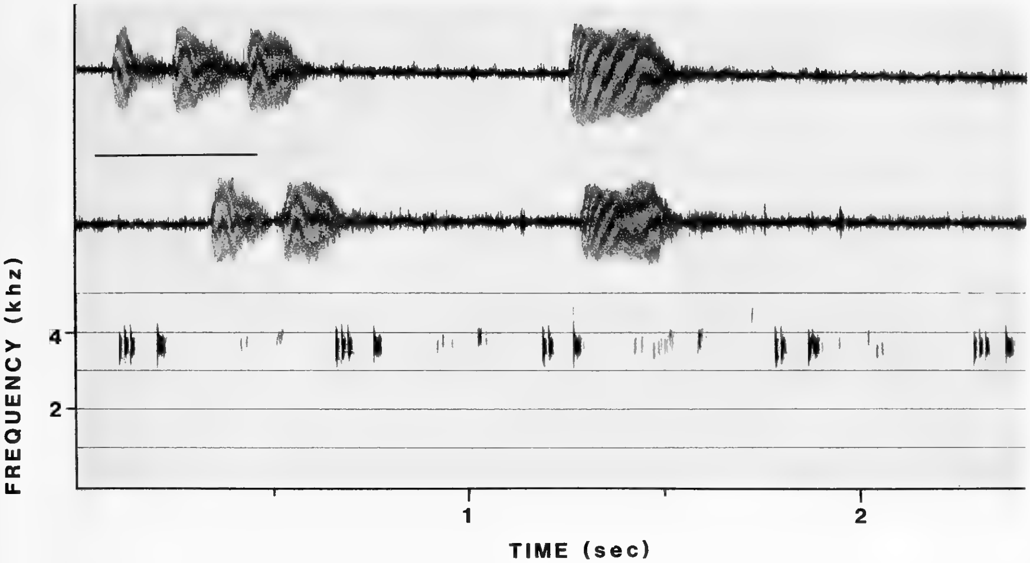


Fig. 10. Audiospectrograms of five advertisement calls of a male *Centrolenella hesperia* (SVL 25.4, FMNH 232499) with a wide-band filter (300 hz). Calls were recorded on 8 May 1987 at the type locality. Waveforms of the first and third calls are shown above the audiospectrogram. Line between waveforms represents 0.034 sec.

scribed. By our calculation about 80% of the recognized species (Frost 1985 and publications since) in the family have been described in the past 30 years and nearly 30 species (>40% of the total described species diversity) in the past 10 years. The number of known but undescribed species also is quite high. In addition to the two we describe here, we know of three others from Peru, four from Ecuador, and four or more from Venezuela that are undescribed; Pedro Ruíz-Carranza (pers. comm.) informed one of us of a large number of undescribed forms from Colombia.

Moreover, the lack of detailed comparative morphological descriptions has precluded a comprehensive phylogenetic treatment of the family. Consequently, the presently recognized genera and species groups do not easily accommodate many of the species being described. This problem stems at least partly from the relatively recent recognition of the family (Taylor 1951) and partly because two of the genera proposed in that paper were inadequately defined and generally have not been accepted (Goin 1964, Savage 1967). When species groups have been proposed (Savage 1967, Savage & Starrett 1967, Starrett & Savage 1973), coverage has been restricted to geographic regions (i.e., Costa Rica or lower Central America), and the groups were subsequently claimed not to accomodate easily some species from other geographic regions (Lynch & Duellman 1973). These latter authors recognized the problems associated with species-group definitions based on geographic subsets (they reported species from Ecuador) of the family and preferred not to alter previous groupings or propose new ones.

We do not attempt to evaluate critically the various groupings that have been proposed within the family. We also recognize that our groups are ones of convenience and may not be monophyletic lineages, but for purposes of comparison we use the following five groups of centrolenids. (1) The genus *Centrolene* Jiménez de la Espada (see Ruíz-Carranza et al. 1986 for diagnostic traits), which includes two described forms (large species, presumably with exposed humeral spines in males) and probably some undescribed ones. (2) Species within the currently recognized genus *Centrolenella* Noble (type *C. antioquiensis* Noble) made up of smaller species, the males of which have humeral spines (part of Savage's [1967] *prosoblepon* group). (3) A second group within *Centrolenella* that includes species in which males lack humeral spines. This cluster of species also is part of Savage's *prosoblepon* group; and if shown to be taxonomically distinct, they would be placed in Taylor's (1951) genus *Cochranella* (type *C. granulosa* Taylor). (4) Another group currently within the genus *Centrolenella* includes several small species with distinguishing characteristics (clear parietal peritoneum, no humeral spines, white color in preservative). This group, originally defined by Savage (1967) and Starrett & Savage (1973), has found general acceptance and has been referred to in the literature (Lynch & Duellman 1973, Cannatella 1980, Cannatella & Lamar 1986) as the *fleishmanni* group. As currently understood, this group has no available taxonomic name. (5) A final group currently placed within *Centrolenella* includes those species with prepollical spines. This trait was recognized by Taylor (1951) in his description of the genus *Teratohyla* (type *C. spinosa* Taylor). Two species (*C. gemmata* and *C. lynchi*) with prepollical spines also have humeral spines (Flores 1985) while the third, *C. spinosa,* does not. For this discussion, we include *C. gemmata* and *C. lynchi* in group 5.

Centrolenella euhystrix lacks humeral spines and therefore is associated with species in our group 3. The absence of humeral spines will distinguish it from all species of *Centrolene* (group 1) and those species of *Centrolenella* in group 2. *Centrolenella euhystrix* also lacks prepollical spines and thus differs from species in group 5. Though similar to members of the *fleischmanni* group (group 4 above) in that they all lack humeral spines and vomerine teeth, *C. euhystrix* is easily distinguished from all species in group 4 (characteristics in parentheses) by the following: larger size (usually less than 25 mm SVL), spinose skin (smoother skin), coloration in life dark green to nearly black without spots (pale green or yellow green with diffuse yellow spots or with pale reticulation) and in preservative dark gray (creamy white), truncate snout (truncate or rounded), distinct canthus (often flattened), and white parietal peritoneum (clear parietal peritoneum).

Centrolenella euhystrix lacks vomerine teeth and so differs from many species in group 3 which also lack humeral spines but have vomerine teeth. The following combination of characters distinguishes *C. euhystrix* from other group 3 species that lack vomerine teeth: green bones, large hands with wide digits and expanded toe tips, extensive toe webbing, color in life dark greenish black without light or dark flecks, spots, or ocelli, dark gray in preservative, and prominent (in males) pale green (life) or white (in preservative) spines on dorsum.

In comparison to the eleven currently recognized species of *Centrolenella* from Peru (Cannatella & Duellman 1982, Flores & McDiarmid 1989), *Centrolenella euhystrix* can be distinguished from all by its larger size, dark coloration in life and in preservative, and the extremely spinose dorsum of males. Other differences from Peruvian species include the following (charcteristics of *euhystrix* in parentheses): *C. azulae, C. spiculata,* and *C. midas* have vomerine teeth (lacking); *C. bergeri* and *C. munozorum* have white bones and concealed tympana (green bones and visible tympanum); and *C. phenax* has a clear parietal peritoneum (white).

The only species on the western versant of northern South America that approaches *C. euhystrix* in size, webbing, and coloration is *C. orejuela* (Duellman & Burrowes 1989), but this species is reported to have vomerine teeth, smooth skin, and white visceral peritoneum. We note that the holotype of *C. orejuela,* reported as an adult female by Duellman & Burrowes (1989:5), in fact is an adult male with vocal slits and large nuptial pads. Also, the paratype (IND-AN 1520) illustrated in Duellman & Burrowes' paper (1989, fig. 1) is listed as a female in the caption but as an adult male in the text.

In many respects (size, coloration, spinose dorsum, absence of vomerine teeth, webbing) *C. euhystrix* is similar to *C. johnelsi* (Cochran & Goin 1970) from northern Colombia. However, *C. johnelsi* has humeral spines and smaller finger discs. The closest relative of *C. euhystrix* may be found among several undescribed species recently collected from the Amazonian side of the Andes in northern Peru, or perhaps in other areas of northern Peru or southern Ecuador (see below).

Centrolenella hesperia (placed in our group 2) has humeral spines and thus is distinct from members of groups 3, 4, and *C. spinosa* in group 5. It also is distinct from *C. gemmata* and *C. lynchi,* two species with both humeral spines and prepollical spines (prepollical spines are lacking in *C. hesperia*). This species is easily distinguished from the described species of *Centrolene* (group 1) by the following traits: smaller size (<30 mm vs. >45 mm in *Centrolene*), concealed humeral spine (exposed in *C. geckoideum*), proportionally broader head (HW/SVL about 36% vs. <28% in *Centrolene*), concealed tympanum (visible), lack of vomerine teeth (present or absent), and light eggs (dark eggs).

Among species in group 2, *C. hesperia* differs from those with vomerine teeth by lacking vomerine teeth, and from many others by having a uniform green dorsum with small spines. It can be distinguished from *C. johnelsi* and *C. pipilata,* two species with spines, by its lavender color in preservative (gray or purplish gray) and concealed (distinct) tympanum. The combination of humeral spines, spiculate and spinose dorsum, concealed tympanum, and moderately sloped snout distinguishes *C. hesperia* from nearly all other species of *Centrolenella.* It is the only described species with a distinct white lateral line, white cloacal patch, and ulnar and tarsal ridges.

Of the described Peruvian species of *Centrolenella, C. hesperia* can be distinguished from all as follows (characters of *C. hesperia* in parentheses): *C. bejaranoi, C. midas, C. ocellata, C. phenax, C. pluvialis, C. spiculata,* and *C. truebae* lack humeral spines in males, have visible tympana, and lack lateral stripes (present, absent, and present, respectively). In addition, *C. midas* and *C. spiculata* have vomerine teeth (absent). *Centrolenella bergeri* and *C. munozorum* have white bones and lack humeral spines and lateral stipes (green bones, spines and stripes present). *Centrolenella azulae* has a visible tympanum and vomerine teeth (tympanum and vomerine teeth absent). *Centrolenella mariae* has a visible tympanum and no lateral stripes (undifferentiated tympanum and lateral stripes). Males of *C. mariae* remain unreported so that the condition of the humeral spine is unknown.

As with *C. euhystrix* from this locality, the closest relative of *C. hesperia* may be found among several undescribed species from Peru's Amazonian slopes. However, some species at Monte Seco are distributed through the Huancabamba Depression area of northern Peru (Amazonian versant), in other areas of northwestern Peru or western Ecuador (Pacific versant), or have their closest relatives in these areas (Fig. 1). Examples include *Dendrophidion brunneum,* which has a narrow distribution along the Pacific versant of Ecuador and northern Peru (Lieb 1988); *Eleutherodactylus lymani,* widely distributed throughout the Huancabamba Depression and southern Ecuador (Lynch 1969); and *Coniophanes longinquus,* which is closely related to *Coniophanes dromiciformis* of southwestern Ecuador (Cadle 1989). *Centrolenella euhystrix, Centrolenella hesperia,* and their close relatives possibly have distributions similar to these, but resolution of this problem must await adequate delineation of species groups within the genus.

Intercalary elements and their descriptors.—Because the family Centrolenidae has been characterized by the presence of cartilaginous intercalary elements between the penultimate and ultimate phalanges (Duellman 1975, Duellman & Trueb 1986, Duellman 1988), our discovery that these elements are mineralized in the two species of *Centrolenella* described herein was, to us, somewhat surprising, although David C. Cannatella (pers. comm.) informed us that this condition is common in centrolenids. Certain descriptors (e.g., "ossified," "mineralized," and "calcified") have been used indiscriminately in the literature to describe the nature of intercalary elements in some frogs. Such use can lead to misinterpretations and subsequent confusion. For example, in their description of *Scarthyla ostinodactyla* Duellman & de Sa (1988) used all three terms to describe the intercalary elements of hylid frogs but did not distinguish clearly among their use. The confusion arises because several types of tissues, including cartilage, can receive deposits of calcium salts by a variety of processes. These tissues then become red with alizarin stain in the standard cleared and stained whole-mount preparations used for anuran osteological studies. Drewes (1984) noted that in most adult hyperoliids, the intercalary "cartilages" are partly or wholly mineralized (i.e., stain red with alizarin), and used the term "intercalary elements" and the descriptor "mineralized" to refer to these structures. We prefer this terminology for the following reasons. The terms "calcified" (as used with reference to cartilage) and "ossified" (used specifically with reference to bone) have precise meanings in the histological and anatomical literature that imply specific processes by which a tissue becomes impregnated with calcium deposits. Calcified cartilage and bone are distinguished, among other things, by differences in vascularity, growth properties, extracellular matrix components, and cell types involved (see Ham & Cormack 1979, Poole et al. 1989). Because these features rarely are studied in evaluating the nature of intercalary elements in anurans, and in any case cannot generally be distinguished in cleared and stained preparations, a need for precise usage of these terms exists. We argue that the term "mineralized" is most appropriate to describe those intercalary elements that have calcium deposits and for which the mechanism of deposition has not been determined histologically; this term does not imply the specific process or histological structure involved. Noble & Jaeckle (1928: 271) reported that the intercalary element in *Polypedates leucomystax* occurs as ". . . fully ossified bone with a marrow cavity. . . ." Drewes (1984) examined histological sections of the intercalary element of *Kassina senegalensis,* a species with a similarly appearing and identically shaped intercalary element to that of *P. leucomystax,* and found only calcified cartilage. This condition appears to be characteristic of nearly all mineralized intercalary elements that have been studied histologically in anurans (David C. Cannatella, pers. comm.). We suggest that "mineralized" be used as a descriptor when only a gross characterization is available (as in cleared and stained preparations).

Our reading of the literature suggests that most workers use the terms "intercalary cartilages" or "cartilaginous intercalary elements" to refer to non-mineralized intercalary cartilages, whereas both "ossified" and "calcified" have commonly referred to intercalary elements composed of calcified cartilage (for which we prefer the term "mineralized"). According to Duellman & de Sa (1988), the only neotropical frogs having "ossified" intercalary elements are the hylines *Sphaenorhynchus carneus, Aplastodiscus perviridis,* and *Scarthyla ostinodactyla,* and species in the pseudid genera *Lysapsus* and *Pseudis.* We now add to this list some species of *Centrolenella.* Both *C. euhystrix* and *C. hesperia,* as well as one preparation of *C. orientalis* (USNM 257182), have mineralized intercalary elements. Two preparations of *C. prosoblepon* (USNM 252617–18) did not show mineralized intercalary elements, but these preparations were only lightly stained with alizarin. We suggest that the lack of evidence for mineralization of these intercalary elements may be an artifact.

The histology of the intercalary elements within the family *Centrolenidae* has not been clarified. Noble (1920:443) stated that *Centrolene* possessed ". . . an intercalary bone (or partly ossified cartilage) . . ." but was less clear about the nature of the element in later papers. Although Noble (1925) defined the Hylidae, into which he placed *Centrolene* and *Centrolenella,* as a group having characters of the Bufonidae but with an intercalary cartilage or bone between the ultimate and penultimate phalanges of each digit, he did not state whether the element in the two genera of concern was cartilage or bone. In his monumental work on the biology of the Amphibia, Noble (1931) referred to the Hylidae as bufonids with intercalary cartilages; no mention was made of bony elements. In defining the family Centrolenidae, Taylor (1951) listed the trait as intercalary cartilages. All subsequent references to the trait in the Centrolenidae have called the structures intercalary cartilages (e.g., Eaton 1958, Duellman 1975, Dowling & Duellman 1978, Duellman 1988) or cartilaginous intercalary elements (Duellman & Trueb 1986). Peters (1964:166) called the structure "intercalary cartilage" and described it as "a phalanx-like cartilaginous (occasionally bony?) element. . . ." Even though one of the other synonyms (intercalary phalanx) listed by Peters (1964) referred to both cartilage or bone intercalated between the normal components of the digit, the use of a question mark suggests to us that Peters was unsure of the nature of the element or confused by previous usage.

Given the prevalence of mineralized intercalary elements among species of centrolenids as evidenced by our observations and those of David C. Cannatella (pers. comm.), we recommend that "mineralized intercalary elements" be recognized as a diagnostic feature of the family Centrolenidae (contra Duellman & Trueb 1986, Duellman 1988).

The Monte Seco area.—The western slopes of the Peruvian Andes generally are arid, through local conditions sometimes permit more humid areas, as in the vicinity of Monte Seco. Koepcke (1961) summarized general features of the vegetation and climate of the western Andean slopes of Peru, including the Río Zaña valley. In general, the western slopes of northern Peru receive more moisture than those in central and southern Peru. The Río Zaña lies at the southern edge of a transition along the Andean slope where the vegetation changes to a more mesic type; humidity increases as one moves north from this area (Weberbauer 1936). Cadle (1989) briefly detailed some aspects of climate in the Monte Seco area. Additional observations from the beginning of the rainy season (January 1989) are noted here.

When Cadle arrived in the Monte Seco area on 13 January, little rain had fallen as evidenced by the dry soil and lack of recent herbaceous and epiphytic growth. No rain fell on several days between 13 and 20 January. Thereafter, each day was characterized by steady rains and much cloud cover. Precipitation fell either as relatively heavy rains lasting for one to several hours during the day, usually in the afternoon, or as steady daytime drizzles of varying intensity. Rain occurring at night was usually of limited intensity and duration, with most falling before midnight. Dense daytime fogs as had happened during the beginning of the dry season (Cadle 1989) did not occur during this period.

The slopes above Monte Seco are steep with relatively few permanent streams and many waterfalls. Because of the topography, nocturnal work along certain portions of streams is difficult and even dangerous. The highest waterfall, Chorro Blanco, drops about 200 m. Many others occur in the study streams (Fig. 2) and vary in height from <1 m to >18 m. During the rainy season, many small temporary streams flow from the hills, and in 1987 some of these lasted into the beginning of the dry season (mid-June) but with greatly reduced flow. In addition to natural streams, local inhabitants have constructed a series of drainage ditches (acequias) along the hillside to channel water for domestic use. Long portions of these ditches extend through forested areas, are well-shaded, and have overhanging vegetation that seemingly could have provided suitable egg-laying sites for *Centrolenella* but none were found. *Centrolenella hesperia* bred along both permanent and temporary streams between 1500 m and 1800 m from the vicinity of the type locality; but *C. euhystrix* was observed only along permanent streams near Cadle's field camp (site 2) and at higher elevations (site 1 and one other nearby site, Fig. 2). Apparently, neither species bred along the drainage ditches. This may reflect differences in substrate quality of the ditches (generally sandy) compared to natural streams (gravelly to rocky), gradient (gradually sloping versus precipitous), or some other unknown variable (e.g., differences in oxygen tension between the ditches and streams). Tadpoles of *Colostethus* sp. were found in the drainage ditches, as well as elsewhere in relatively oxygen-poor, standing water with sandy substrates.

Centrolenella euhystrix and *C. hesperia* were found sympatrically only at the type locality of the latter (Fig. 2). This represented the lowest and highest elevations (1800 m), respectively, at which the two species were observed. Greater elevational overlap in the ranges of the two species probably occurs, but the precipitous nature of the steams precluded adequate exploration of this possibility. Owing to its distinctive call and overt behavior, *C. hesperia* was easily detected and thus appeared to be absent from the sites at 2500 m and above where *C. euhystrix* was observed. Although individuals of *C. euhystrix* were more cryptic, none were observed during a careful search of several waterfalls below 1800 m and at waterfalls along one other permanent stream at about 1800 m. The only other frog which lays eggs along streams in the Monte Seco area is *Telmatobius* sp., but it most likely lays its eggs in the water. Other frogs in the area use terrestrial sites (*Colostethus* and *Eleutherodactylus*) or carry their eggs (*Gastrotheca*). Tadpoles of *Colostethus* sp. were found in the streams (among other sites) at all elevations where adults and eggs of *Centrolenella* were observed. Tadpoles of *Telmatobius* sp. were found only in the streams above 2500 m where *Centrolenella euhystrix* adults (but no tadpoles) were observed; *Gastrotheca* sp. tadpoles were found in ponds or small pools away from streams but only at higher elevations.

Acknowledgments

JEC thanks Robert F. Inger, Michael O. Dillon, and Abundio Sagástegui for encouraging his work at Monte Seco and for discussions and logistic support. Field work was supported by the Field Museum of Natural History and the Academy of Natural Sciences, and was ably assisted by Raul Quiroz, José Santisteban, José Guevara B., Helena Siesniegas, and Segundo Leiva. Local inhabitants of the Monte Seco area, especially Selzo Gil, Ing. Aldo Maquiña, and the family of Francisco Quiroz, made the field work possible. JEC was supported by the National Science Foundation through grant BSR 84-00116 during the 1987 field work. We also thank Ted Kahn for preparing the drawings in Figs. 4, 5, 7, 8, 9; Rex Cocroft for discussions about *Centrolenella* vocalizations and review of the manuscript; Ronn Altig for comments on *Centrolenella* larvae and review of the manuscript; George Steyskal for providing advise on derivations of the species names; Ron Crombie for notable suggestions for the specific epithets (though their meanings did not allow their use in print); David Lellinger for identification of a fern; Cristián Ruíz for help with the Spanish resumen; and Aaron Bauer, James Hanken, John Harshbarger, Ron Heyer, Dave Wake, and George Zug for discussing intercalary elements with us. We extend special thanks to David C. Cannatella for a detailed critique of the manuscript, for sharing with us and allowing us to cite some of his unpublished observations, and for examining specimens for us in the LSUMZ collections.

Literature Cited

Aichinger, M. 1987. Freilandbeobachtungen zum Fortpflanzungsverhalten von *Hyla brevifrons* Duellman & Crump, 1974.—Salamandra 23: 269–276.

Altig, R. 1970. A key to the tadpoles of the continental United States and Canada.—Herpetologica 26:180–207.

Cadle, J. E. 1989. A new species of *Coniophanes* (Serpentes: Colubridae) from northwestern Peru.—Herpetologica 45:411–424.

Cannatella, D. A. 1980. Two new species of *Centrolenella* from Bolivia (Anura: Centrolenidae).—Proceedings of the Biological Society of Washington 93:714–724.

———, & W. E. Duellman. 1982. Two new species of *Centrolenella*, with a brief review of the genus in Peru and Bolivia.—Herpetologica 38:380–388.

———, & W. W. Lamar. 1986. Synonymy and distribution of *Centrolenella orientalis* with notes on its life history (Anura: Centrolenidae).—Journal of Herpetology 20:307–317.

Cochran, D. M., & C. J. Goin. 1970. Frogs of Colombia.—United States National Museum Bulletin 288:1–605.

Dingerkus, G., & L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage.—Stain Technology 52:229–232.

Dowling, H. G., & W. E. Duellman. 1978. Systematic herpetology: a synopsis of families and higher categories. HISS Publications, New York.

Drewes, R. C. 1984. A phylogenetic analysis of the Hyperoliidae (Anura): treefrogs of Africa, Madagascar, and the Seychelles Islands.—Occasional Papers of the California Academy of Sciences. 139:1–70.

Duellman, W. E. 1975. On the classification of frogs.—Occasional Papers on the Museum of Natural History, The University of Kansas 42:1–14.

———. 1988. Evolutionary relationships of the Amphibia. Pp 1-34 *in* B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington, & W. Walkowiak, eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

———, & P. A. Burrowes. 1989. New species of frogs, *Centrolenella*, from the Pacific versant of Ecuador and southern Colombia.—Occasional Papers of the Museum of Natural History, The University of Kansas 132:1–14.

———, & R. O. de Sa. 1988. A new genus and species of South American hylid frog with a highly modified tadpole.—Tropical Zoology 1:117–136.

———, & A. H. Savitzky. 1976. Aggressive behavior in a centrolenid frog, with comments on territoriality in anurans.—Herpetologica 32:401–404.

———, & L. Trueb. 1986. Biology of amphibians. McGraw-Hill Book Company, New York, 670 pp.

Eaton, T. H. 1958. An anatomical study of a neotropical tree frog, *Centrolene prosoblepon* (Salientia: Centrolenidae).—The University of Kansas Science Bulletin 39:459–472.

Flores, G. 1985. A new *Centrolenella* (Anura) from Ecuador, with comments on nuptial pads and prepollical spines in *Centrolenella*.—Journal of Herpetology 19:313–320.

———. 1987. A new *Centrolenella* from the Amazonian lowlands of Colombia.—Journal of Herpetology 21:185–190.

———, & R. W. McDiarmid. 1989. Two new species of South American *Centrolenella* (Anura: Centrolenidae) related to *C. mariae*.—Herpetologica 45:401–411.

Frost, D. R. (ed.). 1985. Amphibian species of the world, a taxonomic and geographical reference. Association of Systematics Collections, Lawrence, Kansas, 732 pp.

Goin, C. J. 1964. Distribution and synonymy of *Centrolenella fleischmanni* in northern South America.—Herpetologica 20:1–8.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification.—Herpetologica 16:183–190.

Ham, A. W., & D. H. Cormack. 1979. Histophysiology of cartilage, bone, and joints. J. B. Lippincott Company, Philadelphia.

Jacobson, S. K. 1985. Reproductive behavior and male mating success in two species of glass frogs (Centrolenidae).—Herpetologica 41:396–404.

Jungfer, K.-H. 1988. Froschlurche von Fortuna, Panama II. Hylidae (2), Centrolenidae, Dendrobatidae.—Herpetofauna 10(56):6–12.

Koepcke, H. W. 1961. Synökologische studien an der westseite der peruanischen Anden.—Bonner Geographische Abhandlungen 29:1–320.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E.

Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Lieb, C. S. 1988. Systematic status of the neotropical snakes *Dendrophidion dendrophis* and *D. nuchalis* (Colubridae).—Herpetologica 44:162–175.

Lynch, J. D. 1969. Taxonomic notes on Ecuadorian frogs (Leptodactylidae: *Eleutherodactylus*).—Herpetologica 25:262–274.

———, & W. E. Duellman. 1973. A review of the centrolenid frogs of Ecuador, with descriptions of new species.—Occasional Papers of the Museum of Natural History, The University of Kansas 16:1–66.

———, P. M. Ruiz, & J. V. Rueda. 1983. Notes on the distribution and reproductive biology of *Centrolene geckoideum* Jiménez de la Espada in Colombia and Ecuador (Amphibia: Centrolenidae).—Studies on Neotropical Fauna and Environment 18:239–243.

McDiarmid, R. W., & K. Adler. 1974. Notes on territorial and vocal behavior of neotropical frogs of the genus *Centrolenella.*—Herpetologica 30: 75–78.

Myers, C. W., & W. E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama.—American Museum Novitates 2752:1–32.

Noble, G. K. 1920. Two new batrachians from Colombia.—Bulletin of the American Museum of Natural History 42:441–446.

———. 1924. Some neotropical batrachians preserved in the United States National Museum with a note on the secondary sexual characters of these and other amphibians.—Proceedings of the Biological Society of Washington 37:65–72.

———. 1925. An outline of the relation of ontogeny to phylogeny within the Amphibia. I.—American Museum Novitates 165:1–17.

———. 1931. The Biology of the Amphibia. McGraw-Hill Book Company, New York. 577 pp.

———, & M. E. Jaeckle. 1928. The digital pads of the tree frogs. A study of the phylogenesis of an adaptive structure.—Journal of Morphology and Physiology 45:259–292.

Peters, J. A. 1964. Dictionary of Herpetology. Hafner Publishing Company, New York. 392 pp.

Poole, A. R., Y. Matsui, A. Hinek, & E. R. Lee. 1989. Cartilage macromolecules and the calcification of cartilage matrix.—The Anatomical Record 224:167–179.

Ruíz-Carranza, P. M., J. Hernândez-Camacho, & M. C. Ardila-Robayo. 1986. Una nueva especie Colombiana del genero *Centrolene* Jiménez de la Espada 1872 (Amphibia: Anura) y redefinición del genero.—Caldasia 15(71–75):431–444.

Savage, J. M. 1967. A new tree-frog (Centrolenidae) from Costa Rica.—Copeia 1967:325–331.

———, & W. R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America.—Beiträge zur Neotropischen Fauna 5(2):111–131.

———, & P. H. Starrett. 1967. A new fringe-limbed tree-frog (Family Centrolenidae) from lower Central America.—Copeia 1967:604–609.

Starrett, P. H., & J. M. Savage. 1973. The systematic status and distribution of Costa Rican glass-frogs, genus *Centrolenella* (Family Centrolenidae), with description of a new species.—Bulletin of the Southern California Academy of Sciences 72: 57–78.

Taylor, E. H. 1949. Costa Rican frogs of the genera *Centrolene* and *Centrolenella.*—The University of Kansas Science Bulletin 33:257–270.

———. 1951. Two new genera and a new family of tropical American frogs.—Proceedings of the Biological Society of Washington 64:33–40.

Weberbauer, A. 1936. Phytogeography of the Peruvian Andes.—Field Museum of Natural History, Botanical Series, 13. Flora of Peru, Part 1: 13–81.

(JEC) Department of Herpetology, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103; and (RWM), United States Fish and Wildlife Service, Biological Survey, National Museum of Natural History, Washington, D.C. 20560.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, SW7 5BD

Applications published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 27 March 1990 in Vol. 47, Part 1 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, ICZN, % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.

2714 *Pleuractis* Verrill, 1864 (Cnidaria, Anthozoa): proposed designation of *Fungia paumotensis* Stutchbury, 1833 as the type species, with conservation of *Lobactis* Verrill, 1864.

2547 CYMATIINAE Iredale, 1913 (1854) (Mollusca, Gastropoda) and CYMATIINAE Walton in Hutchinson, 1940 (Insecta, Heteroptera): proposal to remove the homonymy.

2641 *Limax fibratus* Martyn, 1784 et *Nerita hebraea* Martyn, 1786 (actuellement *Placostylus fibratus* et *Natica hebraea*; Mollusca, Gastropoda): conservation proposée pour les noms spécifiques; et *Placostylus* Beck, 1837: désignation proposée de *L. fibratus* comme espèce-type.

2558 *Proptera* Rafinesque, 1819 (Mollusca, Bivalvia): proposed conservation.

2692 *Mirochernes* Beier, 1930 (Arachnida, Pseudoscorpionida): proposed confirmation of *Chelanops dentatus* Banks, 1895 as the type species.

2725 *Holostaspis subbadius* var. *robustulus* Berlese, 1904 (currently *Macrocheles robustulus*; Arachnida, Acarina): proposed conservation as the correct spelling of the specific name.

2721 *Bathynomus* A. Milne Edwards, 1879 (Crustacea, Isopoda): proposed precedence over *Palaega* Woodward, 1870.

2700 *Carcinochelis* Fieber, 1861 (Insecta, Heteroptera): proposed designation of *Carcinochelis alutaceus* Handlirsch, 1897 as the type species.

2717 *Steno attenuatus* Gray, 1846 (currently *Stenella attenuata*; Mammalia, Cetacea): proposed conservation of the specific name.

2726 *Mammuthus* Brookes, 1828 (Mammalia, Proboscidea): proposed conservation, and *Elephas primigenius* Blumenbach, 1799 (currently *Mammuthus primigenius*): proposed designation as the type species of *Mammuthus,* and designation of a neotype.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 27 March 1990 in Vol. 47, Part 1 of the *Bulletin of Zoological Nomenclature.*

Opinion No.
1567 *Nonion* de Montfort, 1808 (Foraminiferida): *Nautilus faba* Fichtel & Moll, 1798 designated as the type species.
1568 *Hanzawaia* Asano, 1944 (Foraminiferida): conserved.
1569 *Calcarina* d'Orbigny, 1826 (Foraminiferida): conserved.
1570 *Dendritina* d'Orbigny, 1826 (Foraminiferida): conserved.
1571 *Planularia* Defrance, 1826 (Foraminiferida): conserved.
1572 *Nautilus repandus* Fichtel & Moll, 1798 (currently *Eponides repandus*; Foraminiferida): neotype replaced by rediscovered holotype.
1573 *Madrepora limax* Esper, 1797 (currently *Herpolitha limax*) and *Fungia talpina* Lamarck, 1801 (currently *Polyphyllia talpina*; both Cnidaria, Anthozoa): specific names conserved.
1574 *Sphaeroma hookeri* Leach, 1814 (currently *Lekanesphaera hookeri*; Crustacea, Isopoda): specific name conserved.
1575 *Coenobita* Latreille, 1829 (Crustacea, Decapoda): conserved.
1576 *Palaemon longirostris* H. Milne Edwards, 1837 (Crustacea, Decapoda): specific name conserved.
1577 *Hydrobius* Leach, 1815 (Insecta, Coleoptera): *Dytiscus fuscipes* Linnaeus, 1758 conserved as type species, and *Berosus* Leach, 1817 (Insecta, Coleoptera): conserved.
1578 *Vespa triangulum* Fabricius, 1775 (currently *Philanthus triangulum*; Insecta, Hymenoptera): specific name conserved.
1579 *Pycinaster magnificus* Spencer, 1913 (Echinodermata, Asteroidea): specific name conserved.
1580 *Cordylodus? dubius* Rhodes, 1953 (currently *Distomodus dubius*; Conodonta): specific name conserved.
1581 *Hydrolycus* Müller & Troschel, 1844 (Osteichthyes, Cypriniformes): *Hydrocyon scomberoides* Cuvier, 1819 confirmed as the type species.
1582 *Ictiobus* Rafinesque, 1820 (Osteichthyes, Cypriniformes): conserved.
1583 *Scorpaenichthys marmoratus* (Osteichthyes, Scorpaeniformes): Ayres, 1854 to be taken as the author of the specific name.
1584 *Ameiurus* Rafinesque, 1820 (Osteichthyes, Siluriformes): *Silurus lividus* Rafinesque, 1820 designated as the type species.
1585 *Ascalabotes gigas* Bocage, 1875 (currently *Tarentola gigas*; Reptilia, Squamata): specific name conserved.
1586 *Euryotis brantsii* A. Smith, 1834 (currently *Parotomys brantsii*; Mammalia, Rodentia): specific name conserved.

PROC. BIOL. SOC. WASH.
103(3), 1990, pp. 771

BIOLOGICAL SOCIETY OF WASHINGTON

117TH Annual Meeting, 8 May 1990

The meeting was called to order by Kristian Fauchald, President, at 12:30 p.m. in the Waldo Schmitt Room, National Museum of Natural History.

Kristian announced the election results. The new elected officers and council members are listed on the inside front cover of this issue.

Mike Vecchione, Treasurer, presented the report of past Treasurer, Don Wilson. Income from dues in 1989 was slightly higher than that of 1988, and income from subscriptions, sales of past issues of the Proceedings and Bulletins, and page charges was substantially lower. Total income for 1989 was $83,661 and total expenditures were $81,673. The proposed budget for 1990 estimates income of $91,000 and expenditures of $97,000, predicting a potential deficit of $6000.

Brian Robbins, Editor, then presented his report. The four issues of Volume 102 of the Proceedings were published on 29 March, 28 June, 18 October, and 19 December 1989, containing a total of 104 papers and 1085 pages. A copy of the new "Guidelines for Manuscripts" was sent to all members as a Supplement to the first issue of Volume 103. The One-Hundred-Year Index is nearing completion and will be published camera-ready as a Supplement to Volume 100. Rafael Lemaitre replaced Ray Manning as one of the Associated Editors for Invertebrate Zoology.

Kristian noted that Austin Williams replaced Dave Pawson as Back-Issues Custodian and announced that he has appointed an ad-hoc committee to review problems associated with storage and disposition of back issues.

A motion was made and seconded that the meeting be adjourned; the new President, Leslie W. Knapp, adjourned the meeting at 1:15 p.m.

Respectfully submitted,
G. David Johnson
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 Stop 108, Smithsonian Institution, Washington, D.C. 20560.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed in order of receipt by a board of Associate Editors and appropriate referees.

Proofs.—First proofs are submitted to authors for correction and approval. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, changes at proof stages, and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

Presentation.—Manuscripts should be typed **double-spaced throughout** (including tables, legends, and footnotes) on one side of 8½ × 11 inch sheets, with at least one inch of margin all around. Submit three copies complete with tables, figure captions, and figures (plus originals of the illustrations), and retain an author's copy. Pages must be numbered consecutively. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s') Address(es), Appendix, Figure Legends, Figures (each numbered and identified), Tables (**double-spaced throughout,** each table numbered with an Arabic numeral and with heading provided).

Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is required for descriptions and diagnoses. Literature citations in the text should be in abbreviated style (author, date, page), except in botanical synonymies, with unabbreviated citations of journals and books in the Literature Cited sections. Direct quotations in the text must be accompanied by author, date, **and pagination.** The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate figure and table placement in pencil in the margin of the manuscript. Plan illustrations in proportions that will efficiently use space on the type bed of the Proceedings. **Original illustrations should not exceed 15 × 24 inches.** Figures requiring solid black backgrounds should be indicated as such when the manuscript is submitted, but should not be masked.

CONTENTS

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 103 NUMBER 4
19 DECEMBER 1990
ISSN 0006-324X

THE BIOLOGICAL SOCIETY OF WASHINGTON

PROCEEDINGS

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

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

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

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

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 773–783

THE IDENTITY OF *FANNYELLA ROSSII* J. E. GRAY (COELENTERATA: OCTOCORALLIA)

Frederick M. Bayer

Abstract.—The conspecificity of *Ascolepis splendens* Thomson & Rennet, 1931, with *Fannyella rossii* J. E. Gray, 1873, is established. A syntype of *Ascolepis splendens,* register number G-13237 in the Australian Museum, Sydney, is selected as lectotype of the species and simultaneously established as neotype of *Fannyella rossii.* A revised description of the species is provided, illustrated by scanning electron micrographs, in comparison with the original illustrations of *Fannyella rossii* and *Ascolepis splendens.*

During the Antarctic voyage of HMS *Erebus* and *Terror* 1839–1843 under the command of Captain Sir James Clark Ross, a dredge haul made on 19 January 1841 at a depth of 270 fathoms (=494 m) at 72°31′S, 173°39′E, in the vicinity of Cape Hallett, Ross Sea, obtained a "new species of Primnoa, which I name *P. Rossii,*" along with another gorgonian, a scleractinian coral, and some bryozoans (Stokes 1847:258–259). Ross entrusted these, together with some other invertebrates from the expedition, to Charles Stokes for investigation. In 1846, Stokes sent drawings and notes on the specimens to Ross (Stokes 1847:259), who, in turn, gave the drawings to J. E. Gray. They were not published in the volume on the zoology of the expedition, remaining in Gray's custody until 1872, when he presented them together with descriptive text of his own at the meeting of the Zoological Society of London June 18, 1872. According to Gray (1873:744), the specimens by that time had been "lost to science."

Although Stokes (1847) specifically discussed his new *Primnoa rossii,* he referred only to the then unpublished drawings without giving any characters to make the name nomenclaturally available. Gray (1873), in publishing the drawings, established a new genus, *Fannyella,* and used the name *rossii* proposed by Stokes for the species. He seems to have been unaware of the paper published by Stokes. Good though the drawings are, they have not been associated with any gorgonians obtained by later Antarctic expeditions.

Numerous specimens provisionally identified as *Ascolepis splendens* Thomson & Rennet, 1931, a species first obtained at four localities between 92°10′E and 145°21′E by the Australasian Antarctic Expedition, have been taken at various localities around the Antarctic continent by expeditions of the U.S. Antarctic Research Program. This material agrees with the published drawing of *Fannyella rossii,* leaving no doubt that they represent the same species, and comparison with a syntype of *Ascolepis splendens* confirms that the two species also are identical.

Although the generic name *Ascolepis* has been used in keys (see below), the species *A. splendens* Thomson & Rennet, 1931, has not been reported again in the literature since 1931, so no justification exists for retaining it as the valid name for the genus and species in preference over the senior synonym *Fannyella rossii* Gray, 1873, also used only once. In order to place this undoubted but subjective synonymy on an objective basis, the illustrated syntype of *A. splendens* Thomson & Rennet, 1931 (Australian Museum, Sydney, register no. G-13237), is hereby simultaneously selected as lectotype of *As-*

colepis splendens and designated as neotype of *Fannyella rossii* Gray, 1873.

Fannyella J. E. Gray, 1873

Primnoa (part).—Stokes, 1847:260

Fannyella Gray, 1873:744. (Type species, *Fannyella rossii* Gray, 1873, by monotypy.)

Ascolepis Thomson & Rennet, 1931:20.—Bayer, 1981:936 (in key only); 1982:120–122 (passim).—Bayer & Stefani, 1989:454 (in key only). (Type species, *Ascolepis splendens* Thomson & Rennet, 1931, here designated.)

Diagnosis.—Dichotomously branched Primnoidae with verticillate polyps protected by sclerites arranged in distinct longitudinal rows on abaxial and lateral aspects of body; adaxial surface with fewer sclerites, in some cases unarmed except for a few small scales immediately below opercular and circumopercular scales. Body sclerites vertically overlapping, exposed part smooth and distinctly differentiated from strongly tuberculate covered part. Circumopercular (i.e., marginal) scales folding over bases of opercular scales. Outer layer of coenenchyme with thick polygonal, rounded, or irregular plates and many smaller, rounded scales; inner layer with irregularly tuberculate discoidal forms and spindles, which occasionally are triradiate or branched.

Fannyella rossii Gray, 1873
Figs. 1–6

Primnoa Rossii Stokes, 1847:260, 261 (nomen nudum).

Fannyella rossii Gray, 1873:745, pl. 62, figs. 1–3 (Antarctic Ocean).

?*Caligorgia antarctica* Kükenthal, 1912:321, figs. 27–35, pl. 21, fig. 10 (*Gauss*-Station, 385 m).

?*Caligorgia ventilabrum.*—Gravier, 1914: 85, figs. 109–119; pl. 6, fig. 30 (Marguerite Bay, Antarctic Peninsula, 176–230 m).—Molander, 1929:60 (Seymour I., Graham Land, 150 m; South Georgia, 75 m).

Not *Caligorgia ventilabrum* Studer, 1879: 647, pl. 2, fig. 12 (North of New Zealand, 165 m).—Versluys, 1906:74, figs. 83, 84 (illustrates polyp from Studer's type specimen).

Ascolepis splendens Thomson & Rennet, 1931:20, pl. 9, figs. 6, 7; pl. 10, figs. 1, 2; pl. 11, fig. 6 (Off Wilkes Land, from Adelie Coast west to Davis Sea, 46–582 m).

Gray (1873:745) gave no description of the species, but a combined description of genus and species (1873:744), which runs as follows:

> "Coral slightly furcately branched; branches club-shaped, enlarging upwards, and then rapidly contracting at the tip; polypiferous cells many, in numerous close concentric rings, forming regular whorls round the branches, the cells oblong, cylindrical, contracted at the base, and each covered with six longitudinal series of transverse oblong hexangular scales, truncated at top and closed with elongated more or less acute scales, converging to a point when the animal is withdrawn; axis covered with small scales."

The club-shaped branches are related to the small size of the very young colony with only two bifurcations (Fig. 2d), and are not characteristic of fully developed colonies. As the adaxial surface of the polyps is naked save for a few small scales just below the operculum, Gray's description of "six longitudinal series" of scales, rather than the more usual eight, is basically correct.

The more exhaustive description of *Ascolepis splendens* provided by Thomson & Rennet (1931:20) is more nearly definitive. The specimen from *Aurora* station 2, 66°55′S, 145°21′E, 318 fathoms (=582 m), 28 Dec 1913 (Australian Museum no. G-13237) conforms with the specifications cited by Thomson & Rennet (1931:20) and clearly is the specimen upon which the description of *Ascolepis splendens* is based. A photograph of this specimen is given herewith (Fig. 1). The drawing reproduced on Thomson & Rennet's Plate IX, Fig. 6, appears to be a somewhat simplified representation either of the detached branch accompanying the complete specimen, or of a branch of the complete colony as isolated by the artist.

The original description of *A. splendens* is accurate except in regard to the form of the polyp sclerites: "The striking peculiarity is that the main sclerites of the vertical rows have a distinct ascus-like or chalice-like form. That is to say, the basal portion is the substantial very warty support of a delicate cup whose cavity is open to the exterior! The delicate edges of the cups are weakly notched, sometimes almost entire. The cup of the sclerite is broader than the substantial knobbed support, so that the appearance is somewhat like a short-stalked chalice or fruit-basket." The authors go on to say that "We must emphasise the point that the specimen is on the whole like a *Caligorgia,* but its hollow ascus-like sclerites are very far from the ctenoid-scale type" (Thomson & Rennet 1931:20–21).

As is immediately apparent from scanning electron micrographs (Figs. 3–5), the "delicate" cups are an optical illusion. As the calcite of which the sclerites are composed is almost glassy clear, only the edges of the smooth outer portion of the body sclerites are visible as a bright line under the light microscope; the fact that it is solid is not easily detected in a bulk preparation of sclerites. It is, however, readily perceived in intact polyps viewed with a binocular dissecting microscope, and it is a mystery why this was not noticed during preparation of the drawing reproduced by Thomson & Rennet as fig. 7 of Plate IX (Fig. 2b). When sclerites seen by Thomson & Rennet as transparent objects are viewed by SEM as opaque objects, it can be seen that the surface of the exposed part of the body sclerites is sometimes very weakly concave, but as often it is flat or slightly convex and ornamented by rows of low, smooth, elongate granules (Figs. 4, 5).

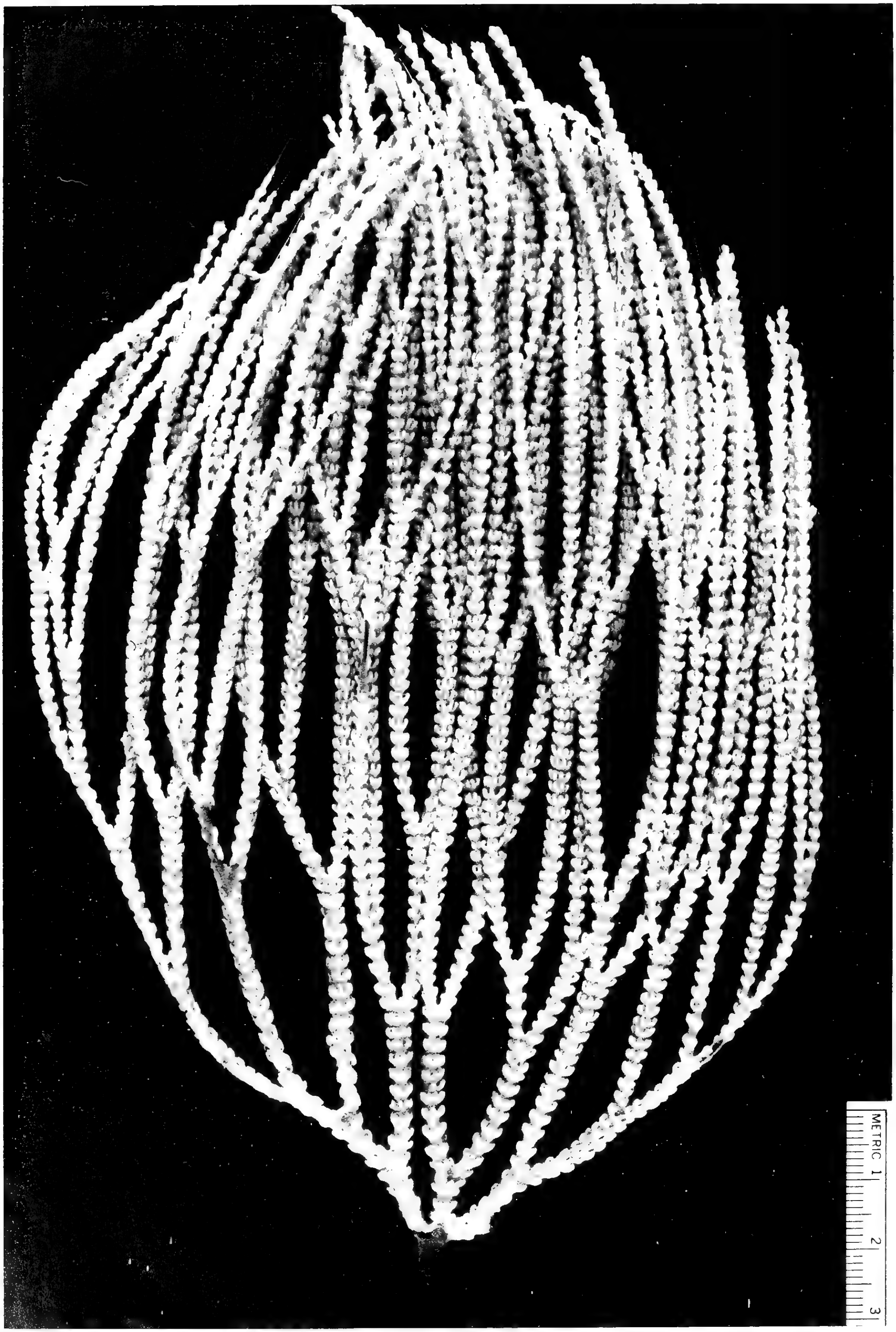
The abaxial and lateral opercular scales are broad and have a marginal point located more or less off center, but the adaxial operculars are narrow and toothlike. The outer lateral rows of body sclerites are well developed and composed of nearly as many scales as the abaxial rows, but these are more rounded in outline and not nearly so "ascus-like" as the abaxial sclerites (Fig. 5). The inner lateral rows are present but short, comprised of only 2 or 3 scales below the operculars, and the adaxial rows are reduced usually to a single small marginal below each opercular (Fig. 4).

In order to show the true form of the sclerites illustrated by Thomson & Rennet, the various types included in their fig. 6 of Plate XI (Fig. 2c) have been photographed under the SEM and arranged so as to reconstruct their illustration (Fig. 6), which appears to have been drawn free-hand.

Distribution.—Circum-Antarctic, 46–852 m. The southernmost locality reported thus far is from 77°13.7′S, 40°03.8′W, off Filchner Ice Shelf (*Polarstern* "Antarktis I" sta. 180); the northernmost record is from 54°22.1′S, 03°38.2′E, off Bouvet Is. (*Marion Dufresne* sta. 17, haul CM 30), which also is the deepest record.

→

Fig. 1. *Fannyella rossii* J. E. Gray, 1873. Neotype colony, natural size. Lectotype of *Ascolepis splendens* Thomson & Rennet, 1931. Australasian Antarctic Expedition, HMS *Aurora* sta. 2. Australian Museum register no. G-13237.


METRIC 1
2
3

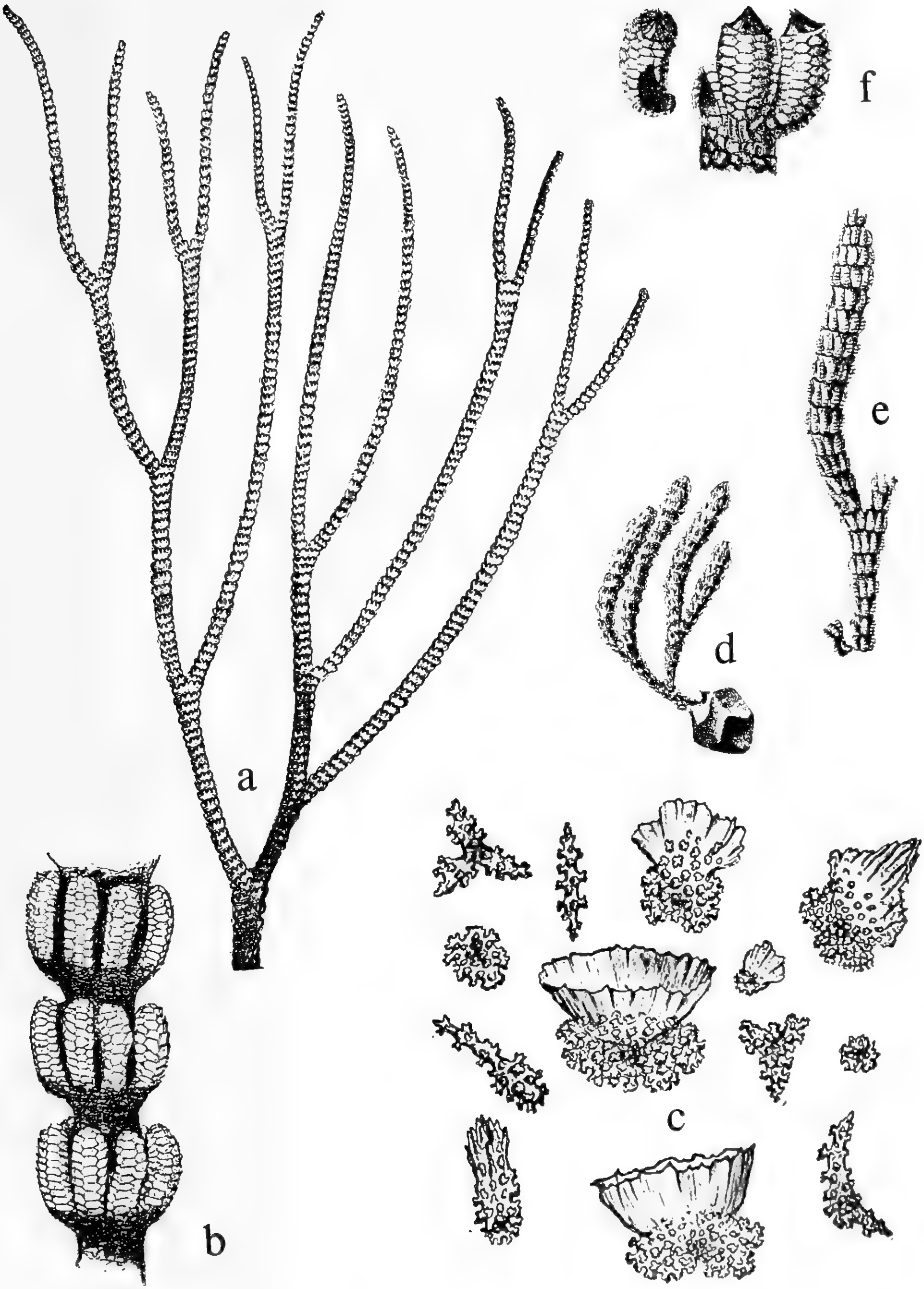


Fig. 2. a–c.—*Ascolepis splendens* Thomson & Rennet, 1931. Original illustrations. a, Copy of pl. IX, fig. 6; b, Copy of pl. IX, fig. 7; c, Copy of pl. XI, fig. 6.—d–f, *Fannyella rossii* Gray, 1873. Original illustrations. Copies of pl. XLII, figs. 1–3.

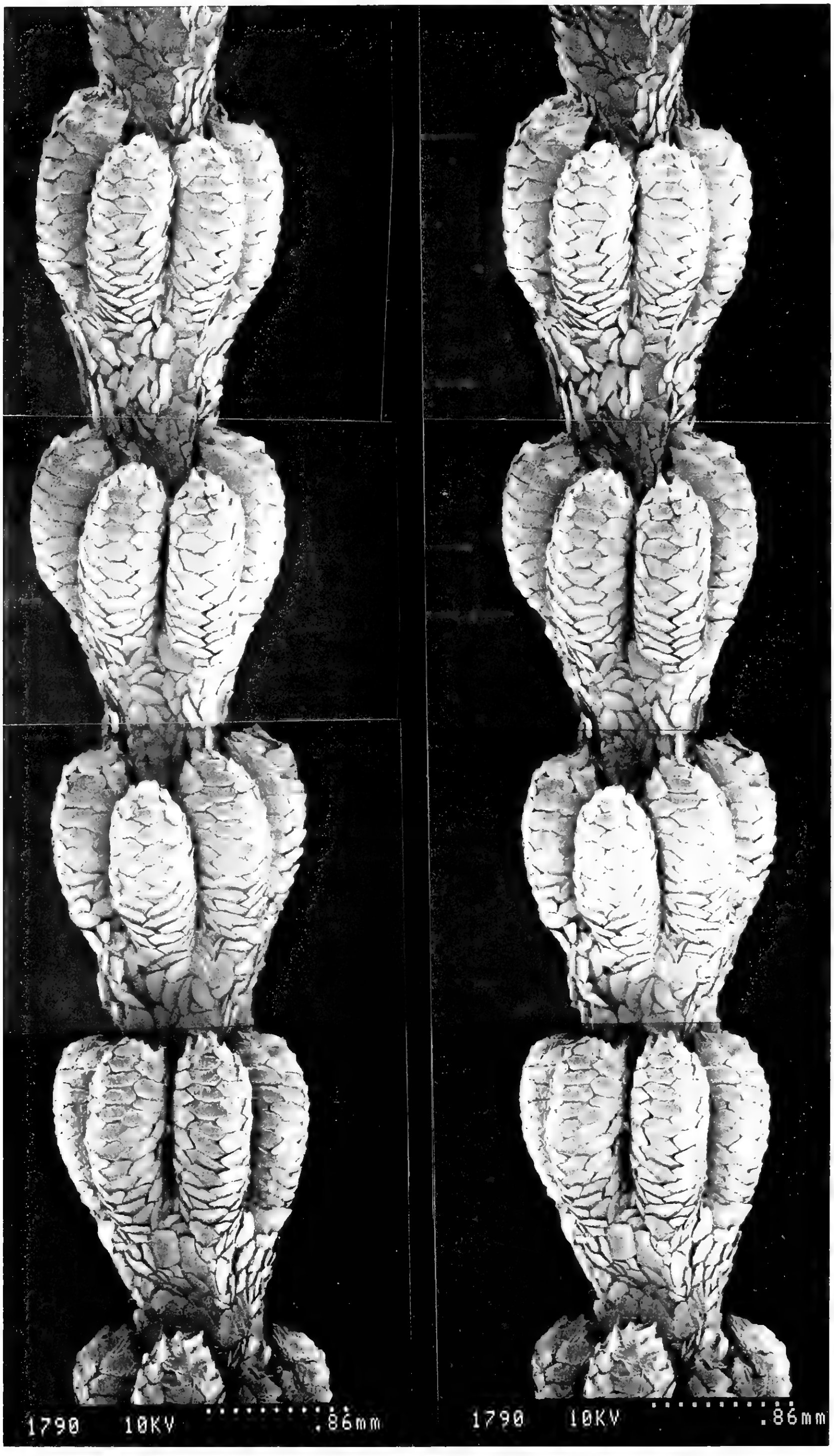


Fig. 3. *Fannyella rossii* J. E. Gray, 1873, neotype =*Ascolepis splendens* Thomson & Rennet, 1931, lectotype. Stereomicrographs of whorls of polyps.

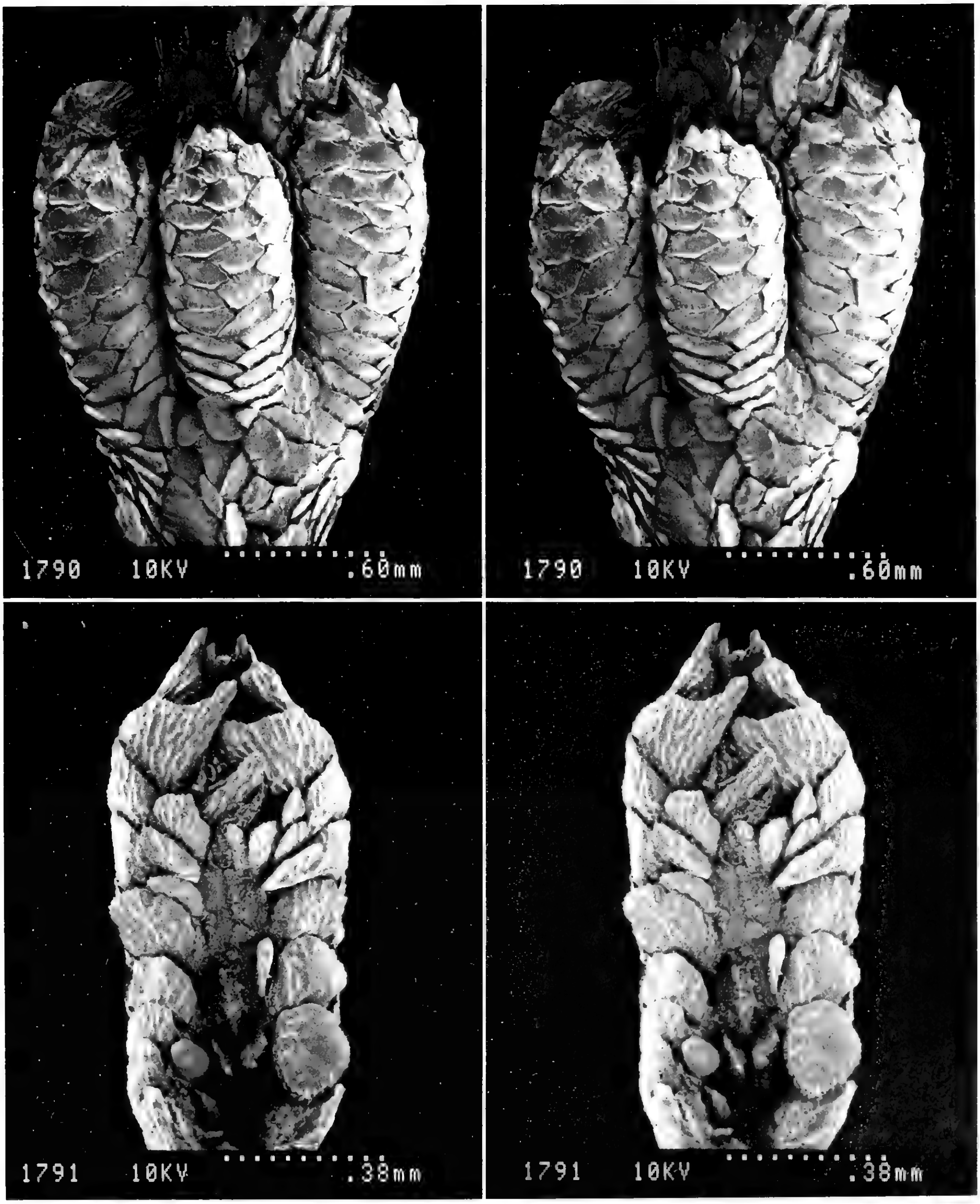


Fig. 4. *Fannyella rossii* J. E. Gray, 1873, neotype =*Ascolepis splendens* Thomson & Rennet, 1931, lectotype. Top, Whorl of polyps. Bottom, Adaxial surface of isolated polyp. Stereomicrographs.

Fannyella rossii is one of the most abundant and widely distributed gorgonians of the Antarctic and sub-Antarctic fauna. It has been taken by various expeditions at the following locations.

U.S. Antarctic Research Program. Specimens in the U.S. National Museum of Natural History:

Ross Sea, off Cape Hallett: 72°32′S, 171°26′E, 337–329 m, USNS *Eltanin* sta.

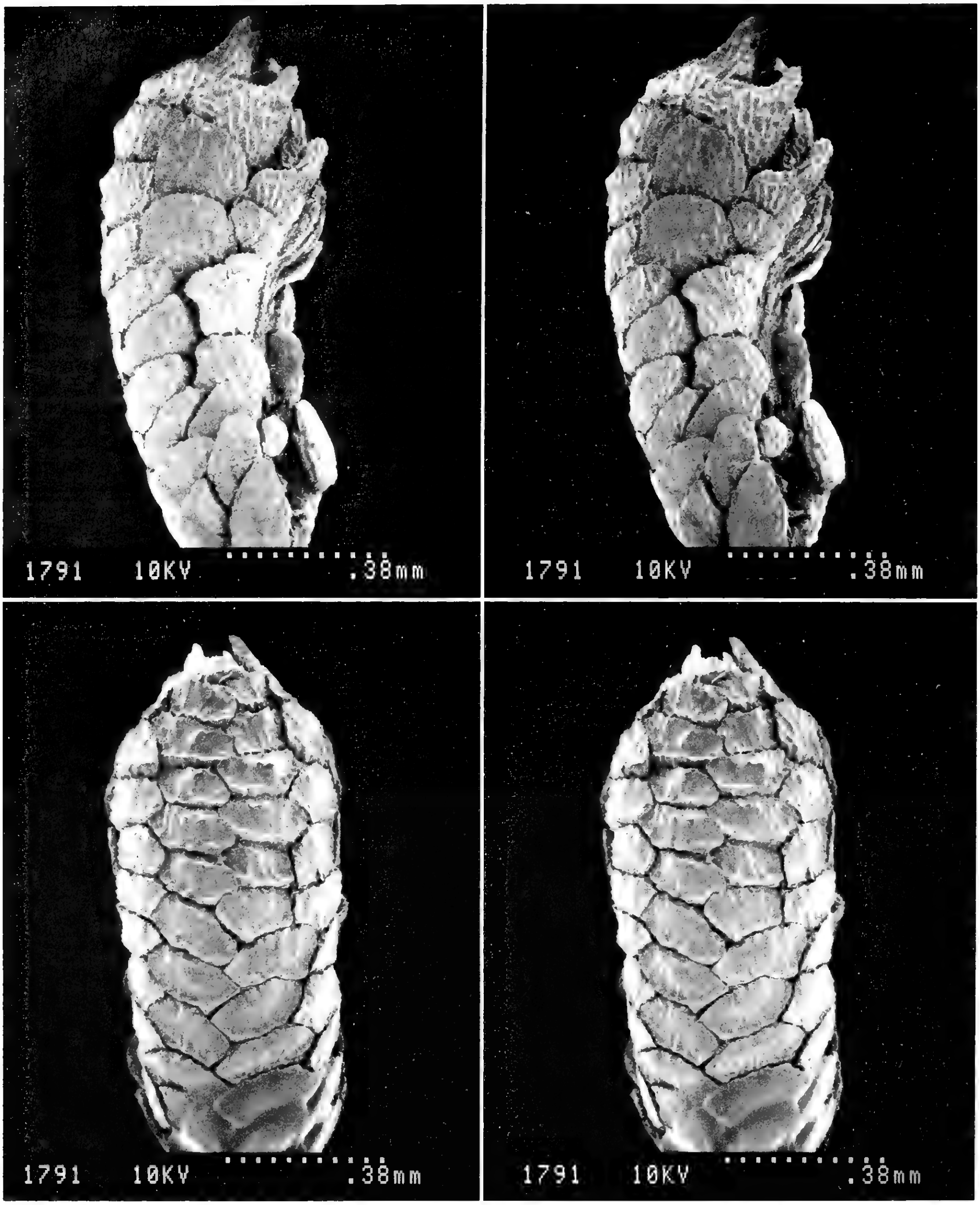


Fig. 5. *Fannyella rossii* J. E. Gray, 1873, neotype =*Ascolepis splendens* Thomson & Rennet, 1931, lectotype. Stereomicrographs of isolated polyp. Top, Lateral view. Bottom, Abaxial view.

1875, 15 Jan 1967. Five large more or less complete colonies without holdfasts, and detached branches, USNM 82949 (SEM 1417, 1427).

Ross Sea, off Cape Washington: 75°01′S, 168°23′E, 334–335 m, USNS *Eltanin* sta. 2036, 18 Jan 1968. One large colony lacking holdfast, USNM 82078 (SEM 1471–1473).

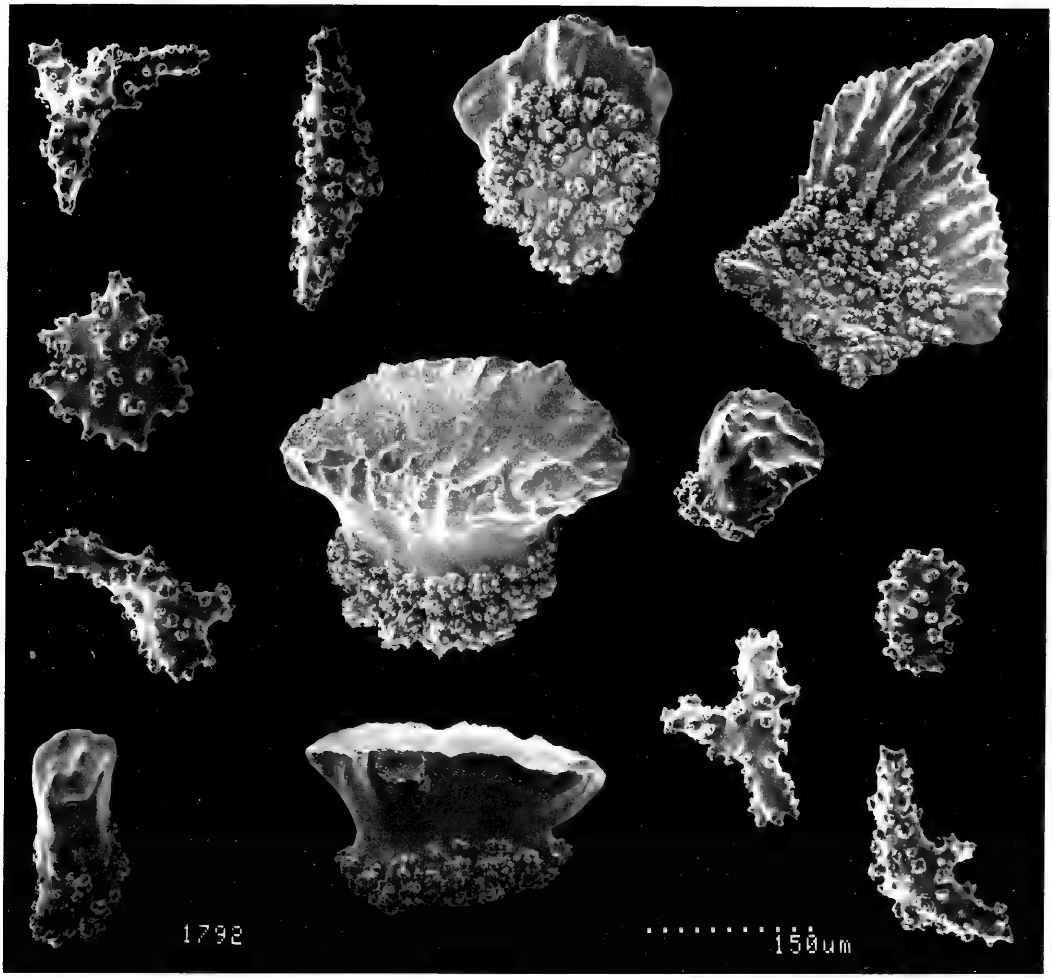


Fig. 6. *Fannyella rossii* J. E. Gray, 1873, neotype =*Ascolepis splendens* Thomson & Rennet, 1931, lectotype. Sclerites. Reconstruction of Thomson & Rennet's plate XI, fig. 6. Scanning electron micrographs.

Ross Sea: 76°00′S, 176°48′W, 566–569 m, USNS *Eltanin* sta. 2045, 20 Jan 1968. One colony and detached branches, USNM 82079 (SEM 1407).

Ross Sea: 76°25′S, 170°24′W, 568 m, USNS *Eltanin* sta. 2075, 30 Jan 1968. One colony without holdfast, and 1 detached branch, USNM 82109.

Ross Sea, Bay of Whales: 76°08′S, 165°04′W, 494–498 m, USNS *Eltanin* sta. 2097, 4 Feb 1968. 2 small incomplete specimens, USNM 82950.

South Shetland Islands: 61°18′S, 56°09′W, 220–240 m, USNS *Eltanin* sta. 410, 31 Dec 1962. One colony lacking holdfast, USNM 82072 (SEM 1404, 1405).

South Shetland Islands: 61°25′S, 56°30′W, 164 fathoms (=300 m), USNS *Eltanin* sta. 993, 13 Mar 1964. One complete colony with holdfast attached to coral, USNM 60342.

South Shetland Islands: 63°26′S, 62°15′W, 119–124 m, R/V *Hero* cruise 691 sta. 26, 10 Feb 1969. One large colony nearly complete but lacking holdfast, and 1 detached branch, USNM 82952 (SEM 1448, 1449).

Antarctic Peninsula, vicinity of Brabant Island: 64°21′24″S, 61°28′12″W, 110–155 m, R/V *Hero* sta. 21-1, 23 Mar 1982, coll. G. Hendler. One large colony complete with holdfast, USNM 77360 (SEM 1798, 1799).

Antarctic Peninsula: 64°46′28″S, 63°26.5′W, 100–150 m, R/V *Hero* cruise 731 sta. 1944, 11 Mar 1973. Three colonies lacking holdfasts, USNM 82071.

Antarctic Peninsula: 64°50′S, 63°12′W, 155 fath. (=283 m); *Eastwind* sta. 66-006, haul 3, coll. D. F. Squires and D. L. Pawson, 29 Jan 1966. Two colonies, USNM 58151 (SEM 303).

Antarctic Peninsula: 65°03.71′S, 63°57.05′W, 360–375 m, R/V *Hero* cruise 833 sta. 8-2, 10 March 1983. One colony lacking holdfast, USNM 82082.

Antarctic Peninsula: 65°06.7′S, 65°00.7′W, 100–180 m, R/V *Hero* cruise 731 sta. 1884. One colony extensively overgrown by hydroids, USNM 82118.

Antarctic Peninsula: 65°54.5′S, 65°15.5′W, 246–270 m, R/V *Hero* cruise 824 sta. 5-1, 16 Mar 1982. Two incomplete colonies, USNM 82119 (SEM 1440–1442).

Weddell Sea off Filchner Ice Shelf: 76°50′S, 40°55′W, 513 m, IWSOE University of Connecticut, USS *Glacier* cruise 2 sta. 0006, 1 Mar 1969. One small branch, USNM 82951.

R/V *Polarstern.* Specimens in Senckenberg Museum Frankfurt:

Off Atka Iceport, Princess Martha Coast: 70°30.3′S, 08°04.0′W, 261–263 m, cruise "Antarktis I" sta. 220, 1 Mar 1983. One large, slender colony without holdfast.

Weddell Sea, off Nantucket Inlet, Lassiter Coast, Antarctic Peninsula: 74°49.9′S, 61°08.3′W, 637 m, cruise "Antarktis II/4" sta. 386, 31 Jan 1984. Two small colonies without holdfasts.

Weddell Sea, off Nantucket Inlet, Lassiter Coast, Antarctic Peninsula: 74°57.3′S, 60°31.4′W, 662 m, cruise "Antarktis II/4" sta. 378, 31 Jan 1984. Six colonies without holdfasts.

Weddell Sea, off Cape Adams, Antarctic Peninsula: 75°00.1′S, 59°38.0′W, 621 m, cruise "Antarktis II/4" sta. 372, 30 Jan 1984. Three colonies without holdfasts and 6 fragments.

Weddell Sea, off Gardner Inlet, Antarctic Peninsula: 75°08.5′S, 59°38.1′W, 627 m, cruise "Antarktis II/4" sta. 369, 30 Jan 1984. Two large and 2 smaller colonies without holdfasts, and many fragments.

Weddell Sea: 75°49.2′S, 56°15.1′W, 456 m, cruise "Antarktis II/4" sta. 450, 8 Feb 1984. Two small colonies with holdfast, 8 small colonies without holdfasts, and 10 fragments.

Weddell Sea, north of Luitpold Coast, Coats Land: 76°08.4′S, 32°37.6′W, 788 m, cruise "Antarktis II/4" sta. 510, 22 Feb 1984. One large incomplete colony.

Weddell Sea: 76°09.7′S, 52°21.4′W, 416 m, cruise "Antarktis II/4" sta. 438, 7 Feb 1984. Two incomplete colonies.

Weddell Sea: 76°38.6′S, 52°10.3′W, 304 m, cruise "Antarktis II/4" sta. 341, 26 Jan 1984. One small colony without holdfast.

Weddell Sea: 76°52.5′S, 50°40.4′W, 259 m, cruise "Antarktis II/4" sta. 308, 20 Jan 1984. One large incomplete colony.

Weddell Sea, off Filchner Ice Shelf: 77°13.7′S, 40°03.8′W, 673–717 m, cruise "Antarktis I" sta. 180, 18 Feb 1983. One large detached branch.

R/V *Marion Dufresne.* Specimen in Muséum National d'Histoire Naturelle, Paris:

East of Bouvet Is.: 54°22.1′S, 03°38.2′E, 965–852 m, sta. 17, Marinovich trawl 30, 22 Aug 1980. One large colony almost complete, with holdfast, and 2 detached branches.

The original material of *Ascolepis splendens* taken by HMS *Aurora* of the Australasian Antarctic Expedition, now preserved in the Australian Museum Sydney, was obtained at station 2, 66°55′S, 145°21′E, 318 fathoms (=582 m), 28 Dec 1913 (AMS no. G-13245 and G-13237 [lectotype]; station 7, 65°42′S, 92°10′E, 60 fathoms (=110 m), 21 Jan 1914 (AMS no. G-13221); station 8, 66°08′S, 94°17′E, 120 fathoms (=219 m), 27 Jan 1914; and at Commonwealth Bay, Adelie Land, in 25–318 fathoms (=47–582 m), 3 Sep 1912 (AMS no. G-13273).

Acknowledgments

In the preparation of this paper I am indebted to Mr. Simon Moore (Natural History Museum, London) and Ms. Penny Berents (Australian Museum, Sydney), for the loan of pertinent material. The records of *Fannyella rossii* from stations of R/V *Polarstern* and R/V *Marion Dufresne* were supplied by Dr. Manfred Grasshoff (Natur-Museum Senckenberg, Frankfurt). As always, I am grateful to Dr. Grasshoff for his perceptive comments and advice in regard to the taxonomic and nomenclatural problems considered in this paper. Dr. Curtis W. Sabrosky, former president of the International Commission on Zoological Nomenclature, provided helpful critical comments on the manuscript, for which I express sincere thanks. The scanning electron micrographs given here were made by Mr. Walter R. Brown, chief of the Scanning Electron Microscope Laboratory, U.S. National Museum of Natural History, Smithsonian Institution.

Literature Cited

Bayer, F. M. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa.—Proceedings of the Biological Society of Washington 94: 902–947, figs. 1–80.

———, 1982. Some new and old species of the primnoid genus Callogorgia Gray, with a revalidation of the related genus Fanellia Gray (Coelenterata: Anthozoa).—Proceedings of the Biological Society of Washington 95:116–160, figs. 1–29.

———, & J. Stefani. 1989. Primnoidae (Gorgonacea) de Nouvelle-Calédonie.—Bulletin du Muséum National d'Histoire Naturelle, Paris (4)10(A no. 3):449–518, including pls. 1–42.

Duncan, F. M. 1937. On the dates of publication of the Society's 'Proceedings,' 1859–1926. With an appendix containing the dates of publication of 'Proceedings,' 1830–1858, compiled by the late F. H. Waterhouse, and of the 'Transactions,' 1833–1869, by the late Henry Peavot, originally published in P.Z.S. 1893, 1913.—Proceedings of the Zoological Society of London (A)107:71–84.

Gravier, C. 1914. Alcyonaires. Deuxième Expédition Antarctique Française (1908–1910). Sciences Naturelles: Documents scientifiques. Pp. 1–118, pls. 1–10.

Gray, J. E. 1873. Notes on corals from the South and Antarctic seas.—Proceedings of the Scientific Meetings of the Zoological Society of London for the year 1872(part 47):744–747, pls. 62–64. [According to Duncan (1937:72), the date of publication of the Proceedings pp. 737–927 is April 1873; Neave (1939:398) records 1873 as the date of *Fannyella*.]

Kükenthal, W. 1912. Die Alcyonarien der deutschen Südpolar-Expedition 1901–1903. Deutsche Südpolar-Expedition 1901–1903, 13 Band.—Zoologie 5(3):289–349, pls. 20–23.

Molander, A. R. 1929. Die Octactiniarien.—Further Zoological Results of the Swedish Antarctic Expedition Expedition 1901–1903, 2(2):i–iv + 1–86, pls. 1–5.

Neave, S. A. (ed.) 1939. Nomenclator zoologicus. Zoological Society, London 2:1–1025.

Stokes, C. 1847. Remarks on some corals obtained from great depths in the Antarctic Ocean, in a letter from Charles Stokes, Esq., F.R.S., F.G.S., &c., to Captain Sir James C. Ross, R.N.—The Edinburgh New Philosophical Journal, exhibiting a view of the Progressive Discoveries and Improvements in the Sciences and the Arts 43: 258–262.

Studer, Th. 1879. Übersicht der Anthozoa Alcyonaria, welche während der Reise S.M.S. Gazelle um die Erde gesammelt wurden.—Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1878:632–688, pls. 1–5.

Thomson, J.A., & N.I. Rennet. 1931. Alcyonaria, Madreporaria, and Antipatharia.—Australasian Antarctic Expedition 1911–14. Scientific Reports. (Series C)9(3):1–46, pls. 8–14.

Versluys, J. 1906. Die Gorgoniden der Siboga Expedition. II. Die Primnoidae.—Siboga-Expeditie Monographie 13a. Pp. 1–187, 178 figs. 10 pls. chart.

Department of Invertebrate Zoology, National Museum of Natural History, NHB-163, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 784–788

MEIOPRIAPULUS FIJIENSIS MORSE (PRIAPULIDA) FROM SOUTH ANDAMAN, ANOTHER EXAMPLE OF LARGE-SCALE GEOGRAPHIC DISTRIBUTION OF INTERSTITIAL MARINE MEIOFAUNA TAXA

Wilfried Westheide

Abstract.—The interstitial priapulid *Meiopriapulus fijiensis* Morse, 1981, is described for the first time outside of its type locality on Fiji from a coral reef on the Andaman Islands. The species identification is based on SEM investigations of cuticular structures.

Priapulids are among the more recent discoveries in the marine meiofauna. Remane (1963) saw the first interstitial representative of this taxon during his investigations in the Red Sea. Van der Land (1968) gave the first description of a meiobenthic priapulid, *Tubiluchus corallicola,* which he found in shallow coral sand from Curaçao. Since that time, four additional *Tubiluchus* species have been described and two genera erected. *Maccabeus* Por, 1973, with at least one species is obviously identical with Salvini-Plawen's (1974) *Chaetostephanus* (Calloway 1988). *Meiopriapulus* Morse, 1981, the most recently discovered genus, is represented by the species *fijiensis* known from a single beach on Viti Levu, Fiji. Details of its integument and anatomy were published by Storch et al. (1989a, 1989b). Nevertheless, priapulids are extremely rare representatives of the interstitial meiofauna. Present records (reviewed by Calloway 1988) appear to indicate their endemic distribution in more or less insular habitats, except for *Tubiluchus corallicola* which is recorded from Curaçao, the Carribean Sea, Bonaire, Barbados and Bermuda (Van der Land 1970). All the more surprising and of zoogeographic interest was the discovery of the Pacific *M. fijiensis* in the Andaman Sea during a short collecting trip by the author to the Andaman Islands in February 1988.

Meiopriapulus fijiensis Morse, 1981

Methods and Materials

Extraction took place in a room of the Hotel Aasiana, Port Blair. The sediment was mixed with a solution of about 8% $MgCl_2$ in tap water to relax any meiofauna present, and sieved through a 63 μm screen. The fraction was placed in fresh sea water and the animals were observed and sorted live using a transportable dissecting microscope. Oocytes were observed in at least two of the specimens. Following narcotization with the $MgCl_2$-solution, the specimens were fixed for several weeks in either 10% formalin or in Bouin's fluid and then transferred into 70% ethanol. The fixed animals exhibited all stages of contraction, invertion, and evertion of the introvert. Four specimens were postfixed with 1% OsO_4 in aqua dest., critical point dried in CO_2, coated with gold and examined with a Cambridge Stereo Scan 250. One specimen was whole-mounted in W 15 mounting medium and examined using interference contrast microscopy.

Results

Material.—Twelve specimens of different size were found. Five of them were used for identification, two were deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.: USNM 128299, and five remain in the collection of the author.

Locality.—Bay of Bengal, Andaman Islands, South Andaman. Coral reef in front of a small village about 10 km south of Port Blair. In water covered patches of clean coral sand between coral clumps in the surf zone of the reef edge; during low tide, 19 Jan 1988.

Measurements.—Length between 1.2 and 1.7 mm; width of the abdomen about 300 μm.

External morphology.—The terminology used is based on the species description of Morse (1981) and also incorporates the findings of Storch et al. (1989a, 1989b). Only cuticular details are described. The overall external morphology totally agrees with the description of Morse (1981): a cylindrical body consisting of a bulbous anterior introvert and an elongate abdomen, the posterior end of which is conical in shape and bears a circle of protruding hooks (Fig. 1A).

The introvert sensory scalids are arranged in three circlets. The eight unornamented elongate scalids of the anterior circlet (length about 70 μm) consist of a basal half with two scale-like cover elements (Fig. 2B) and tubular protrusions at the tip. The upper cover element is triangular (t), and the lower one is comb-like with fine fimbriations (c). Fimbriae in groups or singly may occur proximally to the lower cover element (s). Two small flosculi with circularly arranged papillae ("petals") (f) occur at the base of the scalids. The second and third circlets of alternately-positioned ornamented scalids each consist of eight elongate structures (length about 50 μm) bearing overlapping fimbriated cover elements (Fig. 2A). There are usually fewer cover elements in the posterior third circlet (three or four elements) than in the anterior second circlet (four to six). Each scalid bears three distal tubular protrusions; the middle protrusion is longer than the two lateral ones.

The small introvert locomotory scalids of "semi-palm-tree-like shape" are arranged in rows oblique to the longitudinal body axis. Thirteen to 15 scalids occur in each row. The spoon-shaped scalid hood has about 40 fimbriations (Figs. 1E, 2A).

The pharynx is everted in the form of a buccal cone and bears 16 longitudinal rows of fringed teeth with eight (nine?) teeth in each row (Fig. 1A–D). Teeth of adjacent rows alternate, so that 16 (18?) alternating rings of teeth surround the buccal cone. Three different types of teeth are present. The anterior teeth surround the pharynx opening with comb-like arranged fimbriae of nearly equal length (a); the teeth in the following two rings are scale-like with triangularly arranged fimbriations (m), and have a covering row of small fimbriae of equal length on the upper side and fine fimbriations on the inner side. The teeth at the base of the everted pharynx are tripartite, with a central comb-like structure and two lateral bundles of long fimbriae (b) that extend beyond the central comb.

The cuticle of the abdomen is regularly structured with small spherical protrusions, wrinkled by an irregular pattern of folds due to fixation (Fig. 1A) and characteristic tubercles (less than 1 μm diameter) that appear to be equidistant from each other. Behind the introvert the anterior portion of the abdomen possesses triangular scalids that have fimbriated apical edges and a base width of about 20 μm. The posterior end of the abdomen bears a ring of robust hooks each consisting of two strong prongs and a central tubular projection that Storch et al. (1989b) found to be a sensillum. There are numerous flosculi on the abdomen, which increase in number posterior to the ring of hooks. Often, one or two flosculi are associated with a larger cone-shaped structure with a prominent apical tubular projection and a subdistal ring of short petals ("modified tubulus" in Morse (1981); "setae" in Storch et al. (1989*b*). The flosculi have a

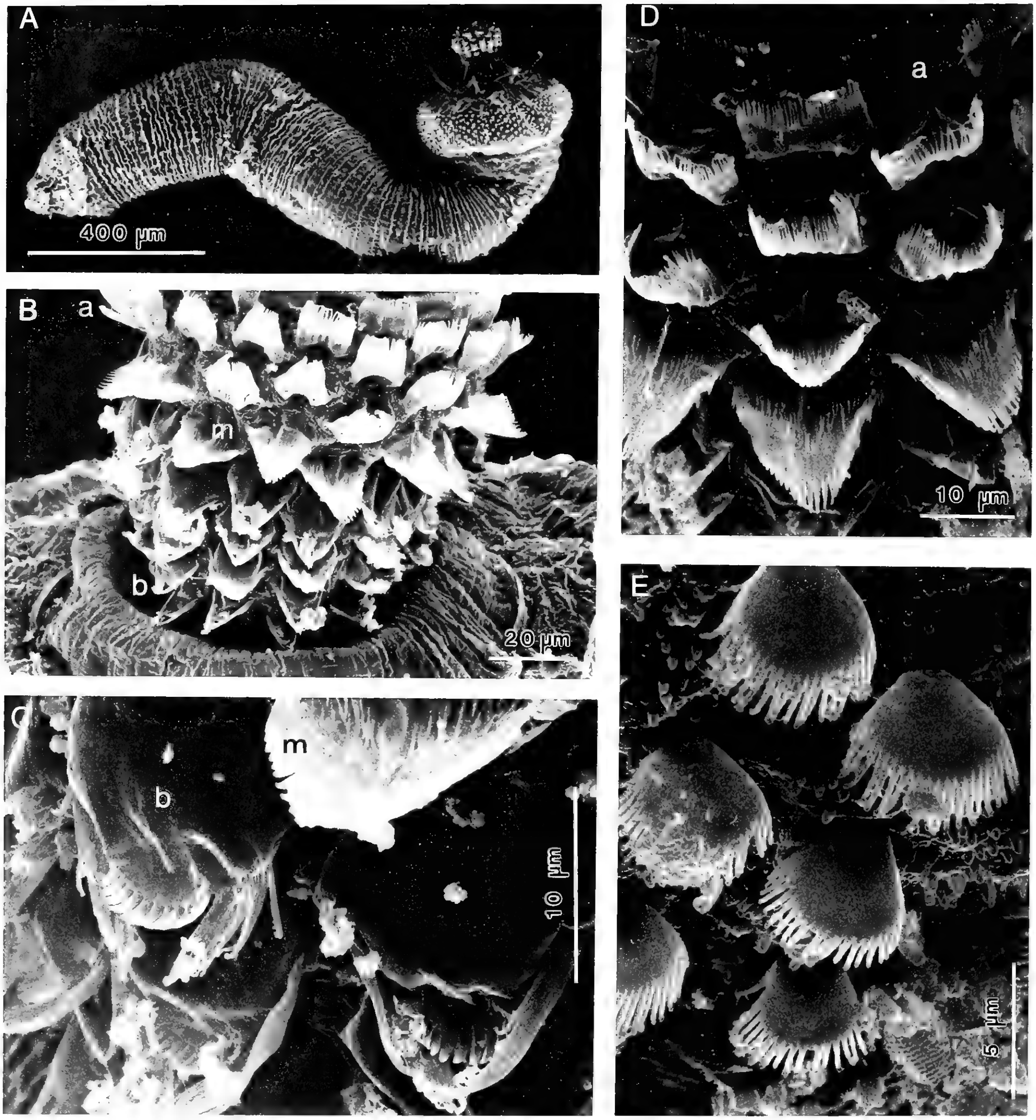


Fig. 1. *Meiopriapulus fijiensis*: A, Whole specimen with pharynx and introvert everted; B, Everted pharynx cone with anterior comb-like teeth (a), middle triangular teeth (m), and basal tripartite teeth (b); C, Close up of middle triangular pharyngeal teeth (*m*) and basal tripartite teeth (*b*); D, Close up of anterior comb-like pharyngeal teeth (*a*) and middle triangular teeth (b); E, Locomotory scalids of introvert.

palisade-like ring of about 14 longer petals, and several smaller inner projections surrounding a central opening.

Discussion

The agreement between the Andaman animals and those from the type-locality (Fiji) (Morse 1981) is extremely high. A few differences, however, exist. The so-called unornamented first circlet scalids of the introvert possess two fimbriate ornamentations, whereas Morse states that they "generally are without ornamentations." Careful examination of additional SEM micrographs of Fijian specimens kindly provided

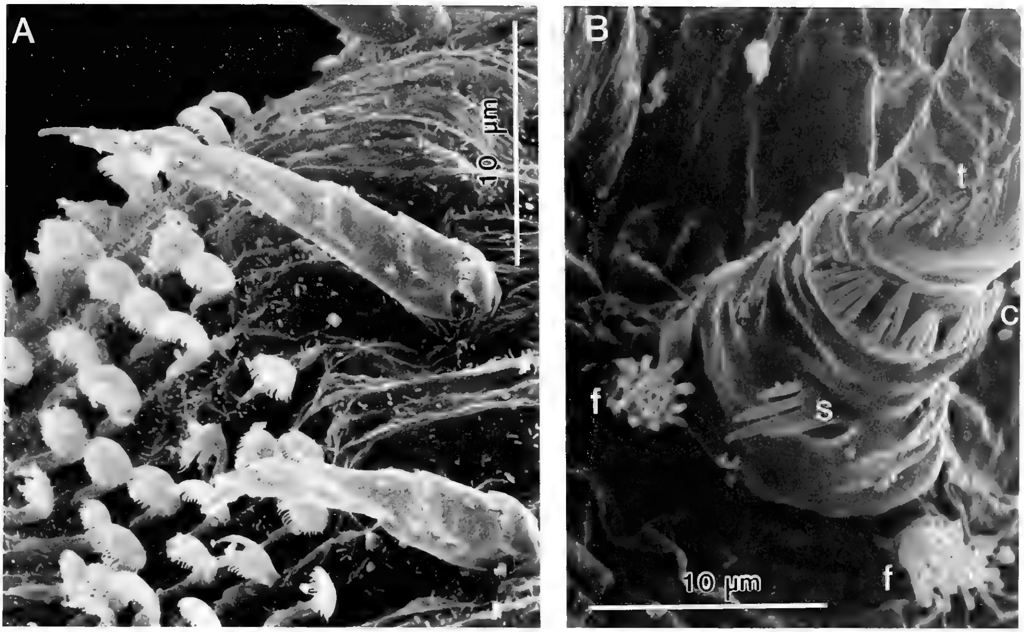


Fig. 2. *Meiopriapulus fijiensis*: A, Locomotory scalids of introvert and sensory "ornamented" scalids of second and third circlet; B, Sensory "unornamented" scalid of first circlet with two flosculi at the base (*f*). *t* = triangular cover element, *c* = comb-like cover element, *s* = small group of fimbriations.

by Dr. Morse shows them to be present there as well, although being more delicate. The number of scale-like cover-elements on ornamented scalids of the second circlet is probably higher (8) than in the Fiji specimens and may be related to age and to moulting (pers. comm. of Morse). Moulting has also been assumed by Storch et al. (1989b).

Storch et al. (1989a) also counted 16 rows of pharyngeal teeth but mention only seven teeth in each row, whereas the Andaman specimens have eight (nine?) teeth per row. The three types of pharyngeal teeth are not described by Morse (1981), but do exist in the Fijian animals (see fig. 5 in Storch et al. 1989a, and fig. 2 in Storch et al. 1989b). Slight quantitative differences also seem to exist in the number of fimbriae of the locomotory scalids, the triangular abdominal scalids and in the number of petals of trunk flosculi, but this may well be due to general variability of these details or because micrographs are unfavorable. The generally less delicate appearance of the fimbriae in the Andaman species may be the result of inadequate fixation.

The absence of distinct differences within the structure-rich details of the body surface suggests that the Andaman and Fiji populations are conspecific. *Meiopriapulus fijiensis* joins the series of intertidal sand inhabiting meiofauna species that appear to exhibit an extremely wide geographic range (Sterrer 1973, Westheide 1977, Ax & Armonies 1987). However, little is known about the taxonomic significance of the external cuticular characters within the Priapulida. Van der Land (1982:333) could find "not a single useful differential character in the adult" between *Tubiluchus corallicola* (from the Carribean Sea) and *T. remanei* (from the Red Sea) unless he examined the peculiar cuticular organs associated with the male genital pores. No such organs appear to exist for comparison of the two *Meio-*

priapulus populations. Further investigations (e.g., by TEM) may elucidate features which may otherwise differentiate between these externally nearly identical members of two widely separated populations, as in the case of the *Microphthalmus listensis* species-complex found on both sides of the Atlantic (Westheide & Rieger 1987).

Acknowledgments

I thank Dr. G. C. Rao for providing transportation on the Andaman Islands. I greatly acknowledge the help of Dr. M. P. Morse, who sent me her *SEM* micrographs for comparison. Dr. R. P. Higgins kindly read the manuscript. W. Mangerich skillfully performed the *SEM* investigations.

Literature Cited

Ax, P., & W. Armonies. 1987. Amphiatlantic identities in the composition of the boreal brackish water community of Plathelminthes. A comparison between the Canadian and European Atlantic Coast.—Microfauna Marina 3:7–80.

Calloway, C. B. 1988. Priapulida. Pp. 322–327 *in* R. P. Higgins and H. Thiel, Introduction to the study of meiofauna. Smithsonian Institution Press, Washington.

Morse, M. P. 1981. *Meiopriapulus fijiensis* n. gen., n. sp.: an interstitial priapulid from coarse sand in Fiji.—Transactions of the American Microscopical Society 100:239–252.

Remane, A. 1963. The systematic position and phylogeny of the pseudocoelomates. Pp. 247–255 *in* E. C. Dougherty et al., eds., The lower Metazoa. Comparative biology and phylogeny. University of California Press, Berkeley.

Salvini-Plawen, L. O. 1974. Zur Morphologie und Systematik der Priapulida: *Chaetostephanus praeposteriens,* der Vertreter einer neuen Ordnung Seticoronaria.—Zeitschrift für Zoologische Systematik und Evolutionsforschung 12: 31–54.

Storch, O., R. P. Higgins, & M. P. Morse. 1989a. Internal anatomy of *Meiopriapulus fijiensis* (Priapulida).—Transactions of the American Microscopical Society 108:245–261.

———. 1989b. The ultrastructure of the integument of *Meiopriapulus fijiensis* (Priapulida).—Transactions of the American Microscopical Society 108:319–331.

Sterrer, W. 1973. Plate tectonics as a mechanism for dispersal and speciation in interstitial sand fauna.—Netherlands Journal of Sea Research 7:200–222.

Van der Land, J. 1968. A new aschelminth, probably related to the Priapulida.—Zoologische Mededelingen 42:237–250.

———. 1970. Systematics, zoogeography, and ecology of the Priapulida.—Zoologische Verhandelingen 112:1–118.

———. 1982. A new species of *Tubiluchus* (Priapulida) from the Red Sea.—Netherlands Journal of Zoology 32:324–335.

Westheide, W. 1977. The geographical distribution of interstitial Polychaeta.—Mikrofauna des Meeresbodens 61:297–302.

———, & R. M. Rieger. 1987. Sytematics of the *Microphthalmus-listensis*-species group (Polychaeta: Hesionidae): facts and concepts for reconstruction of phylogeny and speciation.—Zeitschrift für Zoologische Systematik und Evolutionsforschung 25:12–39.

Spezielle Zoologie, Fachbereich Biologie/Chemie, Universität Osnabrück. D-4500 Osnabrück, Federal Republic of Germany.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 789–802

A CHECKLIST OF THE BRYOZOA OF THE GALAPAGOS

William C. Banta and John C. Redden

Abstract.—The 184 records of Bryozoa known from the Galapagos archipelago (Ecuador) are listed, including 4 new records and 3 unidentified species from Academy Bay, Santa Cruz. Thirty-four species (18%) of Galapagos bryozoans are endemic. Proportionally, there are more endemic stenolaemates (42%) than there are anascans or ascophorans. The Galapagos belongs in the Panamic Province, but is represented disproportionately by colder water species of the Northern Hemisphere with weedier, r-selected tendencies. There is evidence of difficulty in arriving at the Islands and of genetic isolation and local adaptation, especially among stenolaemates.

This report lists all records of Bryozoa we know of from the Galapagos archipelago, Ecuador. The broader zoogeographical implications, discussed in detail by Banta (1991), are summarized herein.

Collections

Previous collections.—There are seven published works describing bryozoan collections from the Galapagos. Hastings (1930) had 37 taxa from 11 shallow-water sites made by C. Crossland (1927). Canu & Bassler (1930) studied 50 species from four stations collected in 1888 and 1891 from the *Albatross* collections of the U.S. Fisheries Commission. One of these stations was from relatively deep water (684 fathoms = 1251 m). Osburn (1950, 1952, 1953) and Osburn and Soule (1953) had extensive collections, from at least 25 stations, some of great depth, made in the 1930s by the *Velero III* expeditions of the Allan Hancock Foundation (see Fraser 1943). Soule (1963b) adds 3 additional records from the Hancock Galapagos collections in his monograph on Bryozoa of the Gulf of California.

New data.—In July, 1980 the senior author collected about 30 species at snorkel depth near boat docks at Academy Bay, Santa Cruz Island. Specimens were dried and wrapped in paper for transport to the laboratory. Where necessary, calcareous specimens were cleaned in dilute KOCl. Specimens are for deposit in the National Museum of Ecuador, Quito.

Four of the specimens collected are new records for the Galapagos: *Lichenopora fimbriata, Membranipora arborescens, Arthropoma circinata* and *Parasmittina crosslandi.* Another three are undetermined species, probably new, unnamed taxa: *Hipporella* sp., with affinities in *H. gorgonensis* (Hastings 1930); *Lagenicella* sp., with affinities in *L. lacunosa* (Bassler 1934); and *Parasmittina* sp., with affinities in *P. hastingsae* Soule & Soule 1973.

Known records in the Galapagos.—The appendix includes every record we were able to find where bryozoan species or subspecies were identified from the Galapagos Islands. Bryozoan subspecies in the Galapagos are based entirely on morphological features; no good criteria are known to distinguish subspecies from species in the area. Authorities for Galapagos records are listed. These are followed by the family of each species and the islands from which each record was taken. The order of the Islands is arbitrary. Where there is more than one name for an Island we use the name in most common use by the inhabitants of the Galapagos (Bowman 1966). The distributions listed are culled from scattered literature. We place each species into one of seven general distribution categories: (1) Cosmopolitan: recorded worldwide from the equator into Arctic and Antarctic waters; (2) Circumglobal: worldwide, but absent from high latitudes above about 60°N and S; (3) Pan American: recorded in both the eastern Pacific and the Caribbean or Gulf of Mexico; present or absent elsewhere in the Atlantic and the Mediterranean; (4) Pacific: known from both the eastern and western Pacific; (5) Eastern Pacific: found exclusively along the western coasts of the Americas, including areas outside the Panamic; (6) Panamic: coastal areas of the Americas from about the U.S. Mexican border to Guayaquil in Ecuador; (7) Endemic: not recorded outside the Galapagos.

Summary of the Zoogeography of Galapagos Bryozoa

One hundred eighty-four species of bryozoans are known from the Galapagos Islands, a number comparable to that of the most diverse bryozoan faunas known. This number is probably an underestimate, especially for the soft-bodied ctenostomes. The sparse data provide no evident patterns of differential distribution of species among the islands, so at least for the purposes of this report, the Galapagos can be treated as a single zoogeographical unit. Although the relative numbers of anascan and ascophoran cheilostomes are near the average for the rest of the world, the proportion of stenolaemates (18%) is about twice as high as that in the rest of the Panamic. Comparable proportions of stenolaemates are found in the Magellanic and Chilean waters off South America, but otherwise there is zoogeographic affinity between these areas and the Galapagos. Relatively low water temperatures and elevated productivities associated with upwelling do not fully explain the high proportion of stenolaemates in Galapagos waters.

At the family level, few absences are conspicuous, except for the Steginoporellidae, characteristic of coral communities, rare in the Galapagos.

Zoogeographically, the Galapagos Islands belong to the Northern Hemisphere, securely in the Panamic Province, with 46% of Galapagos species shared with the rest of the Panamic. The distribution of Panamic bryozoans seems to divide the Panamic into two subprovinces near 10°N. Within the Panamic, strong affinities also are seen among the Galapagos and Cocos Island and the Gulf of California. More distant affinities are seen with the Gulf of Mexico and Indo-Pacific. The fauna seems unrelated to that of the Chilean and Magellanic Provinces of South America. The few shared species are mostly circumglobal or cosmopolitan in distribution.

Thirty-four of 184 species (18%) of Galapagos bryozoans are endemic to the Islands. This proportion is comparable to that of other major groups of shallow-water animals, but smaller than that of the molluscs, especially gastropods. There are 2 endemic genera among 53 in the islands, about 4%. Proportionally, there are more endemic stenolaemates (14 of 33 species, 42%) than endemics in anascans or ascophorans. This difference does not seem to be a simple case of more lumping in the Cheilostomata than among stenolaemates; on the contrary, lumping probably has been more severe among stenolaemates.

Affinities with neighboring zoogeographical provinces are stronger for cheilostomes than for stenolaemate Bryozoa. This, taken together with the higher rate of endemism for stenolaemates, suggests that the dispersal abilities of stenolaemates are inferior to those of cheilostomes. The difference cannot be accounted for by the presence of planktotrophic larvae among some cheilostomes, because Panamic species with planktotrophic larvae are no better represented in the Islands than are those with lecithotrophic larvae.

In general, the Galapagos bryozoan fauna seems to be proportionately more represented by species which range into latitudes higher than about 30 degrees. There also are proportionately more species with geographical ranges wider than those indigenous to waters nearer the Galapagos.

The bryozoan distribution data taken as a whole convey a picture of the Galapagos as a biological isolate belonging securely in the Panamic Province, but represented disproportionately by colder water species of the Northern Hemisphere with weedier, r-selected tendencies. There is evidence of difficulty in arriving at the Islands and of genetic isolation and local adaptation, especially among stenolaemates. The rarity of some habitats, notably estuaries and coral reefs, has contributed to a unique species composition.

The stenolaemates of the Galapagos in particular are disproportionately abundant relative to the rest of the Panamic. There is evidence that the Galapagos stenolaemate fauna may be more isolated and/or more rapidly evolving than the cheilostome fauna.

Acknowledgments

Michael Temkin, Donald Bonyai and Rebecca Beerman helped collect specimens in the Galapagos. Joann Sanner at the U.S. National Museum of Natural History helped with the collections and literature and identified some *Parasmittina* specimens. Alan H. Cheetham, also of the Museum, discussed the subject with me and was a great help with both details and broad ideas included in this paper. Steven Cairns made a number of suggestions and corrected several Latin and Greek names. Thanks also are due the Government of Ecuador, the Charles Darwin Foundation and the Smithsonian Institution for assistance in collecting and studying specimens. Supported in part by an American University Research Award. Contribution 18-89, The American University Biology Department.

Literature Cited

Banta, William C. 1969a. Systematic list of Bryozoa identified from Farnsworth Bank, Santa Catalina Island. Pp. 419–422 *in* O. Hartman, Quantitative survey of the benthos of San Pedro Basin, southern California. Part II, Final results and conclusions.—Allan Hancock Pacific Expeditions 19(2):1–456.

———. 1969b. *Watersipora arcuata,* a new species in the *subovoidea-cucullata-nigra* complex (Bryozoa, Cheilostomata).—Bulletin Southern California Academy of Sciences 68(2):96–102.

———. 1991. Bryozoa of the Galapagos. *in* M. James, ed., Galapagos marine invertebrates: taxonomy, biogeography and evolution in Darwin's islands. Plenum Publishing Company, New York (in press).

———, & Rennate J. M. Carson. 1977. Bryozoa from Costa Rica.—Pacific Science 31(4):381–424.

Borg, F. 1933. On a supposed species of *Heteropora* (Bryozoa).—Annals and Magazine of Natural History (10)12:583–587.

Bowman, R. I. 1966. Comments on the names of the Islands of the Galapagos. P. vxii *in* R. I. Bowman, ed., The Galapagos. Proceedings of the symposium of the Galapagos International Scientific Project. University of California, Berkeley.

Busk, George. 1854. Catalogue of marine Polyzoa in the collection of the British Museum, Part II, Cheilostomata (Part). British Museum pp. i–viii + 55+120. Reprinted 1966, Johnston Reprint Company, New York.

Canu, Ferdinand, & Raymond S. Bassler. 1928a. Fossil and Recent Bryozoa of the Gulf of Mexico region.—Proceedings of the U.S. National Museum 72(14):1–199.

———, & ———. 1928b. Les Bryozoaires du Maroc et de Mauritanie.—Mémories de la Société des Sciences Naturelles du Maroc 18:1–85.

———, & ———. 1929. Contributions to the biology of the Philippine Archipelago and adjacent regions.—Bulletin of the U.S. National Museum 100(9):1–683.

———, & ———. 1930. The bryozoan fauna of the Galapagos Islands.—Proceedings of the U.S. National Museum 76(13):1–78.

Cheetham, Alan H., & Philip A. Sandberg. 1964. Quaternary Bryozoa from Louisiana mudlumps.—Journal of Paleontology 38(6):1013–1046.

Crossland, C. 1927. The expedition to the south Pacific of the S.Y. 'St. George'.—Transactions of the Royal Society of Edinborough 55(2):531–554.

Dick, Matthew H., & June R. P. Ross. 1988. Intertidal Bryozoa (Cheilostomata) of the Kodiak vicinity, Alaska.—Occasional Papers of the Center for Pacific Northwest Studies (Western Washington University, Bellingham, Washington) 23:1–133.

———, & ———. 1985. Intertidal cheilostome bryozoans in rock-pile habitat at Narrow Strait, Kodiak, Alaska. Pp. 87–93 *in* Claus Nielsen & Gilbert P. Larwood, eds., Bryozoa: Ordovician to Recent. Olsen and Olsen, Fredensborg, Denmark.

Fraser, C. McLean. 1943. General account of the scientific work of the *Velero III* in the eastern Pacific, 1931–41. Part III. A ten-year list of the *Velero III* collecting stations.—Allan Hancock Pacific Expeditions 1(3):259–431.

Gordon, Dennis P. 1982. The genera of the Chaperiidae (Bryozoa).—New Zealand Journal of Zoology 9:1–24.

———. 1984. The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge.—Memoirs of the New Zealand Oceanographic Institution 91:1–198.

Harmer, Sidney F. 1926. The Polyzoa of the Siboga Expedition. Part II. Cheilostomata Anasca.—Siboga-Expedite Monograph 28b:181–501.

———. 1934. Polyzoa of the Siboga Expedition. Part III. Cheilostomata Ascophora. I. Family Reteporidae.—Siboga-Expedite Monograph 28c: vii + pp. 503–640.

———. 1957. Polyzoa of the Siboga Expedition. Part IV. Cheilostomata Ascophora. II (Ascophora, except Reteporidae, with additions to part II, Anasca).—Siboga-Expedite Monograph 28d: xv + pp. 641–1147.

Hastings, Anna B. 1930. Cheilostomatous Bryozoa from the vicinity of the Panama Canal collected by Dr. C. Crossland on the cruise of the S.Y. "St. George".—Proceedings of the Zoological Society of London 1929(4):1–17.

———, & ———. 1979. The South African Museum's *Meiring Naude* cruises. Part 13. Bryozoa II.—Annals of the South African Museum 91(1): 1–161.

Hayward, Peter J., & John S. Ryland. 1979. British ascophoran bryozoans. Synopsis of the British Fauna (new series).—Linnean Society, London 14:1–312.

Lagaaij, Robert. 1963. New additions to the bryozoan fauna of the Gulf of Mexico.—Publications of the Texas University Institute of Marine Science 9:162–236.

MacGillivray, Paul H. 1889. On some South Australian Polyzoa.—Transactions and Proceedings of the Royal Society of South Australia 12:24–30.

Marcus, Ernst. 1938. Bryozoarios Brasileiros - II.—Boletins da Faculidade de Philosophia, Ciencias e Letras, Universidad de Sao Paulo 4, Zoologia 2:1–137.

Maturo, Frank J. S. 1968. The distributional pattern of Bryozoa of the east coast of the United States exclusive of New England.—Atti della Societa Italiana di Scienze Naturali 108(36):261–284

———, & Thomas J. M. Schopf. 1968. Ectoproct and entoproct type material: examination of species from New England and Bermuda named by A. E. Verrill, J. W. Dawson, and E. Desor.—Postilla 120:1–95.

Morris, Penny A. 1980. The bryozoan family Hippothoidae (Cheilostomata-Ascophora), with emphasis on the genus *Hippothoa.*—Allan Hancock Monographs in Marine Biology 10:1–145.

Moyano, Hugo. I. 1983. Southern Pacific Bryozoa: a general view with emphasis on Chilean species.—Gayana 46:3–45.

Neviani, Antonio. 1895. Nuove genere e nuove specie di Briozoi fossili.—Rivue Italiana Paleontologica Bologna 1:82–84.

Osburn, Raymond C. 1950. Bryozoa of the Pacific coast of North America. Part I, Cheilostomata-Anasca.—Allan Hancock Pacific Expeditions 14(1):1–269.

———. 1952. Bryozoa of the Pacific coast of North America. Part II, Cheilostomata-Ascophora.—Allan Hancock Pacific Expeditions 14(2):271–611.

———. 1953. Bryozoa of the Pacific coast of America. Part III. Cyclostomata, Ctenostomata, Entoprocta and Addenda.—Allan Hancock Pacific Expeditions 14(3):613–841.

———, & John D. Soule. 1953. Order Ectoprocta, Suborder Ctenostomata. Pp. 726–758 *in* R. C. Osburn, Bryozoa of the Pacific coast of America. Part II. Cyclostomata, Ctenostomata, Entoprocta and Addenda.—Allan Hancock Pacific Expeditions 14(3).

Powell, Neil A. 1967. Polyzoa (Bryozoa) Ascophora from New Zealand.—Discovery Reports 34:199–394.

———. 1971. The marine Bryozoa near the Panama Canal.—Bulletin of Marine Science 21(3):766–778.

Prenant, Marcel, & Genevieve Bobin. 1966. Bryozoaires. Deuxième partie: Chilostomes Anasca.—Fauna de France 68:1–647.

Robertson, Alice. 1908. The incrusting cheilostomatous Bryozoa of the west coast of North America.—University of California Publications in Zoology 4(5):253–344.

Ryland, John S., & Dennis P. Gordon. 1977. Some New Zealand and British species of *Hippothoa* (Bryozoa: Cheilostomata).—Journal of the Royal Society of New Zealand 7(1):17–49.

———, & Peter J. Hayward. 1977. British anascan bryozoans.—Synopsis of the British Fauna (new series) 10:1–188.

Soule, Dorothy F., & John D. Soule. 1964. The Ectoprocta (Bryozoa) of Scammon's Lagoon, Baja California.—American Museum Novitates 2199: 1–56.

———, & ———. 1973. Morphology and speciation of Hawaiian and eastern Pacific Smittinidae (Bryozoa, Ectoprocta).—Bulletin of the American Museum of Natural History 152(6):365–440.

———, & ———. 1975. Species groups in Watersiporidae.—Docummënts Laboratorie Geologie Faculte des Sciences de Lyon 3(2):299–309.

———, & ———. 1985. Effects of oceanographic phenomena such as 'El Niño' on the zoogeography and endemism of tropical/subtropical Pacific Watersiporidae. Pp. 293–300 *in* C. Nielsen and G. P. Larwood, eds., Bryozoa: Ordovician to Recent. Olsen & Olsen, Fredensborg, Denmark.

Soule, John D. 1959. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 6. Anascan Cheilostomata (Bryozoa) of the Gulf of California.—American Museum Novitates 1969:1–54.

———. 1963a. Phylum Bryozoa. Pp. 232–234 *in* L. G. Hertline, ed., Contribution to the biogeography of Cocos Island, including a bibliography.—Proceedings of the California Academy of Sciences 32(8):232–234.

———. 1963b. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 18. Cyclostomata, Ctenostomata (Ectoprocta) and Entoprocta of the Gulf of California.—American Museum Novitates 2144:1–34.

Winston, Judith E. 1982. Marine bryozoans (Ectoprocta) of the Indian River area (Florida).—Bulletin of the American Museum of Natural History 173(2):100–176.

———, & Beverly F. Heimberg. 1986. Bryozoans from Bali, Lombok, and Komodo.—American Museum Novitates 2841:1–106.

Department of Biology, The American University, Washington, D.C. 20016.

Appendix

Bryozoan species known from the Galapagos Archipelago, arranged alphabetically within Orders (there are no Phylactolaemata known).

STENOLAEMATA

Borgiola rugosa (Borg, 1933).—Osburn, 1953:697. Heteroporidae. Islands: Marchena. Distribution: Japan and the Galapagos (Pacific).

Borgiola sp. (Canu & Bassler, 1930).—*Heteropora* sp.—Canu & Bassler, 1930:60. Heteroporidae. Islands: Española. Distribution: Endemic. Apertures measure 0.10 mm in diameter and lunaria are present; we assign it tentatively to *Borgiola,* distinct from *B. rugosa* (Borg, 1933). Probably a new endemic species.

Cavaria praesens Canu & Bassler, 1930.—Canu & Bassler, 1930:58. Lichenoporidae. Islands: Floreana. Distribution: Endemic.

Crisia maxima Robertson, 1910.—Osburn, 1953:682. Crisiidae. Islands: Española, San Cristóbal, Santa Fé. Distribution: British Columbia to the Gulf of California and the Galapagos (Eastern Pacific).

Crisia occidentalis Trask, 1857.—Osburn, 1953:680. Crisiidae. Islands: Seymour. Distribution: British Columbia to Costa Rica and the Galapagos (Eastern Pacific).

Crisia serrulata Osburn, 1953.—Osburn, 1953:679. Crisiidae. Islands: Isabela, Floreana, San Cristóbal, Santa Cruz, Onslow. Distribution: British Columbia, California and the Galapagos (Eastern Pacific).

Crisulipora occidentalis Robertson, 1910.—Osburn, 1953:686. Crisiidae. Islands: Española. Distribution: California, Peru, Japan, Brazil, Panama, Gulf of California, Baja California (Pan American).

Diaperoecia flabellata (Canu & Bassler, 1923).—Canu & Bassler, 1930:52. Diaperoeciidae. Islands: Española. Distribution: Pleistocene of California; Galapagos (Endemic).

Disporella astraea Osburn, 1953.—Osburn, 1953:719. Lichenoporidae. Islands: Floreana, Isabela. Distribution: Endemic.

Disporella octoradiata (Waters, 1904.).—?*Disporella octoradiata.*—Osburn, 1953:718. Lichenoporidae. Islands: Isabela. Distribution: Antarctic, Chile (Moyano 1983:15) (Eastern Pacific). Osburn's query mark reflected his uncertainty about the generic placement, not his confidence in the species determination.

Disporella ovoidea Osburn, 1953.—Osburn, 1953: 713.—*Lichenopora radiata.*—Canu & Bassler, 1928. Lichenoporidae. Islands: Isabela, Española. Distribution: California, Colombia and the Galapagos (Eastern Pacific).

Entalophora sp. Osburn, 1953.—*Entalophora* sp.—Osburn, 1953:669. Entalophoridae. Islands: Isabela. Distribution: Endemic. The animal appears to be distinct; Osburn did not describe it because ovicells were lacking.

Entalophora symmetrica Osburn, 1953.—Osburn, 1953:667. Entalophoridae. Islands: San Cristóbal. Distribution: Endemic.

Heteropora sp. Osburn, 1953.—Osburn, 1953:695. Heteroporidae. Islands: Wenman, San Cristóbal. Distribution: Unknown. Similar to *Heteropora pacifica* Borg, 1933:317 in its measurements, but available specimens are in poor condition.

Lichenopora (Radiopora) pacifica (Osburn, 1953.—*Defrancia stellata.*—Canu & Bassler, 1930:57.—*Disporella stellata* var. *pacifica.*—Osburn, 1953:716. Lichenoporidae. Islands: Wenman, Isabela, Española, Gardner-by-Hood. Distribution: Endemic. This 'variety' surely deserves specific status.

Lichenopora fimbriata Busk, 1875.—Present study. Lichenoporidae. Islands: Santa Cruz. Distribution: British Columbia, California, Chile, Falklands, Tristan de Cunha, Azores, Cape Verde Islands, Australia, New Zealand, Kerguelens, Juan Fernandez (Circumglobal). First record in the Galapagos. For description see Osburn 1952:709.

Lichenopora novae-zelandiae (Busk, 1875).—Osburn, 1953:705. Lichenoporidae. Islands: Floreana. Distribution: New Zealand, Australia, Ceylon, Japan, British Columbia, California (Pacific).

Plagioecia lactea Calvet, 1903.—Canu & Bassler, 1930: 48.—*?Plagioecia lactea.*—Osburn, 1953:653. Diastoporidae. Islands: Wenman, Española. Distribution: Atlantic (France), Galapagos (Pan American). The identity with Atlantic specimens is questionable.

Plagioecia meandrina (Canu & Bassler, 1930).—Osburn, 1953:635.—*Diaperoecia meandrina.*—Canu & Bassler, 1930:51. Diastoporidae. Islands: Wenman, San Cristóbal, Española, Isabela, Floreana, Gardner-by-Hood. Distribution: California, Guadalupe Island (off Mexico), Galapagos (Eastern Pacific).

Plagioecia patina (Lamarck, 1816).—Osburn, 1952:631. Diastoporidae. Islands: Wenman, Isabela, San Cristóbal. Distribution: British Columbia to Baja California and the Galapagos; Atlantic. (Pan American).

Plagioecia sarniensis (Norman, 1864).—Osburn, 1953: 632. Plagioeciidae. Islands: Santa Fé. Distribution: Colombia, California, Washington; "Cosmopolitan" (Osburn 1953:633) (Circumglobal).

Plagioecia striatula Canu & Bassler, 1930.—*Diaperoecia striatula.*—Canu & Bassler, 1930:49. Diaperoeciidae. Islands: Española. Distribution: Endemic. See Osburn (1953:641) regarding generic placement of this species.

Plagioecia subpapyracea Canu & Bassler, 1930.—*Diaperoecia subpapyracea.*—Canu & Bassler, 1930:50. Diaperoeciidae. Islands: Española. Distribution: Endemic. See Osburn (1953:641) regarding the generic placement of this species.

Plagioecia tubiabortiva Canu & Bassler, 1930.—Osburn, 1953:636.—*Microecia tubiabortiva.*—Canu & Bassler, 1930:48. Diastoporidae. Islands: Wenman, Española. Distribution: Endemic.

Platonea expansa Osburn, 1953.—Osburn, 1953:663. Tubuliporidae. Islands: Isabela, Española, Gardner-by-Hood. Distribution: Endemic.

Platonea veleronis Osburn, 1953.—Osburn, 1953:662. Tubuliporidae. Islands: Isabela, Española, Duncan, Floreana, Gardner-by-Hood, Santa Fé. Distribution: Endemic.

Proboscina lamellifera Canu & Bassler, 1930.—Canu & Bassler, 1930:46.–Osburn, 1953:623. Oncousoeciidae. Islands: Wenman, Española, Isabela, Gardner-by-Hood. Distribution: Endemic.

Proboscina major (Johnston, 1847).—Osburn, 1953: 621.—Present study.—*Proboscina* (*Oncousoecia*) *major* Canu & Bassler, 1930:46. Oncousoeciidae. Islands: Española, Isabela, Santiago, Santa Fé, Santa Cruz. Distribution: British Columbia to Costa Rica, Cocos Island, Galapagos; Norway to the Cape Verde Islands; Mediterranean (Osburn 1953:621); Chile (Moyano 1983:15) (Pan American).

Tubulipora flexuosa (Pourtalès, 1867).—Osburn, 1953: 653. Tubuliporidae. Islands: San Salvador. Distribution: California, Cocos Island, the Galapagos, Cuba, Porto Rico and the southern shore of the Caribbean Sea. (Pan American).

Tubulipora liliacea var. *tenuis* Canu & Bassler, 1930.—Canu & Bassler, 1930:55. Tubuliporidae. Islands: Floreana. Distribution: Endemic.

Tubulipora pulchra MacGillivray, 1885.–Osburn, 1953: 653. Tubuliporidae. Islands: San Salvador. Distribution: Australia, California, British Columbia, Mexico, Costa Rica (Pacific).

Tubulipora sp. Canu & Bassler, 1930.—Canu & Bassler, 1930:54. Tubuliporidae. Islands: Española. Distribution: Unknown.

Tubulipora sp. Canu & Bassler, 1930.—Canu & Bassler, 1930:52. Tubuliporidae. Islands: Floreana. Distribution: Not given (Unknown).

CTENOSTOMATA

Amathia vidovici (Heller, 1867).—Osburn & Soule, 1953:741. Vesiculariidae. Islands: Not specified. Distribution: California to Ecuador and Galapagos; Massachusetts to Colombia; France to the Mediterranean and the Cape Verde Islands; eastern; Indian Ocean (Prenant & Bobin 1966:283((Pan American).

Buskia seriata Soule, 1953.—Soule *in* Osburn & Soule, 1953:747. Buskiidae. Islands: Seymour. Distribution: California and the Galapagos (Eastern Pacific).

ANASCA

Aetea anguina (Linnaeus, 1758).—Hastings, 1930: 702.—Osburn, 1950:11. Aeteidae. Islands: Santiago, Santa Cruz, Isabela; Osburn's stations unspecified. Distribution: Arctic, Great Britain, Maine to Brazil, Mediterranean, Indian Ocean, Malay, Australia, Japan, Chile, Patagonia, Juan Fernandez, California, British Columbia, Antarctic (Cosmopolitan). Prenant and Bobin (1966:80) present an extensive synonymy.

Aetea ligulata (Busk, 1852).—Osburn, 1950:13. Aeteidae. Islands: Isabela, San Cristóbal, Bartolomé. Distribution: British Columbia to Chile, Caribbean to Argentina, Red Sea, Baja California, Panama, Colombia, New Zealand, possibly the Mediterranean (Gordon 1984:39); South Atlantic. (Circumglobal).

Aetea recta Hincks, 1861.—Osburn, 1950:12. Aeteidae. Islands: Isabela, Santiago. Distribution: Europe south, Caribbean, Brazil, Gulf of California, Washington, Galapagos, Chile (Pan American). *Velero III* Station converted from Fraser (1943).

Aetea truncata (Landsborough, 1852).—Osburn, 1950: 13. Aeteidae. Islands: Isabela. Distribution: Europe, Indian Ocean, Japan to Australia, Nova Scotia to Brazil, British Columbia, California, Colombia, Peru and the Galapagos; Chile (Cosmopolitan). Synonymy, Prenant and Bobin 1966:86.

Alderina smitti Osburn, 1950.—Osburn, 1950:60. Alderinidae. Islands: Isabela, San Cristóbal. Distribution: Gulf of Mexico, Caribbean, California, Gulf of California, Baja California, Panama (Pan American).

Antropora claustracrassa (Canu & Bassler, 1930).—Osburn, 1950:53.—*Membrendoecium claustracrassum.*—Canu & Bassler, 1930:7. Hincksinidae. Islands: Española, Floreana and unspecified stations of Osburn 1950:53. Distribution: Guaymas (Mexico) to Ecuador and the Galapagos (Panamic).

Antropora tincta (Hastings, 1930).—Osburn, 1950:54.—Present study.—*Crassimarginatella tincta.*—Hastings, 1930:708.—Osburn, 1950:54. Hincksinidae. Islands: Isabela, Santa Cruz; Osburn's collection sites not specified. Distribution: California to the Galapagos (Eastern Pacific). There is much variation in avicularium shape among Pacific specimens.

Aplousina filum (Jullien, 1903).—Canu & Bassler, 1930: 7.—Osburn, 1950:47. Hincksinidae. Islands: Española, Daphne Major. Distribution: Eastern Atlantic, Gulf of Mexico, Gulf of California, Cocos Island (Pan American).

Aplousina major Osburn, 1950.—Osburn, 1950:48. Alderinidae. Islands: Santa Fé. Distribution: California, Mexico, Galapagos, Chile (Eastern Pacific).

Beania mirabilis Johnston, 1840.—Osburn, 1950:170. Bugulidae. Islands: Isabela. Distribution: Scandinavia to the Mediterranean; California to Panama and the Galapagos, Australia, Indian Ocean (Prenant & Bobin 1966:555) (Circumglobal).

Bugula californica Robertson, 1905.—Osburn, 1950: 157. Bugulidae. Islands: San Cristóbal. Distribution: Brazil, British Columbia, California, Gulf of California, Galapagos (Pan American).

Bugula longirostrata Robertson, 1905.—Osburn, 1950: 156. Bugulidae. Islands: Isabela (Tagus Cove), Santiago. Distribution: California, Gulf of California, Galapagos (Eastern Pacific).

Bugula minima (Waters, 1909).—*Bugula neritina* var. *minima.*—Hastings, 1930:704. Bugulidae. Islands: Isabela. Distribution: Gulf of Mexico, Caribbean, Red Sea, Indian Ocean, Malay, Australia; Cocos Island, Costa Rica, Panama and the Galapagos (Osburn 1950:155) (Circumglobal).

Bugula mollis Harmer, 1926.—Hastings, 1930:704.—Osburn, 1950:158. Bugulidae. Islands: Santiago, Isabela. Distribution: New Guinea, Java Sea, California to Panama and the Galapagos (Pacific).

Bugula neritina (Linnaeus, 1758).—Hastings, 1930: 704.—Osburn, 1950:155.—Present study. Bugulidae. Islands: Santiago, Isabela, Floreana, Santa Cruz. Distribution: Worldwide in warm ports (Circumglobal).

Bugula uniserialis Hincks, 1884.—Hastings, 1930:705. Bugulidae. Islands: Isabela. Distribution: Western Australia, California (Pacific).

Callopora horrida (Hincks, 1880).—Osburn, 1950:70. Alderinidae. Islands: Isabela (Tagus Cove), Daphne Major. Distribution: California, Puget Sound, British Columbia, Gulf of California. (Eastern Pacific).

Callopora verrucosa Canu & Bassler, 1929.—Canu & Bassler, 1930:10. Alderinidae. Islands: Española. Distribution: Endemic. Osburn 1950:71 questions the generic assignment.

Cauloramphus brunea Canu & Bassler, 1930.—Canu & Bassler, 1930:10.—Osburn, 1950:56.—Present study. Alderinidae. Islands: Santiago, Isabela, Floreana, Santa Cruz. Distribution: Alaska to Colombia and the Galapagos. (Eastern Pacific). The report of '*Caulorhamphus brunnea*' in Alaska (Dick & Ross 1985:89) is of *C. variegatus* (Dick & Ross 1988:41; California: Banta 1969a:419 (as '*C. brunnea*').

Cauloramphus spiniferum (Hincks, 1838).—Hastings, 1930:713. Alderinidae. Islands: Santiago. Distribution: Britain, Chile, California, British Columbia, Alaska; South Atlantic (see Moyano 1983:18) (Eastern Pacific).

Cellaria diffusa Robertson, 1905.—Osburn, 1950:118. Cellariidae. Islands: Santiago. Distribution: Southern California, Baja California, Galapagos (Eastern Pacific).

Cellaria veleronis Osburn, 1950.—Osburn, 1950:118. Cellariidae. Islands: Isabela, Daphne Major, Marchena, Santiago. Distribution: Clipperton Island, Cocos Island and the Galapagos (Soule 1963a:232) (Panamic).

Chaperiopsis condylata (Canu & Bassler, 1930).—*Chapperia condylata.*—Canu & Bassler, 1930:44.—Osburn, 1950:91. Chaperiidae. Islands: Floreana. Distribution: Southern California to Colombia and the Galapagos; Post-Pleistocene of Louisiana (Cheetham & Sandberg 1964:1020) (Eastern Pacific). =*Chaperiella condylata*: Soule 1963b, Cocos Island. Gordon (1982) discusses the Chaperiidae.

Chaperiopsis frontalis Osburn, 1950.—*Chapperia frontalis.*—Osburn, 1950:93. Chaperiidae. Islands: Española, Isabela, Santa Cruz. Distribution: Endemic.

Copidozoum planum (Hincks, 1880).—Hastings, 1930: 713. Alderinidae. Islands: Santiago. Distribution: Australia; Mediterranean, Japan, California, Colombia, Panama (Osburn 1952:73) (Circumglobal). This record may belong to *C. tenuirostre* (Hincks); see Osburn 1952:72.

Copidozoum tenuirostre (Hincks, 1880).—Osburn, 1952:72.—*Callopora tenuirostris.*—Canu & Bassler, 1929:9. Alderinidae. Islands: Española, Floreana; Osburn's stations are unspecified. Distribution: Western Atlantic, Gulf of Mexico, Caribbean, Brazil; Mediterranean; Indian Ocean, Western Pacific, British Columbia to Peru and the Galapagos (Prenant & Bobin 1966:257) (Circumglobal).

Cupuladria canariensis (Busk, 1885).—Osburn, 1950: 33. Cupuladriidae. Islands: Not given. Distribution: Gulf of California to Ecuador and the Galapagos: Gulf of Mexico; Eastern Atlantic, Mediterranean (Cheetham & Sandberg 1964:1021) (Pan American).

Discoporella umbellata (Defrance, 1823).—Hastings, 1930:719.—Osburn, 1950:113.—*Cupularia umbellata.*—Canu & Bassler, 1930:12. Cupuladriidae. Islands: Santiago, Española; Osburn's stations not specified. Distribution: Gulf of Mexico, Eastern and Western Atlantic; Mediterranean; South Africa, California, Cocos Island and the Galapagos (Cheetham and Sandberg 1964:1022) (Pan American).

Electra bellula var. *bicornis* (Hincks, 1881).—Hastings, 1930:706. Electrinidae. Islands: Floreana. Distribution: Pacific (Pacific).

Membranipora aragoi var. *pacifica* Osburn, 1950.—Osburn, 1950:175. Membraniporidae. Islands: Wenman, Isabela. Distribution: Gulf of California, Baja California, Galapagos (Panamic).

Membranipora arborescens (Canu & Bassler, 1928b) (Morocco).—Present study. Membraniporidae. Islands: Santa Cruz. Distribution: Morocco, West Africa, Panama, Galapagos (Pan American). Closely related and possibly identical to *M. savarti* and *M. tenuis.* If so, it is a circumglobal subtropical to tropical species (see Banta & Carson 1977:387).

Membranipora savarti (Audouin, 1826).—Osburn, 1950.—27.—*Acanthodesia savartii* (Canu & Bassler, 1930:4). Membraniporidae. Islands: Santiago, Española, Santa Cruz, San Cristóbal. Distribution: California, Baja California, Costa Rica, Panama, Gulf of Mexico, Caribbean, Philippines, Australia. (Circumglobal.)

Membranipora tenuis Desor, 1848.—*Acanthodesia denticulata.*—Hastings, 1930:707. Membraniporidae. Islands: Isabela. Distribution: Cape Cod to Brazil; Baja California, Panama, Galapagos, Peru, Gulf of California (Osburn 1950:27). (Pan American.) See Osburn (1950:27) about the identity of *Acanthodesia dentidulata* with *M. tenuis.*

Membranipora tuberculata (Bosc, 1803).—Osburn, 1950:23.—*Nichtina tuberculata.*—Hastings, 1930: 706. Membraniporidae. Islands: Isabela; Osburn's stations not listed. Distribution: British Columbia to Peru, Massachusetts to Patagonia; Europe to Angola; Japan to Australia and New Zealand; Indian Ocean (Gordon 1984:24); Chile (Circumglobal).

Micropora coriacea (Esper, 1794).—Hastings, 1930.—Canu & Bassler, 1930:11.—Osburn, 1950:105. Microporidae. Islands: Española, Santiago, Isabela, Floreana; Osburn's stations not specified. Distribution: British Columbia to Chile, the Juan Fernandez Islands and the Galapagos; Britain to the Mediterranean, Antarctic, South Atlantic, Tasman Sea (Circumglobal).

Micropora coriacea var. *inarmata* Soule, 1959.—Soule, 1959:29. Microporidae. Islands: Marchena, Santa Cruz. Distribution: Baja California, Soccoro Island, Cocos Island, New Zealand (Gordon 1984:52) (Pacific).

Parellisina curvirostris (Hincks, 1862).—Osburn, 1950: 75.—Present study.—*Ellisina curvirostris.*—Hastings, 1930:711.—*Callopora curvirostris* Canu & Bassler 1930:9. Alderinidae. Islands: Isabela, Floreana, Española, Santa Cruz. Distribution: Gulf of Mexico, Caribbean, Mexico to the Cocos Island and the Galapagos, Britain to Morocco, Hawaii, Western Pacific, Indian Ocean, Indonesia (Winston & Heimberg 1986:6 (Circumglobal).

Retevirgula areolata (Canu & Bassler, 1923).—Soule, 1963a:233. Alderinidae. Islands: Not given. Distribution: California to the Galapagos Islands, Cocos; (Soule 1963a); Chile (Moyano 1983:21) (Eastern Pacific). "Common at the Galapagos Islands" (Soule 1963a:233).

Retevirgula lata Osburn, 1950.—Osburn, 1950:87. Calloporidae. Islands: Santiago, off Santa Cruz. Distribution: Endemic.

Retevirgula tubulata (Hastings, 1930).—Osburn, 1952: 86.—*Pyrulella tubulata.*—Hastings, 1930:709. Calloporidae. Islands: Floreana, Marchena, San Cristóbal, Isabela. Distribution: Baja California and the Gulf of California to Panama and the Galapagos (Panamic).

Scruparia ambigua d'Orbigny, 1841.—*Scruparia chelata.*—Hastings, 1930:702. Scrupariidae. Islands: Isabela (Tagus Cove). Distribution: "Distributed throughout the world except in polar waters" (Ryland & Hayward 1977:50) (Circumglobal). Confused with *S. chelata* until about 1941.

Scrupocellaria bertholleti (Audouin, 1826).—Hastings, 1930:733.—*S. bertholetti* (sic).—Osburn, 1950:133. Scrupocellariidae. Islands: Santiago, Floreana, Isabela. Osburn reports it from Galapagos at stations not specified. Distribution: Southern California to Panama and the Galapagos; Atlantic, Mediterranean, Red Sea (Circumglobal).

Scrupocellaria ferox Busk, 1852.—Osburn, 1950:137. Scrupocellariidae. Islands: San Cristóbal, South of Santa Cruz, Isabela (Tagus Cove). Distribution: Widely distributed in the Indian and Pacific oceans, Zanzibar, the eastern Pacific (Circumglobal).

Scrupocellaria harmeri Osburn, 1947.—Osburn, 1950: 138. Scrupocellariidae. Islands: Isabela. Distribution: Caribbean, California, Galapagos (Pan American).

Scrupocellaria panamensis Osburn, 1950.—Osburn, 1950:142. Scrupocellariidae. Islands: Floreana. Distribution: Panama and the Galapagos (Panamic).

Scrupocellaria pugnax Osburn, 1950.—Osburn, 1950: 143. Scrupocellariidae. Islands: Floreana. Distribution: Endemic.

Scrupocellaria scruposa (Linnaeus, 1758).—Hastings, 1930:703. Scrupocellariidae. Islands: Santiago. Distribution: Europe, Madeira, New Zealand. "Widely distributed in warm and temperate seas" (Ryland & Hayward 1977:140) (Circumglobal).

Scrupocellaria unguiculata Osburn, 1950.—Osburn, 1950:149. Scrupocellariidae. Islands: Santiago; south of Santa Cruz; Floreana. Distribution: Endemic.

Sessibugula translucens Osburn, 1950.—Osburn, 1950: 164.—Present study. Bugulidae. Islands: Isabela, Santa Cruz. Distribution: Gulf of California, Costa Rica, Galapagos (Panamic).

Smittipora americana (Canu & Bassler, 1930).—*Velumella americana.*—Osburn, 1950:103. Onychocellidae. Islands: San Cristóbal. Distribution: West Indes, Panama, Galapagos (Pan American).

Thalamoporella californica (Levinsen, 1909).—Hastings, 1930:716.—Osburn, 1950:112. Thalamoporellidae. Islands: Santiago, Santa Cruz, Isabela; Osburn's stations not given. Distribution: California to Colombia and the Galapagos (Eastern Pacific).

ASCOPHORA

Aimulosia palliolata (Canu & Bassler, 1928).—Osburn, 1952:353. Hippoporinidae. Islands: Wenman. Distribution: Florida, Gulf of California and Galapagos (Pan American).

Aimulosia uvulifera (Osburn, 1914).—Osburn, 1952: 352. Hippoporinidae. Islands: South Seymour. Distribution: Florida, Caribbean, Baja California, Costa Rica, Ecuador, Cocos Island (Pan American).

Arthropoma cecili (Audouin, 1826).—Canu & Bassler, 1930:16. Schizoporellidae. Islands: Española. Distribution: Western Pacific, Indian Ocean, Red Sea, Mediterranean, Britain to South Africa, Brazil, British Columbia to the Galapagos (Gordon 1984:85) (Circumglobal).

Arthropoma circinatum (MacGillivray, 1868).—Present study. Schizoporellidae. Islands: Santa Cruz. Distribution: Australia, New Zealand, Tristan da Cunha, Southern California to Colombia and the Galapagos (Osburn 1952:334) (Circumglobal). First record in the Galapagos.

Bellulopora bellula (Osburn, 1950).—*Colletosia bellula.*—Osburn, 1950:189. Cribrilinidae. Islands: Isabela. Distribution: Cape Hatteras to Florida, Gulf of Mexico, Gulf of California, Baja California, Pleistocene of California, Galapagos (Winston 1982:134); Chile (Moyano 1983:17) (Pan American). See Lagaaij (1963:183) regarding generic placement of this species.

Celleporaria albirostris (Hincks, 1884).—*Holoporella albirostris.*—Osburn, 1952:498. Celleporariidae. Islands: Daphne Major. Distribution: Florida, Gulf of Mexico and Caribbean, Indian Ocean, Australia, New Zealand (Circumglobal).

Celleporaria brunnea (Hincks, 1884).—Present study.—*Holoporella brunnea.*—Hastings, 1930:731.—Osburn, 1952:497. Celleporariidae. Islands: Santiago, Santa Cruz, Isabela; Osburn records it from "21 stations in the Galapagos." Distribution: British Columbia to Ecuador, Cocos Island and the Galapagos. (Eastern Pacific.)

Celleporaria hancocki (Osburn, 1952).—*Holoporella hancocki.*—Osburn, 1952:500. Celleporidae. Islands: "Between Seymour and Daphne" and at Daphne Major. Distribution: Endemic.

Celleporaria peristomata (Osburn, 1952).—*Holoporella peristomata.*—Osburn, 1952:501. Celleporidae. Islands: "Between South Seymour and Daphne," Santiago, Isabela. Distribution: Endemic.

Celleporaria quadrispinosa Canu & Bassler, 1930.—*Holoporella quadrispinosa.*—Canu & Bassler, 1930: 38. Celleporidae. Islands: Española, Floreana. Distribution: Baja California and the Galapagos (Panamic).

Celleporella hyalina (Linnaeus, 1767).—*Hippothoa hyalina.*—Hastings, 1930:720.—Osburn, 1953:277. Hippothoidae. Islands: Santiago, Isabela; Osburn's stations not specified. Distribution: Cosmopolitan.

Chorizopora brogniarti (Audouin, 1826).—Canu & Bassler, 1930:14. Chorizoporidae. Islands: Española. Distribution: Australia, New Zealand, Philippines, China, Burma, Sri Lanka, Red Sea, Mediterranean, Britain, South Africa, Galapagos: Gordon 1984:113. (Circumglobal.)

Cigclisula hexagonalis (Canu & Bassler, 1929).—*Holoporella hexagonalis.*—Canu & Bassler, 1930:39.—*Trematooecia hexagonalis.*—Osburn, 1952:503. Stomachetosellidae. Islands: Española, San Cristóbal, Isabela, Floreana, Santa Fé. Distribution: Gulf of California, Mexico, Galapagos (Panamic).

Cigclisula porosa (Canu & Bassler, 1929).—Present study.—*Holoporella porosa.*—Canu & Bassler, 1930: 39.—*Trematooecia porosa.*—Osburn, 1952:503. Stomachetosellidae. Islands: Floreana, Santa Cruz. Distribution: Gulf of California and the Galapagos (Panamic).

Cigclisula tridenticulata (Busk, 1884).—*Holoporella tridenticulata.*—Canu & Bassler, 1930:41.—Osburn, 1952:499. Celleporidae. Islands: Wenman, Floreana, Isabela, San Cristóbal, Santiago. Distribution: Indian Ocean, Australia, New Zealand; Galapagos (Pacific).

Cigclisula turrita (Smitt, 1873).—*Holoporella turrita.*—Hastings, 1930:732. Celleporidae. Islands: Isabela. Distribution: Indian Ocean, China, Philippines, Florida, Pleistocene of Panama (Circumglobal). Powell 1971:773 gives a synonomy. American species of *Cigclisula* are often difficult to distinguish and several species may be confused under this name (Banta & Carson 1977:400).

Cleidochasma contractum (Waters, 1899).—*Perigastrella contracta.*—Hastings, 1930:722.—*Hippoporina contracta.*—Osburn, 1952:347. Cleidochasmatidae. Islands: Santiago, Isabela; Osburn's Galapagos stations not given. Distribution: Madeira; Gulf of Mexico, Caribbean, Massachusetts to Brazil; Gulf of California to Ecuador and the Galapagos (Cheetham & Sandberg 1964:1032 (Pan American).

Cleidochasma porcellanum (Busk, 1860).—Present study.—*Hippoporina porcellana.*—Hastings, 1930: 722.—Osburn, 1952:345.—*Hippoporina cleidostoma.*—Canu & Bassler 1929:19. Cleidochasmatidae. Islands: Santiago, Isabela, Santa Cruz. Distribution: Gulf of Mexico, Caribbean; Gulf of California, Brazil, Pliocene; British Columbia to Peru; Mediterranean, Eastern Central Atlantic, Japan, Indonesia, New Zealand (Gordon 1984:124) (Circumglobal).

Cleidochasma tuberculata Osburn, 1952.—Present study.—*Hippoporina tuberculata.*—Osburn, 1952: 346. Cleidochasmatidae. Islands: San Cristóbal, Santa Cruz. Distribution: Endemic. Absence of spines is a useful character to distinguish *C. tuberculata* from *C. porcellana.*

Codonellina anatina (Canu & Bassler, 1927).—Osburn, 1952:42.—*Codonella granulata.*—Canu & Bassler, 1930:29.—Hastings, 1930:725. Hippoporinidae. Islands: Wenman, Isabela, Santiago, Floreana, Onslow, Española, San Cristóbal, 'Albany.' Distribution: Gulf of California, Galapagos, Hawaii, Gulf of Mexico (Osburn 1952:422) (Pan American). Osburn synonymized *C. granulata* and *C. anatina,* but suggested there may be 'varietal' differences. Galapagos specimens identified as *C. anatina* may be of a distinct species (Soule & Soule 1973:431).

Crepidacantha poissoni (Audouin, 1826).—Present study.—*Hippoporina porcellana.*—Hastings, 1930: 722.—Osburn, 1952:345.—*Hippoporina cleidostoma* Canu & Bassler 1929:19. Crepidacanthidae. Islands: Española, Floreana; Osburn's stations not specified. Distribution: Southern California, Gulf of California, Panama, Cocos Island, Ecuador, Galapagos, Hawaii, Tahiti, New Zealand, Madeira, Indonesia, Red Sea; Florida, Brazil (Gordon 1984:124) (Circumglobal).

Crepidacantha setigera (Smitt, 1873).—Osburn, 1952: 479. Crepidacanthidae. Islands: Wenman, Isabela. Distribution: Florida, Cocos Island, Galapagos (Soule 1963b) (Panamic).

Cyclicopora longipora (MacGillivray, 1883).—Osburn, 1952:285. Cyclicoporidae. Islands: Southwest of Santa Cruz. Distribution: Gulf of California, Galapagos, San Bonito Ids.; Australia (Pacific).

Cycloperiella rosacea Osburn, 1947.—Osburn, 1952: 297. Petraliidae. Islands: Isabela, Santa Cruz. Distribution: Caribbean; Mexico, Panama, Galapagos (Pan American).

Dakaria biserialis (Hincks, 1885).—Osburn, 1952:330. Schizoporellidae. Islands: San Cristóbal. Distribution: New Zealand, Cocos Island, Galapagos, Chile (Pacific). Ascribed to *Arthropoma* by Moyano 1983: 17.

Dakaria sertata Canu & Bassler, 1930.—Canu & Bassler, 1930:57.—Osburn, 1952:329.—Present study. Schizoporellidae. Islands: Floreana, Española, Isabela, Gardner-by-Hood, Santa Cruz. Distribution: Southern California, Gulf of California, Galapagos (Eastern Pacific).

Diplonotos costulatus Canu & Bassler, 1930.—Canu & Bassler, 1930:31 (as *D. costulatum*). Sertellidae. Islands: Española, Marchena. Distribution: Endemic. S. Cairns (pers. comm.) points out *Diplonotos* must be masculine; it could be neuter only if it ended in *-on* or *-um.* The correct name, therefore, appears to be *D. costulatus.*

Enantiosula manica Canu & Bassler, 1929.—Canu & Bassler, 1929.—Osburn, 1952:469.—Present study. Cheiloporinidae. Islands: Isabela, San Cristóbal, Duncan, Gardner, Santiago, Onslow, South Seymour, Floreana. Distribution: Mexico, Gulf of California, Cocos Island, Galapagos (Panamic). Among the most common and characteristic of the Galapagos bryozoans.

Escharella major (Hincks, 1884).—*Mucronella major.*—Osburn, 1952:439. Smittinidae. Islands: Isabela, Santiago, Floreana. Distribution: Southern California, Gulf of California (Eastern Pacific).

Escharina pesanseris Smitt, 1973.—*Mastigophora pesanseris.*—Osburn, 1952:480. Crepidacanthidae. Islands: Wenman, Daphne Major, Isabela. Distribution: Florida, Gulf of Mexico, Caribbean, Brazil; Gulf of California, Panama, Colombia (Pan American).

Escharoides praestans (Hincks, 1882).—Osburn, 1952: 373. Exochellidae. Islands: Wenman, Isabela, Daphne Major. Distribution: Australia, New Zealand, Baja California, Galapagos (Pacific).

Fenestrulina malusi (Audouin, 1826).—Osburn, 1952: 388. Microporellidae. Islands: Wenman, Isabela, Floreana. Distribution: British Columbia to the Galapagos; Gulf of Mexico, Caribbean, Bermuda; north Atlantic, Mediterranean; Western Pacific; Indian Ocean (Cheetham & Sandberg 1964:103); Australia, Chile, southern Atlantic (Moyano 1983:19) (Circumglobal). Possibly a cosmopolitan species, but morphological differences exist between Alaskan specimens and more southern material (Dick & Ross 1988:77).

Hippaliosina rostigera (Smitt, 1873).—Osburn, 1952: 475. Cheiloporinidae. Islands: Isabela. Distribution: Caribbean, Gulf of Mexico, Gulf of California to Colombia and the Galapagos (Cheetham & Sandberg 1964:1044) (Pan American).

Hippomonavella parvicapitata (Canu & Bassler, 1930).—Osburn, 1952:367.—*Hippomonella parvicapitata.*—Canu & Bassler, 1930:19. Hippoporinidae. Islands: Wenman, Española. Distribution: Gulf of California, Ecuador, Colombia (Panamic).

Hippopleurifera mucronata (Smitt, 1873).—Osburn, 1952:301. Umbonulidae. Islands: North Seymour, Isabela, Española. Distribution: Cape Hatteras south (Maturo 1968:278), Gulf of Mexico; Gulf of California to Colombia and the Galapagos (Pan American).

Hippopodinella adpressa (Busk, 1854).—Hastings, 1930: 729.—Osburn, 1952:467.—Present study. Cheiloporinidae. Islands: Santa Cruz, Isabela. "A common species" at unnamed Galapagos stations (Osburn 1952:467). Distribution: Gulf of California to Costa Rica, Panama, Ecuador, Chile, and the Galapagos; Falklands, Antarctic; Britain, Mediterranean (Pan American).

Hippopodinella turrita Osburn, 1952.—Osburn, 1952: 468. Cheiloporinidae. Islands: Floreana, San Christobal. Distribution: Endemic.

Hippoporella gorgonensis Hastings, 1930.—Hastings, 1930:723.—Osburn, 1952:349.—Present study. Cleidochasmatidae. Islands: Wenman, Santiago, Santa Cruz, Santiago, Isabela, Española. Distribution: Southern California to the Galapagos (Eastern Pacific).

Hippoporella rimata Osburn, 1952.—Osburn, 1952: 352. Cleidochasmatidae. Islands: Isabela, San Cristóbal. Distribution: Ecuador, Mexico, Galapagos (Panamic).

Hippoporella species indetermined.—Present study. Hippoporellidae. Islands: Santa Cruz. Distribution: Endemic. Resembles *H. gorgonensis,* but there are six oral spines and the colony is persistently unilaminar.

Hippoporidra granulosa Canu & Bassler, 1930.—Canu & Bassler, 1930:43.—Osburn, 1952:357. Cleidochasmatidae. Islands: San Cristóbal. Distribution: Gulf of California and the Galapagos (Panamic).

Hippoporidra spiculifera (Canu & Bassler, 1930).—Present study.—*Hippotrema spiculifera.*—Canu & Bassler, 1930:43. Cleidochasmatidae. Islands: Española, Floreana, Santa Cruz. Distribution: Mexico, Clarion Island, Panama, Galapagos (Panamic).

Hippoporina ampla Osburn, 1952.—Osburn, 1952:348. Hippoporinidae. Islands: San Cristóbal, Floreana, Santiago. Distribution: Endemic.

Hippoporina pertusa (Esper, 1796).—*Hippodiplosia pertusa.*—Hastings, 1930:724. Hippoporinidae. Islands: Santiago, Isabela. Distribution: Gulf of Mexico, Caribbean, Massachusetts to Brazil; Spitzbergen to the Mediterranean; southern California to Colombia and the Galapagos (Pan American). Cheetham & Sandberg (1964:1041) discuss the generic placement.

Hippoporina verilli Maturo & Schopf, 1968:56.—*Hippodiplosia americana.*—Osburn, 1952:339. Hippoporinidae. Islands: Isabela, Santiago. Distribution: Massachusetts to Brazil, Gulf of Mexico; Gulf of California, to Panama, Costa Rica, and the Galapagos (Winston 1982:139) (Pan American).

Hippothoa divaricata (Lamouroux, 1821).—Osburn, 1952:278. Hippothoidae. Islands: Not listed. Distribution: Widely distributed (Cosmopolitan). Detailed synonymy and distribution in Ryland & Gordon (1977:20). "Typical *H. divaricata* seems to be Atlantic in distribution" Gordon (1984:111). A subspecies occurs in New Zealand.

Hippothoa flagellum Manzoni, 1870.—Osburn, 1952: 278. Hippothoidae. Islands: Not given. Distribution: Europe, Southeastern U.S., Caribbean, Japan, Hawaii, California, Mexico, Galapagos (Morris 1980); Chile, south Atlantic (Moyano 1983:20) (Circumglobal). The world wide synonymy is complex. Ryland & Gordon (1977:25) consider many eastern Pacific specimens to belong to a distinct species.

Lagenicella hippocrepis (Busk, 1856).—*Costazia hippocrepis.*—Hastings, 1930:731.—*Lagenipora hippocrepis* (Busk, 1856).—Osburn, 1952:489. Teuchoporidae. Islands: Wenman, Floreana. Distribution: Southern California to Panama and the Galapagos (Eastern Pacific).

Lagenicella lacunosa Bassler, 1934.—*Lagenipora verrucosa.*—Canu & Bassler, 1930:35.—*Lagenipora lacunosa.*—Osburn, 1952:491. Teuchoporidae. Islands: Wenman, Floreana, Isabela, Santiago, Espãnola, Fernandina. Distribution: southern California to Peru and the Galapagos (Eastern Pacific). The family Teuchoporidae Neviani, 1895 has priority over the Phylactellidae Harmer, 1957:896 (Gordon 1984:80).

Lagenicella marginata Canu & Bassler, 1929.—*Lagenipora marginata.*—Osburn, 1952:490. Teuchoporidae. Islands: Isabela, San Cristóbal, Española, Santa Fé. Distribution: Panama, Cocos Island, Gulf of California, Galapagos; east coast of Florida, Gulf of Mexico (see Winston 1982:144) (Pan American).

Lagenicella punctulata (Gabb & Horn, 1862).—*Lagenipora punctulata.*—Osburn, 1952:486. Teuchoporidae. Islands: Not given. Distribution: Alaska to the Galapagos (Eastern Pacific).

Lagenicella species undetermined.—Present study. Teuchoporidae. Islands: Santa Cruz. Distribution: Endemic. Oligoserial like *L. lacunosa* Bassler, but the zoids are minute for this genus (0.35 × 0.22 mm); peristome low, much shorter than zoids; inner ends of pseudopores circular. No complete ovicells observed.

Lagenicella spinulosa Hincks, 1884.—*Lagenipora spinulosa.*—Hastings, 1930:730. Teuchoporidae. Islands: Santiago. Distribution: Alaska, British Columbia, California, Gulf of California (Osburn 1952: 487) (Eastern Pacific).

Mamillopora cupula Smitt, 1873.—Osburn, 1952: 517.—Canu & Bassler, 1928:45. Mamilloporidae. Islands: Española (Canu & Bassler 1928a:45) 'Abundant about the Galapagos Islands' (Osburn 1952:

518). Distribution: Gulf of California to Panama and the Galapagos; Gulf of Mexico, Caribbean. (Pan American.)

Microporella californica (Busk, 1856).–Osburn, 1952: 382. Microporellidae. Islands: Isabela, Santiago. Distribution: British Columbia to the Galapagos (Eastern Pacific).

Microporella ciliata (Pallas, 1766).—Hastings, 1930: 727.—Osburn, 1952:377. Microporellidae. Islands: Santiago, Isabela; Osburn's stations not given. Distribution: Australia, New Zealand; Philippines, Oregon to the Galapagos; Chile, Falklands, Juan Fernandez, Tristan de Cunha; Britain, Mediterranean (Gordon 1984:101) (Circumglobal).

Microporella gibbosula Canu & Bassler, 1930.—Canu & Bassler, 1930:20.—Osburn, 1952:386.—Present study. Microporellidae. Islands: Española, Santa Cruz; Osburn recorded it from 8 unspecified stations in the Islands. Distribution: Gulf of California, Panama, Costa Rica, Colombia and the Galapagos (Osburn 1952:386) (Panamic).

Microporella marsupiata (Busk, 1860).—Osburn, 1952: 383. Microporellidae. Islands: Isabela, Santiago, Santa Fé, San Cristóbal. Distribution: Gulf of California, Cocos Island and the Galapagos (Pan American). Synonym, *M. coronata* Marcus 1938:235: "Mediterranean, Madeira, Cape Verde Islands, Britain, Gulf of Guinnea, Saint Helena." The synonymy of American species is in doubt (Gordon 1984:102).

Microporella pontifica Osburn, 1952.—Osburn, 1952: 383. Microporellidae. Islands: Isabela. Distribution: Gulf of California to the Galapagos; Post-Pleistocene of Louisiana (Pan American).

Microporella tractabilis Canu & Bassler, 1930.—Canu & Bassler, 1930:22.—Present study. Microporellidae. Islands: Española, Floreana, Santa Cruz. Distribution: Colombia, Panama, Galapagos; Post-Pleistocene of Louisiana (Pan American). Cheetham & Sandberg (1964:1036) found Osburn's descriptions differed in important respects from Canu & Bassler's Galapagos specimens.

Pachycleithonia nigra Canu & Bassler, 1930.—Canu & Bassler, 1930:27. Watersiporidae. Islands: Española. Distribution: Endemic. Osburn (1952:472) considered *P. nigra* a subspecies of *W. cucullata* (Busk 1854). At least some of his *P. nigra* specimens were of *W. arcuata* Banta 1968. See also Soule & Soule (1975:308).

Parasmittina californica (Robertson, 1908).—Osburn, 1952:416. Smittinidae. Islands: Wenman. Distribution: Southern California, Baja California, Galapagos (eastern Pacific). The identity of Galapagos material with that of *Mucronella californica* Robertson 1908:308 is questionable. Confused with and possibly identical to *P. trispinosa* of authors (Soule & Soule 1973:424).

Parasmittina crosslandi (Hastings, 1930).—Present study. Smittinidae. Islands: Santa Cruz. Distribution: Gulf of California, Baja California, Panama and the Galapagos (Panamic). The first record in the Galapagos, if Soule & Soule (1973:382) are correct in regarding all of Canu & Bassler's and Osburn's specimens of *P. crosslandi* as *P. dolobrata.*

Parasmittina dolobrata Soule & Soule, 1973.—*Smittina crosslandi.*—Hastings, 1930:726.—*Parasmittina crosslandi.*—Osburn, 1952:418 (part).—*Parasmittina trispinosa*: Canu & Bassler 1930:27; Osburn 1952:418 (part); *P. spathulata*: Osburn 1952:415 (part); *Parasmittina dolobrata*: Soule & Soule 1973: 421 and 393. See Soule & Soule (1973:421). Smittinidae. Islands: Wenman, Santiago, Santa Cruz, San Cristóbal, Marchena, Floreana, Baltra, Isabela, Española. Distribution: Colombia, Panama, Costa Rica and the Galapagos (Soule & Soule 1973:423) (Panamic).

Parasmittina frazeri Osburn, 1952.—Osburn, 1952:420. Smittinidae. Islands: Isabela. Distribution: Mexico, Ecuador, Galapagos (Panamic).

Parasmittina species undetermined.—Present study. Smittinidae. Islands: Santa Cruz. Distribution: Endemic. Like *P. hastingsae* Soule & Soule 1973:417, but smaller, and the aperture is broader than long.

Phidolipora pacifica (Robertson, 1908).—Osburn, 1952: 449. Sertellidae. Islands: Wenman, Isabela, Santiago. Distribution: Oregon, Gulf of California, to Peru and the Galapagos (Eastern Pacific).

Phylactella aperta Osburn, 1952.—Osburn, 1952:482. Phylactellidae. Islands: Isabela. Distribution: Endemic.

Porella columbiana O'Donoghue, 1923.—Osburn, 1952:398. Smittinidae. Islands: Isabela and at a station between Floreana and Santa Fé. Distribution: British Columbia, Puget Sound, Southern California (Eastern Pacific).

Porella patens Osburn, 1952.—Osburn, 1952:397. Smittinidae. Islands: Wenman. Distribution: Southern California, Baja California, Cocos Island, Galapagos (Eastern Pacific).

Puellina innominata (Couch, 1844).—Canu & Bassler, 1930:13.–Present study. Cribrilinidae. Islands: Española. Distribution: Philippines, India, Mediterranean, Britain, Madeira, Gulf of Mexico, California, Australia, New Zealand (Gordon 1984:64); Peru, Chile (Moyano 1983:19) (Circumglobal). Osburn (1950:187) considered *P. innominata* to be synonymous with *Cribrillaria radiata*; some of his records of *C. radiata* in the Galapagos may be of *P. innominata.*

Puellina radiata (Moll, 1803).—Canu & Bassler, 1930: 13.—Present study.—*Colletosia radiata.*—Osburn, 1950:188. Cribrilinidae. Islands: Floreana, Santa Cruz. Distribution: British Columbia to Peru, Cocos Island and the Galapagos; Gulf of Mexico, Caribbean, North Carolina to Brazil; Western Pacific, Indian Oceans (Circumglobal). The *Cribrilina radiata* of MacGillivray (1889:317) and Powell 1967:223 is probably *C. innominata* (Gordon 1984:64). See Gordon for generic placement.

Puellina setosa (Waters, 1889).—Osburn, 1950:186. Cribrilinidae. Islands: Isabela. Distribution: British Columbia, Puget Sound, Oregon, California, Madeira, Naples (Pan American).

Reptadeonella tubulifera (Canu & Bassler, 1930).—*Adeona tubulifera.*—Canu & Bassler, 1930:34.—Osburn, 1952:442. Adeonidae. Islands: Wenman, Isabela, San Cristóbal, Santa Fé, Santiago, Floreana, Española. Distribution: Ecuador and the Galapagos Islands (Osburn 1952:442) (Eastern Pacific).

Reptadeonella violaecea (Johnston, 1847).—*Adeona violaecea.*—Osburn, 1952:441. Adeonidae. Islands: Not given. Distribution: Britain, Mediterranean, Cape Verde Islands, Western Africa, Gulf of Mexico, Caribbean; Baja California to Colombia and the Galapagos (Hayward & Ryland 1979:82) (Pan American).

Reteporella striata Canu & Bassler, 1930.—*Diplonotos striatum.*—Canu & Bassler, 1930:32. Sertellidae. Islands: Marchena. Distribution: Endemic. See Harmer (1934:624) regarding the tentative generic placement of this species.

Reteporellina denticulata var. *gracilis* Osburn, 1952.—Osburn, 1952:447. Sertellidae. Islands: Wenman, Isabela, South Seymour, Daphne Major, Santiago. Distribution: Costa Rica, Cocos Island, Galapagos (Panamic).

Rhynchozoon rostratum (Busk, 1856).—Hastings, 1930:728.—Osburn, 1952:456.—Present study. Sertellidae. Islands: Santa Cruz; unspecified stations in the Galapagos (Osburn 1952:458). Distribution: Caribbean, Gulf of Mexico, Southern California to Colombia, Panama and the Galapagos; Indonesia (see Winston & Heimberg 1986:38) (Circumtropical). If *R. rostratum* is synonymous with *R. tumulosum* (Soule & Soule 1964:33), the range is Arctic to tropical eastern Pacific (Dick & Ross 1988:84).

Robertsonidra oligopus Osburn, 1952.—Osburn, 1952:295. Petraliidae. Islands: about 30 km northeast of Pinta. Distribution: California, Baja California, Galapagos (eastern Pacific).

Savignyella lafontii (Audouin, 1826).—*Savignyella lafonti.*—Osburn, 1952:288. Savignyellidae. Islands: Isabela. Distribution: Circumglobal in warmer waters, including in America, the Gulf of Mexico, Brazil, California, Colombia, Galapagos (Circumglobal).

Schizmopora anatina Canu & Bassler, 1930.—Osburn, 1952:493.—*Osthimosia anatina.*—Canu & Bassler, 1930:42. Celleporidae. Islands: Isabela, Floreana, South Seymour, Santiago, Española, Marchena, Santa Fé, Gardner, Duncan. Distribution: Gulf of California, Mexico, Panama (Panamic).

Schizmopora margaritacea (Pourtalès, 1867).—Osburn, 1952:495. Celleporidae. Islands: Santiago. Distribution: North Carolina to the Caribbean; Galapagos (Pan American).

Schizoporella cornuta (Gabb & Horn, 1862).—Hastings, 1930:721.—Osburn, 1952:321.—Present study.—*Schizopodrella biaperta.*—Canu & Bassler, 1930:1. Schizoporellidae. Islands: Española, Santiago, Isabela, Santa Cruz; Osburn's stations not listed. Distribution: Alaska to the Galapagos; Gulf of Mexico, Caribbean, Massachusetts to Florida (Cheetham & Sandberg 1964:1030) (Circumglobal).

Schizoporella dissimilis Osburn, 1952.—Osburn, 1952:322. Schizoporellidae. Islands: Isabela, Santiago, Santa Fé. Distribution: Gulf of California and the Galapagos (Panamic).

Schizoporella trichotoma (Waters, 1918).—Hastings, 1930:721.—Osburn, 1952:318. Schizoporellidae. Islands: Wenman, Floreana, San Cristobal, Santa Cruz, Isabela. Distribution: Cape Verde Islands; Gulf of California, Galapagos (Pan American).

Schizoporella unicornis (Johnston, 1847).—Osburn, 1952:317. Schizoporellidae. Islands: Santiago. Distribution: Reported from almost every ocean, but lumping makes many of these records suspect (Cosmopolitan).

Schizotheca umbonata Osburn, 1952.—Osburn, 1952:452. Sertellidae. Islands: Isabela. Distribution: Endemic.

Semihalswellia sulcosa Canu & Bassler, 1930.—Canu & Bassler, 1930:15.—Osburn, 1952:304. Gigantoporidae. Islands: Marchena, Isabela. Distribution: Endemic.

Smittina landsborovi (Johnston, 1847).—Osburn, 1952:401. Smittinidae. Islands: Not listed. Distribution: Western Norway to the western Mediterranean; dubiously recorded world wide (Hayward & Ryland 1979:99) (Cosmopolitan). The identity with European material is questionable.

Smittina smittiella Osburn, 1947.—Osburn, 1952:405. Smittinidae. Islands: Wenman, Santa Cruz, Isabela. Distribution: Gulf of Mexico, Caribbean, Brazil; Ecuador and the Galapagos (Pan American).

Smittoidea pacifica Soule & Soule, 1973.—Osburn, 1952:410.—Soule & Soule, 1973:381.—*Smittina reticulata.*—Canu & Bassler, 1930:27.—*Smittoidea pacifica* Soule & Soule 1973:380. Smittinidae. Islands: Wenman, Isabela, San Cristobal, Duncan, Santiago (Osburn 1952:410); off Floreana (Canu & Bassler 1930:27). Distribution: Hawaii, Galapagos (Soule & Soule 1973:380) (eastern Pacific).

Stephanosella vitrea Osburn, 1952.—Osburn, 1952:370. Hippoporinidae. Islands: San Cristóbal. Distribution: Puget Sound to the Galapagos (eastern Pacific).

Stylopoma informatum (Lonsdale, 1845).—Osburn, 1952:337. Schizoporellidae. Islands: Floreana, Santiago. Distribution: West Indies, Brazil, Galapagos.

I have a specimen from the Gulf of California. (Pan American).

Stylopoma spongites (Pallas, 1766).—Hastings, 1930: 721. Schizoporellidae. Islands: Santiago, Isabela. Distribution: Florida, Gulf of Mexico, Caribbean; Bermuda, Brazil, Pliocene of Panama, Galapagos (Pan American). The taxonomy is discussed by Cheetham & Sandberg (1964:1030).

Tetraplaria veleroae Osburn, 1952.—Osburn, 1952:467. Cheiloporinidae. Islands: About 10 km SSW of Floreana; Isabela. Distribution: Endemic.

Trypostega venusta (Norman, 1864).—Canu & Bassler, 1930:15.—Osburn, 1952:281.—Present study. Hippothoidae. Islands: Española, Floreana, Santa Cruz; Osburn's stations not listed. Distribution: Britain to the Caribbean, Gulf of Mexico; Indian Ocean; California to Cocos Island and Ecuador, the Philippines, Australia, Loyalty Islands, and elsewhere. (Circumglobal).

Watersipora arcuata Banta, 1968.—*Watersipora cucullata.*—Hastings, 1930:729.—*Watersipora cucullata* var. *nigra.*—Osburn, 1952:472. Watersiporidae. Islands: Santiago, Isabela; Osburn's stations in the Galapagos are unspecified. Distribution: California, Baja California, Gulf of California and the Galapagos; Australia and New Zealand (Pacific). Hasting's Pl. 15, figs. 99 and 101, are probably of *W. arcuata.* Some or all of Osburn's records of this species in the Galapagos probably belong here. See Soule & Soule 1975:308.

Watersipora cucullata (Busk, 1854).—Hastings, 1930: 729.—Osburn, 1950:472. Watersiporidae. Islands: Santiago, Isabela; Osburn's stations unspecified. Distribution: Atlantic, Mediterranean, Red Sea, Indian Ocean, Amoy (Circumglobal). This species has not yet been recorded with certainty in the Galapagos; it may be present but lumped with *W. arcuata* and *Pachycleithonia nigra*; see Soule & Soule (1975: 308, 1985:297).

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 803–814

PYRGULOPSIS BRUNEAUENSIS, A NEW SPRINGSNAIL (GASTROPODA: HYDROBIIDAE) FROM THE SNAKE RIVER PLAIN, SOUTHERN IDAHO

Robert Hershler

Abstract.—*Pyrgulopsis bruneauensis*, new species, from thermal springs along Hot Creek and Bruneau River in Owyhee County, Idaho (upper Snake River drainage), is described. Distinguishing features include a combination of small size (<2.8 mm shell height); globose-low conic shell; and penis with an elongate, muscular filament and a small lobe bearing a single distal glandular ridge. *Pyrgulopsis bruneauensis* appears closest morphologically to *P. amargosae* Hershler, 1989, from the Death Valley System to the south, but this opinion may require modification after other congeners from the Snake River region receive anatomical study.

The diverse molluscan fauna of the Snake River drainage includes several gastropods that lack formal description, despite their having been known to malacologists for a number of years. One of these is a springsnail from the Hot Creek area of upper Snake River drainage in northern Owyhee County, Idaho, that was first collected by Borys Malkin in 1952 (letter, W. F. Barr to J. P. E. Morrison, 14 July 1953). Malkin's collection, plus one made by Barr in 1954, were sent to Morrison, who recognized the distinctiveness of the snail and used new manuscript genus and species names for it in the National Museum of Natural History (USNM) collection. Taylor (1982) later pursued additional field and laboratory study of this snail.

Springflows in the Hot Creek area have declined dramatically in recent years because of groundwater mining, and conservation of the Bruneau Hot Springsnail has become an important issue. This species has been proposed for listing under the Endangered Species Act (USDI 1985), and measures currently are being taken to protect remaining populations.

The author visited the Hot Creek area in June 1989 and made collections of the snail, which were used to prepare the following description.

Family Hydrobiidae Troschel, 1857
Genus *Pyrgulopsis* Call and Pilsbry, 1886
Pyrgulopsis bruneauensis, new species
Bruneau Hot Springsnail
Figs. 1–6, Table 1

Bruneau Hot Spring snail.—USDI 1984: 21673.—USDI 1985:33803.
Warm Springs Snail.—Armantrout 1985:35.
"undescribed genus."—Taylor 1985:291.

Material examined.—Spring along west side of Bruneau River, ca. 100 m downflow from Hot Creek's confluence with the river, Owyhee County, Idaho, T 7S, R 6E, SW ¼ sec. 34, USNM 860507 (holotype), USNM 860508 (paratypes; 18 dry shells and a large alcohol series), ANSP 376090 (paratypes; six dry shells), UF 161474 (paratypes; six dry shells).—Seep along south-east side of Hot Creek, ca. 50 m upflow from confluence with Bruneau River, T 8S, R 6E, NE ¼ sec. 3, USNM 860509.—Hot Creek Falls, T 8S, R 6E, NW ¼ sec. 3, USNM 791466 (Malkin coll.), USNM 860510 (Barr coll.).

Diagnosis.—A moderate-sized species with globose to low-conic shell. Penis with

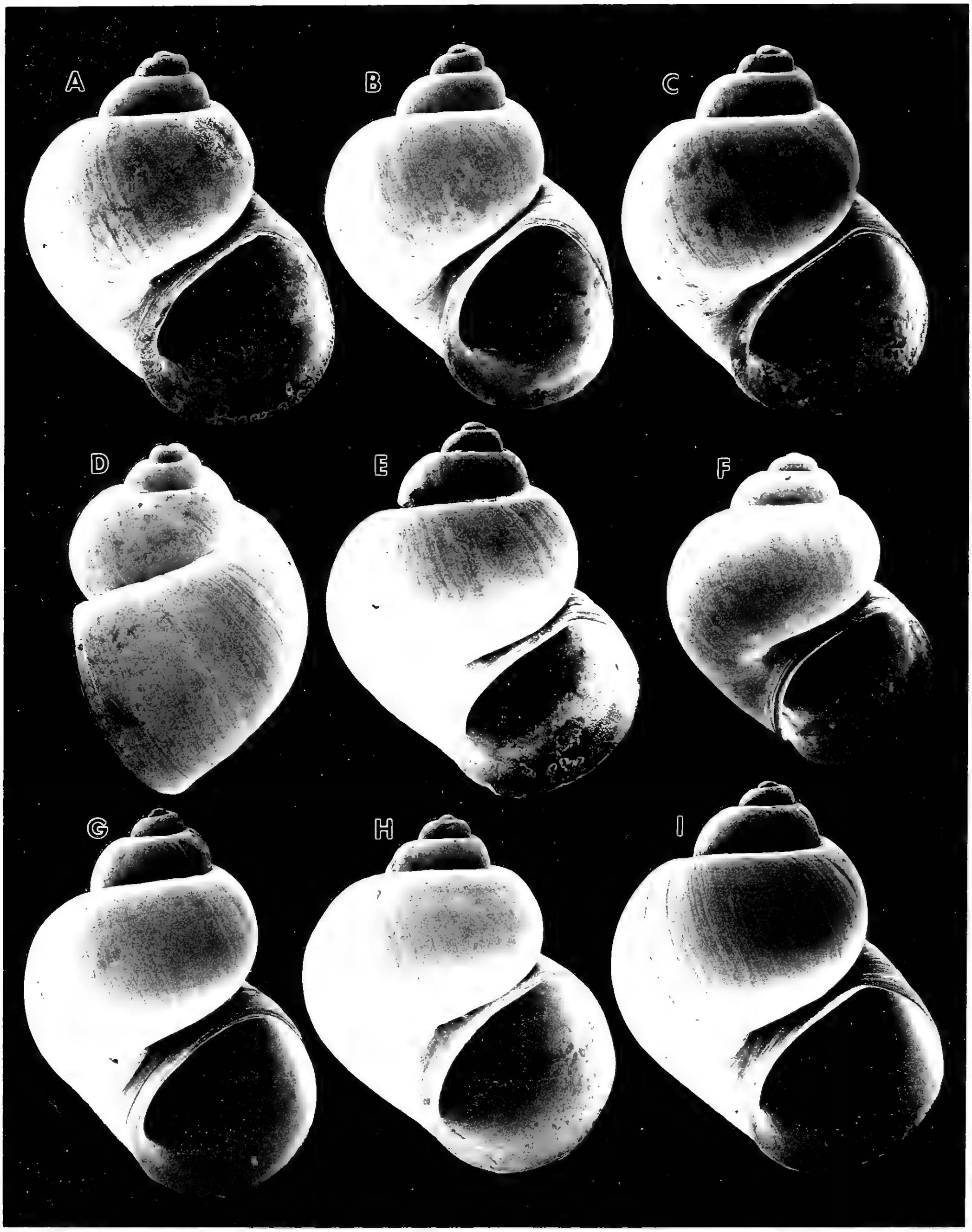


Fig. 1. SEM micrographs of shells of *Pyrgulopsis bruneauensis* Hershler, n. sp. a, Holotype, USNM 860507; b–d, Paratypes, USNM 860508, lot as above; e, f, USNM 791466; g–i, USNM 860509. The holotype is 2.48 mm tall (other micrographs printed to the same scale).

small lobe and elongate, muscular filament. Distal edge of lobe bearing a single glandular ridge.

Description.—Shell (Figs. 1, 2a, b): morphometric data were obtained as described in Hershler (1989) and are in Table 1. Thin, transparent, white-clear, but appearing black because of animal pigmentation. Slightly taller than wide; body whorl large (79–91% of shell height). Whorls, 3.75–4.25, rounded, with pronounced adapical shoulders. Aperture about 55% of shell height, ovate, slightly taller than wide, rounded below, very slightly angled above. Outer lip thin, slightly prosocline (Fig. 1d); inner lip thickened but not reflected, narrowly adnate above or slightly separated from body whorl. Umbilicus broadly open. Protoconch slightly protruding; surface usually whitened and slightly eroded, generally smooth although small area of wrinkled microsculpture sometimes visible (Fig. 2b). Teleoconch growth lines moderately pronounced; numerous faint spiral lines also present.

Operculum (Fig. 3a, b): amber, thin, narrowly ovate, paucispiral, with eccentric nucleus. End farthest from nucleus angled.

Radula (Fig. 4): radular formula, (4-6)-1-(4-6)/1-1, 3-1-3(4), 21–26, 22–26. Width of central tooth, 28–34 μm. Basal cusps of central teeth small, originating from lateral angles; lateral angles well expanded; basal process moderately excavated. Central cusps of central and lateral teeth slightly enlarged.

Anatomy (from relaxed, preserved material; Figs. 2c–f, 3b, d, 5, 6): head-foot and dorsal visceral coil covered with dark, grey-black epithelial pigment. Pigment somewhat lighter around the eyes, on cephalic tentacles (Fig. 5a), along broad strips along the sides of the head-foot, and on dorsal prostate gland (of male). Edge of mantle collar, sole of foot, distal lips of snout, and majority of dorsal operculigerous lobe unpigmented.

Cephalic tentacles without hypertrophied ciliary tufts (Fig. 2c). Ctenidial filaments, ca. 20, triangular, plicate, moderately broad relative to width of pallial cavity. Frontal edges of filaments with two narrow stripes of grey pigment. Osphradium about 25% of ctenidium length, slightly posterior to center of ctenidial axis. Kidney scarcely bulging into pallial cavity; renal opening small, ringed with fleshy lips. Hypobranchial gland not obvious in dissection or section. Stomach and style sac sub-equal in length; small triangular caecal chamber protruding from posterior edge of stomach.

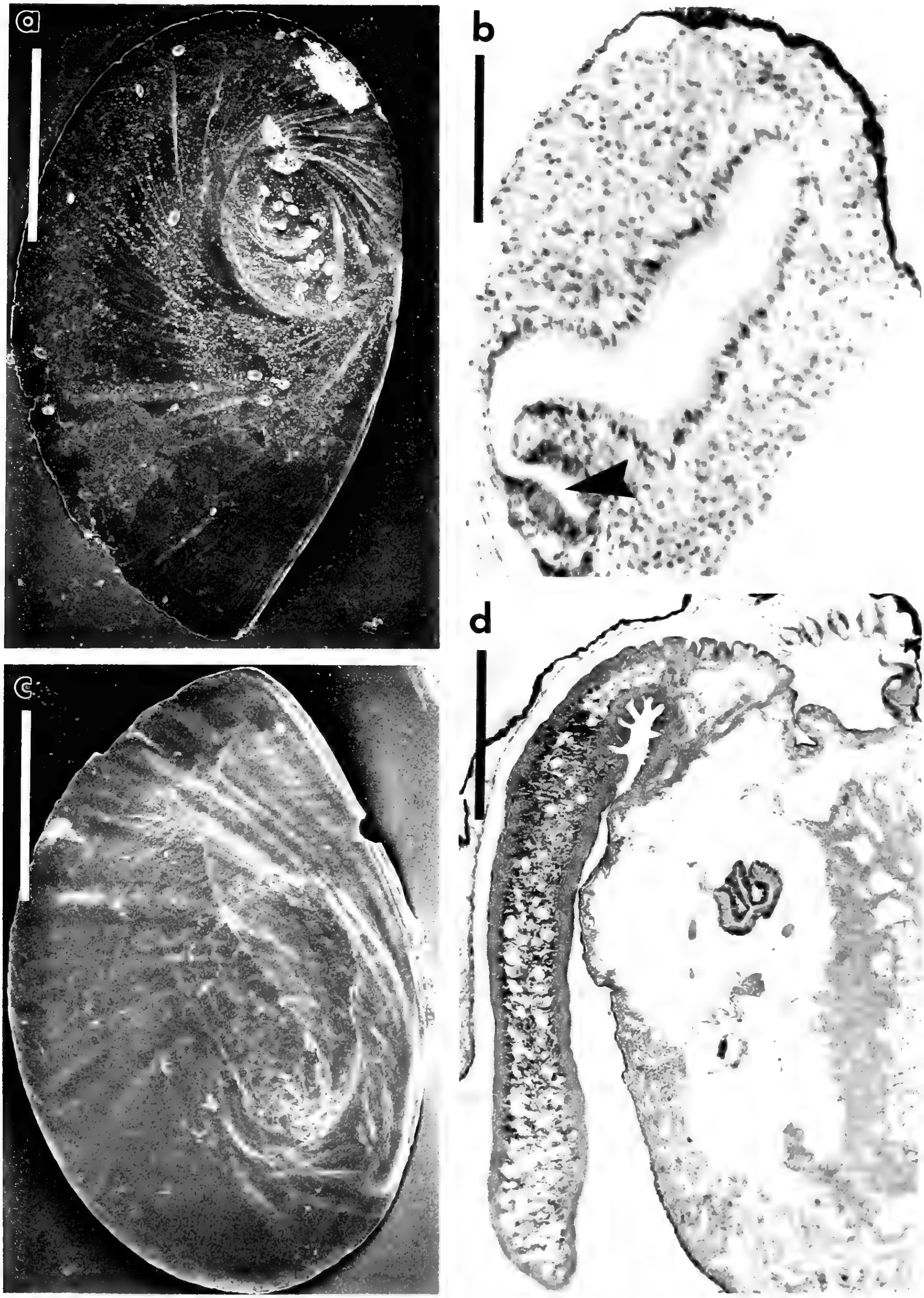
Testis of numerous simple lobes (draining to vas efferens), large (1.5 whorls), filling about 50% of body length and extending from near apical tip of animal to posterior edge of prostate gland (covering stomach). Seminal vesicle of a few thickened coils pressed against posterior edge of stomach. Prostate gland small, bean-shaped, with about 50% of length in pallial roof. Anterior vas deferens exiting proximal to tip of gland. Penis (Figs. 2d–f, 3d, 6) moderate-large, usually uncoiled and protruding beyond edge of mantle collar. Black sub-epithelial pigment dense in virtual entirety of filament, somewhat lighter in lobe and scattered in

→

Fig. 2. SEM micrographs of shell protoconchs and critical point dried bodies of *P. bruneauensis.* a, b, Protoconch, paratypes, USNM 860508 (scale bars = 136 μm, 150 μm); c, Dorsal head, USNM 860509 (200 μm); d, Dorsal aspect of penis, USNM 860508 (250 μm); e, f, Dorsal aspects of head-foot and penis, USNM 860509 (0.43 mm). Pf = penial filament; Pl = penial lobe.

Fig. 3. Operculae and histological sections of *P. bruneauensis,* paratypes, USNM 860508. a, Dorsal operculum (0.38 mm); b, Cross section of mid capsule gland (0.1 mm). Arrow indicates ventral channel of gland; c, Ventral operculum (0.38 mm); d, Cross section of male just posterior to nerve ring (0.25 mm). Note elongate, muscular penis (to left).


a
b
c
d
e
Pl
Pf
f


a
b
c
d

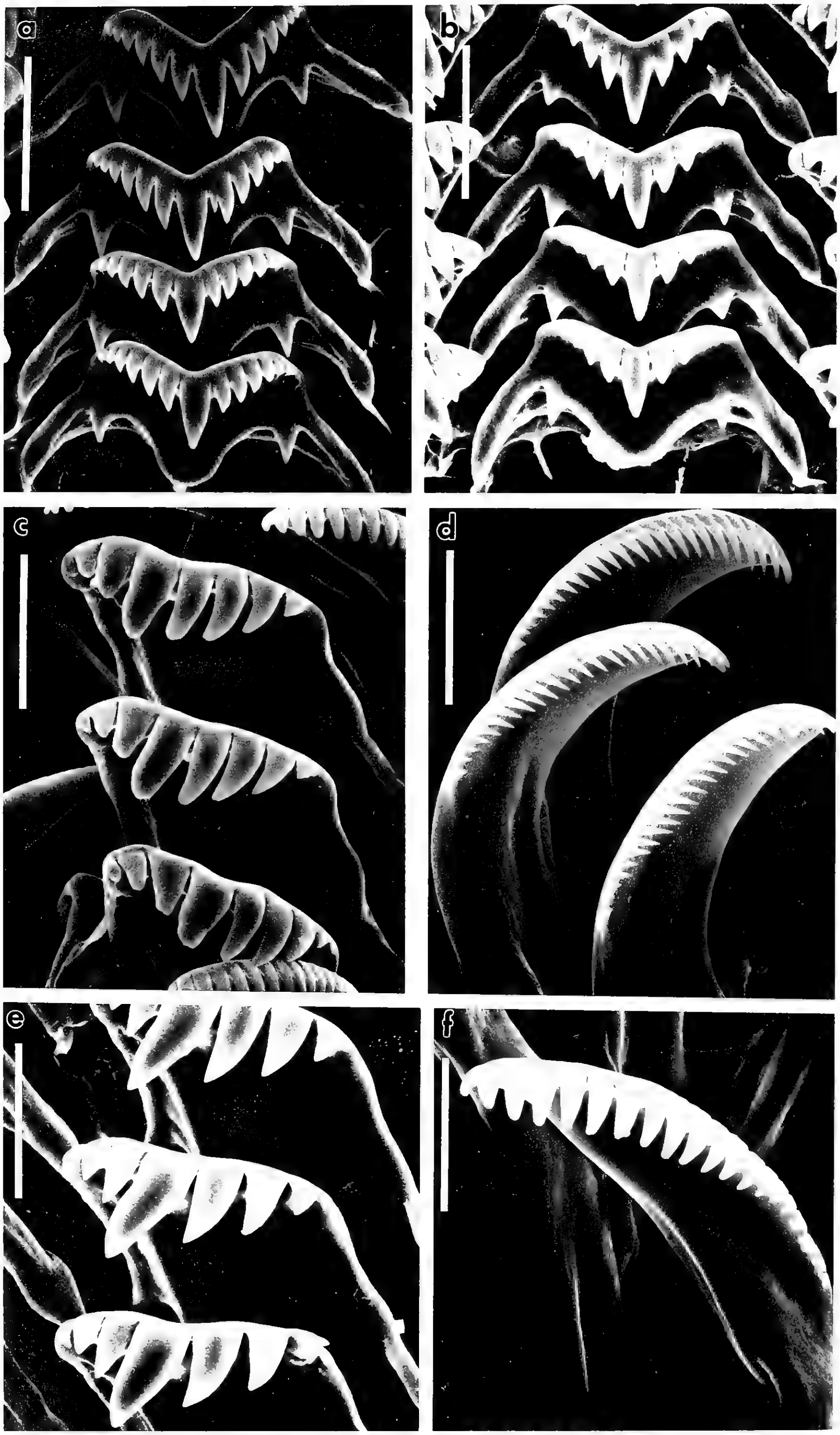


Fig. 4. SEM micrographs of radulae of *P. bruneauensis.* a, Central teeth, paratypes, USNM 860508 (15.0 μm); b, Centrals, USNM 860510 (13.6 μm); c, Laterals, USNM 860508 (12.0 μm); d, Outer marginals, lot as above (7.5 μm). e, Laterals, USNM 860510 (10.0 μm); f, Inner marginal, USNM 860508 (7.5 μm).

remaining penis. Dorsal penis without hypertrophied ciliary patches. Filament narrow, equal to or longer than proximal penis, much longer than lobe. Filament tapering little along most of length, near-circular in cross section. Thick layer of circular muscles of filament obvious in section (Fig. 3d). Lobe stout, slightly tapered distally. Single glandular ridge confined to lobe, usually along distal edge. Vas deferens uncoiled in penis, positioned near outer edge.

Ovary about one whorl, of simple lobes, covering posterior stomach chamber. Albumen gland (Ag) slightly longer than capsule gland (Cg). Renal oviduct (Ov) with large, complex coil on posterior albumen gland. Seminal receptacle (Sr) a small sac with short duct into posterior loop of oviduct. Bursa copulatrix (Bu) moderate-sized, ovate, partly posterior to albumen gland. Duct from bursa copulatrix broad and elongate, traversing much of albumen gland before joining oviduct. Ventral channel (Vc) moderately wide, separated from capsule gland lumen by pronounced fold (Fig. 3b). Capsule gland opening simple, sub-terminal. Distal to opening, edge of gland (base of ventral channel) continued distally (as gutter) to near edge of mantle collar (not illustrated).

Variation.—Shells from the Hot Creek spring and those along the Bruneau River differed significantly in shell measurements (9 of 12 pairwise comparisons [by sex] significant, $P \leq 0.05$, Tukey HSD Test) and translation rate ($0.4 > P > 0.3$), reflecting the larger size and squatter shells from the type locality. These populations also are differentiated by penial form, with males from the type locality (Fig. 6a–d) having smaller penes (scarcely protruding beyond mantle collar) with shorter filaments than those from the Hot Creek spring (Fig. 6f–i). These differences do not, however, appear to justify taxonomic distinction of the populations.

Etymology.—The species name refers to the snail's occurrence in Bruneau River drainage.

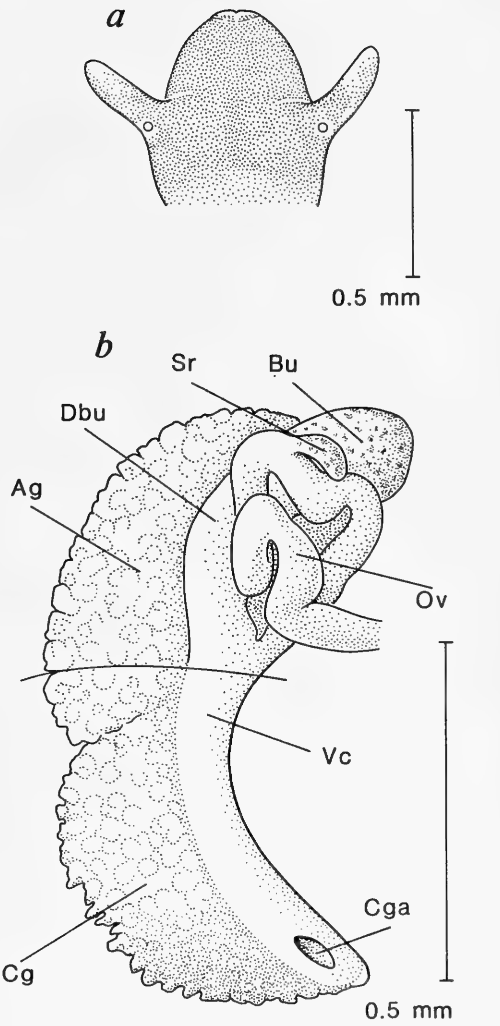


Fig. 5. Anatomy of *P. bruneauensis,* paratypes, USNM 860508. a, Dorsal aspect of head showing typically near-uniform dark pigment; b, Left lateral aspect of pallial oviduct and associated structures. Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Cga = opening of capsule gland; Dbu = duct from the bursa copulatrix; Ov = renal oviduct; Sr = seminal receptacle; Vc = ventral channel of capsule gland.

Remarks.—*Pyrgulopsis bruneauensis* is readily separable from all but one hydrobiid of the Snake River and adjacent areas by its small size and squat shell ("*Fluminicola*" *minutissima* Pilsbry, 1907, from Snake River basin near the Idaho-Oregon border is even smaller and more globose than the

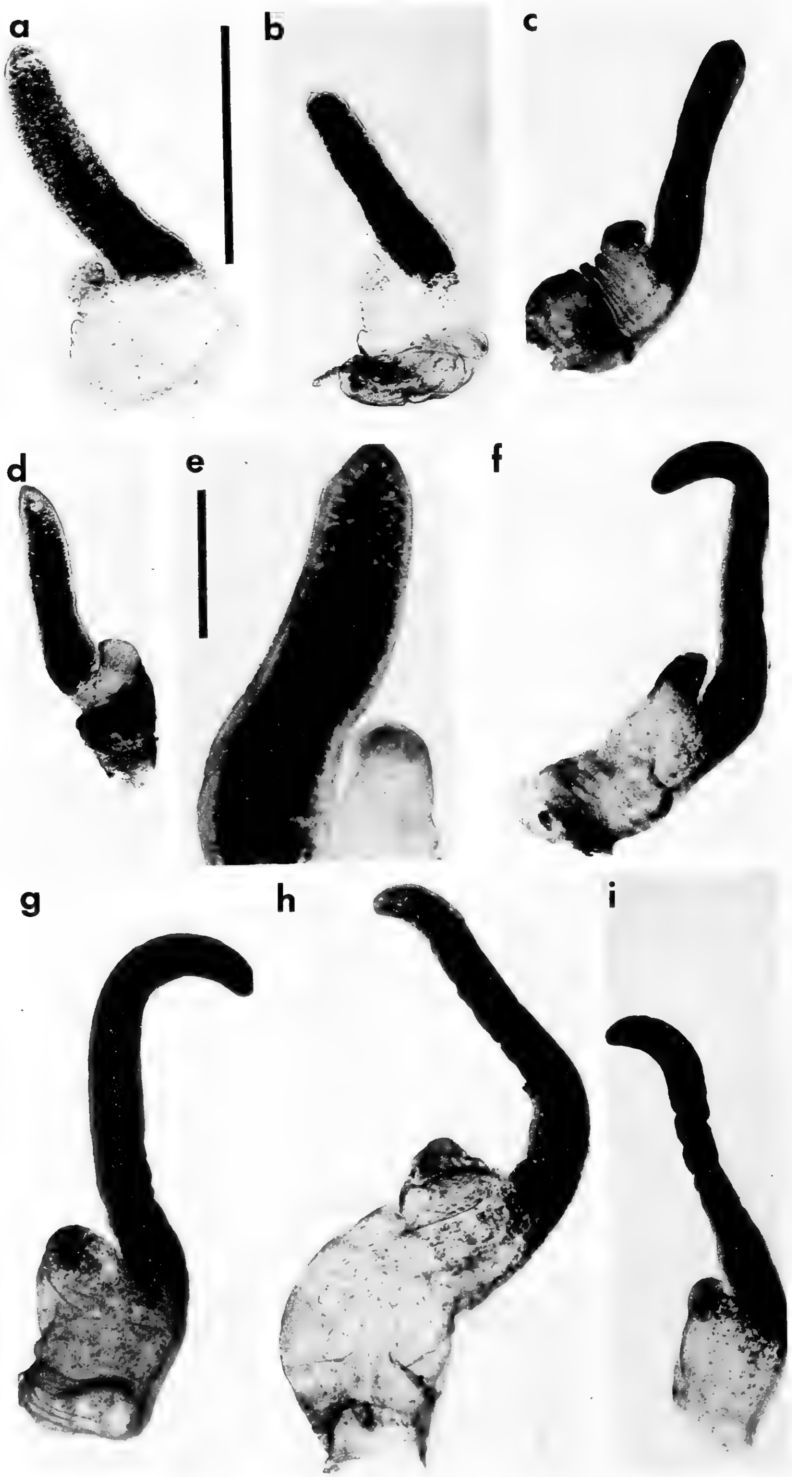

a
b
c
d
e
f
g
h
i

Table 1.—Shell parameters for *Pyrgulopsis bruneauensis*. WH = number of whorls, SH = shell height, SW = shell width, LBW = length of body whorl, WBW = width of body whorl, AL = aperture length, AW = aperture width, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, SA = aperture shape. Measurements are in mm.

		WH	SH	SW	LBW	WBW	AL	AW	W	D	T	SA
USNM 560507												
(holotype)		4.00	2.48	2.03	2.12	1.60	1.39	1.25	1.74	0.60	3.55	1.11
USNM 560508												
(paratypes)	$\bar{X}$	3.81	2.34	1.96	2.01	1.49	1.30	1.22	2.09	0.56	3.88	1.07
(♂, $n = 8$)	s	0.12	0.10	0.12	0.12	0.07	0.07	0.08	0.17	0.04	0.53	0.04
(paratypes)	$\bar{X}$	3.79	2.24	1.79	1.89	1.41	1.21	1.08	2.16	0.54	3.96	1.12
(♀, $n = 7$)	s	0.17	0.15	0.04	0.10	0.05	0.07	0.03	0.37	0.05	0.41	0.04
USNM 560509												
(♂, $n = 10$)	$\bar{X}$	3.90	2.78	2.36	2.35	1.82	1.47	1.35	2.02	0.55	3.29	1.09
	s	0.18	0.16	0.20	0.17	0.13	0.12	0.11	0.19	0.03	0.42	0.07
(♀, $n = 10$)	$\bar{X}$	3.88	2.35	1.96	2.02	1.50	1.36	1.13	2.26	0.53	3.31	1.21
	s	0.21	0.16	0.08	0.12	0.06	0.08	0.05	0.32	0.04	0.43	0.05

above). The penis of *P. bruneauensis* is similar to that of *P. amargosae* from Death Valley System, California, in that the latter also has an elongate filament darkly pigmented with sub-epithelial granules (Hershler 1989:figs. 17b, 18b–e). A close historic relationship between the upper Snake River (prior to its integration with the lower river) and Lahontan drainage to the south (which then was integrated with Death Valley System) was postulated by Minckley et al. (1986: 534, fig. 15.4). A detailed discussion of the relationships of *P. bruneauensis* must, however, await anatomical study of other regional *Pyrgulopsis*.

Distribution and habitat.—The snail occurs in small thermal springs (to 35°C) along Hot Creek and along the Bruneau River in the immediate vicinity of the creek's confluence (Figs. 7, 8).[1] Hot Creek, fed by numerous small springs, flows about one km before entering Bruneau River near the mouth of Bruneau Canyon. Discharge of the creek historically was at least 4.0 cfs (Waring 1965:30). At the upper end of the creek springflow historically drained via Hot Creek Falls into a large pool (Indian Bathtub), which now is virtually dry (compare Fig. 8b and 8c) as a result of water table decline. During a trip to the area on 23 June 1989, the following snail-positive localities were visited:

---

[1] Local endemism of this species appears likely. There are no historic records for the snail from extra-limital areas, and a helicopter survey of thermal springs in southwest Idaho and southeastern Oregon (Bruneau, Jarbridge, South Owyhee River basins) conducted during January 1987 did not reveal additional populations (S. M. Chambers, unpublished report, February 3, 1987; Hershler, personal observations on materials collected on this survey).

←

Fig. 6. Whole mounted penes of *P. bruneauensis*. a–e, Paratypes, USNM 860508 (a–c, dorsal, d, e, ventral aspects). f–i, USNM 860509 (dorsal aspects). The scale bar in "a" equals 1.0 mm. All other photographs are printed to the same scale except "e" (0.25 mm). Note the darkly pigmented filament and small area of glandular ridges in the distal penial lobe (particularly obvious in "e").

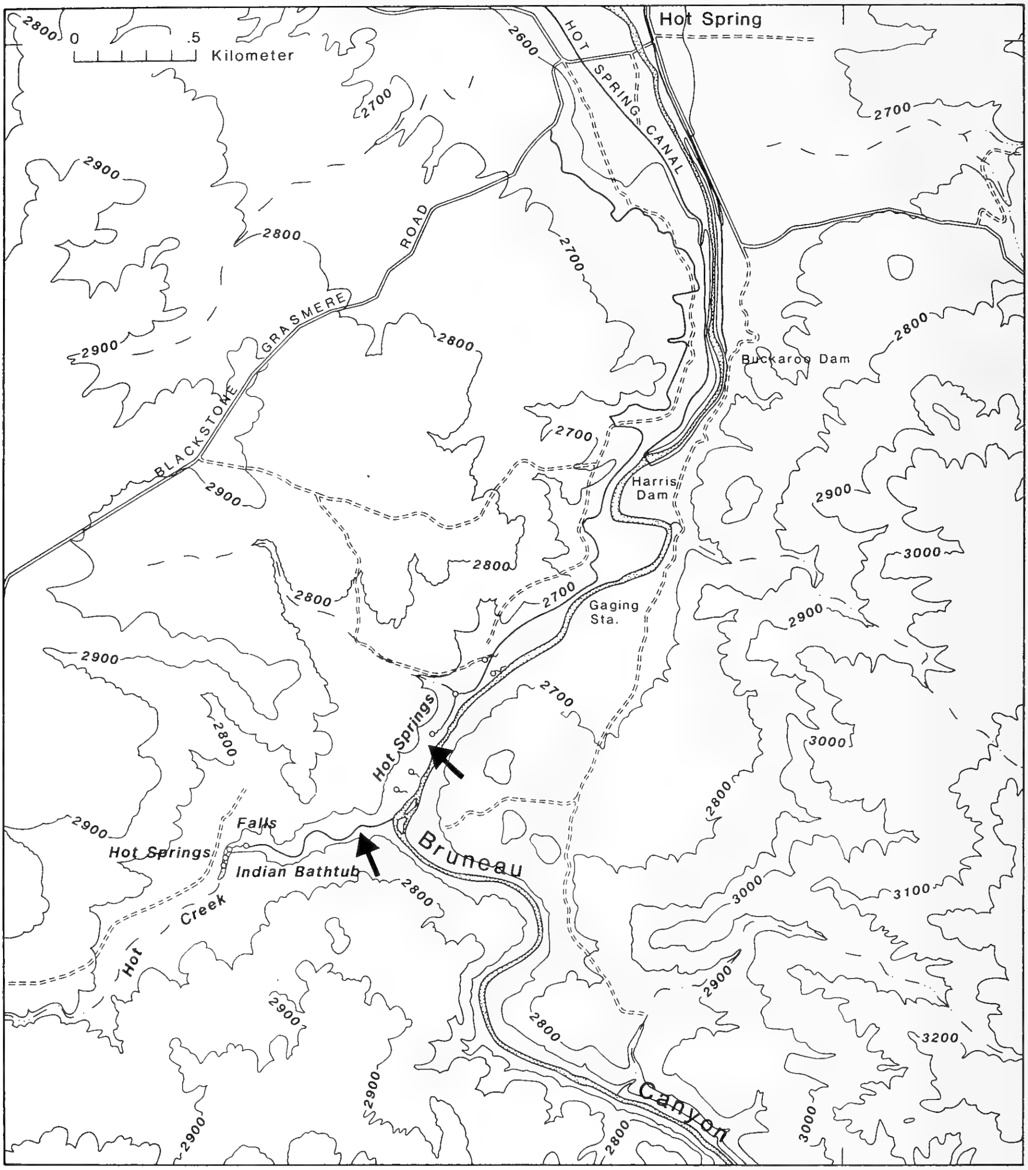


Fig. 7. Map showing collecting localities in Hot Creek area, Owyhee County, Idaho. Modified from USGS 1947 Hot Spring quadrangle (7.5 minute series [topographic]).

(a) Small (ca. 10 cm^2) seep on rock wall just above floor of Indian Bathtub. About four snails were observed (none collected) on the algal-covered drip wall (none found in small pool below).

(b) Small seeps emerging along base of low outcrop on the east side of lower Hot Creek. Snails were common just below spring orifices, on moistened ground covered by grass.

(c) A large (3–4 m high, 3 m across) drip wall on western side of Bruneau River downflow from Hot Creek confluence. Snails were extremely common on the wet, algal-

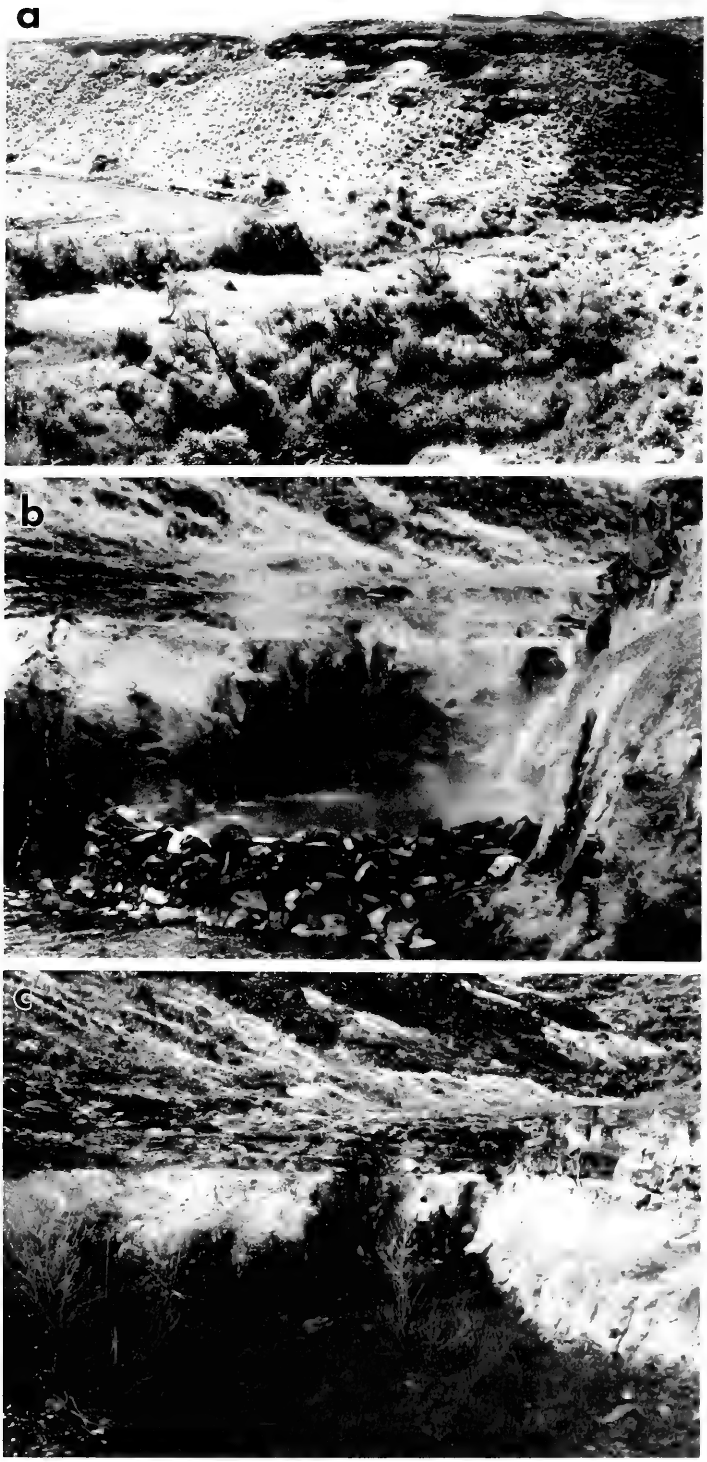


Fig. 8. Photographs of the Hot Creek area. a, Confluence of Hot Creek (to right) and Bruneau River, 9-20-89; b, Indian Bathtub under historic flow conditions, 11-73; c, Indian Bathtub and upper Hot Creek under recent flow conditions, 4-4-89.

covered walls and in a pool below. Snails have also been collected from small thermal spring vents along the east side of the river just upflow from the creek's confluence (P. Olmstead, pers. comm., June 1989).

Several basommatophoran pulmonates were found in association with *P. bruneauensis* in the spring brooks, and an unrelated hydrobiid, *Fluminicola* cf. *hindsi* (Baird), was collected at the confluence of Hot Creek and the Bruneau River.

Acknowledgments

Fieldwork was supported by funds provided by the United States Fish and Wildlife Service (contract to W. Minshall). Assistance in the field was provided by J. Gore (USFWS), P. Olmstead (BLM), G. W. Minshall, and C. T. Robinson. Scanning electron micrographs were taken and developed by W. Brown and S. Braden (NMNH Scanning Electron Microscopy Laboratory). Beth Fricano prepared histological sections and whole mounts. Paul Greenhall and M. Ryan (NMNH, Invertebrate Zoology) measured shells, and prepared line drawings and maps respectively. Peter Bowler and P. Olmstead provided habitat photographs. Useful criticism of the manuscript was provided by P. Bowler, J. Gore, G. W. Minshall, G. Mladenka, and P. Olmstead.

Literature Cited

Armantrout, N. B. 1985. Agency Report. Bureau of Land Management.—Proceedings of the Desert Fishes Council 13:34–37.

Hershler, R. 1989. Springsnails (Gastropoda: Hydrobiidae) of Owens and Amargosa (exclusive of Ash Meadows) River drainages, Death Valley System, California-Nevada.—Proceedings of the Biological Society of Washington 102:176–248.

Minckley, W. L., D. A. Hendrickson, & C. E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pp. 519–613 (+ bibliography) *in* C. H. Hocutt & E. O. Wiley, eds., The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, New York.

Taylor, D. W. 1982. Status report on Bruneau Hot Spring Snail.—Unpublished report submitted to United States Fish and Wildlife Service, Boise Endangered Species Field Office, Idaho, 14 pp.

———. 1985. Evolution of freshwater drainages and molluscs in western North America. Pp. 265–321 *in* C. J. Hocutt & A. B. Leviton, eds., Cenozoic history of the Pacific Northwest. AAAS & California Academy of Sciences, San Francisco, California.

United States Department of the Interior. 1984. Endangered and threatened wildlife and plants; review of invertebrate wildlife for listing as endangered or threatened species.—Federal Register 49:21664-21675.

———. 1985. Endangered and threatened wildlife and plants; proposed endangered status for the Bruneau Hot Spring Snail.—Federal Register 50: 33803–33805.

Waring, G. A. 1965. Thermal springs of the United States and other countries of the world—a summary.—United States Geological Survey Professional Paper 492:1–383.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 815–824

REDISCOVERY OF *TULOTOMA MAGNIFICA* (CONRAD) (GASTROPODA: VIVIPARIDAE)

Robert Hershler, J. Malcolm Pierson, and R. Stephen Krotzer

Abstract.—Recent reports have concluded that the monotypic viviparid snail genus *Tulotoma* Haldeman, 1840, once relatively widespread in lotic waters of the Coosa-Alabama River System, is extinct or reduced to one or two small colonies at most. The authors conducted an extensive survey for the snail during 1988–1989 and discovered five populations in shoal habitat of the Coosa River and its larger tributaries. These populations are separated by unsuitable snail habitat consisting of reaches of impounded river and probably are not in genetic contact with one another.

The genus *Tulotoma* (type species, *Paludina magnifica* Conrad, 1834) is one of many aquatic mollusks endemic to the Coosa-Alabama River System. *Tulotoma magnifica* (commonly known as the tulotoma) is a particularly impressive snail, with a large (>25 mm tall) shell usually ornamented with prominent, spirally arranged knobs (Fig. 1). The genus was erected by Haldeman in 1840 and includes four species described (as *Paludina*) between 1834–1841. While early workers usually recognized at least two of these species (see Wetherby 1877), most recent authors (e.g., Clench 1962, Burch 1982) considered the genus to be monotypic. Note, however, that Patterson (1965) documented differences in chromosome numbers between two tulotoma populations and suggested that several species may be involved.

The historic distribution of the tulotoma, based on examination of various museum collections, is shown in Fig. 2. In the Coosa River System of Alabama, the snail ranged widely from Big Canoe Creek south to Wetumpka, just above the confluence with the Tallapoosa River. Localities included numerous sites on the Coosa River as well as lower reaches of several large tributaries. The snail has been recorded from only two localities in the Alabama River System: the main river in the vicinity of Claiborne (type locality for *T. magnifica*), and Chilatchee Creek southwest of Selma. Records from waters apart from the above are doubtful, in some cases because the material was from Indian middens and probably was transported from original localities (e.g., Black Warrior River records; Clench 1962), and in other cases because the localities are well separated from the general range of the snail and have not been verified by later collecting (e.g., Bridgeport, Jackson Co.; Patsaliga Creek, Crenshaw Co.).

The biology of the tulotoma is virtually unknown, apart from the fact that it broods young and filter-feeds (as do other members of the Viviparidae). Early descriptions indicated that the tulotoma inhabited riffles and shoals, clinging tightly to the undersides of large rocks. Local abundance was common: Hinkley (1904:43) noted that in the Coosa River, "They were generally in colonies; it was not uncommon to find 20 or 30 under a single stone a foot square or more."

Modifications of the Coosa-Alabama River System have been extensive since the description of the tulotoma in 1834. Six major dams were completed along the Coosa River in Alabama between 1914 and 1966, resulting in impoundment of much of the river and lower portions of tributaries. Pol-

Fig. 1. Shells of *Tulotoma magnifica* (Conrad): to left, USNM 858098, Kelley Creek, St. Clair County, Alabama (27.2 mm tall); to right, USNM 858097, Coosa River above Wetumpka, Elmore County, Alabama (22.2 mm).

lution of this drainage also has been on the increase, due to introduction of waste waters of various municipalities (Hurd 1974). Dredging of the Alabama River channel began in 1878 and continues to the present day. Locks and dams on that river were completed in the 1960s.

Decline of the tulotoma has been evident for at least 50 years. The snail no longer could be found at Claiborne by the mid-1930s (Goodrich 1944, Clench 1962), nor has it been found elsewhere in Alabama River drainage in the past 50 years. Reduction of numbers (of all prosobranch snails) in the Coosa River was obvious by 1944, as summarized by Goodrich (1944:1–2):

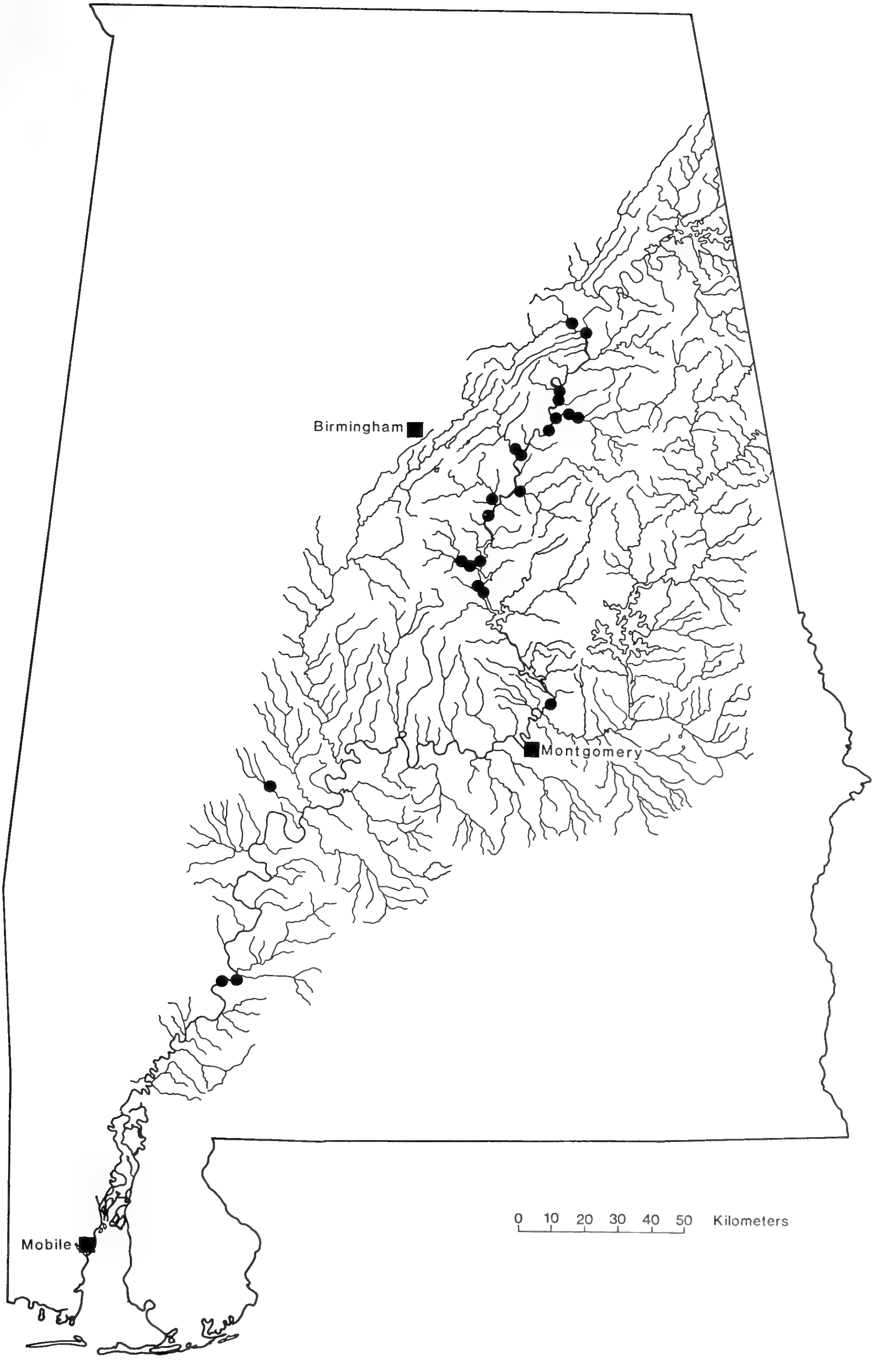
> "For the waters have been backed up behind great dams, miles of reefs are covered and formerly quiet reaches between rapids have been expanded into silt-accumulating lakes. At the foot of the lowermost dam are remains of the old Wetumpka rapids, but I have been told that ten to fifteen feet of water [actually 1–2 m depending on number of turbines operating; Pierson, personal observation] rush over them in the hours that the dynamos are operating. Moreover, upstream sections which once ran clear, Rome to Cedar Bluff, for example, are turbid with field wash, even in a dry August, and one gets specimens, if any, by feeling for them."

The last live collections of the tulotoma were those of Herbert Athearn (*in* Stein 1976), who located three populations in upper Coosa River drainage between 1955–1963 (before completion of Logan Martin Dam), and U.S. Army Corps of Engineers (1981), which found a single live individual in Lay Reservoir below Kelley Creek. Recent reports concluded that the snail is now either extinct or consists of only one or two remaining colonies (Heard 1970, Davis 1974, Stein 1976). The snail currently is a candidate for possible addition to the List

---

→

Fig. 2. Historic distribution of *Tulotoma magnifica.* Map modified from United States Geological Survey 1:500,000 State of Alabama sheet (1970 edition). Filled circles indicate a single or two or more closely spaced localities.


Birmingham
Montgomery
Mobile
0 10 20 30 40 50 Kilometers

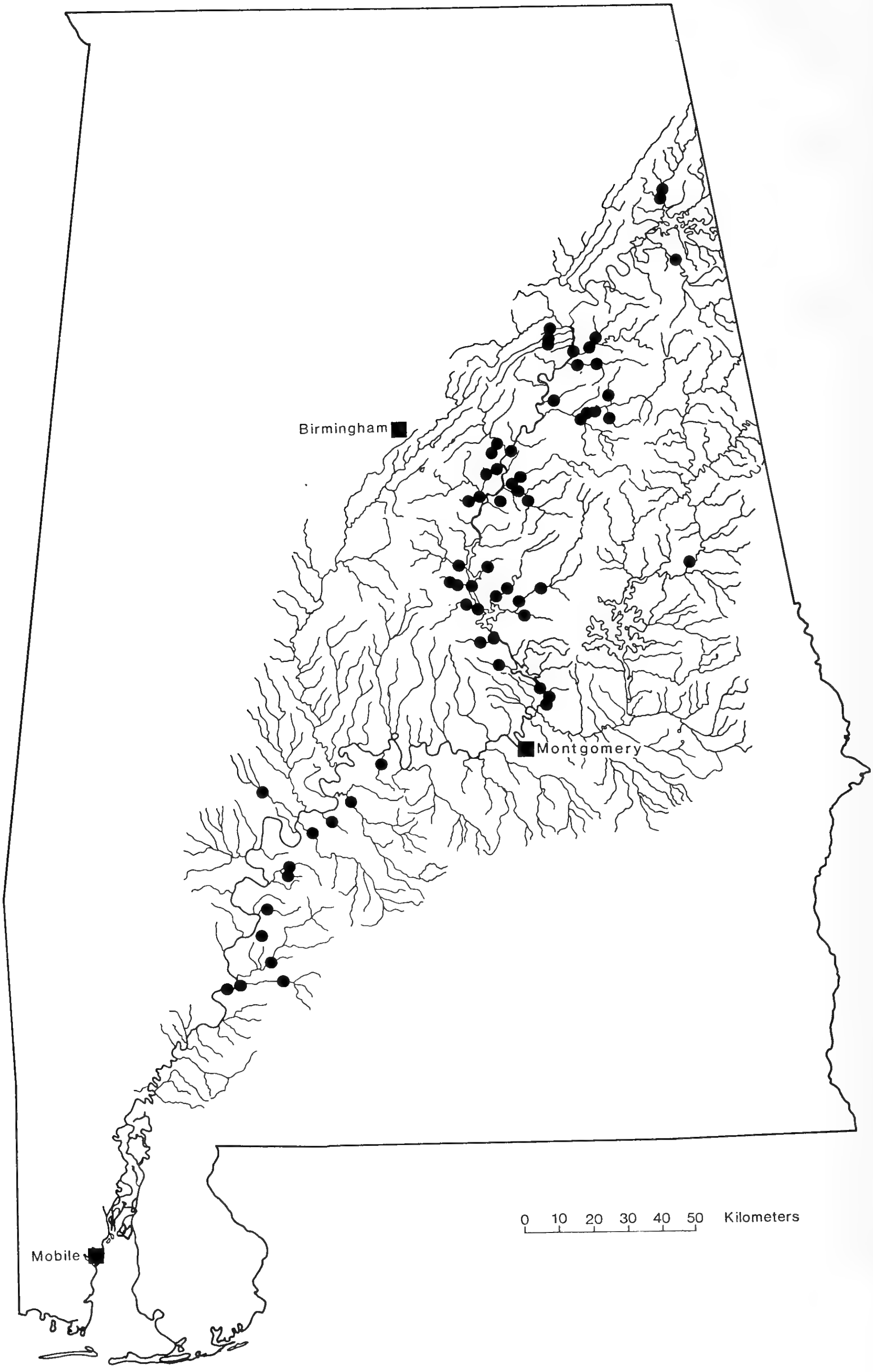


Fig. 3. Localities surveyed (descriptions in Appendix).

of Endangered and Threatened Wildlife (USDI 1989).

During 1988–1989 the authors conducted a field survey for the tulotoma, principally in the Coosa basin, and discovered several live populations, which are reported below. A redescription of this remarkable snail will be published elsewhere.

Methods

Sites visited included those where the tulotoma had been found previously as well as other locales within the historic range of the species. Large tributary creeks and rivers were visited, usually at road crossings. In a number of instances, sites were considered unsuitable for the snail based on scrutiny from bridges and search was not conducted. At potentially suitable sites (e.g., ones in which riffles were present), search was conducted by two or three people, who examined surfaces (particularly undersides) of rocks for time periods of 15 minutes to 3 hours. Boats occasionally were used to reach sampling sites and diving was necessary to gather and/or examine stones from deep water.

Results

Seventy-eight sites (Appendix 1, Fig. 3) were visited, of which fifty-four were intensively searched. The tulotoma was found living in five areas (Fig. 4), which are described below:

1) Ohatchee Creek, Calhoun County: Snails were found in a small shoal several kilometers upstream from the creek's mouth. Substrate consisted of slabs, ledges, and sharp, angular boulders. Snails were rare (six individuals collected) on medium-sized boulders in moderate current. The species was not found at two sites upstream from the above.

2) Kelley Creek, St. Clair County: Snails were collected at various points along a two km section of the moderate-sized stream (generally <1.5 m deep and 8 m wide) beginning at the boat landing about a hundred meters above the mouth (and upstream to SW ¼ sec. 29, T 18S, R 3E). The creek bottom was muddy, and stones were uncommon except in riffles. Snails were found throughout this area but were particularly common in a long riffle zone above the first bridge crossing (border of secs. 29, 32), where up to 20–30 snails were found on single large stones. The stream was subject to a rapid rise in water level when Logan Martin Dam was generating, during which time snails had to be collected by diving for stones. Snails were not found in the Coosa River at or near the mouth of the creek (but note the 1981 Corps of Engineers record cited above).

3) Weogufka Creek, Coosa County: Snails were found commonly in the first set of shoals (rocky bottom, no silt) above Mitchell Reservoir.[1] The tulotoma was much less abundant at two sites 3–4 km above the mouth of creek where fewer than 20 individuals were found after almost 2 hours of searching. At the latter sites the stream was fairly small (3–5 m across, <1 m deep) and predominantly riffle, with the bottom densely littered with small rounded stones covered with green algae. Snails were absent at one site upstream from the above.

4) Hatchet Creek, Coosa County: Snails were found commonly (50–60 individuals on a single large rock) in fast shoals at the lower end of the creek E-NE of Kelly's Crossroads.[1] Snails also were found in the creek ca. 3 km upstream from the confluence with Swamp Creek (ca. 6 km upstream from Mitchell Lake). At this site the creek was about 7 m across and had both short riffles and large pooled areas. Snails were rare: only 6 individuals were collected in 30 minutes. Snails were absent at a site upstream from the above.

---

[1] R. G. Bowker, United States Fish and Wildlife Service (Jackson Field Office) reported finding the tulotoma at the beginning of reservoir influence on both Weogufka and Hatchet Creeks in October, 1989 (letter to RH, 10-23-89).

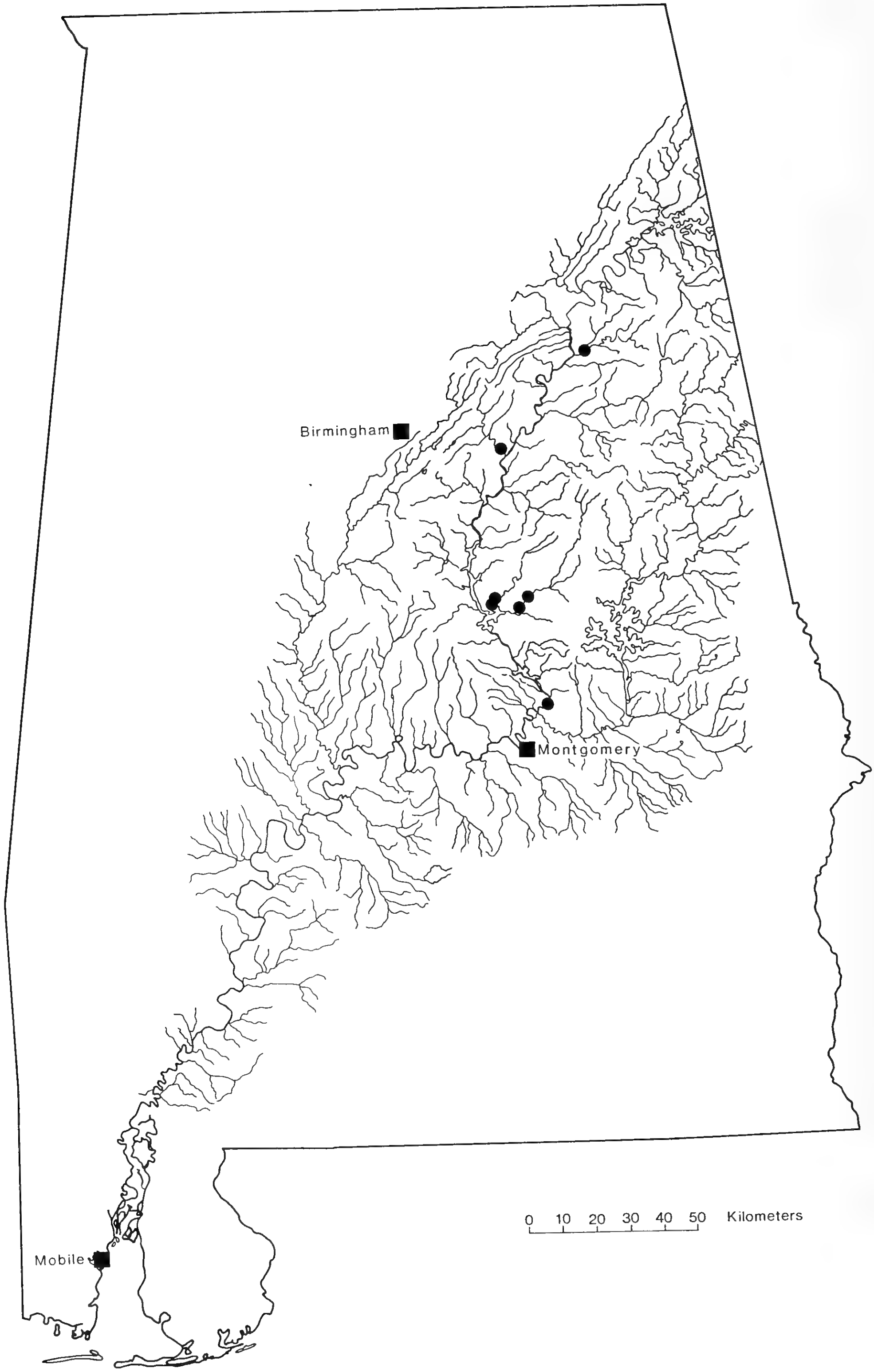


Fig. 4. Current distribution of *Tulotoma magnifica.*

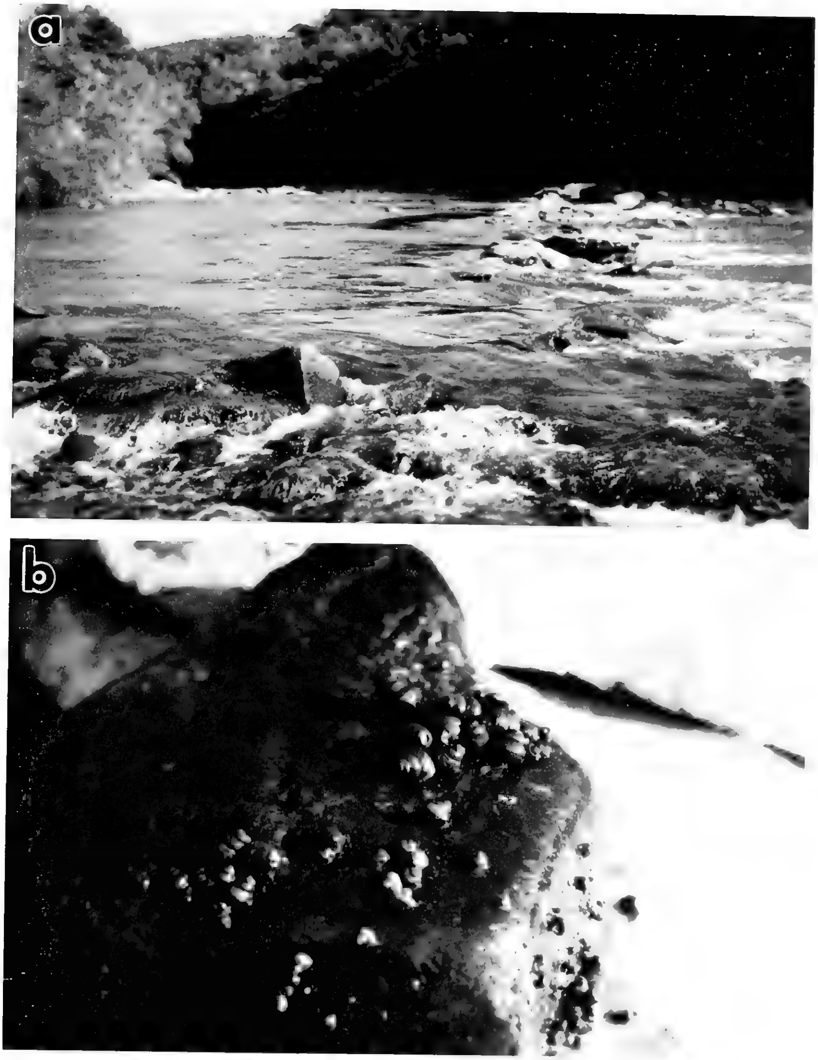


Fig. 5. Photographs of tulotoma site on Hatchet Creek, Coosa County, Alabama: a, snail-bearing shoals; b, underside of large stone showing clustered snails.

5) Coosa River, between Jordan Dam and Wetumpka, Elmore County: The river is free-flowing for at least the upper portion of this area and contains a series of impressive shoals. Snails were collected from two such areas separated by 2–3 km. In both sites the river was constricted by a complex of small islands through which the water rushes. The bottom was gravel-sand and was littered with stones of various sizes. Snails were very common on rocks in narrow riffle areas (up to 40–50 specimens/large stone) and less numerous in pooled areas. During normal daily generation from one turbine (4400 cfs for 2.25 hours) the water level would rise a maximum of 1 m at Moccasin Shoal. Maximum turbine discharge at full gate (21,000 cfs) would raise the river level about 2 m at this location (a very rare event). Snails were absent both from a shoal about

1 km upstream from the above, and downstream at Wetumpka.

Associated molluscan fauna at the above sites included diverse pleurocerid snails and unionid clams, and *Corbicula*.

Discussion

A synthesis of results of this survey and available literature allows a general interpretation of the habitat requirements of the tulotoma. The snail is restricted to cool, well-oxygenated, clean water in free-flowing river and lower portions (ca. lowermost 4–5 km) of large tributary streams (Fig. 5a). The tulotoma never has been recorded from upper reaches of tributaries: perhaps such habitat is unsuitable owing to its small size and/or adverse physiochemical conditions (e.g., softer water compared to downstream). The animal clings to undersides of submerged large stones (which usually rest on hard bottoms), with individuals densely clustered rather than uniformly distributed (Fig. 5b). Densities are highest in riffles or shoals, although snails also occur in pooled areas. Although the tulotoma can tolerate diurnal variation in hydrologic variables (as seen in the Kelley Creek population), continued persistence of the snail in waters where such variation is extreme (as in the river immediately below a dam) appears unlikely.

Perusal of the historic and current distribution maps indicates that a drastic reduction of the tulotoma's range has occurred over the past 150 years (compare Figs. 2 and 4). The snail now is apparently extinct in the Alabama River system and restricted to several km of free-flowing Coosa River below Jordan Dam and short sections of four large creeks tributary to the river. These populations are isolated by reaches of unsuitable tulotoma habitat (impounded river) that are quite long, with the exception of Weogufka and Hatchet Creeks (which discharge into Mitchell Lake at points separated only by a few km), and probably are not in genetic contact with one another. The largest population appears to be that of the Coosa River below Jordan Dam where some tens of thousands of individuals occur. Much of the range reduction can be attributed to unequivocal habitat destruction associated with impoundment of a large portion of the Coosa River in Alabama.

Acknowledgments

Hershler's fieldwork was funded by a contract from the United States Fish and Wildlife Service (Cooperative Agreement No. 14-16-004-87-931). Assistance in the field was provided by H. Athearn, A. Gerberich, P. Greenhall, J. Lochamy, C. Norquist, J. Stewart, and E. Tyberghein. Victor Krantz prepared shell photographs, and M. Ryan and K. Flamer drafted the map.

Literature Cited

Burch, J. B. 1982. North American freshwater snails. Identification keys, generic synonymy, supplemental notes, glossary, references, index.—Walkerana 4:217–365.

Clench, W. J. 1962. A catalogue of the Viviparidae of North America with notes on the distribution of *Viviparus georgianus* Lea.—Occasional Papers on Mollusks, Museum of Comparative Zoology 2:261–287.

Davis, G. M. 1974. Report on the rare and endangered status of a selected number of freshwater gastropods from southeastern U.S.A.—Report to U.S. Department of Interior Fish and Wildlife Service, Contract 14-16-0008-766.

Goodrich, C. 1944. Certain operculates of the Coosa River.—Nautilus 58:1–10.

Heard, W. H. 1970. 3. Eastern freshwater mollusks (II). The South Atlantic and Gulf drainages.—Malacologia 10:23–27.

Hinkley, A. A. 1904. List of Alabama shells collected in October and November, 1903.—Nautilus 18:37–45.

Hurd, J. 1974. Systematics and zoogeography of the unionacean mollusks of the Coosa River drainage of Alabama, Georgia, and Tennessee.—Unpublished Ph.D. dissertation, Auburn University. 240 pp.

Patterson, C. M. 1965. The chromosomes of *Tulotoma angulata* (Streptoneura: Viviparidae).—Malacologia 2:259–265.

Stein, C. B. 1976. Gastropods. Pp. 1–41 *in* H. Boschung, ed., Endangered and threatened plants and animals of Alabama. Bulletin Alabama Museum of Natural History 2.

United States Army Corps of Engineers. 1981. Montgomery to Gadsden Coosa River channel, Alabama. Design memorandum 1. Volume 5. Appendix V—Environmental Systems (EIS Appendix C—Part 2).

United States Department of the Interior. 1989. Endangered and threatened wildlife and plants; animal notice of review.—Federal Register 54:554–579.

Wetherby, A. G. 1877. Review of the genus *Tulotoma,* with remarks on the geographical distribution of the North American Viviparidae—Quarterly Journal of Conchology 11:207–215.

(RH) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (JMP, RSK) G.S.C. #8, Alabama Power Company, Post Office Box 2641, Birmingham, Alabama 35291.

Appendix

Localities surveyed. Data include topographic coordinates and date of visitation. Positive localities are indicated by an asterisk.

ALABAMA. Autauga County: Shoal Creek, State HW 143 (crossing), T 20N, R 16E, SW ¼ sec. 27, 6-2-88.

Calhoun County: Coosa River below Neely Henry Dam, 3.2 km SW of Ohatchee, T 14S, R 6E, SE ¼ sec. 31, 10-11-88.—Ohatchee Creek: N of State HW 62, T 14S, R 6E, SW ¼ sec. 27, 9-20-89; State HW 62, T 14S, R 6E, SW ¼ sec. 27, 6-6-88; *1.9 km S of Ohatchee, T 14S, R 6E, SE ¼ sec. 33, 10-11-88.—Cane Creek: State HW 77, T 15S, R 6E, SW ¼ sec. 18, 9-20-89; County Road 73, T 15S, R 5E, SW ¼ sec. 13, 9-20-89.

Cherokee County: Little River: State HW 35, T 7S R 10E, SE ¼ sec. 30, 6-4-88; State HW 273, 8.8 km NW of Cedar Bluff, T 9S, R 9E, NE ¼ sec. 3, 10-13-88.—Terrapin Creek: 0.6 km S of Ellisville, T 11S, R 9E, SW ¼ sec. 20, 10-13-88; NW of Providence Church, T 11S, R 9E, SE ¼ sec. 34, 9-20-89.

Chilton County: Coosa River, Lay Dam tailrace, T 23N, R 15E, NW ¼ sec. 24, 10-11-88.—Yellowleaf Creek: Crossing S of Page Creek confluence, T 23N, R 15E, SW ¼ sec. 22, 9-13-88; Crossing N of Lime Springs Church, T 23N, R 15E, NE ¼ sec. 20, 9-13-88; 1.6 km SW of Lay Dam, T 23N, R 15E, SW ¼ sec. 25, 10-5-88.—Walnut Creek: County Road 32, T 22N, R 15E, SE ¼ sec. 14, 9-18-89; 10.9 km E-NE of Clanton, T 22N, R 16E, NE ¼ sec. 19, 10-5-88.—Chestnut Creek: State HW 3 at Verbena, T 21N, R 15E, SE ¼ sec. 36, 6-2-88; 8.0 km E-NE of Verbena, T 21N, R 16E, NE ¼ sec. 35, 10-6-88.

Coosa County: Paint Creek, 3.2 km S-SE of Marble Valley, T 24N, R 16E, SE ¼ sec. 35, 10-11-88.—Weogufka Creek: NW of Moriah, T 23N, R 17E, NE ¼ sec. 34, 6-3-88, 10-3-88; *Horse Stomp Campground, T 22N, R 17E, SE ¼ sec. 6, 9-18-89; *Crossing SW of above, T 22N, R 17E, NW ¼ sec. 7, 9-18-89; *First shoals above Mitchell Reservoir, T 22N, R 16E, SE ¼ sec. 13, 10-6-88.—Hatchet Creek, 9-18-89: US 231, T 23N, R 19E, SE ¼ sec. 30, 9-18-89; *SE of Lyle, T 22N R 18E, NW ¼ sec. 19, 9-18-89; *3.7 km N-NE of Kelly's Crossroads, T 22N, R 17E, NW ¼ sec. 25, 10-7-88.—Swamp Creek: State HW 22, T 22N, R 18E, SE ¼ sec. 30, 9-18-89; County Road 29, 2.4 km N of Kelly's Crossroads, T 22N, R 17E, SW ¼ sec. 25, 10-27-88.

Dallas County: Soapstone Creek, US 80, T 16N, R 12E, NW ¼ sec. 31, 6-3-88.—Cedar Creek, State HW 41, T 14N, R 10E, NE ¼ sec. 14, 6-3-88.—Oak Creek, State HW 41, T 13N, R 10E, SW ¼ sec. 8, 6-3-88.

Elmore County: Coosa River: Just below Jordan Dam, T 19N, R 18E, NE ¼ sec. 22, 6-2-88; Shoal ca. 1 km below dam, T 19N, R 18E, SE ¼ sec. 22, 9-14-88; *Moccasin Shoal, ca. 5 km upstream from Wetumpka, T 18N, R 18E, NE ¼ sec. 2, 9-18-89; *Ca. 2.5 km upstream from Wetumpka, T 18N, R 19E, NE ¼ sec. 7, 9-14-88; Vicinity of Wetumpka boat ramp, T 18N, R 19E, NE ¼ sec. 24, 9-14-88.

Monroe County: Tallahatchee Creek, State HW 41, T 10N, R 7E, NE ¼ sec. 20, 6-3-88.—Beaver Creek, State HW 41, T 9N, R 6E, NE ¼ sec. 24, 6-3-88.—Big Flat Creek, State HW 41, T 7N, R 6E, NE ¼ sec. 1, 6-3-88.—Alabama River, 9-14-88: Base of limestone bluff on west side of river, ca. 3.0 km below Claiborne Lock and Dam, T 7N, R 5E, SE ¼ sec. 11; ca. 1.6 km below Claiborne-Murphy Bridge, T 7N, R 5E, NE ¼ sec. 26.—Limestone Creek: State HW 41, T 7N, R 7E, NE ¼ sec. 22, 6-3-88; from mouth to ca. 0.5 km upstream, T 7N, R 6E, SE ¼ sec. 19, 9-14-88.

St. Clair County: Big Canoe Creek, US 231, T 14S, R 4E, SE ¼ sec. 6, 6-4-88.—Beaver Creek, US 231, T 14S, R 3E, NE ¼ sec. 36, 6-4-88.—Shoal Creek, US 231, T 15S, R 3E, SE ¼ sec. 1, 6-4-88.—Coosa River, ca. 0.8 km below Logan Martin Dam, T 18S, R 3E, SW ¼ sec. 33, 9-12-88.—Kelley Creek: *E-NE of Logan Martin Dam substation (upstream from crossing), T 18S, R 3E, SW ¼ sec. 29, 9-21-88, 9-13-89; *Kelley Creek Landing, T 19S, R 3E, NE ¼ sec. 6, 9-12-89; Mouth, T 19S, R 3E, NW ¼ sec. 5, 9-12-89.

Shelby County: Stream tributary to Kelley Creek, W-SW of Macedonia Church, T 18S, R 2E, SE ¼ sec.

23, 6-1-88.—Spring Creek N of Vincent, T 19S, R 2E, SW ¼ sec. 11, 6-1-88.—Morgan Creek NW of Klein, T 20S, R 2E, SE ¼ sec. 17, 6-1-88.—Yellowleaf Creek: State HW 25, T 20S, R 2E, SE ¼ sec. 29, 6-1-88; 6.1 km S-SW of Harpersville, T 20S, R 2E, NE ¼ sec. 18, 10-4-88.—Fourmile Creek, County Road 441, T 20S, R 2E, SE ¼ sec. 30, 6-1-88.—Waxahatchee Creek: 4.8 km S-SW of Shelby, T 24N, R 15E, SE ¼ sec. 7, 10-11-88; State HW 145 S of Shelby, T 24N, R 15E, SE ¼ sec. 20, 6-1-88.

Talladega County: Blue Eye Creek, State HW 77, T 16S, R 5E, SW ¼ sec. 22, 6-6-88.—Eastaboga Creek, in Old Eastaboga, T 16S, R 6E, SW ¼ sec. 33, 6-6-88.—Choccolocco Creek: County Road 399, T 17S, R 6E, NW ¼ sec. 15, 9-19-89; 2.9 km S of Old Eastaboga (near Brick Store Church), T 17S, R 6E, SW ¼ sec. 9, 10-27-88; County Road 5, T 17S, R 6E, SW ¼ sec. 17, 9-19-89; Lower end of Jackson Shoals, T 17S, R 5E, SW ¼ sec. 14, 6-1,4-88, 9-21-88.—Cheaha Creek, County Road 5, T 17S, R 6E, SW ¼ sec. 20, 10-27-88, 9-19-89.—Coosa River, east bank below Logan Martin Dam, T 18S, R 3E, NW ¼ sec. 33, 9-28-88.—Talladega Creek: 5.6 km N-NE of Childersburg, T 20S, R 3E, NE ¼ sec. 3, 9-28-88; At Kymulga, T 19S, R 3E, center of sec. 35, 9-19-89.—Tallasseehatchee Creek: County Road 105, T 20S, R 4E, SE ¼ sec. 30, 9-19-89; N-NW of Friendship Church, T 20S, R 3E, SE ¼ sec. 14, 9-19-89; 3.8 km E-NE of Childersburg, T 20S, R 3E, sec. 22, 9-28-88.—Kahatchee Creek, 6.6 km SW of Childersburg, T 21S, R 2E, NW ¼ sec. 2, 10-4-88.

Tallapoosa County: Tallapoosa River, 10.7 km S-SW of Daviston, T 23N, R 24E, SE ¼ sec. 19, 9-27-88.

Wilcox County: Pine Barren Creek, State HW 41, T 13N, R 9E, SW ¼ sec. 28, 6-3-88.—Pursley Creek, State HW 41, T 11N, R 7E, NE ¼ sec. 2, 6-3-88.—Gravel Creek, State HW 41, T 11N, R 7E, NW ¼ sec. 22, 6-3-88.—Chilatchee Creek, Alberta, T 15N, R 7E, SE ¼ sec. 30, 9-15-88.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 825–838

NEW SPECIES AND NEW RECORDS OF SCALED POLYCHAETES (POLYCHAETA: POLYNOIDAE) FROM THE AXIAL SEAMOUNT CALDERA OF THE JUAN DE FUCA RIDGE IN THE NORTHEAST PACIFIC AND THE EAST PACIFIC OCEAN OFF NORTHERN CALIFORNIA

Marian H. Pettibone

Abstract.—A new species of *Harmothoe globosa* from the Axial Seamount Caldera on the Juan de Fuca Ridge is described. Polynoids from the Gorda Ridge off northern California include *Harmothoe gordae,* new species, in Harmothoinae, from Wood Island; *Parabathynoe brisinga,* new genus, new species, in Arctonoinae, commensal with a brisingid asteroid; *Lepidonotopodium piscesae,* new record, in Lepidonotopodinae; *Levensteiniella kincaidi,* new record, and *L. intermedia,* new species, in Macellicephalinae; and *Branchinotogluma grasslei* and *Opisthotrochopodus tunnicliffeae,* new records, in Branchinotogluminae.

A new species of *Harmothoe* (Subfamily Harmothoinae) has been discovered from fresh basalts up to 100 meters from the hydrothermal vents in the Axial Seamount Caldera of the Juan de Fuca Ridge, collected by DSRV *Alvin.* An additional seven species of polynoids were collected on the Gorda Ridge off northern California by DSRV *Alvin* and in the northern Escanaba Trough of the Gorda Ridge by DSRV *Sea Cliff.* The seven species from the Gorda Ridge include a new species of *Harmothoe*; a new genus and new species (Subfamily Arctoninae) commensal with a brisingid asteroid; new records of *Lepidonotopodium piscesae* (Subfamily Lepidonotopodiinae); a new species of *Levensteiniella* and new records of *L. kincaidi* (Subfamily Macellicephalinae); and new records of *Branchinotogluma grasslei* and *Opisthotrochopodus tunnicliffeae* (Subfamily Branchinotogluminae).

The specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM) and the Scripps Institution of Oceanography (SIO).

Subfamily Harmothoinae Willey, 1902

Genus *Harmothoe* Kinberg, 1856

Harmothoe globosa, new species

Figs. 1, 2

Material examined.—Northeast Pacific, Axial Seamount Caldera, Juan de Fuca Ridge, 45°58′N, 130°03′W, 1570 m, DSRV *Alvin* dive 2087, 15 Aug 1988, from fresh basalts, up to 100 m from hydrothermal vents, holotype (USNM 123368).

Description.—Length of holotype 32 mm, width with setae 12 mm, segments 41, last one minute. Body flattened ventrally, arched dorsally, tapering slightly anteriorly and more so posteriorly, with long parapodia nearly as long as body width. Middorsum brownish with 2 light transverse ciliated bands per segment between bases of elytrophores and dorsal tubercles (Fig. 1A, C). Elytra 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, and 32. Elytra round, subreniform to oval, large, overlapping, covering dorsum, rather thick stiff, with most of surface covered with conical

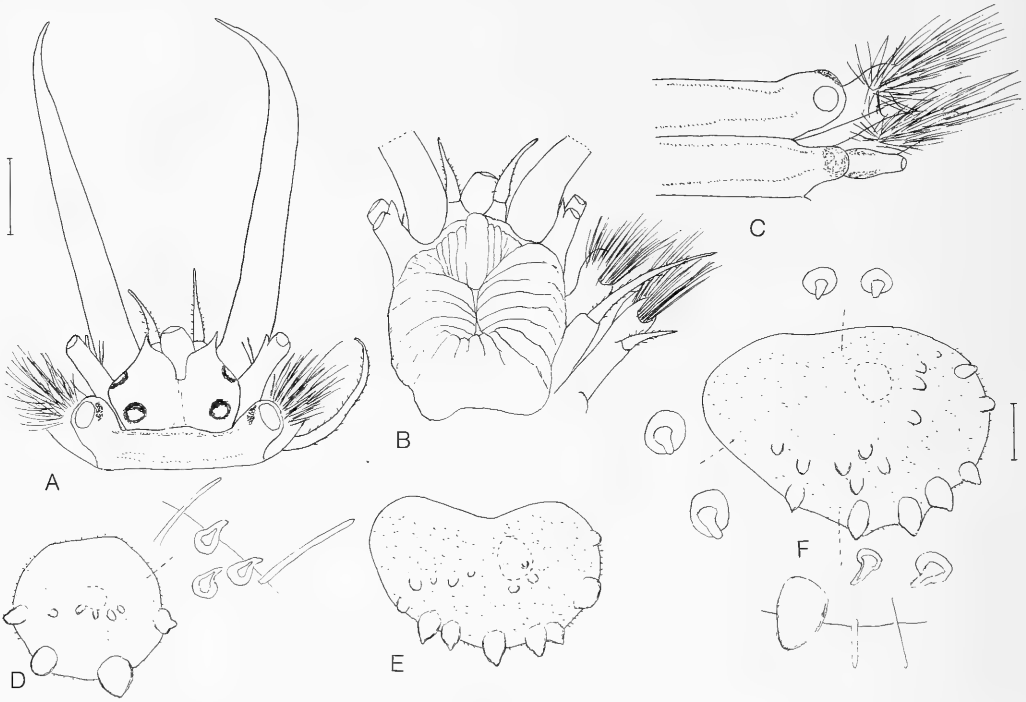


Fig. 1. *Harmothoe globosa,* holotype, USNM 123368: A, Dorsal view of anterior end, styles of median antenna, dorsal and ventral tentacular cirri missing; B, Same, ventral view, right side and palps only partially shown; C, Dorsal view of right half of segments 5 and 6, style of dorsal cirrus on segment 6 missing; D, Right 1st elytron from segment 2, with detail of microtubercles and papillae; E, Right 2nd elytron from segment 4; F, right middle elytron, with detail of macrotubercle, microtubercles and papillae. Scales = 1.0 mm for A–C; 1.0 mm for D–F.

microtubercles, bare region near anteromedial side; additional baloonlike, bulbous macrotubercles with nipple-like tips emerging from wide bases near posterior and lateral borders plus smaller oval macrotubercles on middle part, and some scattered delicate papillae on border and surface (Fig. 1D–F). Elytrophores large, bulbous, reddish glandular area on anterior side (Figs. 1A, C, 2A). Dorsal cirri on segments without elytra; cirrophores long, cylindrical, on posterior sides of notopodia, wider basally and enclosing anterior and posterior reddish glandular areas; styles long, tapering distally, extending beyond setae, with delicate clavate papillae; dorsal tubercles nodular, enclosing reddish glandular areas (Figs. 1C, 2B) smaller from segment 24, indistinct on 9 posterior cirrigerous segments.

Prostomium bilobed, wider than long, with distinct cephalic peaks including delicate tips; median antenna with large cylindrical ceratophore in anterior notch, style missing (probably long); ceratophores of lateral antennae small, inserted ventrally and converging midventrally, with short, subulate, papillate styles; eyes large, anterior pair of anterolateral just anterior to widest part of prostomium, posterior pair posterodorsal; palps stout, long, tapered, minutely papillate (Fig. 1A, B). First segment not distinct dorsally; tentaculophores lateral to prostomium, each with small acicular lobe, 2 setae on inner side, and pair of dorsal and ventral tentacular cirri with styles missing (probably long, similar to buccal cirri); distinct ventrally forming anterior and lateral lips of ventral mouth, with facial ridge but

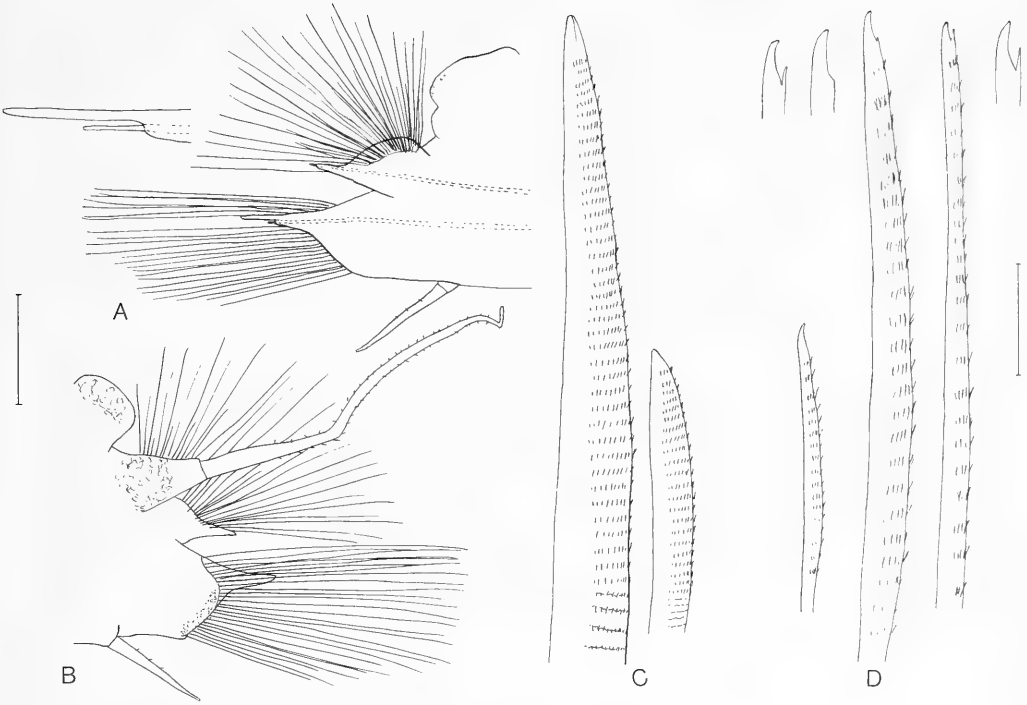


Fig. 2. *Harmothoe globosa,* holotype USNM 123368: A, Right elytrigerous parapodium, anterior view, acicula dotted, with detail of neuropodial supraacicular process; B, Right cirrigerous parapodium, posterior view; C, Long and short notosetae; D, Lower and upper subacicular and supraacicular neurosetae, with detail of tips. Scales = 1.0 mm for A, B; 0.1 mm for C, D.

without distinct facial tubercle (Fig. 1A, B). Second or buccal segment with small nuchal lobe, first pair of large elytrophores, well-developed, biramous parapodia, and long, papillate buccal cirri, and forming posterior lip of ventral mouth (Fig. 1A, B). Pharynx not extended and not examined; dark color of pharynx visible through delicate integument.

Biramous parapodia with both rami well developed, with acicular processes sharply pointed and tips of acicula projecting; notopodium shorter than neuropodium, rounded, with acicular process on lower side; neuropodium with conical presetal acicular lobe, long digitiform supraacicular process and shorter rounded postsetal lobe with reddish glandular area on distal part (Fig. 2A, B). Notosetae very numerous, forming radiating bundle, stouter than neurosetae, of 3 lengths, shorter, curved and longer nearly straight, with numerous rows and tapered blunt bare tips, some of longest ones showing faint longitudinal groove (Fig. 2C). Neurosetae very numerous, forming fan-shaped bundle, with numerous spinous rows; supraacicular neurosetae more slender than subacicular ones; mostly showing delicate secondary tooth or indication of one; lower ones with entire tips (Fig. 2D). Ventral cirri short, tapering, with small clavate papillae (Fig. 2A, B).

Pygidium small, with dorsal anus medial to last pair of parapodia, with pair of anal cirri (styles missing). Nephridial papillae beginning on segment 6, small, oval, on lateral side of rounded, inflated area.

Etymology.—Named *globosa,* referring to the globular macrotubercles on the elytra.

Remarks.—The unusual baloonlike mac-

Table 1.—Comparison of *Harmothoe globosa,* new species and *H. macnabi* Pettibone.

	Harmothoe globosa	*Harmothoe macnabi*
Elytral macrotubercles	balloonlike, near border and on surface (Fig. 1D–F)	extensions on posterior border (Pettibone 1985c, Fig. 6C)
Prostomium	large cephalic peaks; 2 pairs of large eyes (Fig. 1A)	small cephalic peaks; without eyes (Pettibone 1985c, Fig. 6A)
Tentaculophore	with 2 setae (Fig. 1A)	with 6–8 setae (Pettibone 1985c, Fig. 6A, B)
Neuropodial presetal acicular lobe	with well-developed supraacicular process (Fig. 2A)	without supraacicular process (Pettibone 1985c, Fig. 7B)

rotubercles found on the elytra of *Harmothoe globosa* suggest a greater development of the macrotubercles than those found on *H. macnabi* Pettibone (1985c:749, figs. 6, 7), described from the Galapagos Rift in the East Central Pacific. The two species differ as shown in Table 1.

Harmothoe gordae, new species
Fig. 3

Material.—East Pacific Ocean off northern California, Gorda Ridge, *Alvin* dive 2034, 4 Jun 1988, 41°00′N, 127°29′W, 3362 m, Wood Island, holotype (USNM 123367).

Description.—Length of holotype (male with sperm) 17 mm, width with setae 9 mm, segments 36, last one minute. Body flattened dorsoventrally, tapering slightly anteriorly and posteriorly, with long parapodia nearly as long as body width, without color. Elytrophores 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, and 32, large, bulbous (Fig. 3A, C). Elytra (all missing except left 14th on segment 29) large, oval, soft, opaque, nearly covered with conical microtubercles, low, oval on anterior part, bare region near anteromedial side; scattered cylindrical papillae on surface and posterior and lateral borders (Fig. 3B). Dorsal cirri on segments without elytra, with long cylindrical cirrophores on posterior sides of notopodia, wider basally; styles long, extending beyond setae, with slender tips and scattered short papillae; dorsal tubercles prominent, nodular (Fig. 3D).

Prostomium bilobed, with prominent cephalic peaks, without eyes; median antenna with large bulbous ceratophore in anterior notch, with style about twice as long as prostomium, with scattered short papillae; ceratophores of lateral antennae rather large, inserted ventrally, not meeting midventrally, with short, subulate papillate styles; palps stout, tapered, longer than median antenna (Fig. 3A). First segment not distinct dorsally; tentaculophores lateral to prostomium, each with small acicular lobe, 3 setae on inner side and pair of dorsal and ventral tentacular cirri similar to median antenna; ventral surface with facial ridge but without distinct facial tubercle (Fig. 3A). Second or buccal segment with first pair of large elytrophores, well-developed biramous parapodia, and long papillate ventral buccal cirri (Fig. 3A). Pharynx not extended and not examined.

Biramous parapodia with both rami well developed, with projecting acicular lobes and tips of acicula projecting; notopodium shorter than neuropodium, rounded, with projecting acicular process on lower side; neuropodium with conical presetal acicular lobe, with slight indication of rounded supraacicular process; postsetal lobe shorter, rounded (Fig. 3C, D). Notosetae numerous, forming radiating bundle, stouter than neurosetae, short and slightly curved to long

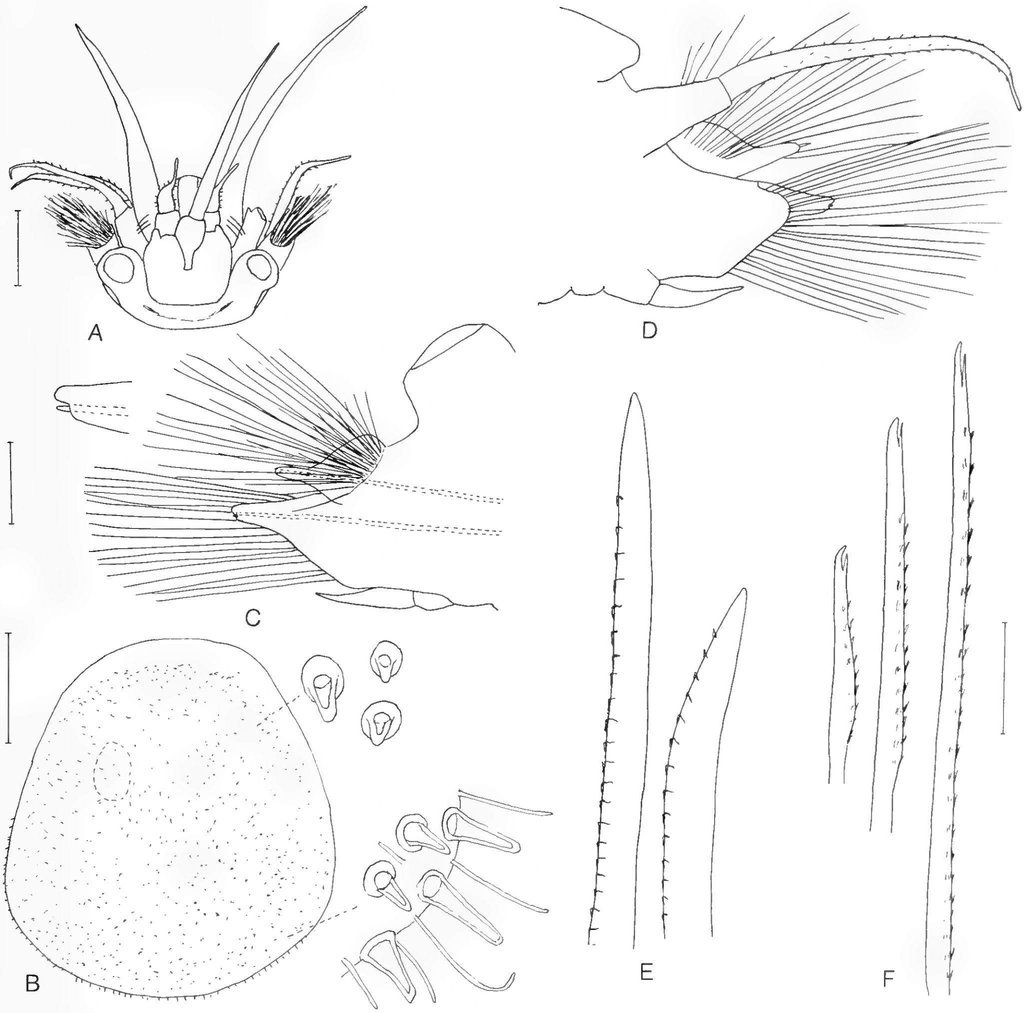


Fig. 3. *Harmothoe gordae,* holotype, USNM 123367: A, Dorsal view of anterior end, right dorsal and ventral tentacular cirri missing; B, Left 14th elytron from segment 29, with detail of microtubercles and papillae; C, Right elytrigerous parapodium, anterior view, acicula dotted; D, Right cirrigerous parapodium, posterior view; E, Long and short notosetae; F, Lower, middle and upper neurosetae. Scales = 1.0 mm for A; 1.0 mm for B; 0.5 mm for C, D; 0.1 mm for E, F.

and straight, with spinous rows and rather long, bare, tapering tips (Fig. 3E). Neurosetae numerous, forming fan-shaped bundle; upper ones more slender, with longer spinous regions, lower ones stouter, with shorter spinous regions; all with bifid tips, with long slender secondary tooth (Fig. 3F). Ventral cirri short, tapering (Fig. 3C, D).

Pygidium small, rectangular, with dorsal anus medial to last pair of small parapodia; anal cirri missing. Nephridial papillae beginning on segment 6, small, on lateral side, projecting dorsally between parapodia.

Etymology.—Named for the collecting site, the Gorda Ridge.

Remarks.—*Harmothoe gordae,* collected on Wood Island on the Gorda Ridge, is close to *H. vagabunda* Pettibone (1985a:146, fig.

Table 2.—Comparison of *Harmothoe gordae,* new species and *H. vagabunda* Pettibone.

	Harmothoe gordae	*Harmothoe vagabunda*
Prostomium	prominent distinct cephalic peaks (Fig. 3A)	very small cephalic peaks (Pettibone 1985a, Fig. 6A)
Neuropodial presetal acicular lobe	with small rounded supraacicular process (Fig. 3C)	without supraacicular process (Pettibone 1985a, Fig. 6B)
Neurosetae	with long slender secondary tooth (Fig. 3F)	with shorter secondary tooth (Pettibone 1985a, Fig. 6E)

6), described from the North Atlantic in the Tongue of the Ocean, Bahamas, and off St. Croix, Virgin Islands, associated with wood panels. The two species differ as indicated in Table 2.

Subfamily Arctonoinae Hanley, 1989

Parabathynoe, new genus

Type species.—*Parabathynoe brisinga,* new species.

Diagnosis.—Body short, up to 46 segments. Elytra and prominent elytrophores 18 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 35, 40, and 43. Elytra thickly covered with conical microtubercles and papillae. Dorsal cirri on segments lacking elytra, with cirrophores and distal styles; dorsal tubercles in line with elytrophores. Prostomium bilobed, rounded, with 2 pairs of large eyes, 2 long palps, and 3 antennae: median antenna with ceratophore and long style inserted in anterior notch; lateral antennae inserted subterminally, ventral to median antenna, with ceratophores and short styles only slightly set off from prostomium. First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, achaetous, with 2 pairs of tentacular cirri; ventral surface with bulbous upper lip. Second or buccal segment with bulbous elytrophores of first pair of elytra, small subbiramous parapodia, ventral buccal cirri, and bulbous lateral and wrinkled lower lips. Parapodia subbiramous; notopodia with small conical acicular lobe and bundle of short acicular notosetae; neuropodia larger, with rounded presetal acicular lobe; postsetal lobe hook-shaped, of two parts: upper part short, rounded; lower part curved dorsally, with thick bushy bundle of long papillae on outer curved border; neurosetae numerous, long, nearly smooth, with tapered, mostly bifid tips; ventral surface of neuropodia thickly papillate. Ventral cirri lacking, except on segment 2. Extended pharynx with 9 pairs of papillae and 2 pairs of chitinous jaws. Commensal with brisingid asteroids.

Etymology.—From the Greek *para,* plus the genus *Bathynoe* Ditlevsen, in the subfamily Arctonoinae; gender feminine.

Remarks.—In comparison with the genera included in the subfamily Arctonoinae by Hanley (1989), *Parabathynoe* is closest to *Bathynoe* Ditlevsen, 1917. Both are relatively short-bodied (less than 50 segments), ventral cirri are present only on segment 2, and lower parts of neuropodial postsetal lobes are curved dorsally and papillated on the curved border. Both are commensal with asteroids.

Bathynoe differs from *Parbathynoe* in a number of features. In the former, the body has prominent middorsal tubercles, lacking in the latter; elytra have a different arrangement and have nodular tubercles and globular micropapillae on the surface, instead of microtubercles and cylindrical papillae; prostomium has short, stumpy palps and has no eyes, instead of long palps and two pairs of eyes; notosetae are absent on subbiramous parapodia, instead of present; and neurosetae are few, short, stout, and strongly hooked, instead of numerous, long, and slender, with minute bifid tips.

Parabathynoe brisinga, new species
Figs. 4, 5

Material.—East Pacific Ocean off northern California, Gorda Ridge, *Alvin* dive 2033, 41°00′N, 127°29′W, 3 Jun 1988, 3356 m, commensal with brisingid asteroid, holotype (USNM 123371), paratype (USNM 123372).

Description.—Length of holotype (female with large yolky eggs in body cavity) 18 mm, width 6 mm with setae, segments 47, last one minute. Paratype incomplete posteriorly, with 32 segments, 11 mm long and 4.5 mm wide. Body flattened ventrally, slightly arched dorsally, tapering slightly anteriorly, and more so posteriorly. Ventral side of body with 2 pairs of large, rounded papillae per segment and numerous small papillae on ventral side of parapodia (Fig. 4E). Elytra 18 pairs, large, covering dorsum, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 35, 40, 43. Elytra oval to subreniform, thickly covered with conical microtubercles and papillae; thicker, slightly raised area across posterior fifth or sixth of surface (Fig. 5 E–G); elytrophores large and prominent (Figs. 4A, C, 5A). Dorsal cirri on segments lacking elytra, with short cylindrical cirrophores and styles extending beyond neuropodia, styles with proximal ⅔ cylindrical and slightly bulbous, distal ⅓ filamentous, with long papillae on lower side of cylindrical part; dorsal tubercles nodular, in line with elytrophores (Figs. 4A, B, D, 5B).

Prostomium oval, bilobed, wider than long, with 2 pairs of eyes on lateral sides, anterior pair very large, twice as large as posterior pair; median antenna with bulbous ceratophore in anterior notch, style about twice as long as prostomium, with filamentous tip; lateral antennae with ceratophores indistinctly set off from prostomium and inserted ventral to median antenna; short styles with clavate enlargements and filamentous tips; palps stout, cylindrical, with filamentous tips; tentaculophores lateral to prostomium, with small acicular lobe on inner side, achaetous; dorsal and ventral tentacular cirri bulbous subdistally with filamentous tips; facial ridge on bulbous anterior lip of ventral mouth (Fig. 4A, B).

Second or buccal segment without nuchal lobe, with first pair of large elytrophores, subbiramous parapodia much smaller than following parapodia, ventral buccal cirri, similar to tentacular cirri, and bulbous lateral and posterior lips enclosing ventral mouth (Fig. 4A–C).

Parapodia from segment 3 on larger, subbiramous, with small conical notopodial acicular lobe on anterodorsal side of larger neuropodium with longer, rounded presetal acicular lobe with low rounded upper part; shorter, hook-shaped postsetal lobe consisting of short rounded upper half and longer lower half curving dorsally, with bushy bundle of long papillae on outer curved border of lower part (Figs. 4B, 5A, B). Without ventral cirri. Notosetae extending to tip of neuropodium, in small bundle, short, acicular, slightly stouter than neurosetae, nearly smooth, with faint close-set spinous rows and entire tips (Fig. 5C). Neurosetae very numerous, forming fan-shaped bundle, long, enlarged subdistally, tapering to slightly hooked tips, mostly with very small secondary tooth, others entire; upper few (5 or so) with split tips (Fig. 5D). Pharynx (cut open) with 9 pairs of marginal papillae and 2 pairs of amber-colored jaws. Pygidium short, rectancular, between posterior, minute parapodia, with anal cirri (missing).

Etymology.—The species is named for its commensal relationship with brisingid asteroids.

Subfamily Lepidonotopodiinae
Pettibone, 1983

Genus *Lepidonotopodium* Pettibone, 1983

Lepidonotopodium piscesae Pettibone, 1988

Lepidonotopodium piscesae Pettibone 1988: 193, figs. 1–4.

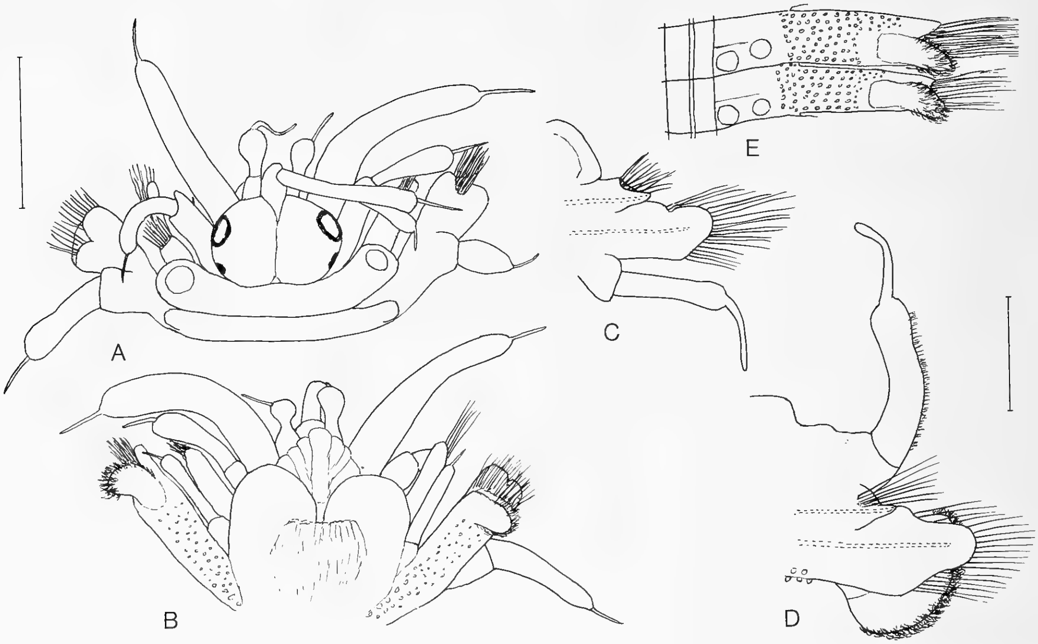


Fig. 4. *Parabathynoe brisinga,* A–D, holotype USNM 123371: A, Dorsal view of anterior end, left ventral tentacular cirrus missing; B, Same, ventral view; C, Left elytrigerous parapodium from segment 2, anterior view, acicula dotted; D, Left cirrigerous parapodium from segment 3, anterior view, acicula dotted; E, Ventral view of left side of two middle segments lateral to midventral neural groove. Scales = 1.0 mm for A, B, E; 0.5 mm for C, D.

Lepidonotopodium pettibonae Detinova, 1988:858, fig. 1a–h.

Material.—East Pacific Ocean off northern California, Gorda Ridge, in northern Escanaba Trough, *Sea Cliff* dive 764, 3 Sep 1988, 41°00′N, 127°30′W, 3500 m, 11 specimens (USNM 123369, SIO).

Remarks.—The specimens from the Gorda Ridge agree with the specimens from the hydrothermal vents of the Northeast Pacific Explorer and Juan de Fuca Ridges, described earlier as *Lepidonotopodium piscesae* by Pettibone (1988, 29 April) and as *L. pettibonae* by Detinova (1988, June). Unfortunately, the former name has priority.

The eleven specimens from the Gorda Ridge were collected in the northern Escanaba Trough in a heavily sedimented area with a large clump of vestimentiferans, including *Rigia* spp., and long filamentous bacteria. The elytra and setae of the polynoids were covered with foreign material, including sediment and bacteria. The larger specimens measured 20–22 mm in length, 10–11 mm in width, with 25–26 segments.

Distribution.—Hydrothermal vents of Northeast Pacific Explorer and Juan de Fuca Ridges, in 1500–2208 m and northern Escanaba Trough of Gorda Ridge, in 3500 m.

Subfamily Macellicephalinae Hartmann-Schröder, 1971; emended Pettibone, 1976

Genus *Levensteiniella* Pettibone, 1985

The genus includes *L. kincaidi,* described from the Galapagos Rift and the East Pacific Rise at 21°N by Pettibone (1985c), with additional records from the Northeast Pacific Explorer and Juan de Fuca Ridges by Pettibone (1988), and *L. raisae,* described from the Western Pacific in the Mariana Back-

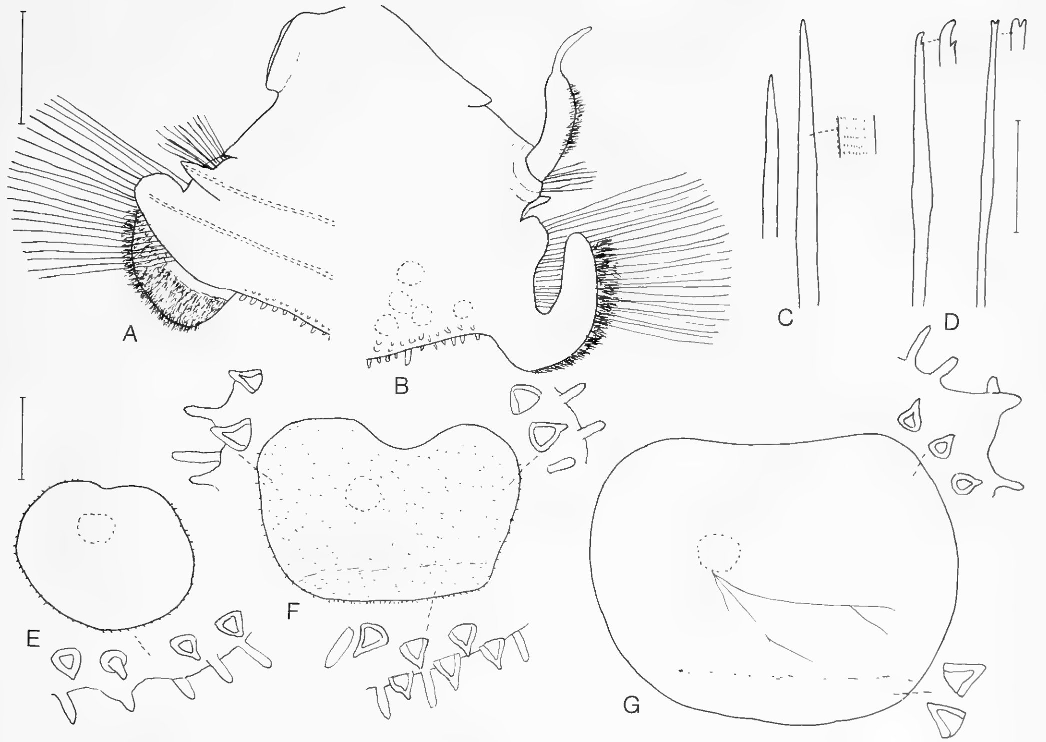


Fig. 5. *Parabathynoe brisinga,* holotype, USNM 123371: A, Right elytrigerous parapodium from segment 15, anterior view, acicula dotted; B, Right cirrigerous parapodium from segment 16, posterior view (few eggs in body cavity dotted); C, Notosetae, with detail of faint spinous rows; D, Middle and upper neurosetae, with detail of tips; E, Left 1st elytron from segment 2, with detail of microtubercles and papillae; F, Left 2nd elytron from segment 4, with detail of microtubercles and papillae; G, Left middle elytron, with detail of microtubercles and papillae. Scales = 0.5 mm for A, B; 0.1 mm for C, D.

Arc Basin by Pettibone (1989b). From the Gorda Ridge, additional records of *L. kincaidi* showing some varietal differences are added and a new species is described below.

Levensteiniella kincaidi Pettibone, 1985
Fig. 6

Levensteiniella kincaidi Pettibone, 1985c: 741, figs. 1–3; 1988:199, fig. 5; 1989b: 159.

Material.—East Pacific Ocean off northern California, Gorda Ridge, *Alvin* dive 2036, 6 Jun 1988, 41°00′N, 127°29′W, 3240 m, 1 specimen (USNM 123366). Gorda Ridge in northern Escanaba Trough, *Sea Cliff* dive 764, 3 Sep 1988, 41°00′N, 127°30′W, 3500 m, 5 specimens (USNM 123365; SIO).

Description of specimen from Alvin *dive 2036.*—Length 19 mm, width with setae 10 mm, with 26 segments and 11 pairs of elytra. Some elytra with papillae on posterior and lateral borders enlarged basally; papillae on border and surface variable in shape (Fig. 6G–I). Prostomium, tentacular and first buccal segments as described earlier (Fig. 6A). Dorsal cirri and dorsal tubercles, biramous parapodia, notosetae and neurosetae, and ventral cirri, as described earlier (Fig. 6C–F). Body without 2 pairs of long ventral papillae on segments 11 and 12 but with small rounded paired papillae near basal sides of parapodia on segments 11–19

(Fig. 6B); as reported earlier, long ventral papillae found on only some adults (Pettibone, 1985c, fig. 1D; 1988).

Remarks.—The setae of the specimens from the Escanaba Trough, collected on heavily sedimented fresh basalts, were covered with numerous round and long filamentous bacteria; one was covered with stalked peritrich protozoa.

The elytra of the stem form of *L. kincaidi,* described from the Galapagos Rift and 21°N, have only cylindrical micropapillae near the border and on the surface (Pettibone, 1985c, fig. 1E). The elytra of the varietal form, described on a small specimen from the Juan de Fuca Ridge (Pettibone, 1988, fig. 5A, B) and described here from the Gorda Ridge (Fig. 6G–I) have some additional border papillae enlarged basally.

Distribution.—Hydrothermal vents of tropical East Pacific, Galapagos Rift and East Pacific Rise at 21°N, in 2450–2633 m; Northeast Pacific Explorer Ridge, Endeavour Segment and Axial Seamount, Juan de Fuca Ridge, in 1546–2213 m; and off northern California Gorda Ridge, in 3240–3500 m.

Levensteiniella intermedia,
new species
Figs 7, 8

Material.—East Pacific Ocean off northern California, Gorda Ridge, *Alvin* dive 2042, 12 Jun 1988, 41°00′N, 127°29′W, 3271 m, "clam washings," holotype (USNM 123370).

Description.—Body flattened ventrally, arched dorsally, slightly tapered anteriorly and more so posteriorly, with parapodia about as long as body width. Eleven pairs of elytra, oval to subreniform, thick, stiff, opaque, with thick oval raised areas or projections on posterior border and some scattered oval micropapillae on surface (Fig. 7D–G).

Prostomium wider than long, deeply bilobed with subtriangular lobes projecting anteriorly, with terminal filaments; without eyes; ceratophore of median antenna large, bulbous, in anterior notch; style missing; palps long, stout, tapered; tentaculophores lateral to prostomium, achaetous, with small acicular lobe on inner side; dorsal and ventral tentacular cirri about same length as palps (Fig. 7A, B) Segment 2 with first pair of large elytrophores, biramous parapodia, and ventral buccal cirri attached basally lateral to ventral mouth, longer than following ventral cirri (Fig. 7A, B).

Biramous parapodia with notopodium shorter than neuropodium, notopodium rounded with projecting acicular lobe on lower side; neuropodium with conical projecting presetal acicular lobe; postsetal lobe shorter, rounded, deeply cut on dorsal side (Fig. 8A, B). Notosetae very numerous, forming radiating bundle, much stouter than neurosetae, of several lengths, stout, tapering to bare, blunt tips, with smooth or with widely spaced spines along one side (Fig. 8C). Neurosetae very numerous, forming fan-shaped bundle; supraacicular neurosetae with longer spinous regions, with 2 rows of widely spaced spines along borders, with shorter close-set spines on tapered tips (Fig. 8E); subacicular neurosetae with slightly hooked bare tips and close-set minute spines along one border (Fig. 8D). Dorsal cirri with cylindrical cirrophores on anterior side of notopodia; styles with long filamentous tips, extending to about tips of neurosetae; dorsal tubercles nodular to truncate; ventral cirri short, tapering, and extending to distal end of ventral side of neuropodia (Fig. 8B).

Single pair of long ventral papillae on segment 11, much wider basally and extending almost to tip of neuropodium and ending in distal knob and subdistal filament (Fig. 7C). Pygidium small rounded lobe between bases of posterior small parapodia; anal cirri missing.

Etymology.—The species is named based on its intermediate position between the other two species of *Levensteiniella.*

Comparisons.—Important characters separating *L. intermedia* and the other two

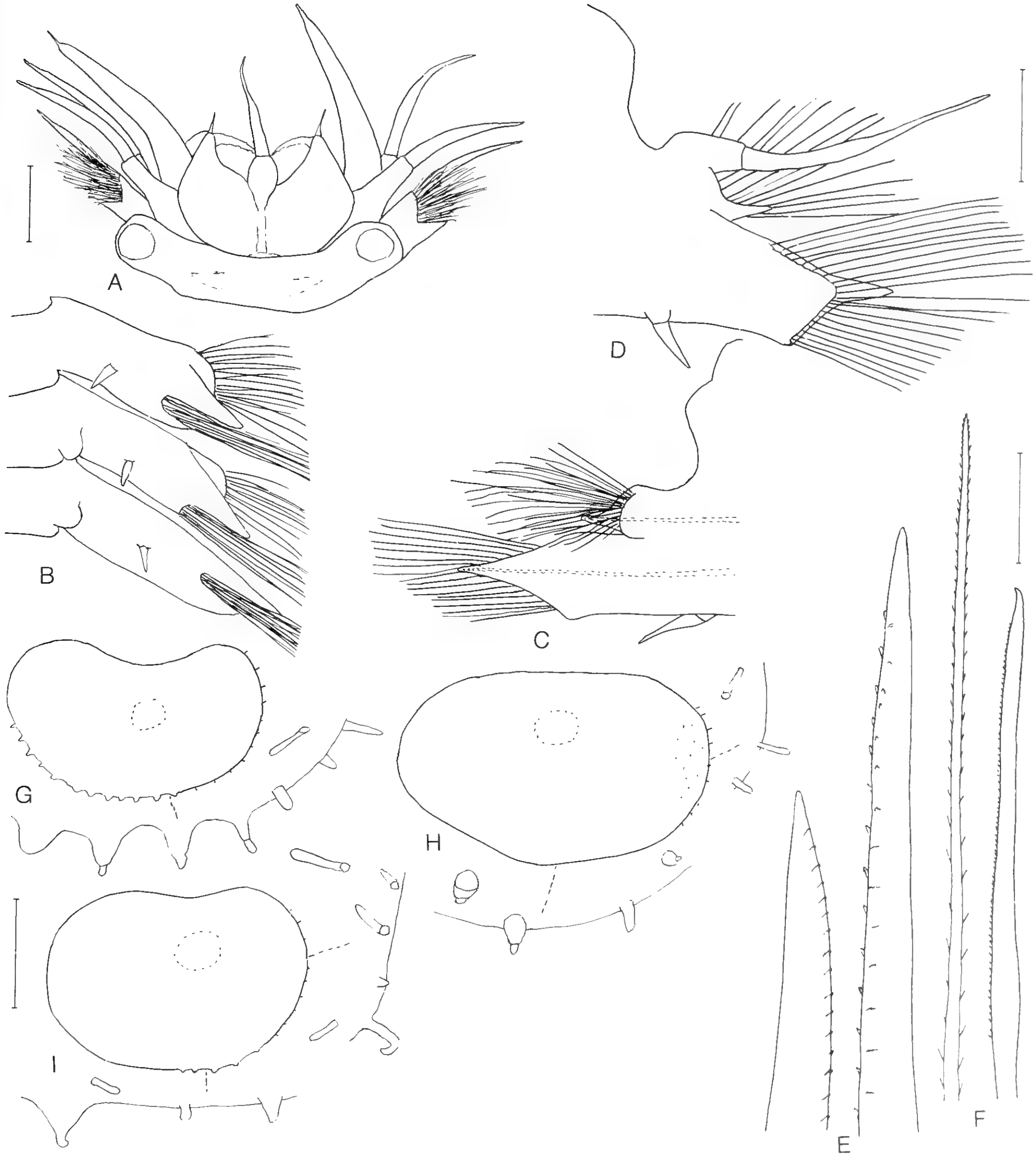


Fig. 6. *Levensteiniella kincaidi,* variety, USNM 123366: A, Dorsal view of anterior end; B, Ventral view of left side of segments 10–12, showing rounded papillae on segments 11 and 12; C, Right elytrigerous parapodium, anterior view, acicula dotted; D, Right cirrigerous parapodium, posterior view; E, Short and long notosetae; F, Tip of supraacicular and subacicular neurosetae; G, Right 2nd elytron from segment 4, with detail of papillae; H, Right 5th elytron from Segment 9, with detail of surface and border papillae; I, Right 10th elytron from segment 19, with detail of papillae. Scales = 1.0 mm for A, B; 1.0 mm for C, D; 0.1 mm for E, F; 2.0 mm for G–I.

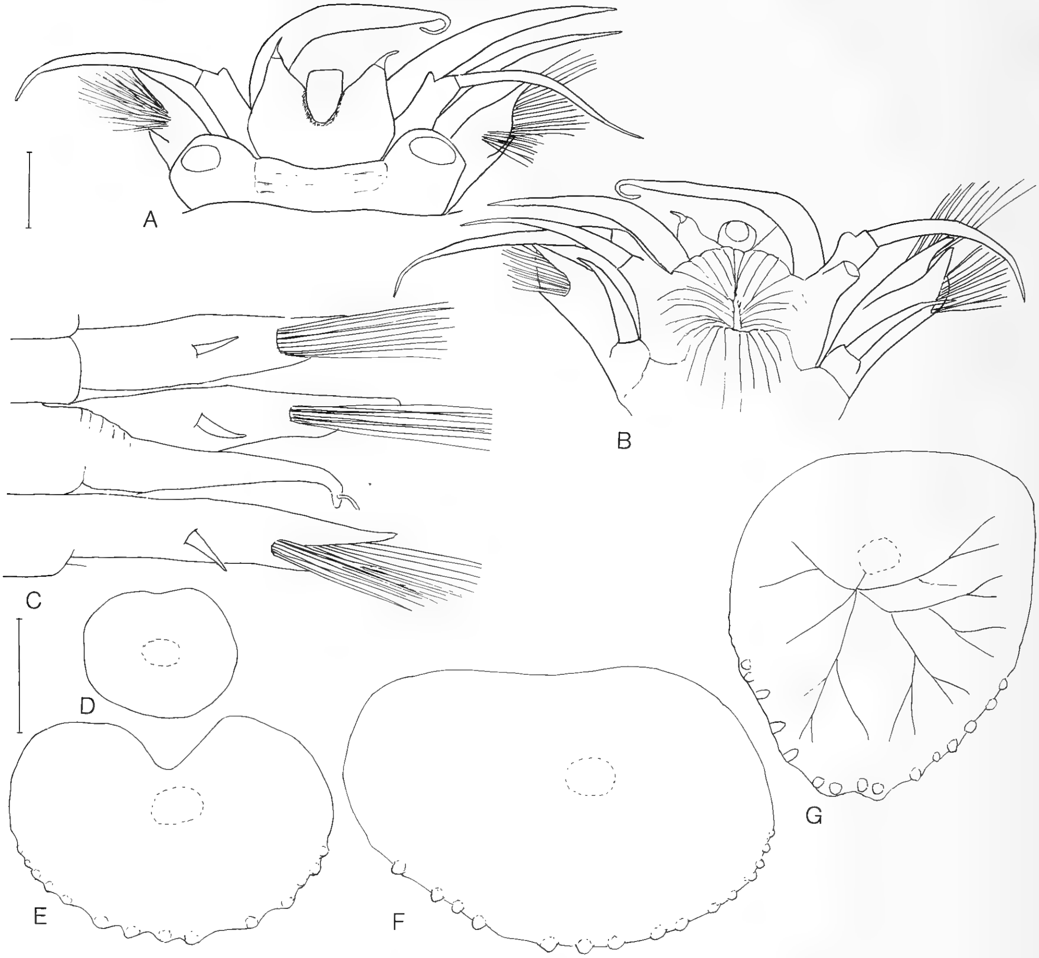


Fig. 7. *Levensteiniella intermedia,* holotype, USNM 123370: A, Dorsal view of anterior end, styles of median antenna and left ventral tentacular cirrus missing; B, Ventral view of same; C, Ventral view of left side of segments 10–12, showing long ventral papilla on segment 11; D, Right 1st elytron from segment 2; E, Right 2nd elytron from segment 4; F, Right middle elytron; G, Left posterior elytron. Scales = 1.0 mm for A–C; 2.0 mm for D–G.

species of *Levensteiniella* are indicated in Table 3.

Subfamily Branchinotogluminae Pettibone, 1985

Genus *Branchinotogluma* Pettibone, 1985

Branchinotogluma grasslei Pettibone, 1985

Branchinotogluma grasslei Pettibone, 1985b:457, figs. 5, 6; 1988:199; 1989b:157.

Material.—East Pacific Ocean off northern California, Gorda Ridge, *Alvin* dive 2036, 6 Jun 1988, 41°00′N, 127°29′W, 3240 m, 9 specimens (USNM 123363); *Alvin* dive 2037, 7 Jun 1988, 3261 m, washings from vestimentiferans and alvinellids, 2 specimens (USNM 123362). Gorda Ridge, in northern Escanaba Trough, *Sea Cliff* dive 764, 3 Sep 1988, 41°00′N, 127°30′W, 3500 m, heavily sedimented area with vestimentiferans and long filamentous bacteria, 4 specimens (USNM 123364; SIO).

Remarks.—The 15 specimens from the Gorda Ridge, in 3240–3500 m, agree with the specimens previously described from the

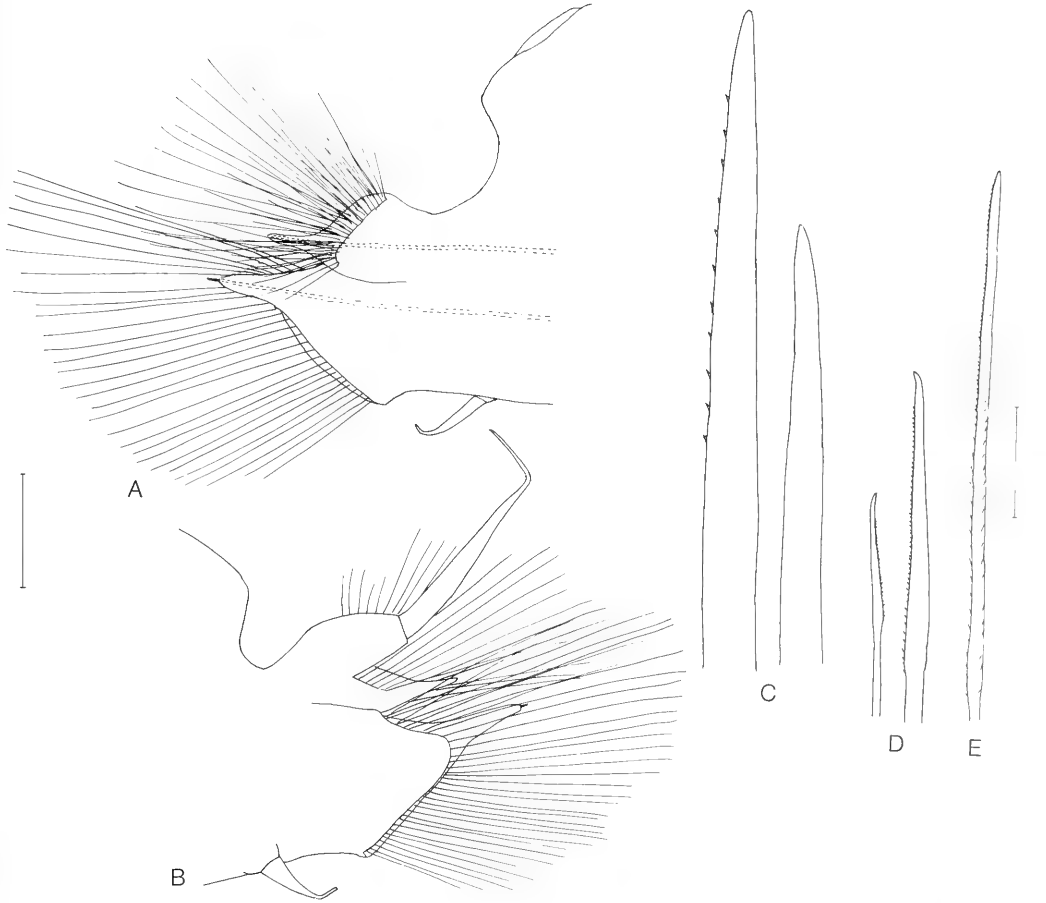


Fig. 8. *Levensteiniella intermedia,* holotype, USNM 123370: A, Right elytrigerous parapodium, anterior view, acicula dotted; B, Right cirrigerous parapodium, posterior view; C, Long and short notosetae; D, Lower and upper supraacicular neurosetae; E, Supraacicular neuroseta. Scales = 1.0 mm for A, B; 0.1 mm for C–E.

Table 3.—Comparison of three species of *Levensteiniella.*

	L. kincaidi Pettibone, 1985c	*L. raisae* Pettibone, 1989	*L. intermedia* n. sp.
Elytra	with filiform micropapillae on border & surface; some with enlarged bases on posterior border (Fig. 6G–I)	with macro- and microtubercle-papillae on surface and posterior border (Pettibone 1989a, Fig. 1G)	with thickened bulbous projections on posterior border and oval micropapillae on surface (Fig. 7D–F)
Notosetae	with spinous rows (Fig. 6E)	with widely spaced spines along one side (Pettibone 1989a, Fig. 2E)	smooth or with widely spaced spines along one side (Fig. 8C)
Long paired ventral papillae	2 pairs on segments 11 & 12 (Pettibone 1985c, Fig. 1D)	2 pairs on segments 11 & 12 (Pettibone 1989a, Fig. 1E)	single large pair on segment 11 (Fig. 7C)

Galapagos Rift and 21°N vent sites (Pettibone 1985b) and reported from the Explorer and Juan de Fuca Ridges (Pettibone 1988) and the Guaymas Basin (Pettibone, 1989b), in 1495–2633 m, associated with vestimentiferans. The specimens measured 9–22 mm in length, 5–11 mm in width, with 21 segments.

Genus *Opisthotrochopodus* Pettibone, 1985b

Opisthotrochopodus tunnicliffeae Pettibone, 1988

Opisthotrochopodus tunnicliffeae Pettibone, 1988:203, figs. 6–9

Material.—East Pacific Ocean off northern California, Gorda Ridge, *Alvin* dive 2036, 6 Jun 1988, 41°00′N, 127°29′W, 3240 m, 5 specimens (USNM 123375); *Alvin* dive 2037, 7 Jun 1988, 3261 m, washings from vestimentiferans and alvinellids, 1 specimen (USNM 123376). Gorda Ridge, in northern Escanaba Trough, *Sea Cliff* dive 764, 3 Sep 1988, 41°00′N, 127°30′W, 3500 m, heavily sedimented area with vestimentiferans and long filamentous bacteria, 7 specimens (USNM 123374; SIO).

Remarks.—The 13 specimens from the Gorda Ridge, in 3240–3500 m, agree with the specimens previously described from the Explorer and Juan de Fuca Ridges, in 1818–1533 m. The larger specimens from the Gorda Ridge measured 19–22 mm in length, 9–12 mm in width, with 21 segments. One specimen from the *Sea Cliff* dive had a long coiled parasitic copepod in the body cavity and extending to the outside.

Acknowledgments

I wish to thank Verena Tunnicliffe of the University of Victoria for the specimen from the Juan de Fuca Ridge, J. Frederick Grassle and Rosemarie Petrecca of the Woods Hole Oceanographic Institution for the DSRV *Alvin* specimens, and Michael A. Boudrias of the Scripps Institution of Oceanography for the DSRV *Sea Cliff* specimens from the Gorda Ridge. The manuscript benefited from the reviews of Thomas H. Perkins and James A. Blake.

Literature Cited

Detinova, N. N. 1988. New species of polychaetous annelids from hydrothermal vents of the Juan de Fuca Ridge (Pacific Ocean).—Zoologichesky Zhurnal 67(6):858–864. (In Russian, English summary.)

Hanley, J. R. 1989. Revision of the scaleworm genera *Arctonoe* Chamberlin and *Gastrolepidia* Schmarda (Polychaeta: Polynoidae) with the erection of a new subfamily Arctonoinae. —The Beagle, Records of the Northern Territory Museum of Arts and Sciences 6:1–34.

Pettibone, M. H. 1985a. Polychaete worms from a cave in the Bahamas and from experimental wood panels in deep water of the North Atlantic (Polynoidae: Macellicephalinae, Harmothoinae).—Proceedings of the Biological Society of Washington 98:127–149.

———. 1985b. Additional branchiate scale-worms (Polychaeta: Polynoidae) from Galapagos hydrothermal vent and rift-area off Western Mexico at 21°N.—Proceedings of the Biological Society of Washington 98:447–469.

———. 1985c. New genera and species of deep-sea Macellicephalinae and Harmothoinae (Polychaeta: Polynoidae) from the hydrothermal rift areas off the Galapagos and Western Mexico at 21°N and from the Catalina Channel.—Proceedings of the Biological Society of Washington 98:740–756.

———. 1988. New species and new records of scaled polychaetes (Polychaeta: Polynoidae) from hydrothermal vents of the Northeast Pacific Explorer and Juan de Fuca Ridges.—Proceedings of the Biological Society of Washington 101: 192–208.

———. 1989a. New species of scale-worms (Polychaeta: Polynoidae) from the hydrothermal rift-area of the Mariana Back-arc Basin in the western central Pacific.—Proceedings of the Biological Society of Washington 102:137–153.

———. 1989b. Polynoidae and Sigalionidae (Polychaeta) from the Guaymas Basin, with descriptions of two new species, and additional records from hydrothermal vents of the Galapagos rift, 21°N, and seep-sites in the Gulf of Mexico (Florida and Louisiana).—Proceedings of the Biological Society of Washington 102:154–168.

Department of Invertebrate Zoology, National Museum of Natural History, Washington, D.C. 20560

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 839–846

REDEFINITION OF *TENERIDRILUS* HOLMQUIST (OLIGOCHAETA: TUBIFICIDAE), WITH DESCRIPTION OF TWO NEW SPECIES FROM NORTH AMERICA

Christer Erséus, Jarl K. Hiltunen, Ralph O. Brinkhurst, and
Don W. Schloesser

Abstract.—The tubificid genus *Teneridrilus* Holmquist, 1985 (subfamily Tubificinae) is redefined. The genus was originally monotypic for the type species, formerly classified as *Ilyodrilus mastix* Brinkhurst, 1978. The genus now includes *Teneridrilus columbiensis* (Brinkhurst & Diaz, 1985), a new combination for *Isochaetides columbiensis,* and two new species. The first of these, *Teneridrilus calvus,* is described by Erséus & Brinkhurst, and the second, *Teneridrilus* flexus, by Erséus & Hiltunen. Synapomorphies for the genus are strongly modified chaetae in II and an enlarged eversible pharynx. The genus is distributed from China to British Columbia, Washington, and California in freshwater near the mouths of large rivers, and in the St. Marys River, which connects Lake Superior with Lakes Michigan and Huron.

An aberrant freshwater tubificid with modified chaetae in segment II and greatly enlarged mouth and pharynx was described as *Ilyodrilus mastix* by Brinkhurst (1978) from the Fraser River in British Columbia, and later recorded by Erséus and Qi (1985) from the Pearl River in China. Holmquist (1985:343), who re-examined the type series, challenged the original generic position: "The species *mastix* with its quite differently built male apparatus, its entire lack of spermathecae, and the peculiarly built head region is not compatible with any of the above species, nor with any of the other members of the '*Ilyodrilus*' complex scrutinized, but holds its own position." She accordingly established a monotypic genus, *Teneridrilus,* for *I. mastix,* an action that was supported by the original author (Brinkhurst, pers. comm., in Erséus & Qi 1985:194).

The male efferent duct of *T. mastix* consists of a narrow vas deferens, a stout atrium bearing a small prostate gland, and a small cone-shaped penis without thickened cuticle (see Holmquist 1985 for details and dimensions). All atrial epithelial cells are of one type, unlike those of the tubificine genus *Tubificoides.* Although clearly a member of the Tubificinae, the species has a simple male apparatus atypical of most species in the subfamily. There are large ovaries but no spermathecae—the latter feature usually attributed to self-fertilizing or parthenogenetic species in the Tubificidae (see Brinkhurst 1986a). Species with these characteristics are commonly classified together with species that have normal reproductive systems in genera defined by phylogenetic principles. These involve recognizing shared apomorphies (synapomorphies) that indicate descent from a common ancestor despite more recent adaptations. *Teneridrilus mastix* was originally found in the tidal freshwater part of the Fraser River, British Columbia. *Tubificoides fraseri* Brinkhurst was described from more seaward sites in the same estuary in more saline water (Brinkhurst 1986b). It, too, is a suspected parthenogen with a simplified reproductive system (spermathecae lacking), but is recognizable as a true *Tubificoides.* Because such an adaptation is not seen as a generic character, we recognize three additional members of the genus *Teneridrilus* that share the peculiar modified chaetae of II and the enlarged pharynx of the type species but which have more elaborate male reproductive systems than that of *T. mastix. Teneridrilus columbiensis* and *T. calvus,* n. sp. are both found in tidal freshwaters in the Pacific Rim, but *T. flexus,* n. sp. is known only from the exit channel from Lake Superior.

Material and Methods

Specimens of *Teneridrilus mastix* and *T. calvus,* n. sp. were found during a study in the Sacramento-San Joaquin Delta in California, and were placed at our disposal by Dr. W. C. Fields, Jr. (Newcastle, California). Specimens of *T. flexus,* n. sp. were collected in St. Marys River, the exit channel from Lake Superior, by one of us (D.W.S.). All specimens were mounted whole in Canada balsam and studied with a light microscope.

The type series of the new species are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Family Tubificidae
Subfamily Tubificinae
Teneridrilus Holmquist, 1985

Definition (emended).—Small tubificids. Prostomium small. Anterior end of worm wide and rather bluntly rounded; pharynx large, eversible, forming a folded diverticulum when withdrawn inside animal. All chaetae of II bifid, but modified: stouter, and with distal tooth thinner and shorter than bifid chaetae of other segments. Hair chaetae present in dorsal bundles (in *T. mastix*) or absent. Modified (grooved) spermathecal chaetae present (in *T. columbiensis*) or absent. Modified penial chaetae absent. Male pores paired in XI. Spermathecal pores absent (in *T. mastix*) or paired in X. Coelomocytes of the "rhyacodriline-type" absent. Male ducts paired. Vasa deferentia narrow, confined to XI. Atria cylindrical, small, each bearing one small, solid prostate gland (not yet confirmed for *T. flexus,* n. sp.). Penes present, sometimes with thickened cuticular sheath (*T. columbiensis* and *T. calvus,* n. sp.), generally enclosed in muscular sacs. Spermathecae (absent in *T. mastix*) with roundish ampullae and narrow ducts. Sperm as short and broad spermatozeugmata (in *T. columbiensis*), or random, in spermathecae.

Type species.—Ilyodrilus mastix Brinkhurst, 1978.

Other species.—Teneridrilus columbiensis (Brinkhurst & Diaz, 1985), n. comb., *T. calvus* Erséus & Brinkhurst n. sp., and *T. flexus* Erséus & Hiltunen n. sp.

Remarks.—Monophyly of *Teneridrilus* is indicated by two synapomorphies in the four species of the genus: the large, modified feeding apparatus, and the modified bifid chaetae in segment II. All other features appear homologous to states known also from other Tubificinae. Most of these traits are thus likely to prove to be plesiomorphic and should not be used as a basis for a phylogenetic definition of the genus.

The four species of the genus are all freshwater forms, mostly occurring in riverine habitats.

Teneridrilus mastix (Brinkhurst, 1978)

Ilyodrilus mastix Brinkhurst, 1978:2171–2173, fig. 3.—Erséus & Qi 1985:193–194, fig. 1.

Teneridrilus mastix.—Holmquist 1985:332–334, 336–341, 357–360, figs. 18, 21D–E, 22E, 23K–L, 24P–R, 31A.

New material (studied by, and in collection of, R. O. Brinkhurst).—Several specimens from various sites in the Sacramento-San Joaquin Delta, in fine sediments with slow water flows (collected on several dates since April 1984; W. C. Fields, Jr.).

Remarks.—This species, the type of the genus, is in fact the most atypical member of *Teneridrilus*. Unlike the other three species, it bears both hairs and bifid chaetae in the dorsal bundles. It has very simple penes in penial sacs that are not particularly muscular, and lacks spermathecae.

Teneridrilus mastix is likely to be a reproductive opportunist, not reproducing by normal cross-fertilization.

Distribution and habitat.—British Columbia and California (new record), southern China. Fine sediments of rivers; in freshwater.

Teneridrilus columbiensis
(Brinkhurst and Diaz, 1985),
new combination

Isochaetides columbiensis Brinkhurst & Diaz, 1985:949–952, figs. 1–2.

Remarks.—Originally placed in *Isochaetides* Hrabě, the monophyletic state of which is highly questionable (Brinkhurst 1986a), this species is here transferred to *Teneridrilus* because it has the synapomorphies now recognized for the genus.

Teneridrilus columbiensis is further characterized by lack of hair chaetae, possession of grooved spermathecal chaetae in segment X, and atria appearing as "simple widenings of vasa deferentia, with prostates attached near midpoints" (Brinkhurst and Diaz 1985: 950). Short ejaculatory ducts connect the atria with muscular penial bulbs that bear short, rounded to blunt-ended penis sheaths. The spermathecal ampullae are large and spherical and have short and broad spermatozeugmata.

Distribution and habitat.—Known only from Columbia River, Oregon. Tidal freshwater marsh, muddy sediment.

Teneridrilus calvus Erséus & Brinkhurst,
new species
Fig. 1

Type material.—USNM 123377, holotype, whole-mounted specimen from the Sacramento-San Joaquin Delta, Sacramento, California, muddy silt and clay (26 February 1987, W. C. Fields, Jr.). USNM 123378–123380, paratypes, 3 whole-mounted specimens from type locality.

Other material.—Several specimens from the type locality, in the collections of R. O. Brinkhurst and C. Erséus.

Etymology.—The epithet "*calvus*" is Latin for "bald, without hair," and refers to the lack of hair chaetae in this species.

Description.—Holotype 6.9 mm long, but not complete, consisting of the first 29 anterior segments. Paratypes 4.6–5.3 mm long, with 22–33 segments. Width at XI (compressed specimens) 0.21–0.31 mm. Prostomium (Fig. 1A, pro) triangular, small. Body wall with scattered particles on surface. Clitellum extending over XI–XII. Chaetae all bifid, those of II (Fig. 1B) stout, 30–35 μm long, about 2.5 μm thick, 2–3 per bundle; with distal tooth distinctly thinner and shorter than proximal. Chaetae of other anteclitellar segments (Fig. 1C) about 50 μm long, 2.0–2.5 μm thick, up to 5(6) per bundle, with distal tooth almost as thick as, but longer than, proximal. Postclitellar chaetae up to about 40 μm long, about 2 μm thick, 2 per bundle, with teeth about equal in length and thickness. Chaetae absent ventrally in XI. Male pores paired in line with ventral chaetae in XI. Spermathecal pores immediately anterolateral to ventral chaetae in X.

Mouth and pharynx (Fig. 1A) enlarged and complexly folded (semi-schematical in drawing), apparently forming a massive, eversible feeding apparatus. In all specimens studied, esophagus and gut filled (and distended) with sediment and detritus along most of worm, indicating that large amounts are engulfed. Pharyngeal glands not observed. Male genitalia (Fig. 1D) paired. Vas deferens 6–9 μm wide, much longer than atrium, entering apical end of latter. Atrium 45–60 μm long, 20–28 μm wide, somewhat comma-shaped or spindle-shaped, with apical end tilted over to posterior. Atrium with ventral bulge bearing (somewhat broadly at-

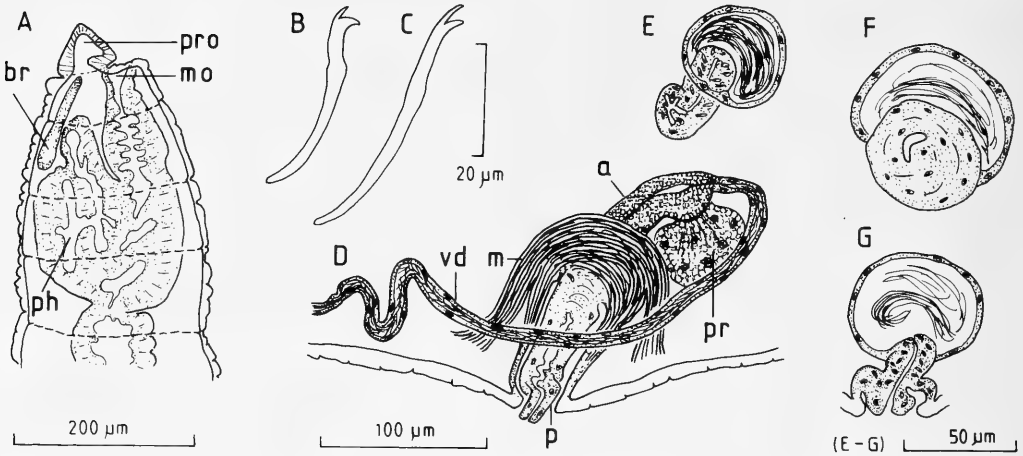


Fig. 1. *Teneridrilus calvus* Erséus & Brinkhurst, n. sp.: A, Anterior end of worm, with folding of pharynx semi-schematically drawn; B, Chaeta of segment II; C, Chaeta of segment IV; D, Male genitalia; E, Spermatheca from one specimen; F–G, Spermathecae from another specimen. Abbreviations: a atrium; br brain; m muscular bulb; mo mouth; p penis; ph pharynx; pr prostate gland; pro prostomium; vd vas deferens.

tached?) discrete prostate gland. Atrium entering heavily muscular bulb, interior to which is a hollow sac with a cylindrical or somewhat tapering penis. Penis 60–95 µm long, 18–30 µm wide, with thin but distinct cuticular lining (= a cylindrical sheath) along most of its length, but with 'soft' and somewhat pointed tip, protruding from opening of sheath. Spermathecae (Fig. 1E–G) with wide and distinct ducts, and spherical or oval ampullae; body wall thickened and somewhat folded at pore, often with a circular groove surrounding pore (but details not clear in available material); ampullae 30–60 µm long, 25–70 µm wide; sperm random or as loose bundles in ampullae.

Remarks.—This species is distinguished from *T. mastix* and *T. columbiensis* by its characteristic, slender penes (Fig. 1D), which, however, are not as long as those of *T. flexus,* n. sp. (see below).

The complex spermathecal pores of *T. calvus* (Fig. 1G) are unique within the genus. The corresponding pores are inconspicuous in *T. columbiensis* and *T. flexus,* and absent in *T. mastix.*

Distribution and habitat.—Known only from the Sacramento-San Joaquin Delta in California, where it is commonly associated with the following invertebrates (W. C. Fields, Jr., pers. comm.): *Corbicula fluminea, Corophium stimpsoni, Anisogammarus ramellus, Limnodrilus angustipenis, L. hoffmeisteri, Bothrioneurum vejdovskyanum, Aulodrilus limnobius, Nereis limnicola,* and *Prostoma graecense.* Freshwater muddy sediments.

Teneridrilus flexus Erséus & Hiltunen, new species

Fig. 2

Type material.—USNM 123381, holotype, whole-mounted specimen from St. Marys River, exit channel from Lake Superior, Chippewa Co., Michigan, U.S.A. (June 1985, D. W. Schloesser). USNM 123382–123383, paratypes, 2 whole-mounted specimens (one represented by fragments only) from type locality.

Etymology.—The epithet "*flexus*" is Latin for "winding" and refers to the flexible shape of the penes in this species.

Description.—Length of holotype 4.1 mm, about 32 segments (worm coiled and distorted), paratypes not complete. Width at

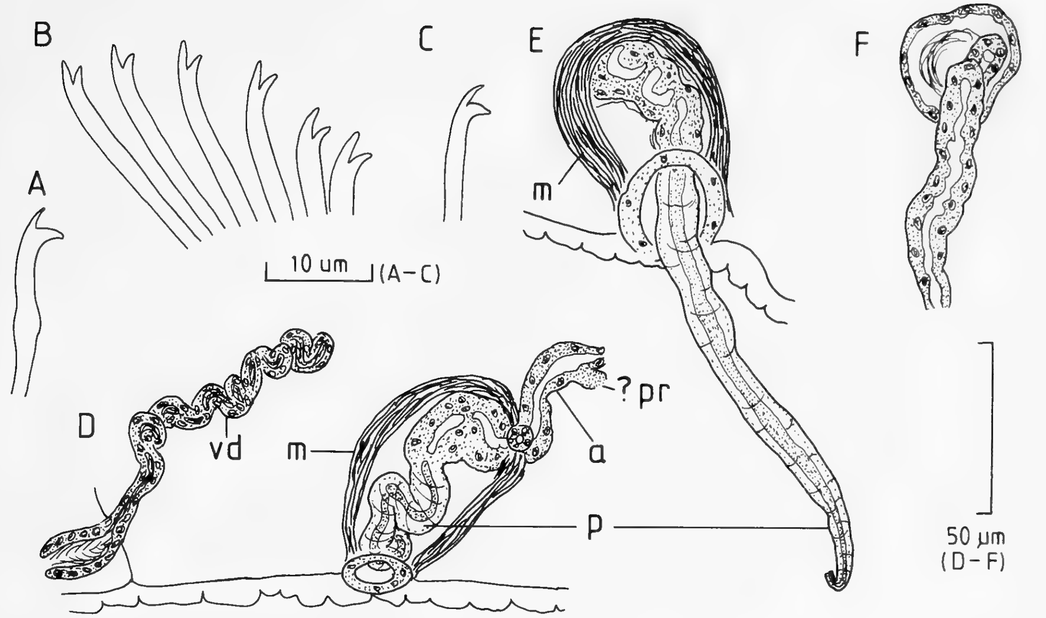


Fig. 2. *Teneridrilus flexus* Erséus & Hiltunen, n. sp.: A, Chaeta from segment II; B, Bundle of chaetae from segment V; C, Chaeta from postclitellar segment; D, Male genitalia from one side of much distorted specimen (paratype), with prostate gland (if present at all?) and vas deferens detached from atrium; E, Copulatory organ of other paratype, with penis protruded; F, Spermatheca. Abbreviations: a atrium; m muscular bulb; p penis; ?pr possible attachment of prostate gland; vd vas deferens.

XI (compressed specimens) 0.24–0.25 mm. Prostomium somewhat triangular, small. Body wall without adhering particles. Clitellum extending over XI–XII. Chaetae all bifid, those of II (Fig. 2A) stout, about 30 μm long, about 2 μm thick, 2–3 per bundle, with distal tooth distinctly thinner and shorter than proximal. Chaetae of segments III through VII or thereabouts (Fig. 2B) clearly longer than those of II, 40–47 μm long, 2.0–2.5 μm thick, 4–6 per bundle, with distal tooth about as thick as the proximal, but clearly longer. Chaetae of mid-body and posterior part of worm (Fig. 2C) about 35 μm long, about 1.5 μm thick, 1–3 per bundle (bundles sometimes missing?), somewhat similar in shape to those of II. Chaetae absent ventrally in XI. Male and spermathecal pores paired, ventrally in XI and X, respectively, but exact position in relation to chaetal lines difficult to see in available material.

Mouth and pharynx modified as in *T. calvus* (see Fig. 1A); esophagus and gut filled with sediment along most of worm. Pharyngeal glands not observed. Male genitalia (Fig. 2D–E) paired. Vas deferens about 5–7 μm wide, longer than atrium, but detached from atrium in the paratype, where it is best visible (Fig. 2D). Atrium inconspicuous (visible only in one paratype; Fig. 2D), slender, about 40 μm long, 9–11 μm wide, with non-muscular outer lining and virtually non-granulated inner epithelium. Prostate gland not observed, but a small structure may be remains of a prostate stalk in (much distorted) paratype (Fig. 2D:?pr). Atrium entering heavily muscular bulb, interior of which is a hollow sac with a very long, tapering, flexible penis. Penis about 150–200 μm long, 15–20 μm wide at base, only about 5 μm wide at tip, either coiled and retained within sac (Fig. 2D) or protruding through male pore, reaching far out from worm (Fig.

2E). Penis appearing somewhat cuticularized, but distinct sheath not formed. Spermathecae (Fig. 2F) small, with very slender ducts, 80–90 μm long, 12–15 μm wide, and round or oval ampullae, 35–40 μm long, 30–35 μm wide. Sperm as loose bundle or random mass in ampullae.

Remarks.—This species is easily distinguished from the closely related *T. calvus* by its clearly longer penes and more slender spermathecal ducts (cf. Figs. 1–2).

Distribution.—Known only from type locality (St. Marys River).

Discussion

Aulodrilus paucichaeta Brinkhurst & Barbour, 1985, known from freshwater marshes in Maryland (and possibly North Carolina), is a very large form, up to 50 mm long, which has some features in common with these smaller *Teneridrilus* species. The small atria, intimately associated with large, spherical, muscular penial bulbs, the wedge to spherical shaped penes, and the bundled sperm in the spermathecae make *A. paucichaeta* similar to the taxa treated here. However, in *A. paucichaeta* the chaetae of segment II are not much different from those of the following segments, and the pharynx does not appear to be modified in the *Teneridrilus* manner (observations on some of the original specimens of *A. paucichaeta* in Brinkhurst's collection). Therefore, the species is excluded from *Teneridrilus.*

The European *Peipsidrilus,* established by Timm (1977) for *P. pusillus* Timm, 1977, later revised by Finogenova (1983) to include *Umbadrilus saamicus* Timm, 1978 (described in Timm & Popchenko 1978), and further revised by Giani et al. (1984) to include *Neoaulodrilus libanus* Giani et al., 1982, is probably closely related to *Teneridrilus.* The three species of *Peipsidrilus* are also small freshwater forms (length 6–8 mm), with simple atria and small penes enclosed in muscular sacs. In *P. pusillus,* the chaetae of segment II, as well as those of the postclitellar segments, have teeth that are equally long, whereas the chaetae of other segments have distal teeth that are longer than the proximal ones (Finogenova 1983). This is noteworthy, as it foreshadows the state in *Teneridrilus,* in which the distal tooth of the segment II chaetae is shorter than the proximal. Similarly, although none of the descriptions of *P. pusillus* (Timm 1977, Finogenova 1983) mentions any modification of the feeding apparatus, the original drawing by Timm (1977:fig. 1) gives the impression that the pharynx is slightly wider than in other tubificids, and thus appears transitional toward the modification seen in *Teneridrilus.* These circumstances suggest that *P. pusillus* in fact may be the plesiomorphic sister taxon to *Teneridrilus,* but whether the two genera should be united cannot be determined until the states of these characters (chaetae of II and feeding apparatus) in all species of *Peipsidrilus* have been carefully reexamined.

The taxa discussed so far are only a part of a whole complex within the Tubificinae characterized by rather simple atria and penes, and by a tendency toward bearing random sperm instead of spermatozeugmata in the spermathecae. Some loose sperm were observed in the spermathecae of *T. columbiensis* by one of us (C.E.) but the significance of this is unclear until tubificines with the same feature are examined. Genera involved in this complex are *Aulodrilus* Bretscher (Giani et al. 1984), *Isochaetides* Hrabě emend., Brinkhurst (Brinkhurst 1984, 1986a), *Peipsidrilus* Timm (1977), *Krenedrilus* Dumnicka (Giani et al. 1990), and *Sketodrilus* Karaman, 1976. The morphological features of these often appear to be plesiomorphic and the species in question are thus likely to be less derived Tubificinae. However, some of the species may be advanced members of the subfamily; i.e., their lack of genital complexity is due to regression linked with reduction in body size or modification in reproductive strategy (see comments on *T. mastix* in Introduction).

For instance, some species of *Aulodrilus* combine relatively simple genitalia with presumed advanced traits such as modified and very numerous chaetae, tube-dwelling, and asexual reproduction. Phylogenetic analysis to determine such questions should be attempted after some of the generic definitions have been clarified.

The scarcity of unequivocal apomorphic states has made it difficult to resolve the phylogenetic relationships within the lower Tubificinae, and the generic classification has to a great extent represented phenetic similarity and unique combinations of characters rather than monophyletic groups based on synapomorphies—a statement that unfortunately is true also for many other tubificids. In the present paper, we do not attempt to rectify this difficulty for other genera, but we claim that there is evidence that the four *Teneridrilus* species constitute a true monophyly.

Acknowledgments

We are grateful to Dr. W. C. Fields, Jr. for placing oligochaete material at our disposal, and to Ms. Barbro Löfnertz and Ms. Aino Falck-Wahlström (University of Göteborg) for technical assistance. This paper is Contribution 742 of the National Fisheries Research Center–Great Lakes, U.S. Fish and Wildlife Service, Ann Arbor, Michigan 48105.

Literature Cited

Brinkhurst, R. O. 1978. Freshwater Oligochaeta in Canada.—Canadian Journal of Zoology 56: 2166–2175.

———. 1984. A revision of the Tubificidae and Lycodrilidae (Annelida, Oligochaeta) known from Lake Baikal.—Canadian Journal of Zoology 62: 494–509.

———. 1986a. Guide to the freshwater aquatic microdrile oligochaetes of North America.—Canadian Special Publication of Fisheries and Aquatic Sciences 84:1–259.

———. 1986b. Taxonomy of the genus *Tubificoides* Lastochin (Oligochaeta, Tubificidae): Species with bifid setae.—Canadian Journal of Zoology 64:1270–1279.

———, & M. T. Barbour. 1985. A new species of *Aulodrilus* Bretscher (Oligochaeta:Tubificidae) from North America.—Proceedings of the Biological Society of Washington 98:931–934.

———, & R. J. Diaz. 1985. *Isochaetides columbiensis,* new species (Oligochaeta:Tubificidae) from the Columbia River, Oregon.—Proceedings of the Biological Society of Washington 98:949–953.

Erséus, C., & Qi Sang. 1985. Two aberrant Tubificidae (Oligochaeta) from Pearl River in the People's Republic of China.—Hydrobiologia 127: 193–196.

Finogenova, N. P. 1983. A revision of the genera *Peipsidrilus* Timm, 1977 and *Umbadrilus* Timm, 1978 (Tubificidae, Oligochaeta). Pp. 199–203 *in* Limnologicheskie issledovaniya na zalive Onezhskogo ozera Bol'shoye Onego:Sbornik nauchnykh trudov. Academy of Sciences U.S.S.R., Zoological Institute, Leningrad. [In Russian.]

Giani, N., C. Erséus, & E. Martinez-Ansemil. 1990. Redefinition of the subterranean genus *Krenedrilus* Dumnicka with a redescription of *K. papillatus* Dumnicka, 1983 and the description of two new species.—Stygologia 5:55–65.

———, E. Martinez-Ansemil, & R. O. Brinkhurst. 1984. Revision du statut taxonomique des Aulodrilinae (Tubificidae, Oligochaeta).—Bulletin de la Societe d'Histoire Naturelle de Toulouse 120:17–22.

———, E. Martinez-Ansemil, Z. Moubayed, & A. Dia. 1982. Les Oligochetes aquatiques du Liban. I. *Neoaulodrilus libanus* n. g., n. sp. et *Nais iorensis* Pataridze.—Annales de Limnologie 18:179–190.

Holmquist, C. 1985. A revision of the genera *Tubifex* Lamarck, *Ilyodrilus* Eisen, and *Potamothrix* Vejdovsky & Mràzek (Oligochaeta, Tubificidae), with extensions to some connected genera.—Zoologische Jahrbücher (Systematik) 112: 311–366.

Karaman, S. 1976. The second contribution to the knowledge of the freshwater Oligochaeta of Slovenia.—Bioloski Vestnik 24:201–207.

Timm, T. 1977. *Peipsidrilus pusillus* gen. n. sp. n. (Oligochaeta, Tubificidae).—Eesti NSV Teaduste Akadeemia Toimetised 26 (Biologia):279–283.

———, & V. Popchenko. 1978. The aquatic Oligochaeta of the Murmansk region. Pp. 71–132 *in* Hydrobiological researches VII. Seasonal phenomena in fresh-water biology. Academy of Sciences of the Estonian S.S.R., Institute of Zoology and Botany, Tartu. [In Russian, with English summary.]

(CE) Zoo-tax, Swedish Museum of Natural History, Stockholm, and (postal address) Department of Zoology, University of Göteborg, Box 25059, S-400 31 Göteborg, Sweden; (JKH and DWS) National Fisheries Research Center–Great Lakes, 1451 Green Road, Ann Arbor, Michigan 48105; (ROB) Institute of Ocean Sciences, P.O. Box 6000, Sidney, British Columbia V8L 4B2, Canada.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 847–853

ADDITIONAL RECORDS OF STOMATOPOD CRUSTACEANS FROM ISLA DEL COCO AND GOLFO DE PAPAGAYO, EAST PACIFIC OCEAN

David K. Camp and Hans G. Kuck

Abstract.—Four species of stomatopod crustaceans are reported from Isla del Coco, East Pacific Ocean: *Gonodactylus zacae* Manning, 1972; *Pseudosquilla adiastalta* Manning, 1964; *Crenatosquilla oculinova* (Glassell, 1942); and *Heterosquilloides mccullochae* (Schmitt, 1940). Three of the species, *G. zacae, C. oculinova,* and *H. mccullochae,* are reported from Isla del Coco for the first time. The only other stomatopod known from there is *Neocoronida cocosiana* (Manning, 1972). A monodactyla postlarva, tentatively assigned to *P. adiastalta,* is briefly characterized and illustrated. Records from the Golfo de Papagayo, Costa Rica, of *Squilla panamensis* Bigelow, 1891, and the poorly known *S. biformis* Bigelow, 1891, are also presented. The original definition of *Crenatosquilla* Manning, 1984, contained errors that are corrected here. *Heterosquilloides mccullochae* is shown to differ from the current definition of every family in the superfamily to which the species is assigned.

Isla del Coco is an isolated oceanic island located at 5°32′57″N, 86°59′17″W, approximately 500 km southwest of Costa Rica and 630 km northeast of the Galápagos Archipelago (see Bakus 1975, Hogue & Miller 1981, and Abele & Kim 1984 for general information, biogeography, and ecology of the island; see Hertlein 1963 for faunal checklist and bibliography). Although the molluscan fauna of Isla del Coco has been extensively sampled (e.g., Hanna & Hertlein 1938, Hertlein 1963, Shasky 1983), little effort has been directed toward surveying the Stomatopoda until now. Collections made during 1932–1933 and 1938 by the R/V *Velero III* of the Allan Hancock Foundation, University of Southern California (AHF), proved that a rich crustacean fauna existed on and around the island, but no stomatopods were collected (John S. Garth and Janet Haig, AHF, pers. comm.). Hertlein (1963) reported fifty species of Crustacea from the island, but none were stomatopods. Few additional species of crustaceans have been reported from Isla del Coco since that time (Manning 1972, Abele & Kim 1984).

Forty-two species of stomatopods are known to occur in the tropical eastern Pacific (Salgado-Barragán & Illescas-Monterroso 1987:159). Reaka & Manning (1980) reviewed the stomatopod fauna of Pacific Costa Rica and nearby offshore islands. They listed only two species known from Isla del Coco: *Neocoronida cocosiana* (Manning, 1972), the only stomatopod endemic to the island, and *Pseudosquilla adiastalta* Manning, 1964, the only species of *Pseudosquilla* known from the East Pacific Region (Reaka & Manning 1987:15).

In 1988 one of us (HGK) participated in a general collecting expedition to Parque Nacional Isla del Coco (Fig. 1) aboard the schooner M/S *Victoria af Carlstad.* The present report is principally based on small collections of stomatopods taken during that trip by personnel from the Natural History Museum of Los Angeles County (LACM) using SCUBA (3–43 m depths). Also included in this note are specimens collected

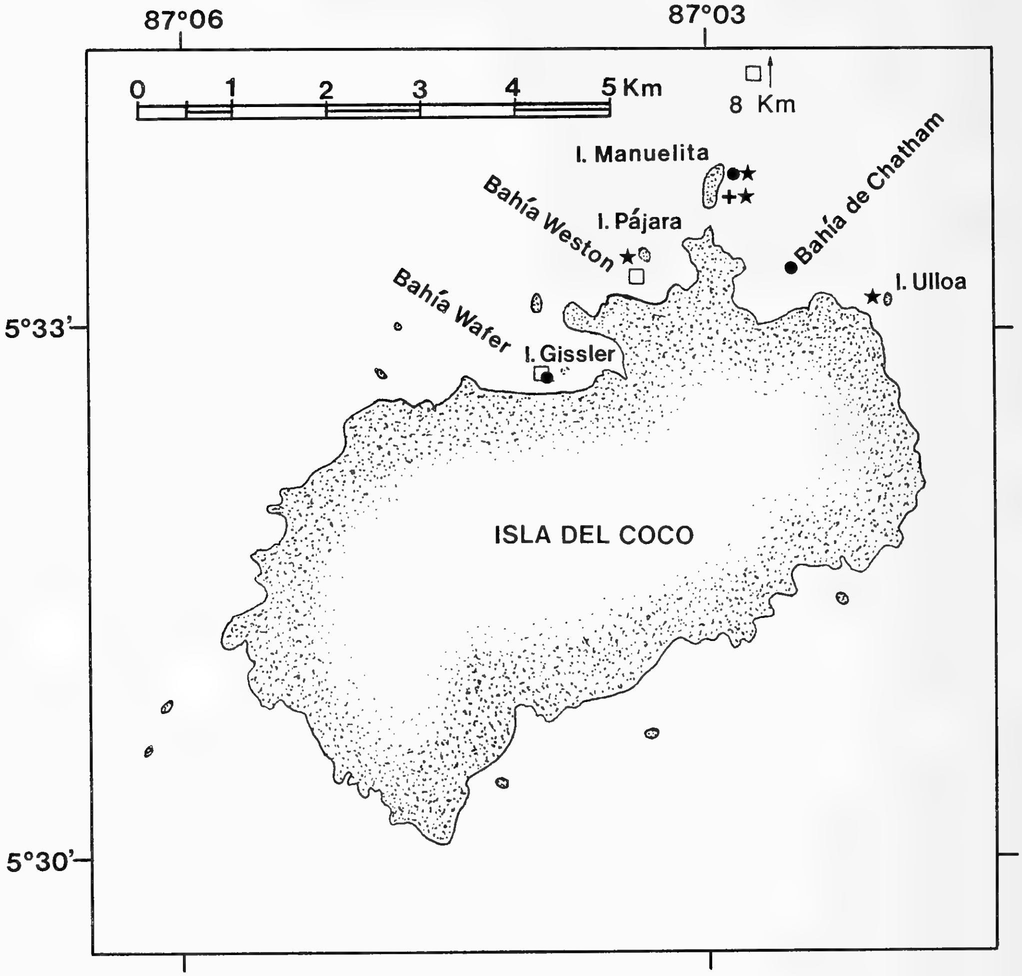


Fig. 1. Isla del Coco, showing sites at which stomatopods were collected. Closed circle = *Gonodactylus zacae*; Open square = *Pseudosquilla adiastalta*; Cross = *Crenatosquilla oculinova*; Star = *Heterosquilloides mccullochae*.

at Isla del Coco by Kirstie Kaiser, Michel Montoya, and Douglas von Kriegelstein using trawl, dredge, and tangle net (18–46 m depths) during March 1989 and donated to LACM. Finally, specimens captured by trawling (66–276 m depths) in the Golfo de Papagayo, Costa Rica (Fig. 2), by William Bussing aboard the Japanese vessel R/V *Nisshin Maru* during 1987–1988 are listed.

The waters at Isla del Coco abound with suitable habitats for stomatopods. During the 1988 trip, inclement weather prevented collecting anywhere but in and around the protected bays of the north side of the island. Specimens reported here were found in several habitats. Some specimens were collected in sand and rubble beneath dead patches of the coral *Porites lobata* Dana, 1846. Others were collected from deep within the branches of living colonies of the much less abundant *Pocillopora capitata* Verrill, 1864. Many specimens were found in the medium-grained, light brown to white sand under basaltic rocks in the wide talus zones at the bases of the many islets surrounding Isla del Coco. The sheer rock walls of some islets and seamounts have many crevices and holes with stomatopods, but

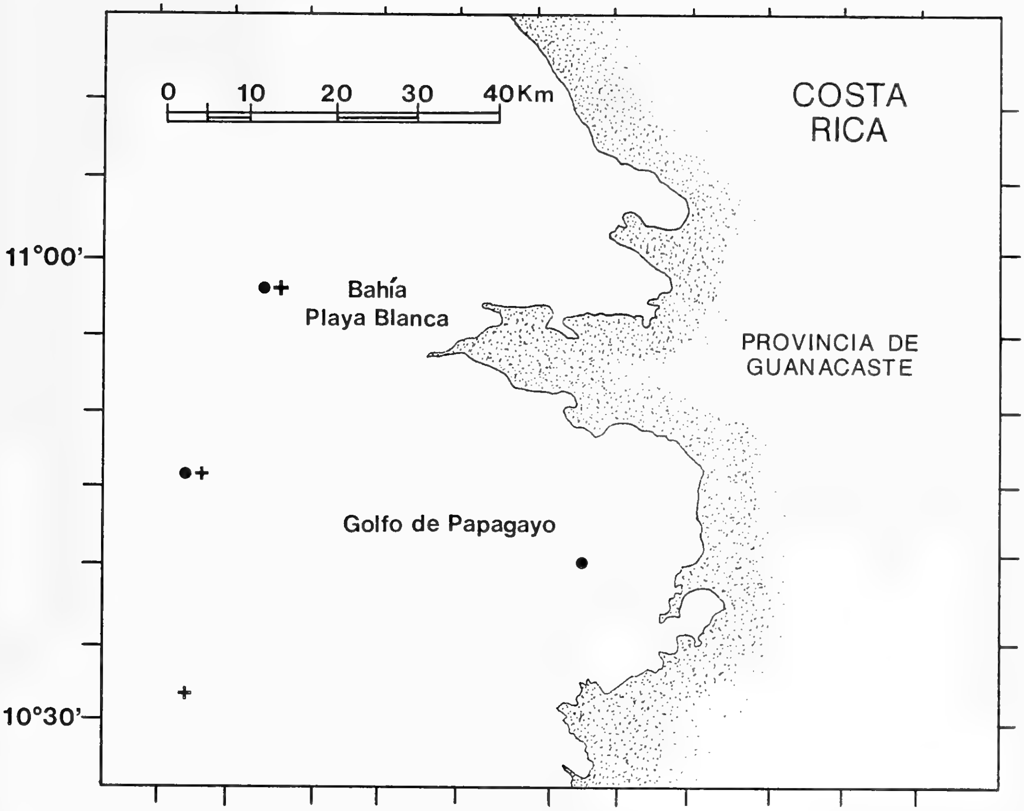


Fig. 2. Golfo de Papagayo, Pacific coast of Costa Rica, showing sites at which stomatopods were collected. Cross = *Squilla biformis*; Closed circle = *Squilla panamensis*.

specimens are difficult to collect because of the depth to which the stomatopods recede within the crevices and because of the strong currents in those habitats, which make diving difficult.

Carapace length (cl) is measured on the midline and does not include the rostral plate, but total length does include the plate. All specimens have been deposited at LACM and at the Florida Marine Research Institute, Marine Invertebrate Collection (catalog number prefix FSBC I).

Family Gonodactylidae Giesbrecht, 1910

Gonodactylus zacae Manning, 1972

Material.—Isla del Coco: Northeast of Isla Manuelita, seamount, 5°33.88′N, 87°02.78′W, depth 18–43 m; leg. H. G. Kuck and A. Jahn, 29 Apr 1988; 1 male, cl = 2.5 mm; LACM 88-38.1.—Bahía Wafer, *Porites* reef, east side of Isla Gissler, 5°32.8′N, 87°03.82′W, depth 3–6 m; leg. H. G. Kuck and R. W. Peck, 25 Apr 1988; 1 female, cl = 4.3 mm; FSBC I 34187 (LACM 88-12).—Bahía de Chatham, depth 46 m; leg. K. Kaiser, 26 Mar 1989; 1 male, cl = 2.7 mm; LACM 89-28.1.

Remarks.—The specimens reported here agree well with the illustrations of *G. zacae* presented by Manning (1974:fig. 1), except that the lateral margins of the ocular scales are not as concave as those he depicted. The species has not been reported before from Isla del Coco, but its occurrence there is not surprising. *Gonodactylus zacae* is thought to be the most widely distributed gonodactylid and the most common *Gonodactylus* in the East Pacific Region (Manning 1974: 104, Reaka & Manning 1980:9).

Family Pseudosquillidae Manning, 1977
Pseudosquilla adiastalta Manning, 1964

Material.—Isla del Coco: Bahía Wafer, *Porites* reef, east side of Isla Gissler, 5°32.8′N, 87°03.82′W, depth 3–6 m; leg. H. G. Kuck and R. W. Peck, 25 Apr 1988; 1 male, 2 females, cl = 4.6–6.7 mm; LACM 88-12.1.—Bahía Weston, *Porites* reef, southwest side of Isla Pajara, 5°33.28′N, 87°03.45′W, depth 9–15 m; leg. R. W. Peck and H. G. Kuck, 27 Apr 1988; 1 male, cl = 14.8 mm; FSBC I 34188 (LACM 88-23).—Approx. 8 km north of Bahía de Chatham, 5°38.0′N, 87°02.55′W, from stomach of yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788) (approx. length 1 m, approx. weight 165 kg, hook and line); leg. M. Dell' Aquila, 30 Apr 1988; 1 monodactyla postlarva, cl = 4.4 mm; LACM 88-41.1

Remarks.—The subadult male with carapace length 4.6 mm (LACM 88-12.1) lacks the two large patches of dark chromatophores on the carapace that are usually characteristic of adults (see Manning 1964:fig. 1). The white spots on that specimen are relatively larger than similar spots on adults and are positioned evenly over the dorsal surface of the entire body.

We have assigned to this species the postlarva (LACM 88-41.1) found in the stomach contents of a tuna caught north of Isla del Coco, even though the specimen is not in good condition and the postlarval stage of *P. adiastalta* has never been described. Manning (1969) reviewed the morphological characteristics of postlarvae of the Atlantic species *P. ciliata* (Fabricius, 1787) and *P. oculata* (Brullé, 1837). The specimen from off Isla del Coco differs from *P. ciliata* in the same way that *P. oculata* does (see Manning 1969:270, 277). The specimen is more similar to the postlarva of *P. oculata,* which shares the following characteristics. Total length of the specimen is 25 mm. The eyes are large, with broadened cornea, and the rostral plate is cordiform (Fig. 3a). The sixth abdominal somite has submedian spines but lacks intermediate spines (Fig. 3b). The median cleft of the telson is pronounced. The outer margin of the uropod is armed with ten movable spines, and the proximal segment of the outer ramus of the uropod is more than three times the length of the distal segment (Fig. 3b, d). The outer spine of the basal prolongation of the uropod is longer than the inner, and the inner margin of the outer spine of the prolongation is angled. There are posterolateral spines on the fifth and sixth abdominal somites; however, unlike the postlarva of *P. oculata,* the fourth somite is acutely angled posterolaterally and lacks a spine (Fig. 3c). A complete description of the postlarva of *P. adiastalta* must await collection of more suitable material from the area.

Family Squillidae Latreille, 1803
Crenatosquilla oculinova (Glassell, 1942)

Material.—Isla del Coco: East side of Isla Manuelita, depth 18 m; leg. M. Montoya and K. Kaiser, 21 Mar 1989; 1 female, cl = 5.1 mm; LACM 89-29.1.

Remarks.—The specimen agrees well with Glassell's (1942) description of the species. Manning (1984) erected the monotypic genus *Crenatosquilla* for *Squilla oculinova.* His definition of *Crenatosquilla* contained two errors: 1) specimens of *C. oculinova* have three epipods on the maxillipeds, not four as Manning stated; and 2) the dorsal ridge of the carpus of the raptorial claw, rather than being indistinct, is prominent and ends in a distal tooth (see Glassell 1942:54).

Crenatosquilla oculinova has not been reported before from Isla del Coco. Reaka & Manning (1980:16) reported the species to be the most common stomatopod collected in their study of Pacific Costa Rica.

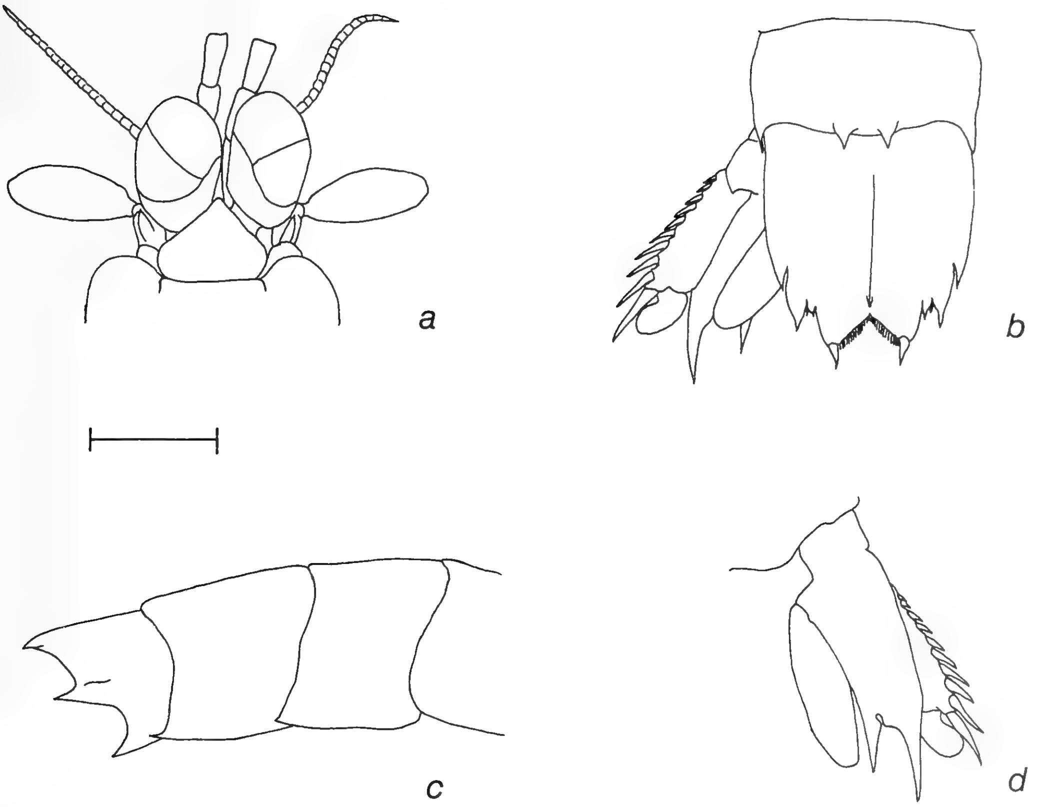


Fig. 3. *Pseudosquilla adiastalta* postlarva, LACM 88-41.1: a, Anterior portion of body, dorsal view, setae and antennular flagella omitted; b, Sixth abdominal somite, telson and left uropod, dorsal view, setae omitted; c, Abdominal somites 3–6, lateral view of right side; d, Left uropod, ventral view, setae omitted. (Scale line = 2 mm.)

Squilla biformis Bigelow, 1891

Material.—Costa Rica, Provincia de Guanacaste: Golfo de Papagayo, 10°45.0′N, 86°12.0′W–10°46.2′N, 86°13.0′W, depth 206–208 m; leg. W. Bussing, R/V *Nisshin Maru,* 7 Dec 1987; 1 female, cl = 28.3 mm; FSBC I 34185 (LACM 87-217).—Golfo de Papagayo, 10°30.5′N, 86°13.6′W–10°32.0′N, 86°14.6′W, depth 268–276 m; leg. W. Bussing, R/V *Nisshin Maru,* 10 Dec 1987; 2 females, 1 male, cl = 30.5–33.2 mm; LACM 87-216.1.—Bahía Playa Blanca, northwest of Golfo de Papagayo, 10°58.4′N, 86°07.5′W–10°00.1′N, 86°08.1′W, depth 131–139 m; leg. W. Bussing, R/V *Nisshin Maru,* 9 Jan 1988; 1 female, cl = 30.8 mm; LACM 88-108.1.

Remarks.—*Squilla biformis* is captured infrequently despite its rather wide distribution in the tropical East Pacific. It has been reported only from the Golfo de California, the Golfo de Panamá, and off Peru (Manning 1974:108).

Squilla panamensis Bigelow, 1891

Material.—Costa Rica, Provincia de Guanacaste: Golfo de Papagayo, 10°45.0′N, 86°12.0′W–10°46.2′N, 86°13.0′W, depth

206–208 m; leg. W. Bussing, R/V *Nisshin Maru,* 7 Dec 1987; 1 male, cl = 24.2 mm; FSBC I 34186 (LACM 87-217).—Golfo de Papagayo, 10°40.7′N, 85°46.3′W–10°42.1′N, 85°47.2′W, depth 66–67 m; leg. W. Bussing, R/V *Nisshin Maru,* 13 Nov 1987; 2 females, cl = 14.9–approx. 22 mm (latter damaged), 1 female abdomen and telson only, 1 male, cl = 22.7 mm; LACM 87-214.1.—Bahía Playa Blanca, northwest of Golfo de Papagayo, 10°58.4′N, 86°07.5′W–10°00.1′N, 86°08.1′W, depth 131–139 m; leg. W. Bussing, R/V *Nisshin Maru,* 9 Jan 1988; 1 female, 1 male (abdomens and telsons only); LACM 88-108.1

Remarks.—This species is known from Bahía Petatlán, México, to Tumbes, Peru (Manning 1974:108).

Family Lysiosquillidae Giesbrecht, 1910

Heterosquilloides mccullochae (Schmitt, 1940)

Material.—Isla del Coco: *Porites* reef, northeast side of Isla Manuelita, 5°33.87′N, 87°02.12′W, depth 12–20 m; leg. R. W. Peck and H. G. Kuck, 26 Apr 1988; 2 females, cl = 10.6–14.8 mm; LACM 88-19.1.—*Porites* reef, east side of Isla Manuelita, 5°33.8′N, 87°02.07′W, depth 9–12 m; leg. H. G. Kuck and R. W. Peck, 26 Apr 1988; 1 male, cl = 10.3 mm; LACM 88-20.1.—Bahía Weston, west side of Isla Pajara, 5°33.48′N, 87°03.40′W, depth 21 m; leg. K. Burke, 27 Apr 1988; 1 male, cl = 9.8 mm; LACM 88-24.1.—Bahía de Chatham, boulder talus zone at base of wall, west side of Isla Ulloa, 5°33.20′N, 87°02.07′W, depth 8–26 m; leg. R. W. Peck, H. G. Kuck, and M. Dell' Aquila, 29 Apr 1988; 1 female, cl = 13.8 mm; FSBC I 34189 (LACM 88-36).

Remarks.—The specimens agree well with descriptions of the species published by Schmitt (1940:197) and Manning (1969:55); all have the distinctive chromatophore pattern illustrated by Schmitt. *Heterosquilloides mccullochae,* although relatively uncommon, has the widest distribution of any stomatopod (Reaka & Manning 1987:15). It is a circumtropical species, known from the East Pacific, West Atlantic, Central Atlantic (Ascension Island), and Indian oceans (Reaka & Manning 1980:11, 1987:15).

A new family might have to be erected to receive this species. Manning (1980:367–368) revised the superfamilies, families, and genera of Recent stomatopods. Characters of *Heterosquilloides mccullochae* do not fit the definition of any of the three families (Lysiosquillidae, Coronididae, and Nannosquillidae) that he placed within the superfamily Lysiosquilloidea, nor do the characters fit the more recently discovered Erythrosquillidae, also tentatively placed in the Lysiosquilloidea (see Manning & Bruce 1984:332). *Heterosquilloides mccullochae* differs from members of the Lysiosquillidae and the Erythrosquillidae by having the endopods of the first two walking legs subcircular rather than slender and strap-like, from members of the Nannosquillidae by lacking a proximal fold on the outer margin of the uropodal endopod, and from members of the Coronididae by lacking the basal inflation of the dactylus of the raptorial claw. Because of the morphological characteristics and unusually broad distributional pattern of *Heterosquilloides mccullochae,* the species is certainly unique within the Lysiosquilloidea.

Acknowledgments

The 1988 collecting trip in which HGK participated was sponsored by the Ichthyology Section of the Natural History Museum of Los Angeles County, Los Angeles, California, and funded by the LACM Life Science Research Fund and the Taylor Research Fund through a grant to Robert J. Lavenberg (Curator of Fishes, LACM). We extend our gratitude to Robert Lavenberg for providing financial support for HGK to participate in the 1988 expedition; Manuel Murillo, Michel Montoya, and William Bussing of the Universidad de Costa Rica, Museo de Zoología for providing lab space, specimens, logistical support, and hospitality during the 1988 stay of HGK in Costa Rica; Robert W. Peck, formerly of LACM, for his keen eye in spotting stomatopods during many dives off Isla del Coco; the crew of the M/S *Victoria af Carlstad* for excellent logistical support and good companionship during the expedition; John S. Garth and Janet Haig (AHF) for information and data on early AHF expeditions to Isla del Coco; Kirstie Kaiser and Douglas von Kriegelstein for the donation of specimens to LACM; Raymond B. Manning (Smithsonian Institution) for discussion of the familial placement of *Heterosquilloides mccullochae* and for reading an early draft of the manuscript; Joel W. Martin (LACM) for his motivation, guidance to HGK, and editorial comments; Judy Leiby, William G. Lyons, Thomas H. Perkins and James F. Quinn, Jr. (Florida Marine Research Institute, FMRI) for advice about the manuscript; and Llyn French (FMRI) for assistance with the figures.

Literature Cited

Abele, L. G., & W. Kim. 1984. Notes on the freshwater shrimps of Isla del Coco with the description of *Macrobrachium cocoense,* new species.—Proceedings of the Biological Society of Washington 97:951–960.

Bakus, G. J. 1975. Marine zonation and ecology of Cocos Island, off Central America.—Atoll Research Bulletin 179:1–11.

Glassell, S. A. 1942. A new stomatopod crustacean from the west coast of Mexico.—Proceedings of the United States National Museum 92(3138): 53–56.

Hanna, G. D., & L. G. Hertlein. 1938. Land and brackish water Mollusca of Cocos Island.—Allan Hancock Pacific Expeditions 2(8):123–135.

Hertlein, L. G. 1963. Contribution to the biogeography of Cocos Island, including a bibliography.—Proceedings of the California Academy of Sciences 32(8):219–289.

Hogue, C. L., & S. E. Miller. 1981. Entomofauna of Cocos Island, Costa Rica.—Atoll Research Bulletin 250:1–29.

Manning, R. B. 1964. A new West American species of *Pseudosquilla* (Stomatopoda).—Crustaceana 6(4):303–308.

———. 1969. Stomatopod Crustacea of the western Atlantic.—Studies in Tropical Oceanography, Miami, 8:viii + 380 pp.

———. 1972. Three new stomatopod crustaceans of the family Lysiosquillidae from the eastern Pacific region.—Proceedings of the Biological Society of Washington 85(21):271–278.

———. 1974. Stomatopods collected by Th. Mortensen in the eastern Pacific region (Crustacea, Stomatopoda).—Steenstrupia 3(11):101–109.

———. 1980. The superfamilies, families, and genera of Recent stomatopod Crustacea, with diagnoses of six new families.—Proceedings of the Biological Society of Washington 93:362–372.

———. 1984. *Crenatosquilla,* a new genus of stomatopod crustacean from the East Pacific.—Proceedings of the Biological Society of Washington 97:191–193.

———, & A. J. Bruce. 1984. *Erythrosquilla megalops,* a remarkable new stomatopod from the western Indian Ocean.—Journal of Crustacean Biology 4(2):329–332.

Reaka, M. L., & R. B. Manning. 1980. The distributional ecology and zoogeographical relationships of stomatopod Crustacea from Pacific Costa Rica.—Smithsonian Contributions to the Marine Sciences 7:iii + 29 pp.

———. 1987. The significance of body size, dispersal potential, and habitat for rates of morphological evolution in stomatopod Crustacea.—Smithsonian Contributions to Zoology 448:iii + 46 pp.

Salgado-Barragán, J., & C. Illescas-Monterroso. 1987. First record of *Lysiosquilla panamica* Manning, 1977 (Crustacea: Stomatopoda) in the Pacific waters of Mexico.—Revista de Biología Tropical 35(1):159–160.

Schmitt, W. L. 1940. The stomatopods of the west coast of America, based on collections made by the Allan Hancock Expeditions, 1933–38.—Allan Hancock Pacific Expeditions 5(4):129–225.

Shasky, D. R. 1983. New records of Indo-Pacific Mollusca from Cocos Island, Costa Rica.—The Nautilus 97(4):144–145.

(DKC) Florida Marine Research Institute, 100 Eighth Avenue, S.E., Saint Petersburg, Florida 33701-5095; (HGK) Section of Invertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 854–860

A NEW SPECIES OF CHIROSTYLID CRUSTACEAN (DECAPODA: ANOMURA) FROM OFF THE WEST COAST OF NORTH AMERICA

Keiji Baba and Janet Haig

Abstract.—A new chirostylid, *Gastroptychus iaspis,* is described from depths of 600–1189 m off Mexico, California and Oregon. Its affinities to *Gastroptychus defensa* (Benedict, 1902) from the Galapagos Islands are discussed based on examination of two syntypes of that species. This is the fifth species of the genus in the eastern Pacific.

In the course of studying benthic communities of deep hard bottom seamounts Dr. Amatzia Genin of the Hebrew University of Jerusalem, then of the Scripps Institution of Oceanography, has observed specimens of an anomuran crustacean belonging to the chirostylid genus *Gastroptychus* on Jasper Seamount off Baja California. According to him, this chirostylid was a very important member of the seamount community at the 600 to 1100 m depth interval, usually seen on gorgonians and antipatharians (A. Genin, pers. comm.). Two specimens of this chirostylid were collected; one is deposited in the Smithsonian Institution (USNM) and the other in the Allan Hancock Foundation (AHF). The specimens were made available for study by the courtesy of Dr. Genin and Dr. Austin B. Williams of the National Marine Fisheries Service. In the meantime one of us (JH) found that the following specimens were identical with those from the Jasper Seamount: four AHF specimens taken in 950–1189 m off California, and reported by Wicksten (1982:245) as *Chirostylus* sp.; 12 USNM specimens on loan to AHF, collected off Oregon in 914 m by the *Commando,* U.S. Bureau of Commercial Fisheries–AEC Project; and material from British Columbia and Washington described and illustrated as *Chirostylus* sp. by Hart (1982:166, fig. 65). Their identity was confirmed also by K. Baba during a visit to the Allan Hancock Foundation in 1989 and they represent an undescribed species. The measurements of the specimens examined are given in parentheses under "Material," indicating postorbital carapace lengths.

Gastroptychus iaspis, new species
Figs. 1, 2

Chirostylus sp. Wicksten, 1982: 245 (in Table 1).

Chirostylus sp. Hart, 1982: 166, fig. 65.

Type material.—MEXICO: 1 ovig. ♀ (17.7 mm), holotype, AHF 861, Jasper seamount off Baja California (30°25.6′N, 122°43.7′W to 30°25.5′N, 122°44.3′W), 950–840 m, rock dredge, 1 Nov 1986, *Seatomado* Expedition Sta 12; 1 ♂ (26.5 mm), USNM 234412, Jasper Seamount (30°25′N, 122°45′W), 600–800 m, dredge, 20 Oct 1984. CALIFORNIA: 1 ♂ (30.0 mm), 2 ovig. ♀ (24.0, 25.5 mm), AHF 787, W of Tanner Bank (32°46′41″N, 119°59′23″W), 950 m, baited fish traps, 1978, coll. commercial fishing boat; 1 ovig. ♀ (25.0 mm), AHF 7720, off (inside) San Clemente Island (approx. 33°N, 118°W), 1189 m, sablefish trap, 25 July 1977, coll. boat *Pete Boy.* OREGON: 7 ♂ (11.9–18.5 mm), 3 ovig. ♀ (19.8–21.0 mm), 2 ♀ (15.0, 15.4 mm), USNM 243911, SW of Columbia River mouth (46°02.7′N, 124°57.3′W), 914 m, 72-foot shrimp trawl, 30 May 1964, coll. *Commando,* U.S. Bureau of Commercial Fisheries–AEC Project.

Description.—Rostrum nearly one-third to barely one-fourth as long as postorbital carapace length, rostral base laterally ridged, rostral spine curving dorsad. Outer orbital angle rounded. Carapace, excluding rostrum, 1.1–1.2 times as long as its greatest width. Lateral margins strongly convex in posterior two-thirds of length, with distinct constriction at one-third from anterior end, bearing spines as figured (Fig. 1a, b), anterolateral spine much pronounced. Gastric region convex, distinctly separated from cardiac region by wide depression (cervical groove), indistinctly from anterior branchial region, bearing 6 prominent spines in hexagonal arrangement with another spine in center (left posterior spine of hexagon set well back from level of right posterior one in holotype), occasionally accompanied by few additional smaller spines inside, beside or behind hexagon. Mid-cervical groove slightly anterior to midlength of carapace. Anterior branchial region with 2 convexities bordered by deep groove, each with 1 or 2 pronounced central spines, occasionally with small accompanying spine, anterior convexity weakly elevated and indistinctly separated from gastric region, posterior convexity well elevated and bordered by deep posterior groove. Cardiac region indistinctly defined, with pair of prominent anterior spines, usually followed by few small or somewhat pronounced spines. Branchial and intestinal spines as figured (Fig. 1a); elevation along posterior margin of carapace with several erect spines. Pterygostomian flap spinulose, anterior end with prominent spine, occasionally accompanied by second smaller spine behind it.

First segment of abdomen bearing posterior transverse elevation with 5–11 spines (usually 5, 6 or 7, rarely 8, 9 or 11), lacking pleura. Second segment having tergum with low hump-like elevations in transverse line, each elevation with few simple or pointed granules, occasionally lacking granules, pleuron separated by deep groove from tergum, tapering, transversely hollowed, bearing elevation with 1–5 small dorsal spines along anterolateral margin. Third and fourth segments similar, terga feebly elevated, pleura more weakly tapering than preceding; pleuron of third segment with 1 or 2, or, rarely 3 or 4 small posterior marginal spines in addition to terminal one, rarely spineless; that of fourth segment usually tapering, occasionally rounded, with 2 or 3 (rarely 1 or 4) posterior marginal spines or without spines. Fifth segment having pleuron ending in rounded margin, bearing 1–7 (usually 2 or 3) small spines on posterolateral margin, occasionally with 1 or 2 small spines on surface; tergum unarmed. Tergum of sixth segment usually with 3 prominent posterior marginal and 6 dorsal spines, rarely with few more spines; pleuron usually spineless, rarely with few (on surface) to 7 or 8 spines (on posterolateral margin). Telson divided into anterior and posterior lobes, posterior lobe slightly wider than, and barely twice as long as anterior lobe, fully twice as wide as long.

Eyes barely reaching end of rostral spine, cornea dilated and distinctly wider than remaining eyestalk.

Basal segment of antennule simple, spineless. Antennal peduncle having second segment with small distolateral spine, ultimate segment about 3 times as long as penultimate, bearing slender distoventral spine, penultimate segment with tiny distoventral spine; antennal scale rudimentary.

Third maxilliped having coxa with slender but prominent ventral spine; ischium half as long as merus, with 12–22 (average 16) denticles on mesial ridge; merus with dorsodistal spine; carpus with distinct distolateral spine; propodus shorter than merus, with ventral margin somewhat expanded on distal portion.

Sternite at base of third maxilliped bluntly produced on anteromedian margin, usually with pair of small, low spines somewhat posterior to anterior end, rarely with 3 additional spines: 2 on anterior margin and 1 somewhat posterior to left anterior ventral spine. Next sternite at base of cheliped with 2 pairs of strong spines on anterolateral margins, pair of very tiny, tubercle-like spines between first lateral pair, and another pair of larger spines between posterior limits of posterolateral margins.

Chelipeds 5 times as long as carapace, subcylindrical, sparsely provided with long coarse setae. Coxa ventrally bearing well developed distomesial spine and few tubercular processes. Merus with 6 regular rows of spines. Carpus equalling length of palm, with lines of spines continued from merus. Palm, exclusive of spines, 7 times longer than wide, 1.3 times as long as movable finger, bearing 7 regular rows of spines: 2 dorsal, 1 mesial, 1 lateral, 1 ventromesial, and 2 ventral. Fingers largely gaping, slender, subcylindrical; opposable margins with line of tubercular teeth, prominent truncate basal tooth on movable finger opposed to 2 somewhat smaller ones on fixed finger; mesial margin of movable finger with few tiny spines proximally.

Walking legs slender, laterally compressed distally, sparsely provided with stiff setae. First walking leg falling short of end of carpus of cheliped when extended forward; coxa with 2 prominent mesial marginal spines near ventral surface; merus about twice as long as carpus, 1.5 times as long as propodus, bearing 6 rows of spines continued onto carpus; propodus with dorsal, mesial and dorsolateral spines in rows, all small and fixed, dorsolateral ones less numerous; ventral margin with more than 20 movable slender, closely set spinules including distal pair; dactylus distinctly less than one-third length of propodus, terminating in acute curved corneous claw, ventrally bearing 11 or 12 slender spinules. Second walking leg similar to first, third walking leg with longer propodus.

Diameters of ova measuring 1.7 mm in holotype, 1.1–1.2 mm in paratypes.

Male with 2 pairs of gonopods similar to those illustrated for *G. hawaiiensis* Baba, 1977 (see Baba 1977a:fig. 2f, g).

Etymology.—The specific name is a noun in apposition from the Greek "iaspis," jasper, alluding to the type locality.

Remarks.—From the eastern Pacific Ocean four species of *Gastroptychus* are known (Baba 1977b:205). The new species resembles *G. defensa* (Benedict, 1902) from the Galapagos Islands in the arrangement of the gastric spines and the less spinose terga of the abdominal segments. Although the original description of the latter species is brief, the following characters seem unique to *G. defensa*: 1) the carapace has more prominent spines than in *G. iaspis* and fewer interspersed small ones on the posterior dorsal surface; 2) the second abdominal segment bears prominent spines on the tergum, and the next three segments bear distinct spines on the pleura; 3) the telson has a longer posterior lobe (if Benedict's figure 44 is correctly depicted); and 4) the branchial region of the carapace bears less numerous but prominent dorsal spines. In addition, Chace's notes on *G. defensa* (see Haig 1968: 276) concerning the sternite at the base of the cheliped that lacks tubercles between the lateral spines, and the chelipeds that have the spination widely spaced and irregular, also seem helpful to separate it from the new species.

Examination of two syntypes (one male and one female, USNM 20563) of *Gastroptychus defensa* taken from *Albatross* Station 2818, northeast of Indefatigable Island, Galapagos Islands, in 717 m (392 fms), showed that most of the above characteristics are true in the male (12.9 mm in postorbital carapace length) upon which Benedict's description is based. In the female (8.7 mm), however, the carapace, and its posterior half in particular, bears fewer small dorsal spines interspersed among prominent ones; spines on the chelipeds are fewer and widely spaced between spines on rows; the spinules on the abdominal pleura are very reduced in both size and number so as to be discernible only

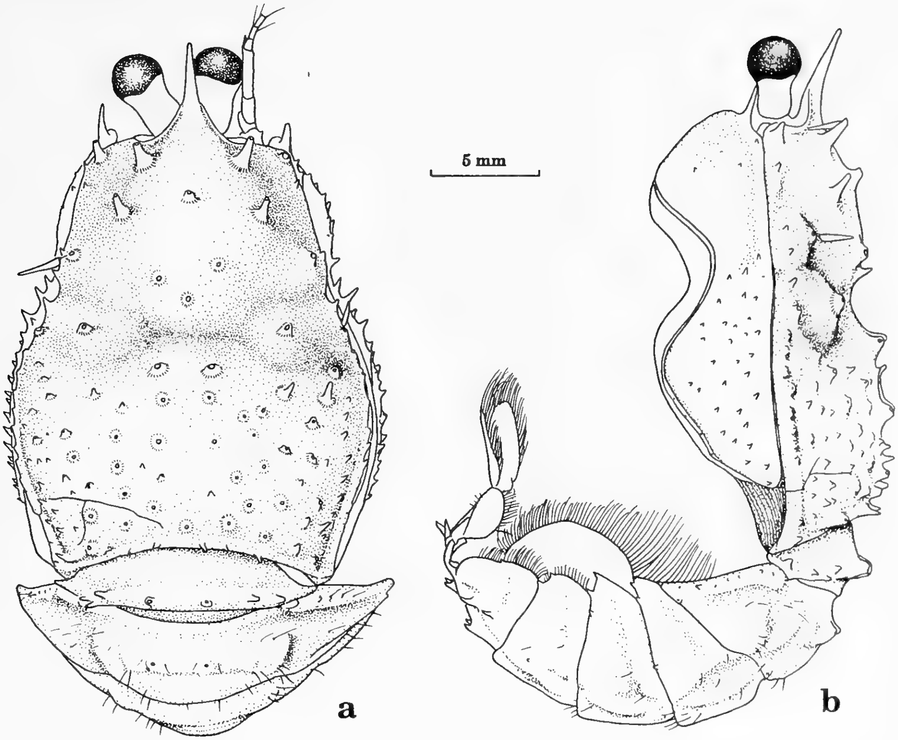


Fig. 1. *Gastroptychus iaspis,* new species, ovigerous female holotype (AHF 861): a, carapace and abdomen, dorsal view; b: same, lateral view.

under high magnification; the terga of the third to fifth segments are elevated from levels of pleura, bearing a distinct spine on the lateral extremity; the sixth abdominal tergum is less spinose; width-length ratio of the posterior lobe of the telson is 1.87 in the female syntype, 1.84 in the male syntype, instead of 2.25 in the new species. In both syntypes, the spination of the carapace is much more pronounced than in the new species; in particular, prominent spines on the posterior half of the carapace are arranged in four longitudinal rows (Fig. 3a, b); chelipeds are comparatively slender, and the spines are arranged more irregularly than in the new species; the carapace is relatively long, the length-width ratios being 1.32 in the male syntype, 1.28 in the female syntype, while 1.18 (average) in the males and 1.13 (average) in the females of the new species.

The hexagonal arrangement of the gastric spines is also known in the Indo-West Pacific *G. hendersoni* (Alcock & Anderson, 1899), though a few additional accompanying spinules are occasionally present within or directly behind the hexagon (Alcock & Anderson 1899: pl. 45: figs. 2, 2a; Baba 1988:14). That species differs from the new species in the very spinose pleura of the abdominal segments.

Color.—Hart (1982:166) noted in detail the color of living specimens from British Columbia and Washington. The San Clemente specimen (AHF 7720) when fresh, was dark carrot-orange in color (M. K. Wicksten, pers. comm.).

Key to the eastern Pacific species of *Gastroptychus*

1. Abdominal segments very spinose 2

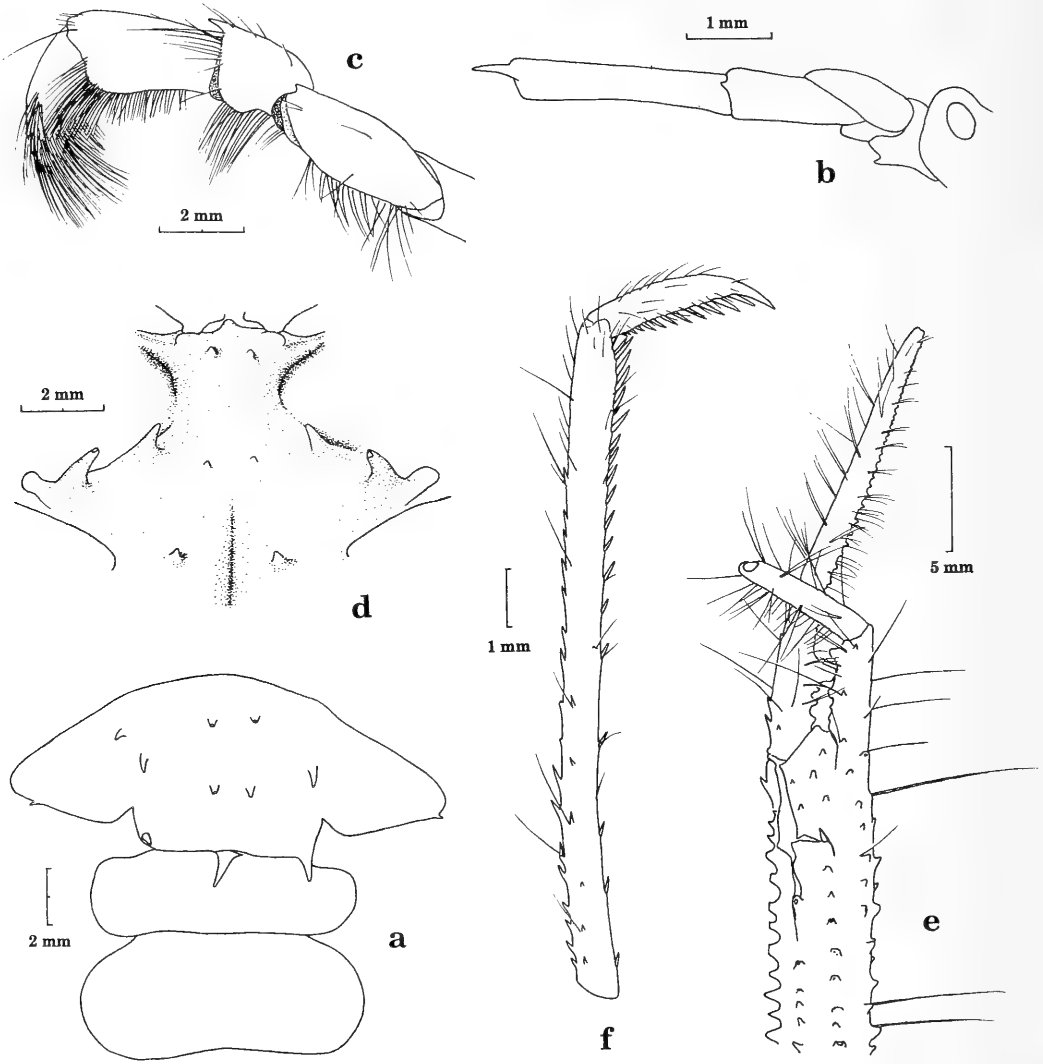


Fig. 2. *Gastroptychus iaspis,* new species, ovigerous female holotype (AHF 861): a, sixth abdominal segment and telson, extended, dorsal view; b, right antennal peduncle, ventral view; c, endopod of left third maxilliped, ischium omitted, lateral view; d, anterior part of sternum; e, distal portion of right chela, dorsal view; f, distal segments of right first walking leg, lateral view.

– At least third and fourth abdominal segments nearly spineless 3

2. Propodus of third maxilliped with distinct dorsal spines . . . . *G. milneedwardsi* (Henderson, 1885:418) (Southern Chile, 732 m)

– Propodus of third maxilliped unarmed *G. cavimurus* Baba, 1977b:202 (Off northern Peru and Ecuador, 388–500 m)

3. Carapace with many small spines interspersed among prominent ones; mid-cervical groove distinctly an-

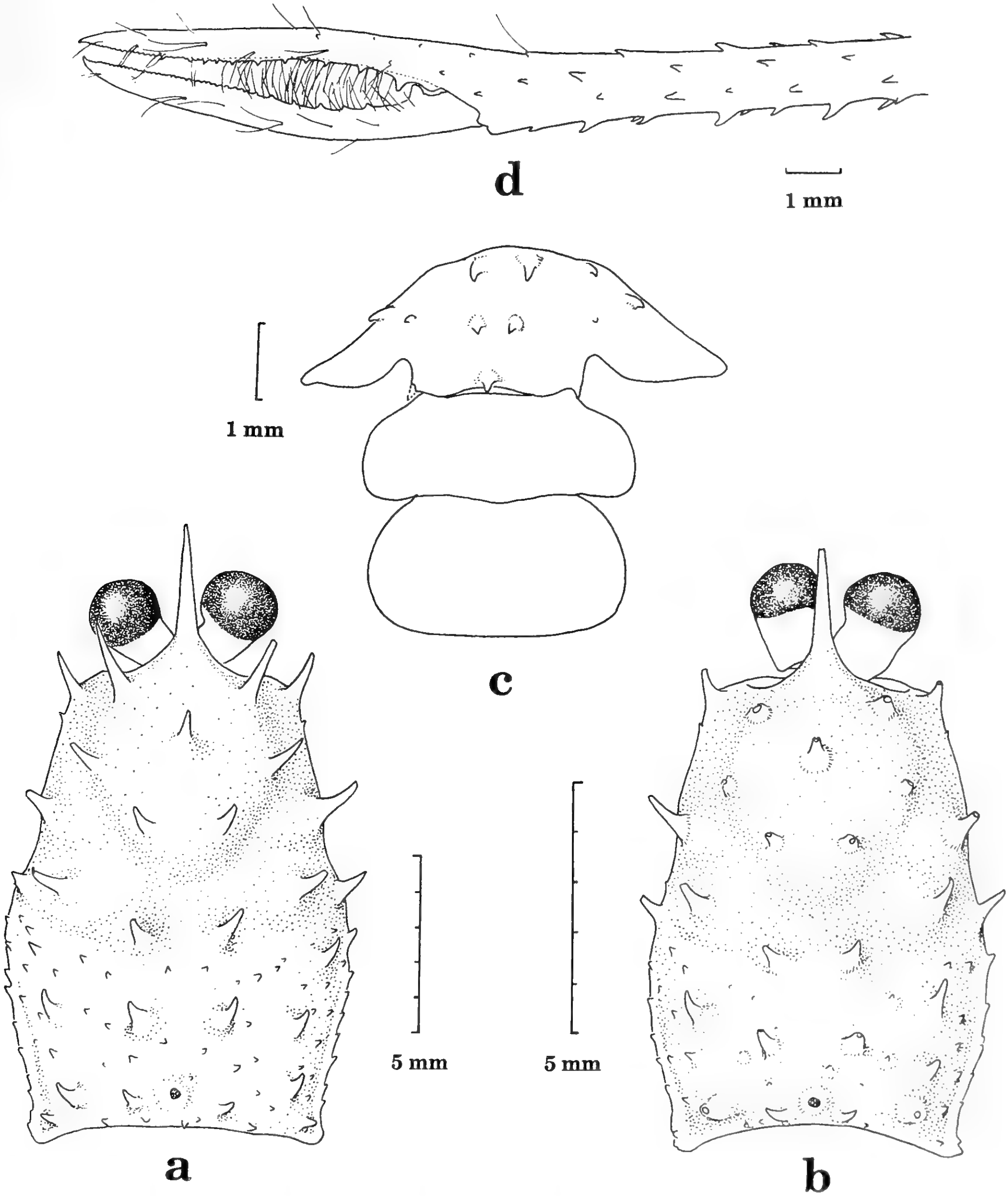


Fig. 3. *Gastroptychus defensa* (Benedict, 1902), syntypes (USNM 20563): a, male carapace, dorsal view; b, female carapace, dorsal view; c, sixth abdominal segment and telson of same, extended, dorsal view; d, distal part of right cheliped of same, dorsal view.

terior to midlength of carapace . . .
. . . . . . *G. perarmatus* (Haig, 1968:272)
(Off California, 229 m)

– Carapace with prominent spines and few interspersed ones, gastric region with prominent spines arranged in hexagon with central spine; mid-cervical groove about at midlength of carapace 4

4. Terga of third to fifth abdominal

segments lacking spines near pleura; sternite at base of cheliped with 2 anterior spines between first lateral marginal spines *G. iaspis,* new species (Off northern Mexico to British Columbia, 600–1189 m)

– Terga of third to fifth abdominal segments provided with spines at least on lateral extremities near pleura; sternite at base of cheliped lacking spine between first lateral marginal spines .... *G. defensa* (Benedict, 1902:299) (Galapagos Islands, 717 m)

Acknowledgments

We thank A. Genin and A. B. Williams for the opportunity of studying the Jasper Seamount specimens. We also thank Raymond B. Manning for loaning type material of *Ptychogaster defensa* Benedict, and A. B. Williams and two anonymous reviewers for critical reading of the manuscript.

Literature Cited

Alcock, A., & A. R. S. Anderson. 1899. Illustrations of the Zoology of the Royal Indian Marine Surveying Steamer "Investigator." Crustacea, part 7, pls. 36–45. Calcutta.

Baba, K. 1977a. Five new species of chirostylid crustaceans (Decapoda, Anomura) from off Midway Island.—Bulletin of the National Science Museum, Tokyo, series A (Zoology) 3(3):141–156.

———. 1977b. *Gastroptychus cavimurus* sp. nov., a new chirostylid (Crustacea, Decapoda, Anomura) from off the western coast of South America.—Zoologische Mededelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden 52(16):201–207.

———. 1988. Chirostylid and galatheid crustaceans (Decapoda: Anomura) of the "Albatross" Philippine Expedition, 1907–1910.—Researches on Crustacea, The Carcinological Society of Japan, Special Number 2:v + 203 pp.

Benedict, J. E. 1902. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species.—Proceedings of the United States National Museum 26:243–334.

Haig, J. 1968. First report of the crab family Chirostylidae off California, and description of a new species of *Chirostylus.*—California Fish and Game 54(4):270–277.

Hart, J. F. L. 1982. Crabs and their relatives of British Columbia.—British Columbia Provincial Museum Handbook 40:iii + 266 pp., 12 pls.

Henderson, J. R. 1885. Diagnoses of the new species of Galatheidea collected during the "Challenger" Expedition.—Annals and Magazine of Natural History (5)16:407–421.

Wicksten, M. K. 1982. Crustaceans from baited traps and gill nets off southern California.—California Fish and Game 68:244–248.

(KB) Faculty of Education, Kumamoto University, Kumamoto, 860 Japan; (JH) Allan Hancock Foundation, University of Southern California, Los Angeles, California 90089-0371.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 861-890

NEW SPECIES, CLARIFICATIONS, AND CHANGES IN STATUS WITHIN *EOSENTOMON* BERLESE (HEXAPODA: PROTURA: EOSENTOMIDAE) FROM THE UNITED STATES

Ernest C. Bernard

Abstract.—Nine new species of *Eosentomon* Berlese are described from the United States: seven from South Carolina (*E. crypticum, E. hargrovei, E. nudilabratum, E. renateae, E. richardi, E. savannahense, E. xenomystax*; one from Arkansas (*E. osageorum*); and one from Michigan (*E. snideri*). *Eosentomon brassicae* Bernard is synonymized with *E. pusillum* Ewing, which is redescribed from the holotype. *Eosentomon pusillum ewingi* Bonet is redescribed and raised to specific rank as *E. ewingi* Bonet.

The genus *Eosentomon* Berlese (Eosentomidae), the largest genus among the Protura, now contains more than 180 species. Recently, Dr. R. J. Snider, Michigan State University, sent to me several thousand specimens of Protura collected from the U.S. Department of Energy's Savannah River Site (SRS) in South Carolina. In this collection were 13 *Eosentomon* species, of which seven are undescribed. In addition, specimens in collections from Arkansas and Michigan were determined to represent other undescribed species of *Eosentomon.* Also, type specimens of *E. pusillum* Ewing and *E. pusillum ewingi* Bonet were redescribed as a step in the evaluation of the South Carolina material.

Materials and Methods

Protura were extracted from soil and litter in Tullgren funnels and preserved in 95% ethanol. Specimens were cleared, expanded, and mounted in a polyvinyl alcohol-lactophenol medium. Slides were dried overnight in an oven at 60°C. Most drawings were made with the use of a drawing tube on an interference-contrast microscope. Female genital structures were interpreted with brightfield and interference-contrast optics, and relative sclerotization of the parts was estimated with a phase-contrast microscope. Head and labral lengths were generally measured in dorsal view. For most species, only females were used for descriptions because of difficulties in identifying males and juveniles. All holotypes and some paratypes are deposited in the National Museum of Natural History (NMNH). Remaining paratypes, except as designated, are in the Apterygote Section of the University of Tennessee Entomology Museum (UTEM). Unless otherwise noted, all specimens were collected by W. W. Hargrove.

Terminology

Terms and designations, except as noted below, are used as given in Tuxen (1964). Szeptycki (1984) has been followed for designations of anterior additional head seta (*aa*), posterior additional head seta (*pa*), anterior sensillum (*as*), posterior sensillum (*ps*), median subposterior seta (*sp*), and median posterior seta (*p*). In this paper, the other paired, median head setae are designated for convention as follows, from anterior to *sp*: *rs* (median rostral seta) and *cs* (clypeal seta) (Copeland 1964), *m1, m2, m3, m4,* and *m5*; *rs, cs, m2, m3, m5, sp,* and *p* are considered the innermost setae of transverse rows of setae (Fig. 8). Identification of these rows greatly facilitates the location of *aa* and *as*. Seta *m4* is present in all the species described in this paper, but is absent in *E. vermiforme* Ewing.

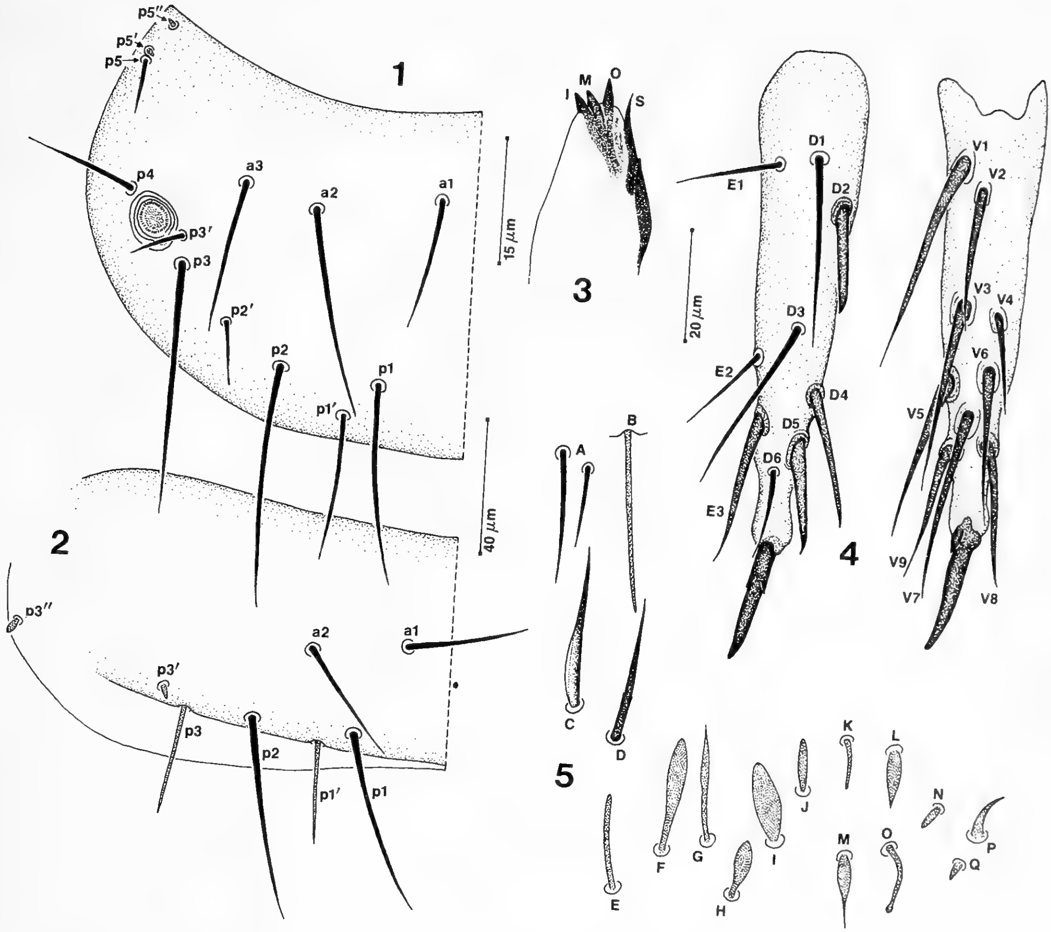
The form of the galea is similar among *Eosentomon* spp., with an external spine and three apical projections (Fig. 3). The shape of the projections, here termed digits (outer, median, inner), varies among species and is a very useful supplementary taxonomic character.

The mesonotum and metanotum each have certain characters not hitherto used in eosentomid systematics. On each segment, seta *p3′* may be setiform, lanceolate, claviform, or ovate. Mesonotal seta *p2′* is almost always setiform but occasionally mimics a modified *p3′*. On the metanotum, *p5* is associated with two minute microchaetae near the anterolateral margin (Fig. 1), which for convention may be designated *p5′* and *p5″*. The bases of seta *p5* and *p5′* are usually contiguous, although occasionally there is discernible space between them, useful as a supplementary character. Imadate (1989) observed and sketched the location of these microchaetae in *Eosentomon woroae* Imadate.

Bernard (1975a) noted that, in addition to the 5+5 posterior setae usually reported on abdominal tergite I, there was an additional microchaeta (*p3″*) near each posterior corner (Fig. 2). The socket of *p3″* is much less distinct than that of *p3′*, making it more difficult to detect. All *Eosentomon* spp. I have examined possess *p3″*, but Imadate (1989) recently reported that *E. woroae* Imadate does not possess it. The tergite I setal formula introduced by Copeland (1964) is used in this paper. A formula of 3:1:2 means three normal setae, one delicate seta, and two microchaetae.

The microchaetae, sensilla, and setae of eosentomids display a wide variety of shapes. Terms that define these shapes are given (Fig. 5); some of these terms have been in use for many years. A "delicate" seta (Tuxen 1964) is one found in the posterior rows of the terga, less sclerotized than the normal setae and without a pronounced socket. Inflated and indented setae are unusual forms of the median rostral setae; inflated setae are swollen in the basal half, while indented setae suddenly narrow in the middle third. Copeland (1964) has referred to the inflated type as "alate." Sensilla are those specialized sensory setae found on the forelegs. Microchaetae are the small sensory setae found on the head, terga, middle legs, and hind legs. Among the more specialized forms, "aristate" refers to a lanceolate microchaeta with a terminal filament; "capitulate" (small-headed) applies to minutely capitate microchaetae on tergum VIII, and "gemmate" (bud-like) refers to the minute microchaetae of the metanotum and sometimes tergum VIII.

The metatarsus possesses, at least in North American species, a constant number and arrangement of setae, some of which are variable in thickness and length. A numbering system for the metatarsal setae is proposed and illustrated in Fig. 4. Six dorsal setae (D1–6) are arranged in an irregular zigzag row; the most variable of these is D2, referred to as the basal seta (*bs*) by Szeptycki (1984). Since BS is already used for a foretarsal ratio, it is desirable to use a different term for this metatarsal seta. D2 varies from a thin seta to a thick spine. D5 is always a distinct spine but its thickness varies. D4 is variably spiniform, while D1, D3, and D6 are setiform. On the exterior surface, E1 and E2 are setiform, while E3 is spiniform. All nine ventral setae (V1–V9) are rather heavy spines, whose length may vary among species; V4 is the shortest of the ventral setae. The interior side is considered to be free of setae. In this paper, usually only the view that best shows D2 is illustrated.



Figs. 1–5. *Eosentomon vermiforme*: 1, metanotum, left side; 2, abdominal tergum I, left side; 3, galea (S: exterior spine; O: outer digit; M: median digit; I: inner digit); 4, metatarsus, dorsal and ventral views (D: dorsal setae; E: exterior setae; V: ventral setae). *Eosentomon* spp.: 5, Setal types (A–D, setae: A, normal; B, delicate; C, inflated; D, indented. E–J, sensilla: E, linear; F, rounded spatulate; G, pointed spatulate; H, claviform; I, oval; J, oblong. K–Q, microchaetae: K, linear; L, lanceolate; M, aristate; N, oblong; O, capitulate; P, falcate; Q, gemmate).

Eosentomon crypticum, new species
Figs. 6–17; Table 1

Color and dimensions.—Body weakly sclerotized, yellow-amber posteriorly. Length 795 µm; length of head 99 µm; length of foretarsus without claw 64 µm. LR = 12.3; PR = 7.0; TR unknown (foretarsal claw broken).

Morphology.—Pseudoculus oval with a few longitudinal striae (Fig. 8). Clypeal apodeme small but robust, with thick anterior bar and a central keel-like appendage extended posteriorly (Fig. 10). Labral margins coarsely scalloped anteriorly, apices rounded to a very narrow U-shaped notch; labral setae present, extended well past labrum apex (Fig. 10). Rostral setae greatly inflated. Mandible slender with two apical teeth; galea with cylindrical, apically rounded outer digit and slender-conoid middle and inner digits, the middle digit shorter than the inner; outer lobe of lacinia slender, slightly curved at apex, not serrate; inner lacinial lobe slender and curved anteriorly, not hooked (Fig. 9).

Empodia of middle and hind tarsi short.

Central lobe of praecosta sinuate (Fig. 15). Female squama genitalis (Fig. 17) with very thin caput processus bent sharply toward inner stylus margins; corpus processus extending as a narrow lobe anteriorly past the caput, and without prominent alae; median sclerotizations present, rod-like; proximolateral sclerotizations very heavy and well-developed. Filum processes short, stylus apex bluntly pointed.

Chaetotaxy.—Cephalic seta *aa* absent, *pa* present, anterior sensillum present (Fig. 8). Setae *sp* and *p* about equal in length.

On mesonotum and metanotum (Figs. 12, 13), lengths of *p1* and *p1'* equal, *p2'* two-thirds the length of *p2, p3* setiform and shorter than *p2'*; on mesonotum, *p5* very short, its base contiguous with that of *p5'*.

On foretarsus (Figs. 6, 7), all sensilla present; *b, a', b'2,* and *t* narrowly spatulate; *b'1* very large and ovate, nearly level with *b'*2; *e* and *g* rounded-spatulate and large; *f1* linear, long; *d* broken near base; *t3* robust; sensilla *a, c, f2,* and *c'* short and slender. Sensillum *t1* closer to $\alpha 3$ than to $\alpha 3'$; BS = 0.81. Metatarsal seta D2 of moderate thickness (Fig. 11).

Abdominal setal composition given in Table 1. Tergite I formula 3:1:2, *p1'* longer than *p1*. On tergites II–VI, *p1'* and *p2'* twice the length of *p1* and *p2*; *p4'* delicate and shorter than *p4* (Fig. 14) but becoming progressively longer and stronger on tergites V–VII. On tergite VII, *p1'* short and weakly capitulate, *p2'* longer than *p2.* On tergite VIII, *pc, p1'* and *p1"* aristate, the filament short; *p2'* clearly capitulate (Fig. 16).

Collection data.—Holotype female collected from wet sand and liverworts along Road 5, SRS, Barnwell County, South Carolina, 9 Sep 1983; deposited in NMNH.

Derivation of name.—The latinized Greek word *crypticum* means "hidden," and refers both to the small size of the holotype and my failure to find it initially in the thousands of SRS proturans.

Diagnosis.—*Eosentomon crypticum* is distinguished from all other *Eosentomon* spp. by the large, anteriorly displaced foretarsal sensillum *b'1.* The structure of the corpus processus is reminiscent of the "*transitorium*" species group (Tuxen 1964), but the very thin caput processus is distinctive.

Eosentomon ewingi Bonet, new status

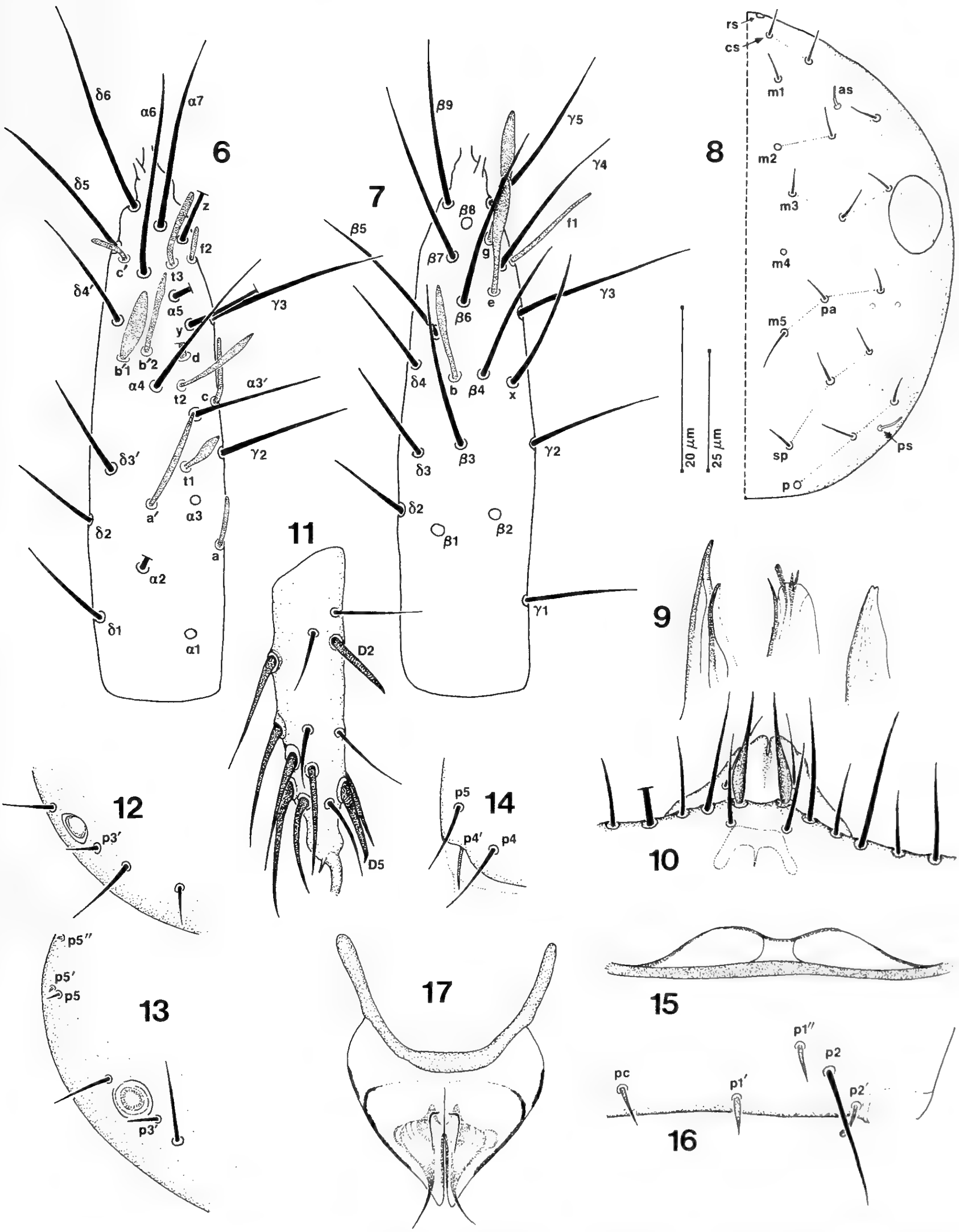
Figs. 18–29; Table 2

Eosentomon pusillum f. *ewingi* Bonet 1950: 113; Tuxen 1964:112, fig. 131.

Ewing (1940), in his description of *E. pusillum,* included three specimens from North Carolina in the type series. Bonet (1950) considered these specimens a distinct form of *E. pusillum* because they lacked anterior setae on sternite VIII, and designated them as forma *ewingi.* Tuxen (1964:112) noted the very shrivelled state of the specimens and considered that "It seems advisable . . . to omit this form from the catalogue." This action, apparently a recommendation to declare *E. pusillum* f. *ewingi* a *forma inquirenda,* has no validity since specimens and a published, albeit very inadequate, description exist.

With the collection of many undescribed species from South Carolina, it became necessary to reassess *E. pusillum* f. *ewingi.* A male proturan collected from Great Smoky Mountains National Park is nearly identical to Ewing's specimens and is used to complete the following description, which is based on the specimen designated as lectotype (Type #65881, USNM) by Tuxen. Characters determined from the male are described in parentheses, following the designation GRSM.

Color and dimensions.—Body small and



Figs. 6–17. *Eosentomon crypticum*: 6, Foretarsus, dorsal view; 7, Foretarsus, ventral view; 8, Right side of head, dorsal view; 9, Lacinia, galea, mandible; 10, Labrum and rostral region; 11, Metatarsus, exterior view; 12, Mesonotal margin; 13, Metanotal margin; 14, Posterior corner of tergum IV; 15, Praecosta of tergum VI; 16, Posterior margin of tergum VIII; 17, Squama genitalis. (20 µm scale applies to Figs. 6–7, 9–11, 15–17, 25 µm scale to all others.)

Table 1.—Abdominal chaetotaxy of *Eosentomon crypticum*, n. sp.

	I	II–III	IV	V–VI	VII	VIII	IX–X	XI	XII
Dorsal	4/12	10/16	10/16	8[1]/16	6[2]/16	6/9	8	8	9
Ventral	4/4	6/4	6/10	6/10	6/10	0/7	6	8	12

[1] Seta *a3* absent.
[2] Setae *a1, a3* absent.

slender, weakly sclerotized, light amber. Length 603 μm (GRSM: 868 μm); head length about 70 μm (GRSM: 82 μm); PR approximately 3.6 (GRSM: 4.5); (GRSM: foretarsus length 65 μm). LR: (GRSM 9.9); TR: (GRSM 4.4).

Morphology.—Pseudoculus extremely large, appearing round or broadly oval with at least three prominent longitudinal striae (Figs. 20, 21). Labrum, mouthparts, and clypeal apodeme all unobservable on lectotype. (GRSM: Labrum rounded-truncate anteriorly, the lobes angled inward to a small V-shaped notch, labral setae present [Fig. 22]. Median rostral setae inflated. Mandible tridentate with small subapical and two apical teeth; on galea, outer digit the longest, inner digit the shortest [Fig. 23]; lacinia not clearly observable. Clypeal apodeme stout, side arms short and heavy.)

Empodium of middle leg almost a third the length of the unguis, EUII = 0.29 (GRSM: 0.31); empodium of hind leg long, EU = 0.69 (GRSM: 0.70) (Fig. 24).

Central lobe of praecosta slightly incised (Fig. 27). Styli of female squama genitalis presenting slightly different appearances (Fig. 29): caput processus semicircular; thickened rods in corpus processus united to form a Y-shape, the Y spread to the exterior edge on the left stylus but in the usual position on the right stylus. Median sclerotizations linear; proximo-lateral sclerotizations distinct. Filum processus very long and slender; stylus apices narrowly rounded.

Chaetotaxy.—Cephalic seta *aa* not observed on lectotype, *pa* present (Fig. 20); (GRSM: *aa* and *pa* present, anterior sensillum present [Fig. 21]). Seta *sp* 1.6× the length of seta *p* (GRSM: 1.5).

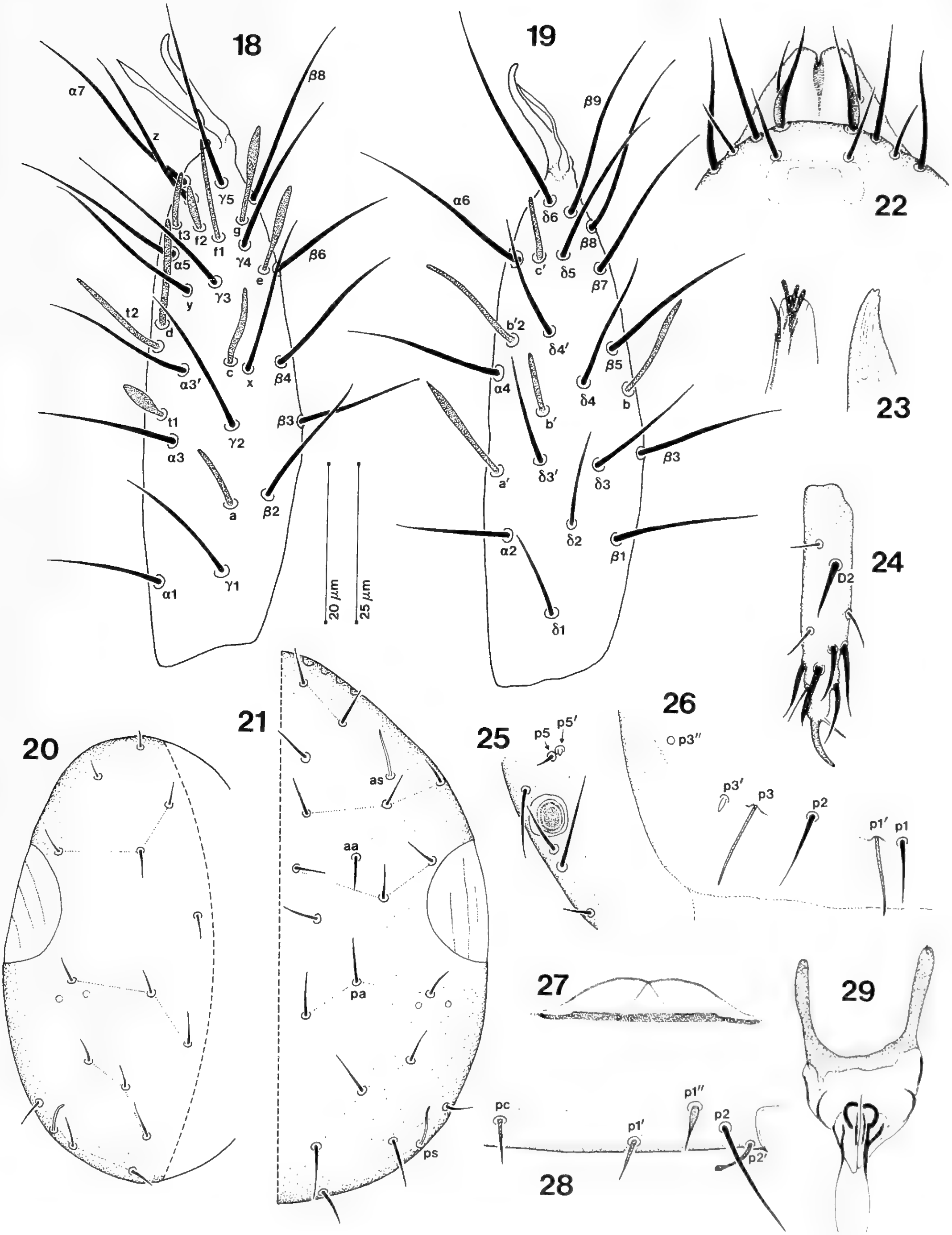
Mesonotal seta *p2′* and *p3′* short; on metanotum, seta *p3′* longer than *p2′*, *p5* very short and contiguous with *p5′* (Fig. 25).

Foretarsi absent on lectotype. (GRSM: foretarsus [Figs. 18, 19] broad, all sensilla present. Sensilla *a′* and *b* narrowly spatulate; *b′2*, *f1*, and *t2* long and slender; *f2* ovate; sensillum *t1* closer to *α3* than to *α3′*, BS = 0.94.) Metatarsal seta D2 a spine of moderate thickness; D5 relatively slender (Fig. 24).

Abdominal setal composition given in Table 2. Tergite I formula 2:2:2, *p3* delicate (Fig. 26). (GRSM: on tergites II–VI, *p1′* and *p2′* longer than *p1* and *p2*; *p4* delicate and slightly longer than *p1* on tergite II, delicate and equal to *p4* on tergites III–VII. On tergite VII, *p1′* short and capitulate, *p2* and *p2′* of equal lengths; on tergite VIII [Fig. 28], *p1′* and *p1″* aristate, *p2′* capitulate).

Material examined.—Lectotype female (USNM Type #65881) collected in peach orchard soil by W. F. Turner, Moore County, North Carolina, 8 May 1937; one male collected by E. Bernard from Great Smoky Mountains National Park, North Carolina, Swain County, southern face of Mine Ridge, elev. 817 m, in mixed hemlock-oak forest, deposited in UTEM.

Diagnosis.—*Eosentomon ewingi* is distinguished from most *Eosentomon* spp. by the enormous pseudoculus, long metatarsal empodium, and semicircular caput processus.



Figs. 18–29. *Eosentomon ewingi*: 18, Foretarsus, exterior view (GRSM); 19, Interior view (GRSM); 20, Left side of head (lectotype); 21, Right side of head (GRSM); 22, Labrum and rostral region (GRSM); 23, Galea and mandible (GRSM); 24, Metatarsus (lectotype); 25, Metanotal margin (lectotype); 26, Posterior setae of tergum I (lectotype); 27, Clypeal apodeme (lectotype); 28, Posterior margin of tergum VIII (GRSM); 29, Squama genitalis (lectotype). (25 μm scale refers to Figs. 20–21, 20 μm scale to all others.)

Table 2.—Abdominal chaetotaxy of *Eosentomon ewingi* Bonet.

	I	II–III	IV–VI	VII	VIII	IX–X	XI	XII
Dorsal	4[1]/(12)	10/16	10/16	6[2]/16	6/9	8	8	(9)
Ventral	(4)/(4)	(6)/(4)	6/10	6/10	0/7	6	8	(12)

[1] Setal formulas in parentheses determined from male collected in Great Smoky Mountains National Park.

[2] Setae *a1, a3* absent.

It shares these characters with *E. brevicorpusculum* Yin (1965, 1982), but lacks anterior setae on sternite VIII (two setae in *E. brevicorpusculum*) and has a much longer foretarsal sensillum f1. *Eosentomon ewingi* does not bear any special relationship to *E. pusillum*; on the basis of the squama genitalis, *E. ewingi* is related to *E. yosemitense* Ewing, while *E. pusillum* is allied to *E. udagawai.*

Eosentomon hargrovei, new species

Figs. 30–40; Table 3

Color and Dimensions.—Body moderately sclerotized, yellowish. Length of fully expanded female 1097 μm. Length of foretarsus without claw 64 μm. Length of head without labrum 98 μm. LR = 14.2; PR = 10.6; TR = 5.1.

Morphology.—Pseudoculus broadly oval, with obscure linear and circular depressions in the posterior half (Fig. 34). Clypeal apodeme not visible. Labrum in lateral view short, with labral setae extending past anterior edge of labrum (Fig. 32). Central pair of rostral setae inflated basally. Mandible (Fig. 32) with two apical and one subapical teeth. Galea of maxilla with slender outer spine; median apical lobe slightly clavate and rounded, two inner apical lobes adjacent, fused on galeal blade; outer lobe of lacinia short, almost straight, broadly rounded apically, without inner teeth, inner lobe thin and slightly curved, not hooked at apex (Fig. 33).

Empodium of foretarsus almost as long as claw, EU = 0.96. Empodia of middle and hind legs very short, less than one-fifth the length of the claws.

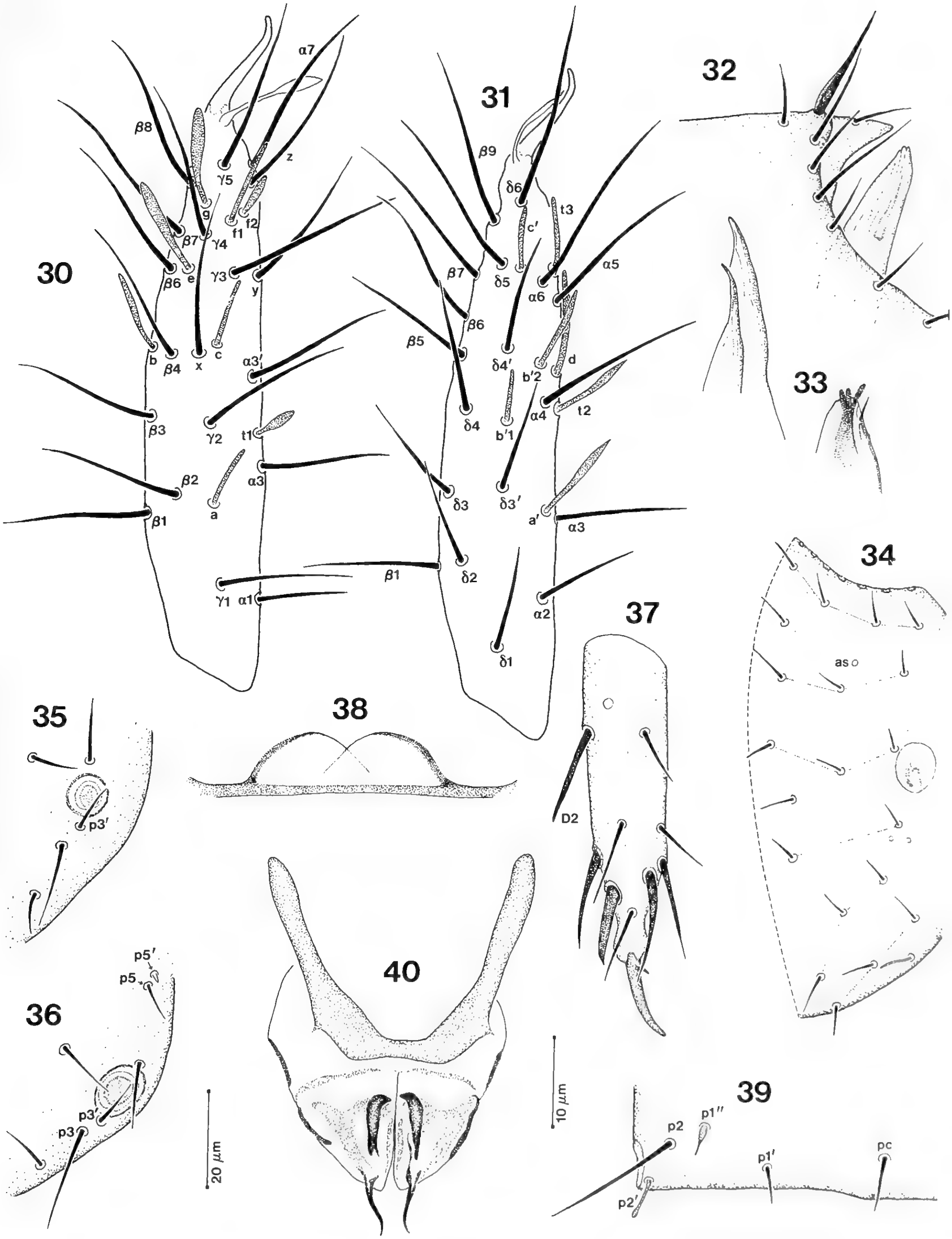
Central lobe of praecosta incised (Fig. 38). Squama genitalis of female (Fig. 40) short and broad, basal apodeme thick and heavy. Median sclerotization of each stylus weakly developed; caput processus strong, curving and tapering to a narrowly rounded point; corpus processus weakly sclerotized, extending as a lobe to the inner edge of the stylus and with distinct ala; lateral sclerotizations of perigynium and stylus present; filum short, less than half the length of the stylus; apex of stylus rounded.

Chaetotaxy.—Cephalic setae *aa* and *pa* absent, anterior sensillum present (Fig. 34). Seta *sp* about 1.4× the length of seta *p.*

On mesonotum and metanotum, seta *p1'* about equal in length to *p1*; *p2'* much shorter than *p2*; seta *p3'* normal, length equal to spiracle width (Figs. 35, 36). On metanotum, seta *p5* as long as *p3'*, its base close to but not contiguous to *p5'* (Fig. 36).

On foretarsus (Figs. 30, 31), sensilla *b'1* and *c'* present; sensillum *a* short and slender, *b* reaching the base of *β6, c* reaching *γ3*; *d* reaching *α6*; *f1* slender, *f2* shorter and broader than *f1.* Sensilla *a'*, *b'2,* and *t2* narrowly spatulate, *e* and *g* broadly spatulate. Sensillum *t1* closer to *α3* than to *α3'*, BS = 0.81; *t3* long and slender. Metatarsal seta D2 a long, slender spine (Fig. 37).

Abdominal setal composition given in Table 3. Tergum I setal formula 3:1:2. Seta *p'1* longer than *p1* on terga I–VI, very short



Figs. 30–40. *Eosentomon hargrovei*: 30, Foretarsus, exterior view; 31, Foretarsus, interior view; 32, Labral region and mandible; 33, Lacinia and galea; 34, Right side of head, dorsal view; 35, Mesonotal margin; 36, Metanotal margin; 37, Metatarsus; 38, Praecosta of tergum VI; 39, Posterior margin of tergum VIII; 40, Squama genitalis. (20 μm scale applies to Figs. 34–36, 10 μm scale to all others.)

Table 3.—Abdominal chaetotaxy of *Eosentomon hargrovei,* n. sp.

	I	II–III	IV–VI	VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{10}{16}$	$\frac{8[1]}{16}$	$\frac{7[1,2]}{16}$	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{6}{10}$	$\frac{2}{7}$	4	8	12

[1] Seta *a3* absent.

[2] Setae *a4* absent on right side of holotype.

and weakly claviform on tergum VII. Seta *p'2* longer than *p2* on terga II–VI, equal to *p2* on tergum VII. Accessory seta *p'4* similar in appearance to but slightly shorter than *p4*. On tergum VIII, *p1″* aristate (Fig. 39).

Collection data.—Holotype female extracted from deciduous litter along Road F past Road 4, SRS, Aiken County, South Carolina, 18 May 1984, deposited in NMNH.

Derivation of name.—This species is named with gratitude after Mr. William W. Hargrove, who collected most of the proturan material described in this paper.

Diagnosis.—*Eosentomon hargrovei* can be separated from other members of the genus by the very strong caput processus and well developed corpus process with prominent lateral alae. The squama genitalis is reminiscent of that in some "*wheeleri*" group species (Copeland 1964, Tuxen 1964), but otherwise *E. hargrovei* bears no resemblance to them.

Eosentomon nudilabratum,
new species
Figs. 41–53; Table 4

Color and dimensions.—Body moderately sclerotized, yellowish. Mean length of partially expanded adults 792 μm (699–892, $n = 4$). Length of foretarsus without claw 64 μm (61–67, $n = 4$). Length of head without labrum 96 μm (91–100, $n = 4$). LR = 0.17 (0.15–0.20, $n = 4$), PR = 8.8 (7.5–9.7, $n = 6$); TR = 6.1 (5.6–7.1, $n = 7$).

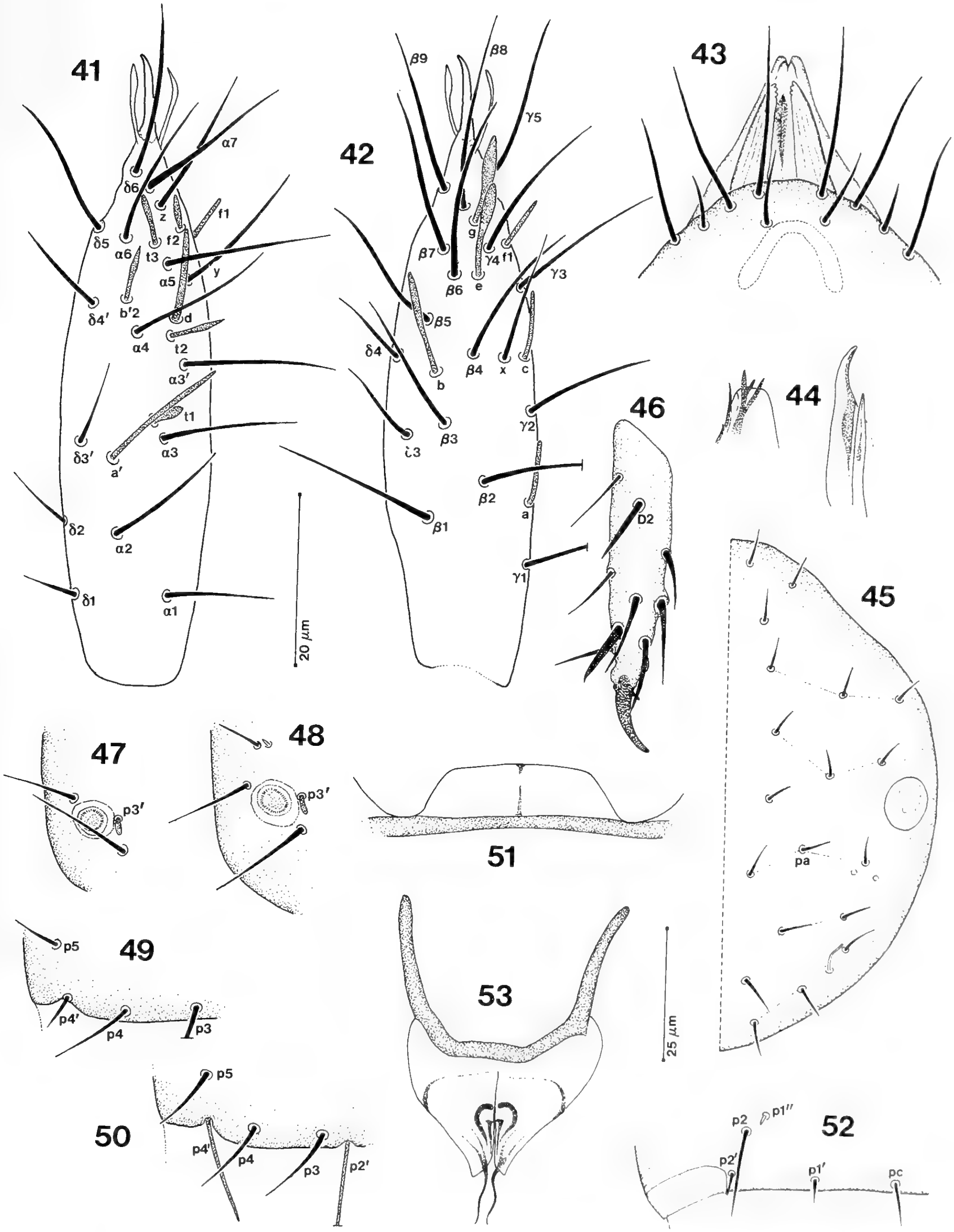
Morphology.—Pseudoculus broadly oval, with a small circular, central depression and several longitudinal striae (Fig. 45). Clypeal apodeme (Fig. 43) stout, the side arms heavy and slightly enlarged posteriorly. Labrum prominent, tapering anteriorly to small, rounded apices and a V-shaped notch; labral setae absent (Fig. 43). Median pair of rostral setae not inflated or otherwise modified. Mandible (Fig. 43) with three to five minute teeth along the inner edge. Galea of maxilla with outer spine, tapering outer digit and minute median and inner digits, all three digits appearing bluntly pointed; outer lobe of lacinia smoothly curved, not serrate; inner lobe tapering and straight (Fig. 44).

Empodium of foretarsus slightly longer than the claw, EU = 1.08 (0.95–1.15, $n = 7$). Empodia of middle and hind legs very short, less than one-fifth the length of the claws.

Central lobe of praecosta trapezoidal, not incised (Fig. 51). Squama genitalis of female (Fig. 53) small, each stylus tapering to a point; median sclerotization strong, capitate proximally; caput processus thin and smoothly curved, shaped like a question mark; corpus processus weakly developed, bifurcate; filum short, about half the length of the stylus.

Chaetotaxy.—Cephalic seta *aa* absent, *pa* present; anterior sensillum absent (Fig. 45). Seta *sp* 1–1.3× the length of seta *p*.

Seta *p1′* on mesonotum and metanotum slightly shorter than *p1′*; seta *p3′* short and clavate; on metanotum, seta *p5* nearly as long as *p2′*, its base close to that of *p5′* (Figs. 47, 48).



Figs. 41–53. *Eosentomon nudilabratum*: 41, Foretarsus, dorsal view; 42, Foretarsus, ventral view; 43, Labrum and rostral region; 44, Galea and lacinia; 45, Right side of head, dorsal view; 46, Metatarsus, subdorsal view; 47, Mesonotal margin; 48, Metanotal margin; 49, Posterior margin of tergum III; 50, Posterior margin of tergum IV; 51, Praecosta of tergum VI; 52, Posterior margin of tergum VIII; 53, Squama genitalis. (25 μm scale applies to Figs. 45, 47–50, 20 μm scale to all others.)

Table 4.—Abdominal chaetotaxy of *Eosentomon nudilabratum,* n. sp.

	I	II–III	IV–VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{8^1}{16}$	$\frac{8^1}{16}$	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{0}{7}$	6	8	12

[1] Seta *a3* absent.

On foretarsus (Figs. 41, 42), sensilla *b'1* and *c'* absent; sensillum *a* not reaching *γ2, b* long and nearly reaching *β7, c* reaching *γ3, d* extending to *f2*; *f1* short and linear, *f2* oblong; *e* and *g* spatulate. Sensilla *t2* and *b'2* narrowly spatulate; *t3* reaching the base of *α7*; *a'* long and slender. Sensillum *t1* close to *α3,* BS = 0.94 (0.87–1.00, *n* = 7).

Abdominal setal composition given in Table 4. Tergum I setal formula 3:1:2; *p1'* almost twice the length of *p1.* On tergites II–VI, *p1'* and *p2'* longer than *p1* and *p2*; p4' tergites II–III setiform, short (Fig. 49), but on tergites IV–VII, p4' longer than p4 and delicate (Fig. 50). Seta p1' short and slightly capitulate on tergum VII. On tergite VIII, *p1"* minute, oblong (Fig. 52); p2' pointed, not clubbed.

Collection data.—Holotype female and two paratype females extracted from wet oak and Spanish moss litter, SRS near Dunbarton, Barnwell County, South Carolina, 13 Apr 1984; one paratype female, same locality, 18 May 1984. Holotype and one paratype in NMNH, two paratypes in UTEM.

Derivation of name.—The specific epithet is a compound Latin word meaning "provided with a naked lip," referring to the lack of labral setae.

Diagnosis.—*Eosentomon nudilabratum* is distinguished from all other *Eosentomon* spp. by the lack of labral setae, mandibles with three to five inner teeth, foretarsal sensillum *t1* very close to *α3,* and claviform seta *p3'* on the mesonotum and metanotum. The squama genitalis is somewhat similar to that of *E. pomari* Bernard, which also lacks labral setae, but possesses median sclerotizations of the styli (absent in *E. pomari*). In addition, *E. nudilabratum* lacks foretarsal sensillum *c'* (*c'* present in *E. pomari*) and has eight anterior setae on abdominal terga II–VI (ten in *E. pomari*).

Eosentomon osageorum,
new species
Figs. 54–66; Table 5

Color and dimensions.—Body well sclerotized, amber brown. Mean length of fully expanded individuals 1332 μm (1217–1446, *n* = 6). Length of foretarsus without claw 103 μm (101–106, *n* = 9). Length of head without labrum 124 μm (122–127, *n* = 6). LR = 11.2 (8.9–13.5, *n* = 6); PR = 10.0 (9.1–12.0, *n* = 9); TR = 6.4 (5.9–6.6, *n* = 9).

Morphology.—Pseudoculus oval, with several weak longitudinal striae in the anterior half (Fig. 48). Clypeal apodeme indistinct. Labrum with truncated apices sloping inward to a U-shaped notch, inner corners with fine, curved striae (Fig. 56); labral setae present and reaching just past labral apices. Median rostral setae slightly inflated basally. Mandible tridentate, with two apical and one subapical teeth (Fig. 56). Digits of galea well-developed and rounded apically, the median and inner digits of equal length; outer lobe of lacinia smoothly curved and tapering, distinctly serrate on the inner edge; margin of inner lobe bent at tip to form finger-like process supporting a thin inner lamina (Fig. 57).

Foretarsal empodium shorter than the

claw, EU = 0.87 (0.79–0.84, $n = 7$). Empodia of both middle and hind legs long, EU of middle leg 0.59 (0.52–0.67, $n = 10$), EU of hind leg 0.66 (0.61–0.74, $n = 11$) (Figs. 59–61). Central lobe of praecosta weakly incised on tergites IV–V, very weak and linear on tergites VI–VII (Figs. 64, 65).

Styli of female squama genitalis (Fig. 63) elongate, median sclerotizations present and with small median spurs. Caput processus thin, smoothly curved, and reaching stylus edge, not heavily sclerotized; outer and inner edges of corpus process heavily sclerotized, the outer edge thickened and clavate proximally. Filum processus long and slender; tips of styli bluntly pointed.

Chaetotaxy.—Cephalic setae *aa* and *pa* present, anterior sensillum present (Fig. 58); seta *sp* 1.2–1.3 × the length of seta *p*.

Seta *p1'* on meso- and metanotum slightly shorter than *p1*; *p3'* normal, longer than the width of the spiracles; on metanotum, *p5* remote from *p5'* (Fig. 62).

On foretarsus (Figs. 54, 55), *c'* present, *b'1* absent. Most sensilla long and slender; *c, d, f1,* and *b'2* all about of equal length; *a'* nearly reaching *d*; sensillum *e* long and slender, not spatulate; *g* weakly spatulate. Sensillum *t1* much closer to $\alpha 3$ than to $\alpha 3'$, BS = 1.09 (1.02–1.12, $n = 9$). Metatarsal seta D2 a very stout spine, nearly as large as D5 (Fig. 61).

Abdominal setal composition given in Table 5. Tergum I setal formula 3:1:2; *p1'* 1.5 × the length of *p1*. Accessory setae *p1'* and *p2'* longer than *p1* and *p2* on terga II–VI, *p4'* short and delicate but becoming stronger on each succeeding segment. On tergum VII, *p1'* much shorter than *p1,* rounded but not capitulate at its apex. On tergum VIII, *p1'* and *p1"* aristate, *p2'* slender, very slightly capitulate apically (Fig. 66).

Collection data.—Holotype female and three male, three female, and two maturus junior paratypes collected from swampy soil near Pine Bluff, Jefferson County, Arkansas, 8 Jul 1988, N. Elkassabany and M. A. Muegge, coll. Holotype and four paratypes deposited in NMNH, four paratypes in UTEM.

Derivation of name.—The specific epithet is derived from the name of a Native American tribe, the Osage, who inhabited parts of what is now Arkansas.

Diagnosis.—*Eosentomon osageorum,* in its possession of long mesotarsal and metatarsal empodia, differs from all *Eosentomon* spp. except *E. saharense* Conde and *E. adakense* Bernard, but differs radically from both in the structure of the corpus processus, which appears similar to that of the Japanese *E. asahi* Imadate. The combination of linear foretarsal sensillum *e* and spatulate *g* appears to be unique within the Eosentomidae; *Madagascarentomon* Nosek has both sensilla long and setiform.

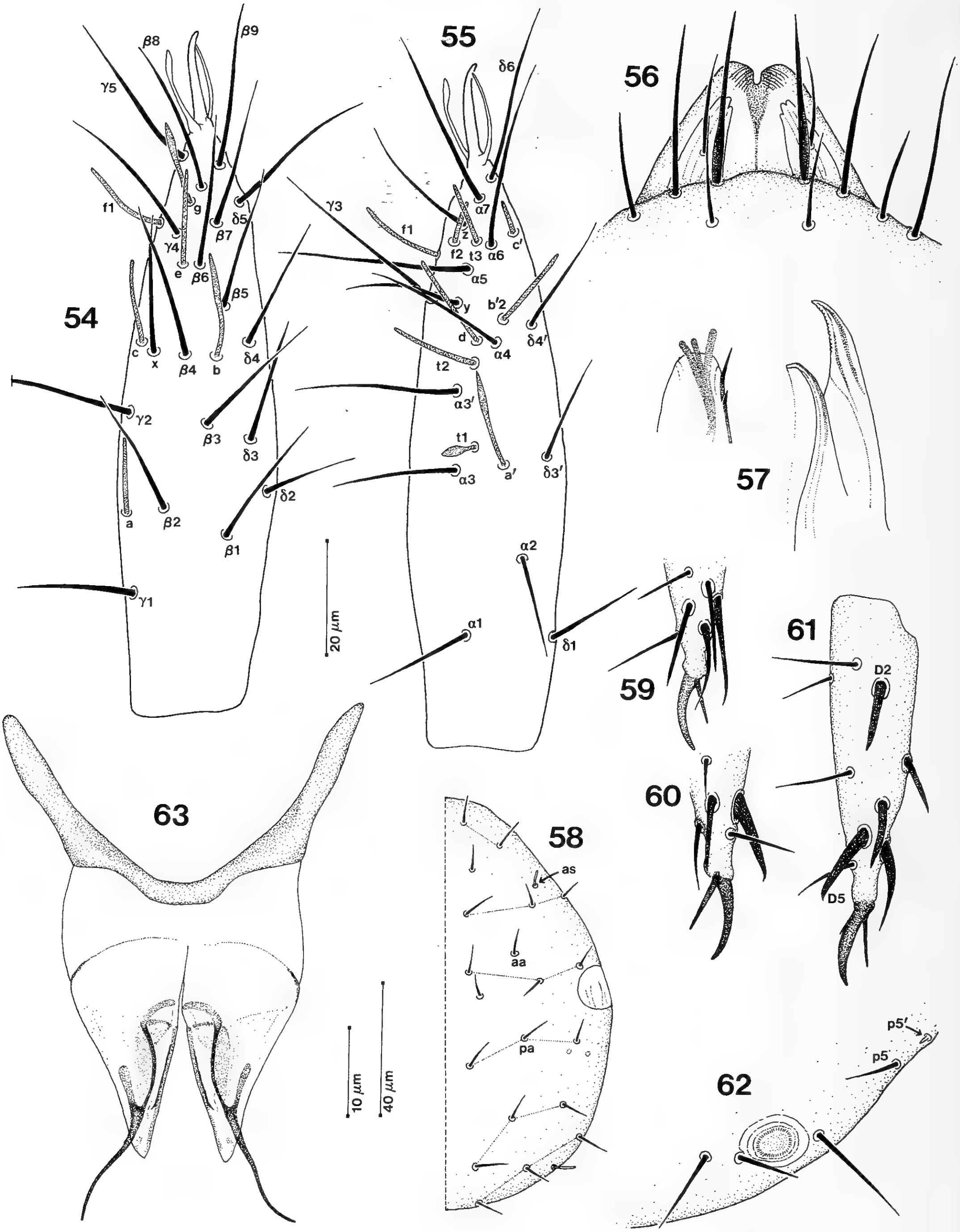
Eosentomon pusillum Ewing
Figs. 67–75; Table 6

Eosentomon pusillum Ewing, 1940:527, fig. 13.—Bonet, 1950:111.—Bonet and Tuxen, 1960:281, figs. 37–42.—Tuxen, 1964: 110–112, figs. 128–130.—Tuxen, 1976: 436, fig. 19.

Eosentomon brassicae Bernard, 1975b:167–169, figs. 31–40. New synonymy.

This species, known originally from a single specimen collected in Florida, has been examined several times and until 1976 was considered to have a short hind empodium (Bonet & Tuxen 1960, Tuxen 1964). Tuxen (1976) studied the holotype once again and found it possessed foretarsal sensillum *b'1* and a long metatarsal empodium. However, many characters are still not described, necessitating yet another restudy of the holotype. After this reexamination, it is obvious that *E. brassicae* Bernard from Michigan is a junior synonym of *E. pusillum*; references to *E. brassicae* below are in parentheses and designated MS (Michigan specimens).

Color and dimensions.—Body lightly sclerotized, amber. Length 570 μm (MS: 918). Length of head without labrum 87 μm



Figs. 54–63. *Eosentomon osageorum*: 54, Foretarsus, dorsal view; 55, Foretarsus, ventral view; 56, Labrum and rostral region; 57, Galea and lacinia; 58, Right side of head, dorsal view; 59, Apical half of mesotarsus; 60, Apical half of metatarsus, lateral view; 61, Metatarsus, dorsal view; 62, Postero-lateral margin of metanotum; 63, Squama genitalis. (10 µm scale refers to Figs. 56, 57, 63; 40 µm scale to Fig. 58; 20 µm scale to all others.)

Table 5.—Abdominal chaetotaxy of *Eosentomon osageorum*, n. sp.

	I	II–III	IV–VI	VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{10}{16}$	$\frac{10}{16}$	$\frac{8^{1}}{16}$	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{6}{10}$	$\frac{0}{7}$	4	4	12

[1] Seta *a3* absent.

(MS:85). Length of foretarsus without claw 55 μm (MS:62). LR = 17.6; PR = 6.1 (MS: 5.6). TR = 5.6 (MS:6.4).

Morphology.—Pseudoculus very large but obscure in holotype, (MS: broadly oval, three longitudinal striae). Clypeal apodeme stout, side arms hooked inward (Fig. 70). Labrum short, apices broadly rounded, medially with a deep V-shaped notch; labral setae present, extending past labral tip (Fig. 70). Rostral setae not inflated. Mandible with two apical teeth and a minute subapical denticle; galea with slender outer digit, rudimentary middle digit, and short, slender inner digit; outer lobe of lacinia short, stout, and slightly curved, inner lobe curved inward at apex but not hooked (Fig. 71).

Empodium of foretarsus about equal to claw, EU = 1.0 (Tuxen [1964]: 0.9, MS 1.0). Empodium of middle leg less than one-fourth the length of its unguis, EU = 0.22; empodium of hind leg nearly two-thirds the length of its unguis, EU = 0.63 (MS:0.64) (Fig. 72).

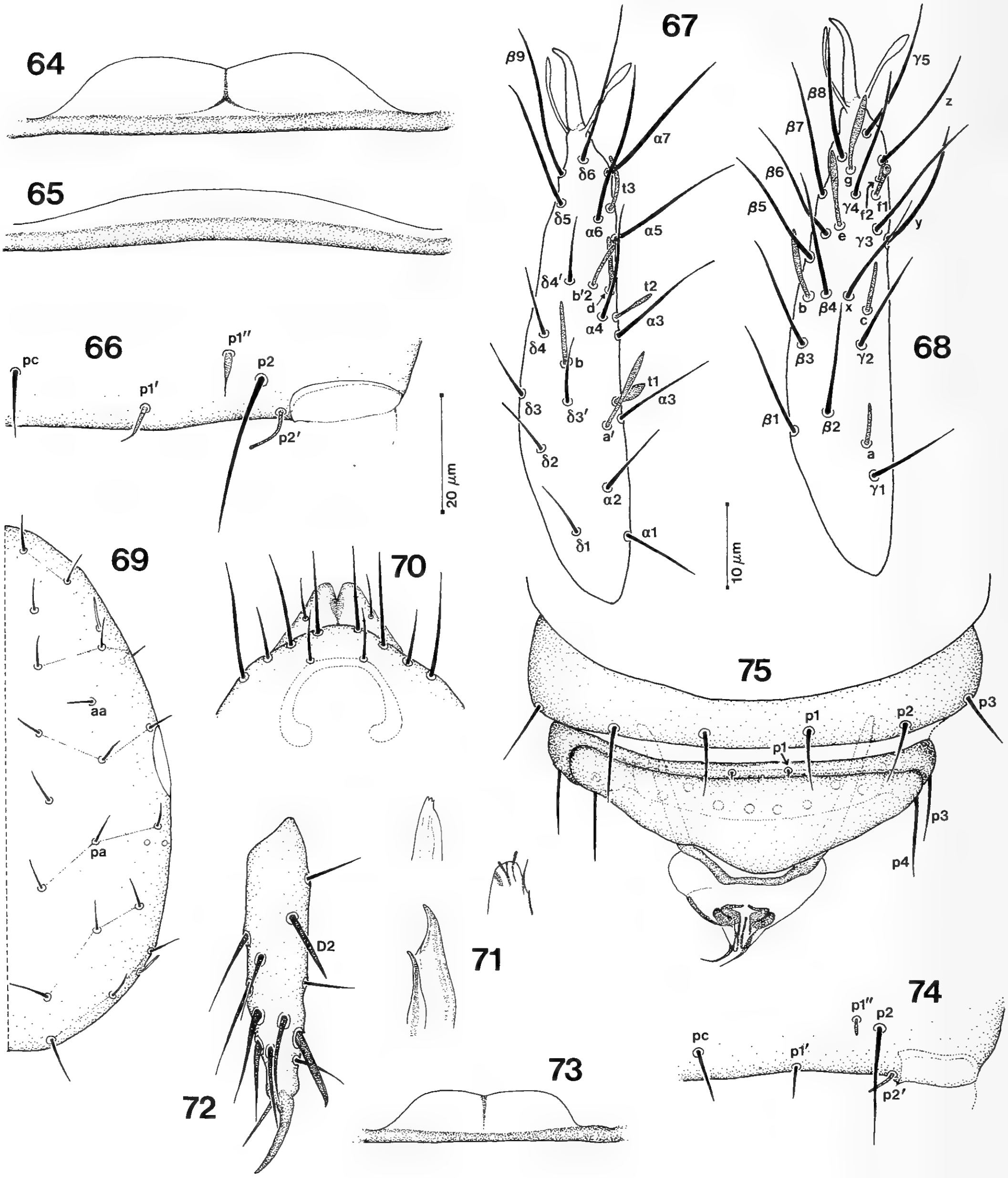
Central lobe of praecosta very weakly incised (Fig. 73). Female squama genitalis (Fig. 75) distorted, the basal apodeme lying in the horizontal plane but the remainder turned sharply upward. Proximo-lateral sclerotizations present; caput processus shaped somewhat like a duck's head, the apex slightly recurved anteriorly; caput and ala processus appearing to be combined into an S-shape. Median sclerotizations present but thin; filum processus of medium length; stylus apex narrowly rounded.

Chaetotaxy.—Cephalic setae *aa* and *pa* present, anterior sensillum present (Fig. 69). Seta *sp* about equal to seta *p*. Setae *p1* and *p1′* of equal length on mesonotum and metanotum; seta *p3′* the same length as the spiracle width; on metanotum, bases of *p5* and *p5′* contiguous.

On foretarsus (Figs. 67, 68) sensillum *c′* absent; *b, a′*, and *t2* narrowly spatulate; *e* and *g* rounded spatulate, *f1* spatulate but turned upward and foreshortened; sensillum *b1′* present; *f2* not clearly visible but appearing oblong; *t1* very close to *α3,* BS = 0.75; *t3* thin, curving, reaching the level of *δ6.* Metatarsal seta D2 a slender spine, slightly thicker than D4 (Fig. 72).

Abdominal setal composition given in Table 6. Setal formula of tergum I 3:1:2; *p1′* longer than *p1*. On terga II–VI, *p1′* and *p2′* longer than *p1* and *p2*; *p4′* delicate and shorter than *p4*. Seta *p1″* on tergite VIII oblong, minute, *p1′* setiform but very short; *p2′* not capitulate (Fig. 74). Tergum XI with only six setae (*p2* absent), the middle pair minute (Fig. 75).

Diagnosis.—*Eosentomon pusillum* is similar to the "*kumei*" group of Tuxen (1964) and Imadate (1974), and to *E. udagawai* Imadate in the S-shaped form of the caput processus + ala processus. It differs from all but *E. udagawai* in the presence of a long metatarsal empodium. *Eosentomon pusillum* differs from *E. udagawai* in the presence of labral setae and lack of foretarsal sensillum *c′* (in *E. udagawai,* labral setae absent, sensillum *c′* present). In Bernard (1985), *E. pusillum* will key to *brassicae,* a species here synonymized with *E. pusillum.*



Figs. 64–75. *Eosentomon osageorum*: 64, Praecosta, tergum V; 65, Praecosta, tergum VI; 66, Posterior margin of tergum VIII. *Eosentomon pusillum,* holotype: 67, Foretarsus, interior view; 68, Foretarsus, exterior view; 69, Right side of head, dorsal view; 70, Labrum and rostral region; 71, Mandible, galea, and lacinia; 72, Metatarsus; 73, Praecosta of tergum VI; 74, Posterior margin of tergum VIII; 75, Posterior abdominal segments with extruded squama genitalis (dotted circles: setal bases of sternite XI; setae of abdominal segment XII not shown). (20 µm scale refers to Figs. 66, 69; 10 µm scale to all others.)

Table 6.—Abdominal chaetotaxy of *Eosentomon pusillum* Ewing.

	I	II–III	IV–VI	VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{10}{16}$	$\frac{10}{16}$	$\frac{6[1]}{16}$	$\frac{6}{9}$	8	6[2]	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{6}{10}$	$\frac{2}{7}$	6	8	12

[1] Setae *a1, a3* absent.
[2] Seta *p2* absent.

Eosentomon renateae, new species
Figs 76–86; Table 7

Color and dimensions.—Body moderately sclerotized, yellowish. Mean length of females with various degrees of expansion 884 μm (675–1024, $n = 3$). Length of head without labrum 106 μm (97–110, $n = 3$). Length of foretarsus without claw 67 μm (66–68, $n = 5$). LR = 12.2 (10.7–14.0, $n = 3$); PR = 10.2 (9.6–10.7, $n = 2$); TR = 5.1 (4.8–5.9), $n = 5$).

Morphology.—Pseudoculus round, with several very obscure circular depressions in the center (Fig. 80). Clypeal apodeme moderately developed, side arms slightly clavate (Fig. 78). Labrum with rounded apices and deep U-shaped notch; labral setae present, extending past anterior margin (Fig. 78). Central pair of rostral setae indented, apical three-fifths of each seta much narrower than the basal part. Mandible with two apical and one subapical teeth; digits of galea rounded, the outer digit curving outward and longer than the other two digits; outer lobe of lacinia curved and tapering distally and not serrate, inner lobe hooked at apex (Fig. 79).

Empodium of foretarsus shorter than unguis, EU = 0.91 (0.86–0.96, $n = 5$). Empodia of middle and hind legs less than one-sixth the lengths of their ungues.

Central lobe of praecosta incised (Fig. 84). Female squama genitalis (Fig. 86) with short, wide styli; weak proximo-lateral sclerotizations present; caput processus thin and shaped like a boomerang, angled toward inner stylus margin; corpus processus extending nearly to inner stylus margin; median sclerotizations very well-developed; filum processus almost as long as stylus; stylus apices tapering to finely rounded tips.

Chaetotaxy.—Cephalic setae *aa* and *pa* present, anterior sensillum also present (Fig. 80). Seta *sp* 1.5× the length of seta *p*.

On mesonotum, *p2′* and *p3′* lanceolate (Fig. 82), *p1* and *p1′* of equal length; metanotal chaetotaxy similar except *p2′* setiform; bases of *p5* and *p5′* contiguous (Fig. 83).

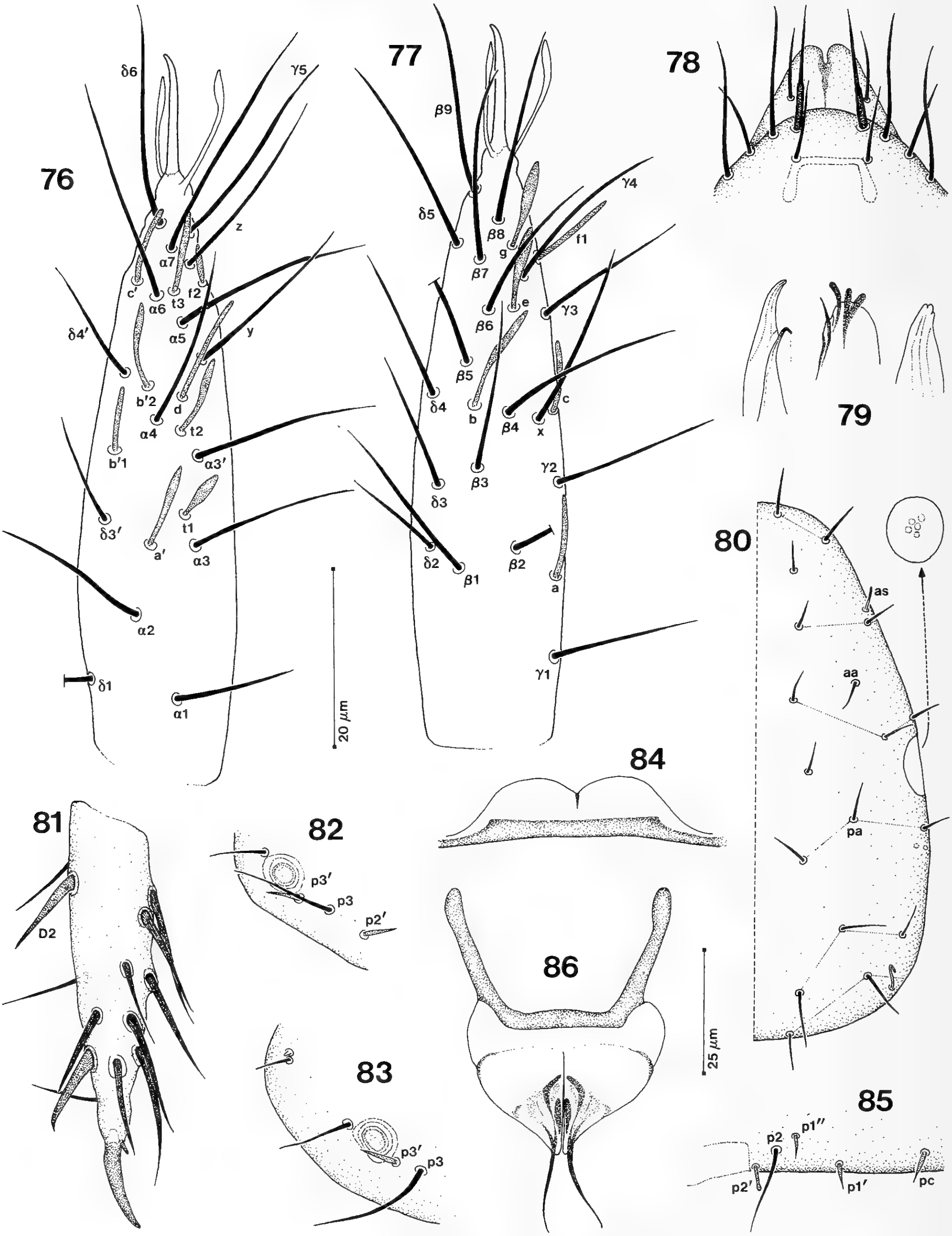
All sensilla present on foretarsus (Figs. 76, 77), sensilla *b, e, g, t2, a′*, and *b′2* spatulate; *a, c, d, f1, b′1, c′*, and *t3* linear, but *t3* slightly broader than the others; *f2* oblong. Sensillum *t1* closer to $\alpha3$ than to $\alpha3'$, BS = 0.84 Metatarsal seta D2 spiniform, stouter than D4 (Fig. 81).

Abdominal setal composition given in Table 7. Tergum I setal formula 3:1:2, *p1′* longer than *p1*. On terga II–VI, *p1′* and *p2′* longer than *p1* and *p2*, *p4′* about half the length of *p4* and less robust.

On tergum VII, *p1′* short and capitulate, *p4′* nearly the length of *p4* and equally robust. On tergum VIII, *pc, p1′*, and *p1″* all aristate, *p2′* clearly capitulate (Fig. 85).

Collection data.—Holotype female and one paratype female extracted from decaying wood, Upper Three Runs Creek and Road F, SRS, Aiken County, South Carolina, 17 Aug 1983; one paratype female from mixed pine-deciduous litter, SRS, Barnwell County, Road F near the guard rail, 4 Jan 1984. Holotype and one paratype in NMNH; one paratype in UTEM.

Derivation of name.—It is a pleasure to



Figs. 76–86. *Eosentomon renateae*: 76, Foretarsus, dorsal view; 77, Foretarsus, ventral view; 78, Labrum and rostral region; 79, Lacinia, galea, and mandible; 80, right side of head, dorsal view, and pseudoculus; 81, Metatarsus; 82, Posterior margin of mesonotum; 83, Posterior margin of metanotum; 84, Praecosta of tergum VI; 85, Posterior margin of tergum VIII; 86, Squama genitalis. (25 μm scale refers to Figs. 80, 82, 83, 85; 20 μm scale refers to all others.)

Table 7.—Abdominal chaetotaxy of *Eosentomon renateae,* n. sp.

	I	II–III	IV	V–VI	VII	VIII	IX–X	XI	XII
Dorsal	4/12	10/16	10/16	8[1]/16	4[2]/16	6/9	8	8	9
Ventral	4/4	6/4	6/10	6/10	6/10	0/7	6	8	12

[1] Seta *a3* absent.

[2] Setae *a1, a2, a3* absent.

name this species for Dr. Renate M. Snider, Michigan State University, who has made significant contributions to our knowledge of soil arthropod ecology.

Diagnosis.—*Eosentomon renateae* is similar to *E. richardi* (this paper) in most chaetotaxic and foretarsal characteristics, but differs primarily in the squama genitalis. In *E. renateae,* the caput processus is boomerang-shaped and the median sclerotizations are strong and prominent, whereas in *E. richardi* the caput processus is shaped like the head of a duck and bent sharply, and the median sclerotizations are thin and rod-like. Also, *E. renateae* has indented median rostral setae, while those of *E. richardi* are thin and not modified. The squama genitalis of *E. renateae* is similar to that of *E. asakawaense* Imadate, but lacks the distinct accessory sclerotization described for that species, and possesses prominent median sclerotizations (very thin in *E. asakawaense*).

Eosentomon richardi,
new species
Figs. 87–95; Table 8

Color and dimensions.—Body moderately sclerotized, yellow-orange. Mean length 782 μm (699–892, $n = 9$). Length of foretarsus 71 μm (69–74, $n = 13$). Length of head without labrum 103 μm (93–115, $n = 9$). LR = 10.7 (9.0–11.3, $n = 9$); PR = 11.0 (9.1–13.3, $n = 110$; tr = 4.5 (4.1–5.3, $n = 13$).

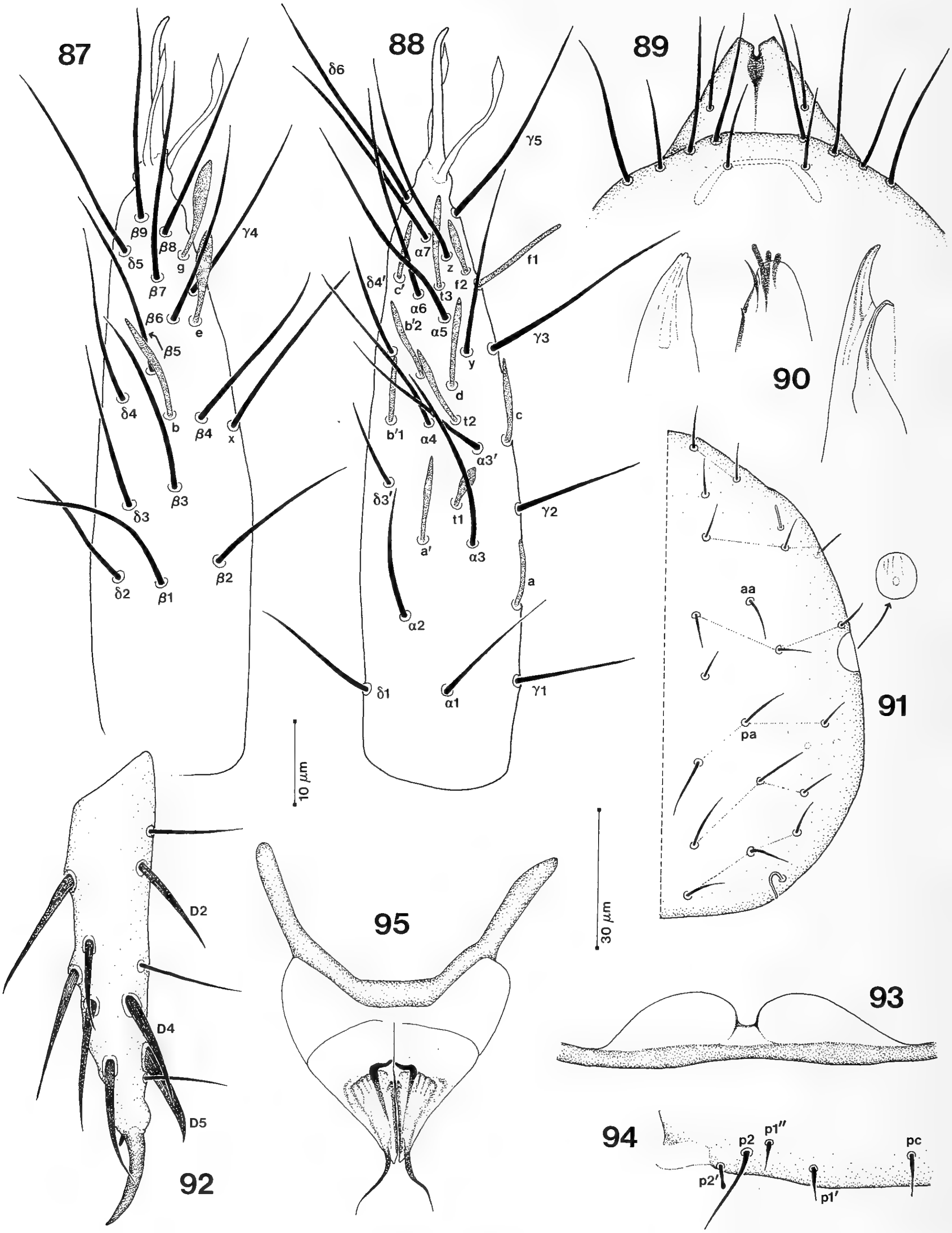
Morphology.—Pseudoculus round, with an oval median depression and a few faint, longitudinal striae in the anterior half (Fig. 91). Clypeal apodeme thin, side arms divergent. Labrum with truncate apices angled inward and terminating medially as a U-shaped notch; labral setae present, extending past tip of labrum (Fig. 89). Central pair of rostral setae not inflated. Mandible with three apical teeth, the middle teeth slightly larger than the others; digits of galea cylindrical and rounded apically, the outer digit about twice the length of the other two; outer lacinial lobe tapering, slightly curved, and without serrations; inner lacinial lobe sharply bent at apex (Fig. 90).

Empodium of foretarsus about the same length as the unguis, EU = 0.97 (0.89–1.07, $n = 10$). Empodia of middle and hind legs less than one-fifth the lengths of their ungues.

Central lobe of praecosta deeply sinuate (Fig. 93). Female squama genitalis (Fig. 95) with caput processus in the shape of a duck's head; corpus processus weakly developed, appearing striate in the proximal part, with outlines of the alae processus distinct; median sclerotizations rod-like, filum processus of medium length; stylus apices bluntly pointed.

Chaetotaxy.—Cephalic setae *aa* and *pa* present, anterior sensillum present; seta *sp* 1.2–1.5× the length of seta *p* (Fig. 91).

Seta *p1′* on mesonotum much longer than, and on metanotum slightly longer than, *p1*; *p3′* setiform, slightly longer than spiracle width; sockets of *p5* and *p5′* on metanotum contiguous.



Figs. 87–95. *Eosentomon richardi*: 87, Foretarsus, ventral view; 88, Foretarsus, dorsal view; 89, labrum and rostral region; 90, Mandible, galea, lacinia; 91, Right side of head and pseudoculus; 92, Metatarsus; 93, Praecosta of tergum VI; 94, Posterior margin of tergum VIII; 95, Squama genitalis. (30 μm scale applies to Figs. 91, 94; 10 μm scale to all others.)

Table 8.—Abdominal chaetotaxy of *Eosentomon richardi,* n. sp.

	I	II–III	IV–VI	VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{10}{16}$	$\frac{8^1}{16}$	$\frac{4^2}{16}$	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{6}{10}$	$\frac{0}{7}$	6	8	12

[1] Seta *a3* absent.

[2] Setae *a1, a2, a3* absent.

All sensilla present on foretarsus (Fig. 97, 88); *b, c, a', b'2, t2* and *t3* very weakly spatulate, *e* and *g* broadly spatulate; *f2* oblong, unusually large; all other sensilla except *t1* linear; sensilla *d, a', b'2, t2,* and *t3* all about equal in length. Sensillum *t1* closer to *α3* than to *α3'*, BS = 0.83 (0.76–0.91, *n* = 13). Metatarsal seta D2 a slender spine, weaker than D4 (Fig. 92).

Abdominal setal composition given in Table 8. Tergum I formula 3:1:2, *p1'* longer than *p1*. On terga II–VI, *p1'* and *p2'* longer than *p1* and *p2*; *p4'* shorter than *p4* but robust. On tergum VII, *p1'* short and weakly capitulate, *p2'* shorter than *p2*. On tergum VIII, *pc, p1'*, and *p1"* aristate and rather slender, *p2'* capitulate (Fig. 94).

Collection data.—Holotype female, two male paratypes, and two female paratypes collected from deciduous litter near the Road F guard rail SRS, Aiken County, South Carolina, 26 Mar 1984; one male and two female paratypes from soil under a log in deciduous forest along Road F, SRS, Barnwell County, South Carolina, 18 Jul 1983; one female paratype, decaying wood from Upper Three Runs Creek at Road F, SRS, Aiken County, South Carolina, 17 Aug 1983. Holotype and three paratypes deposited in NMNH, five paratypes in UTEM.

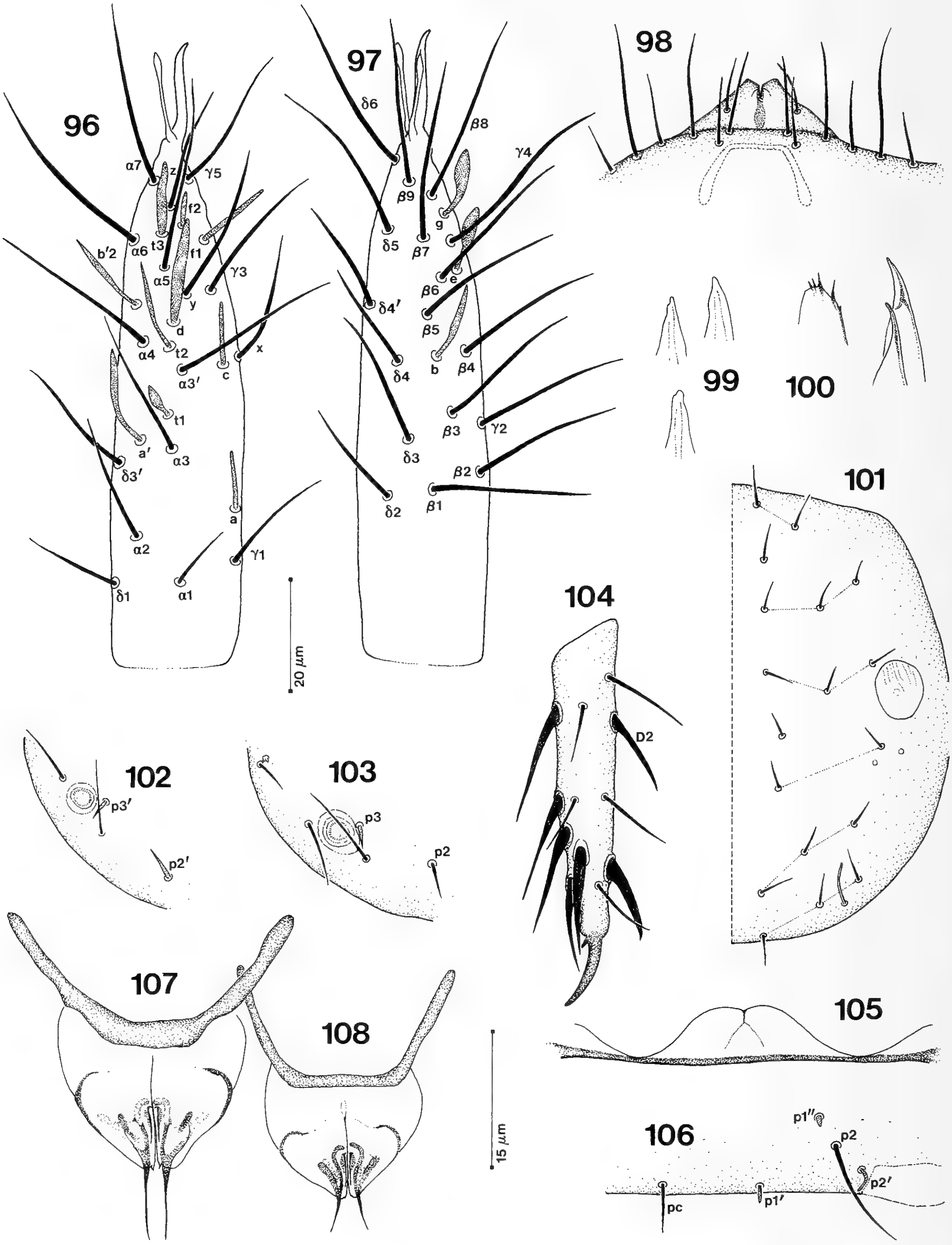
Derivation of name.—This species is named for Dr. Richard J. Snider, Michigan State University, who generously allowed me to examine the many proturans collected from the SRS.

Diagnosis.—*Eosentomon richardi* is one of the few known North American representatives of the mostly European "*transitorium*" group (Tuxen, 1964), species of which are distinguished by the sharply bent and recurved caput processus, resembling a duck's head. The presence of the two cephalic setae, *aa* and *pa,* places it among the subset named "*delicatum*" group by Szeptycki (1985) where it will key to *E. zodion* Szeptycki. It differs from this and the other "*delicatum*" group species, and from the North American species *E. vermontense* Nosek and *E. bernardi* Nosek (Nosek & Kevan 1984), in the presence of foretarsal sensillum b'1, the presence of eight, rather than ten, anterior setae on abdominal tergum IV, and the presence of six, not four, setae on sternites IX–X.

Eosentomon savannahense,
new species
Figs. 96–108; Table 9

Color and dimensions.—Body moderately sclerotized, yellowish. Mean length of females with various degrees of expansion 759 μm (603–1036, *n* = 9). Length of head without labrum 82 μm (70–95, *n* = 9). Length of foretarsus without claw 57 μm (48–63, *n* = 17). LR = 15.3 (11.8–18.5, *n* = 9); PR = 6.1 (5.6–6.5, *n* = 6); TR = 5.8 (5.3–6.4, *n* = 16).

Morphology.—Pseudoculus broadly oval, with several faint longitudinal striae in the anterior half and a small, circular central depression (Fig. 101). Clypeal apodeme with thin connecting bar and bulbous side arms (Fig. 98). Labrum small, much wider than



Figs. 96–108. *Eosentomon savannahense*: 96, Foretarsus, dorsal view; 97, Foretarsus, ventral view; 98, Labrum and rostral region; 99, Mandibles; 100, Galea and lacinia; 101, Right side of head, dorsal view; 102, Posterior margin of mesonotum; 103, Posterior margin of metanotum; 104, Metatarsus; 105, Praecosta of tergum VI; 106, Posterior margin of tergum VIII; 107, Variation in squama genitalis. (20 μm scale applies to Figs. 101–103, 15 μm scale to all others.)

Table 9.—Abdominal chaetotaxy of *Eosentomon savannahense*, n. sp.

	I	II–III	IV–VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{8}{16}$[1]	$\frac{8}{16}$[1]	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{2}{7}$	4	8	12

[1] Seta *a3* absent.

long, apices truncated to form a shallow V (Fig. 98); labral setae present. Central pair of rostral setae not inflated. Mandible (Fig. 99) slender, rounded terminally or with an obscure, rounded subapical protuberance. Digits of galea spine-like, the outer digit the longest; outer lacinial lobe slightly curved, not serrate, inner lacinial lobe slender and curved but not bent near apex (Fig. 100).

Empodium of foretarsus usually shorter than the unguis, EU = 0.90 (0.85–1.0, *n* = 14). Empodia of middle and hind tarsi less than one-sixth the lengths of their ungues.

Central lobe of praecosta slightly incised (Fig. 105). Female squama genitalis (Figs. 107, 108) with well developed, clubbed or hooked median sclerotizations and weakly sclerotized, semi-circular caput processus; corpus processus reduced except for well-developed alae processus; filum of variable length; stylus apices broadly rounded with a weak to well-developed subterminal spur. Basal apodeme rather thin; proximo-lateral sclerotizations clearly present.

Chaetotaxy.—Cephalic setae *aa* and *pa* and anterior sensillum all absent (Fig. 101). Seta *sp* 1.1–1.4× the length of seta *p*; posterior sensillum longer than the posterior setae.

On mesonotum and metanotum, setae *p1* and *p1′* of equal lengths; *p3′* lanceolate and as long as width of spiracle (Fig. 102). On mesonotum, *p2′* similar in shape to *p3′*; on metanotum *p2′* setiform; *p5* about equal to *p2′* and contiguous with *p5′* (Fig. 103).

On foretarsus (Figs. 96, 97), sensilla *b′1* and *c′* absent; *b, a′*, *b′2* and *t2* all pointed-spatulate; lengths of *b′2* and *t2* variable; sensillum *d* long and broad, reaching or bypassing the base of *f2*; *t3* broad, half the length of *d*; *f1* linear. Sensillum *t1* closer to *α3* than to *α3′*, BS = 0.91 (0.83–0.96, *n* = 17). Metatarsal seta D2 a slender spine, much thinner than D5 (Fig. 104).

Abdominal setal composition given in Table 9. Tergum I setal formula 3:1:2; seta *p1′* twice the length of *p1*. On terga II–VI, *p1′* and *p2′* longer than their primary setae; *p4′* delicate and longer than *p4* on terga II–V, robust and shorter than *p4* on terga VI and VII. On tergum VII, *p1′* two-thirds the length of *p1* and capitulate, *p2′* longer than *p2*. On tergum VIII, seta *p1′* oblong, *p1″* gemmate, *p2′* short, not noticeably capitulate (Fig. 106).

Collection data.—Holotype female and two paratype females collected from oak litter, Road F near Dunbarton, SRS, Barnwell County, South Carolina, 18 May 1984; one paratype female, rotted wood and deciduous litter, same general locality, junction of Road 6 and Road C, 10 Mar 1982; one paratype female, soil cores near Road C, SRS, Barnwell County, 26 Sep 1983; one paratype female, soil cores in live oak stand, near Road F—Road B junction, SRS, Barnwell County, 10 Oct 1983; two paratype females, deciduous litter near Road 6 and guard rail, SRS, Barnwell County, 4 Jan 1984; one paratype female, pitfall trap in deciduous swamp near Road 4 and guard rail, SRS, Aiken County, 2 Mar 1984; one paratype female, wet oak and Spanish moss litter near Dunbarton, SRS, Barnwell County, 13 Apr 1984; one paratype female, oak litter in U.S. Forest Service pine plantation, SRS, Aiken County, 15 May 1984; one paratype female, deciduous litter near Road F guard rail, SRS, Aiken County, 23 Jul 1984. Holotype and four paratypes deposited in NMNH, the remaining paratypes in UTEM.

Derivation of name.—This species is named after the Savannah River, which flows near the type locality.

Diagnosis.—*Eosentomon savannahense* is very similar to *E. ewingi*, *E. pseudoyosemitense* Copeland and White, and *E. yosemitense* Ewing in the form of the squama genitalis. The following key will serve to separate the four species:

1. Sternum VII with two anterior setae; terga II–VII each with eight anterior setae 2
– Sternum VIII without anterior setae; tergum VII with four or six anterior setae 3
2. Foretarsal sensillum *b′1* present; sterna IX–X each with six setae; median rostral setae indented . . . . *E. pseudoyosemitense*
– Foretarsal sensillum b′1 absent; sterna IX–X each with four setae; median rostral setae thin . . . . *E. savannahense*
3. Empodium of metatarsus short; tergum VII with four anterior setae . . . . *E. yosemitense*
– Empodium of metatarsus long; tergum VII with six anterior setae . . . . *E. ewingi*

Eosentomon snideri, new species
Figs. 109–118; Table 10

Eosentomon australicum Womersley of Bernard, 1975b:187, figs. 1–5.

The specimens of this new species from southern Michigan were identified originally as *E. australicum* Wormersley 1939 by Bernard (1975b). After reexamination of the specimens with the aid of interference contrast microscopy, and especially with a reinterpretation of the female genitalia, it is clear they represent a species allied to east Asian taxa such as *E. udagawai* Imadate.

Color and dimensions.—Body moderately sclerotized, amber-yellow. Mean length of adults 1183 μm (940–1362, *n* = 6). Length of head without labrum 134 μm (121–148, *n* = 6). Length of foretarsus without claw 88 μm (83–90, *n* = 11). LR = 11.0 (10.1–12.1, *n* = 6); PR = 11.9 (10.2–12.1, *n* = 12); TR = 4.8 (4.2–5.2, *n* = 11).

Morphology.—Pseudoculus broadly oval with two small, contiguous, oval median depressions (Fig. 113). Labrum robust, apices rounded-truncate, with several fine, longitudinal lines distally; median notch a rounded U-shape; labral setae present, extending past labral apex (Fig. 111). Clypeal apodeme with large, clavate side arms. Rostral setae inflated. Mandible with two apical and one minute inner teeth; digits of galea cylindrical and apically rounded, the median and inner digits about two-thirds the length of the outer digit; outer lobe of lacinia tapering and curved inward slightly, not serrate on the inner margin; inner lacinial lobe hooked at apex (Fig. 112).

Empodium of foretarsus slightly shorter than the unguis, EU = 0.92 (0.85–1.03, *n* = 11). Empodia of middle and hind legs less than one-fifth the lengths of their ungues.

Central lobe of praecosta sinuate (Fig. 116). Processus sternalis of female squama genitalis (Fig. 118) formed into an S-shape by the caput processus and an ala processus, the caput processus shaped like a duck's head; median sclerotization very broad but weakly sclerotized; filum processus nearly as long as stylus; stylus pointed apically.

Chaetotaxy.—Cephalic seta *aa* and *pa* present, anterior sensillum present (Fig. 113). Seta *sp* 1.3–1.5× the length of seta *p*.

On mesonotum and metanotum, *p3′* setiform, slightly longer than spiracle width; *p1′* longer than *p1*; on metanotum, *p5* nearly as long as *p3′*, bases of *p5* and *p5′* nearly contiguous (Fig. 114).

On foretarsus (Figs. 109–110), sensillum *b′1* absent; sensilla *b*, *f1*, and *a′* slender and spatulate, *e* and *g* rounded-spatulate; *f2* clearly claviform; except for *t1,* all other sensilla linear. Sensillum *d* nearly reaching *f2*; *t3* and *c'* of equal length; *a* reaching $\gamma 2$. Sensillum *t1* closer to $\alpha 3'$ than to $\alpha 3$, BS = 1.00 (0.93–1.05, *n* = 11). Metatarsal seta D2 a robust spine; most of the ventral spiniform setae very long and slender (Fig. 115).

Abdominal setal composition given in Table 10. Tergum I formula 3:1:2, *p1'* longer than *p1*. On terga II–VI, *p1'* and *p2'* longer than *p1* and *p2*; *p4'* a normal seta, two-thirds of the length of p4. On tergum VII, *p1'* capitulate, very short, less than one-fifth the length of *p2'*. Setae *p1"* and *p2'* on tergum VIII aristate, base of *pc* far from margin (Fig. 117).

Collection data.—Holotype female and two paratype females extracted from moss near Monahan Lake, Livingston County, Michigan, 19 May 1974, E. Bernard, coll.; three paratype females, pine forest soil, Kellogg Forest, Kalamazoo County, Michigan, 23 Jun 1963. Holotype and one paratype deposited in NMNH, three paratypes in UTEM, and one paratype in the Michigan State University Entomology Museum.

Derivation of name.—This species is named with pleasure for Dr. Richard J. Snider, world authority on the Collembola and my first mentor for studies on apterygote insects.

Diagnosis.—*Eosentomon snideri* is similar to *E. kumei* Imadate and Yosii from Japan and *E. udagawai* Imadate from Japan and China (Imadate 1974) but differs in tergal chaetotaxy, length of metatarsal empodium, and details of the squama genitalis. *Eosentomon snideri* has a short metatarsal empodium (long in *E. udagawai*), ten *a*-setae on terga IV–V, four *a*-setae on tergum VII, no *a*-setae on sternite VIII, and four setae on sternites IX–X (in *E. kumei,* eight *a*-setae on terga IV–V; in *E. udagawai,* six *a*-setae on terga IV–V, two *a*-setae on sternite VIII, and six setae on sternites IX–X). The squama genitalis of *E. snideri* has a compact "S" formed from the caput processus and ala processus well anterior to the stylus apex, as in *E. udagawai* ("S" large in *E. kumei* and close to stylus apex), possesses median sclerotizations (absent in *E. kumei*), and has sublateral alae (absent in *E. kumei* and *E. udagawai*).

Eosentomon xenomystax,
new species

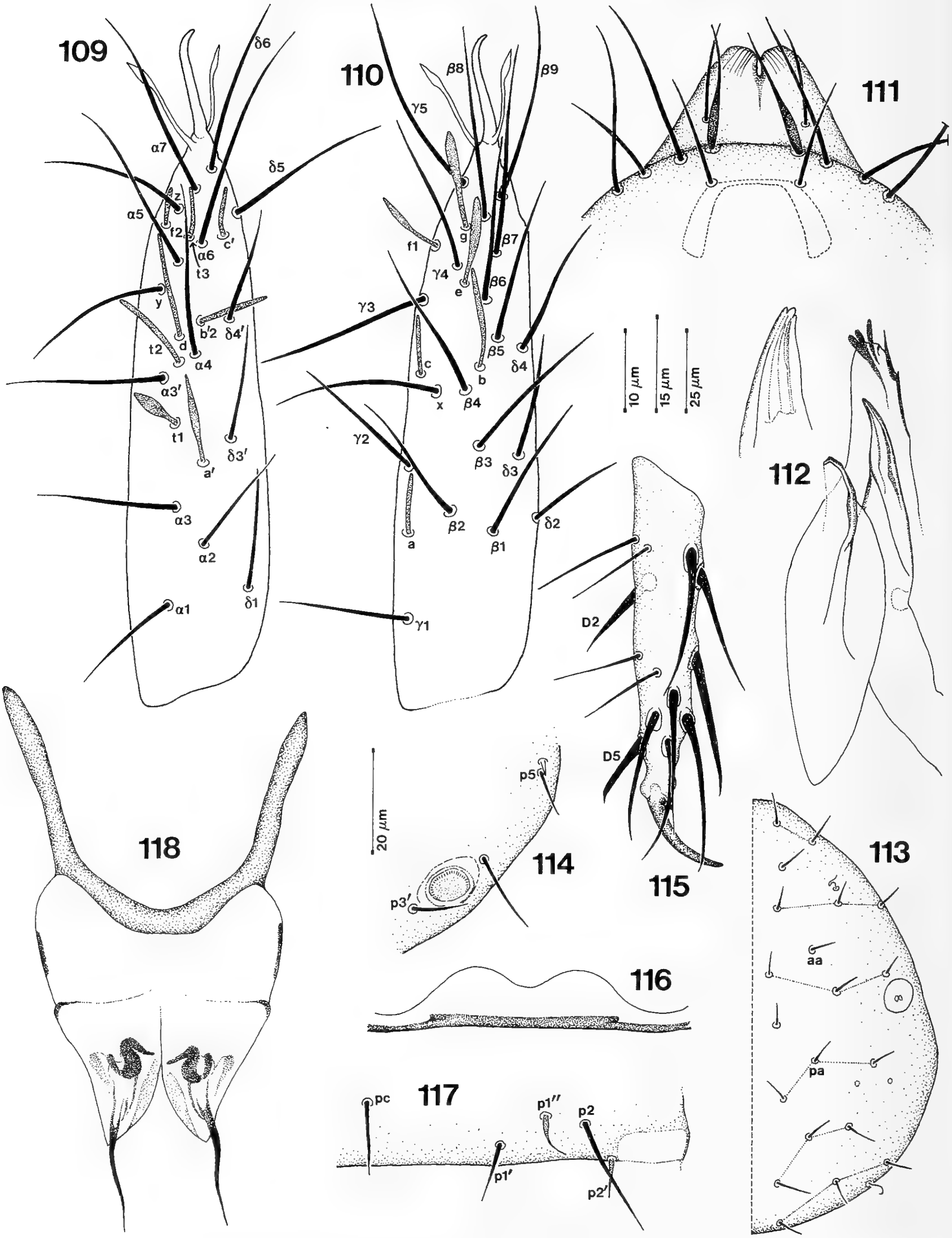
Figs. 119–129; Table 11

Color and dimensions.—Body lightly sclerotized except posteriorly, yellowish amber. Mean length of expanded adults 759 μm (627–831, *n* = 4). Length of foretarsus without claw 51 μm (49–54, *n* = 6). Length of head without labrum 81 μm (75–87, *n* = 4). LR = 8.9 (7.2–10.3, *n* = 4); PR = 7.4 (6.8–8.0, *n* = 8); TR = 5.7 (5.4–6.3, *n* = 6).

Morphology.—Pseudoculus nearly round, with median line, a few obscure lines anteriorly, and two small circular depressions near its center (Fig. 123). Clypeal apodeme thin, side arms slightly swollen. Labrum of a peculiar shape, the sides concave in the distal half and tapering to small, truncated apices and a minute U-shaped cleft; labral setae present but minute, much shorter than the labrum (Fig. 121). Central pair of rostral setae not inflated. Mandible small and bidentate, with an apical tooth and an inner retrorse tooth; galea of maxilla with the usual outer spine and thin, delicate digits, the outer digit the longest; all three digits fused on the galeal blade; each lacinial lobe curved and evenly tapering, serrations not observed on the outer lobe (Fig. 122).

Empodium of foretarsus generally slightly shorter than the unguis, EU = 0.9 (0.8–1.0, *n* = 7). Empodia of middle and hind legs less than one-sixth the lengths of their ungues.

Central lobe of praecosta trapezoidal, not incised (Fig. 126). Female squama genitalis (Fig. 129) with well-developed sclerotizations of the perigynium and stylus; caput process thin but distinct, smoothly curved to the inner stylus edge; corpus processus



Figs. 109–118. *Eosentomon snideri*: 109, Foretarsus, dorsal view; 110, Foretarsus, ventral view; 111, Labrum and rostral region; 112, Mandible and head of maxilla; 113, Right side of head, dorsal view; 114, Posterior margin of metanotum; 115, Metatarsus; 116, Praecosta of tergum VI; 117, Posterior margin of tergum VIII; 118, Squama genitalis. (10 μm scale applies to Figs. 111, 112, 118; 15 μm scale applies to Figs. 109, 110, 115–117; 20 μm scale applies to Fig. 114; 25 μm scale applies to Fig. 113.)

Table 10.—Abdominal chaetotaxy of *Eosentomon snideri*, n. sp.

	I	II–III	IV–V	VI	VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{10}{16}$	$\frac{10}{16}$	$\frac{8^{1}}{16}$	$\frac{4^{2}}{16}$	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{6}{10}$	$\frac{6}{10}$	$\frac{0}{7}$	4	8	12

[1] Seta *a3* absent in holotype and four adult paratypes, present in one adult paratype.
[2] Setae *a1, a2, a3* absent.

well developed and variably thickened, scalloped on anterior edge, and extending as ala processus to the outer stylus edge; median sclerotizations long and thin, doubled in the proximal fourth. Filum processus short, stylus tips rounded.

Chaetotaxy.—Cephalic seta *aa* absent, *pa* present; anterior sensillum absent (Fig. 123). Seta *sp* 0.9–1.4× the length of seta *p*.

Seta *p1′* on mesonotum and metanotum similar to *p1* and of the same length; seta *p3′* short and asymmetrically claviform with flattened, oblique tip appearing minutely crenulate (Fig. 124). On metanotum, bases of *p5* and *p5′* close but not contiguous.

On foretarsus (Figs. 119, 120), sensillum *c′* absent; *b′1* present, setiform. Sensillum *a* nearly reaching $\gamma 2$, *a′* reaching *t2*, *b* long and thinly spatulate, *c* reaching $\alpha 3$; *t1* closer to $\alpha 3$ than to $\alpha 3'$; BS = 0.94 (0.91–0.96, *n* = 6); *t2* and *b′2* of moderate length and pointed-spatulate; *d* and *t3* each long, *t3* particularly robust and reaching nearly to the base of the claw. Sensilla *e* and *g* spatulate; *f1* linear; *f2* shorter than *f1* and ovate. Metatarsal setae D2, D4, and D5 very stout (Fig. 125).

Abdominal setal composition given in Table 11. Tergum I setal formula 3:1:2; *p1′* almost twice as long as *p1*. On terga II–VI, *p1′* and *p2′* nearly twice the length of *p1* and *p2*; *p4′* on terga II–III setiform and much shorter than *p4* but delicate and longer than *p4* on terga IV–VI; on tergum VII *p4′* equal in length to *p4*, *p1′* more than half the length of *p1* and not noticeably capitulate (Fig. 127). On tergum VIII, *p1″* minute and bluntly pointed, *p2′* very weakly capitulate (Fig. 128).

Collection data.—Holotype female and two paratype females collected from wet oak and Spanish moss litter near Dunbarton, SRS, Barnwell County, South Carolina, 13 Apr 1984; one paratype female, same location, from oak litter, 18 May 1984. Holotype and one paratype deposited in NMNH; two paratypes deposited in UTEM.

Derivation of name.—The specific epithet is a compound Greek word meaning "strange upper lip," in reference to the unusual labrum with very short setae.

Diagnosis.—*Eosentomon xenomystax* possesses many unusual characteristics that separate it from other *Eosentomon* spp.: labral setae very short; foretarsal sensillum *t3* long and strong, equal in length to *d*; seta *p3′* on the mesonotum and metanotum claviform-truncate; caput processus shaped like a barbless fishhook, median sclerotizations doubled proximally. The Minorcan species *E. coiffaiti* Conde has very short labral setae but is otherwise dissimilar. The squama genitalis is reminiscent of that of *E. pseudoyosemitense* Copeland & White but differs from that species in many characters, including those listed above.

Remarks

In addition to the seven new species described herein from the SRS, six other eosentomid species were collected from the same area: *Eosentomon pallidum* Ewing, *E. pseudoyosemitense* Copeland & White, *E.*

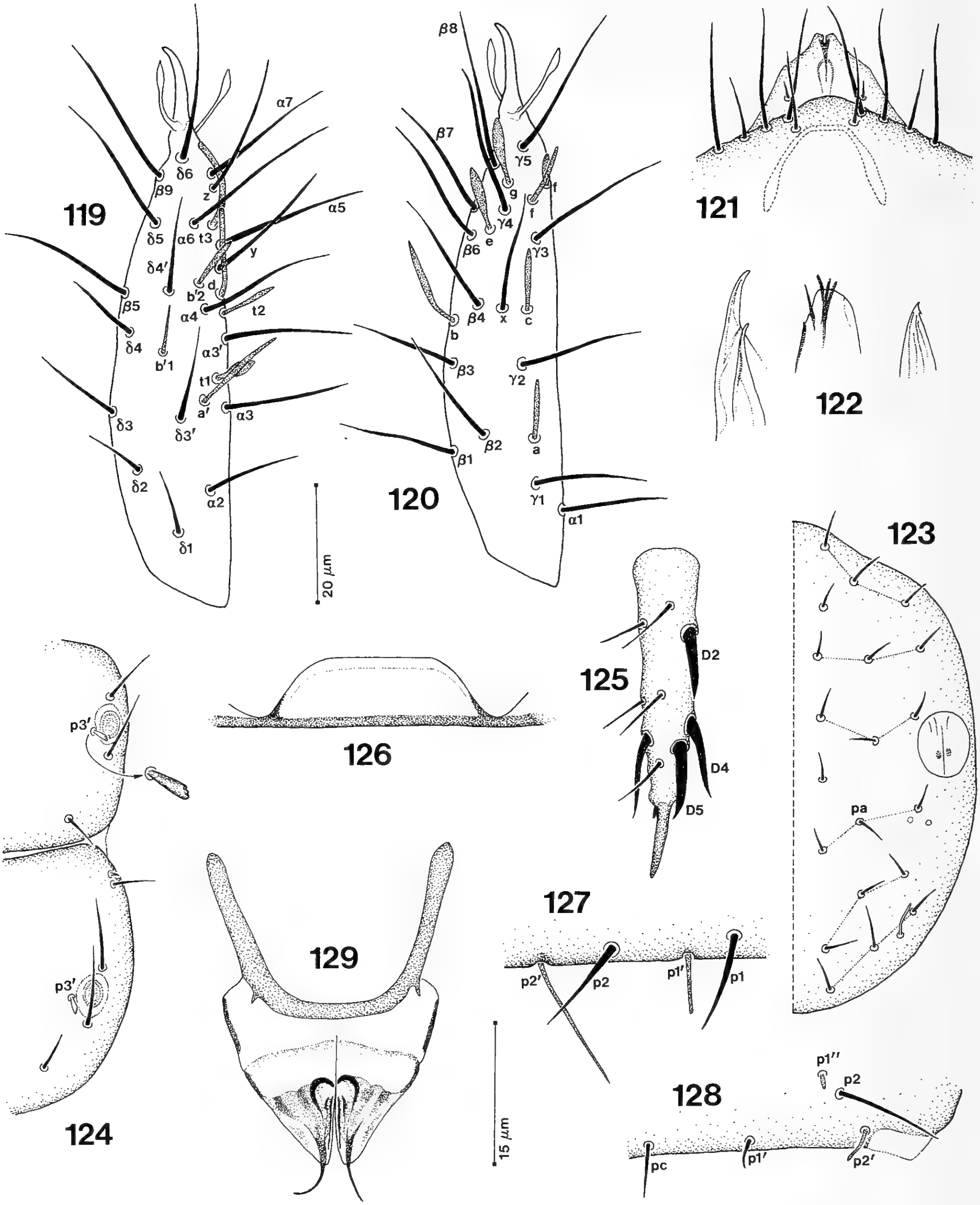


Fig. 119–129. *Eosentomon xenomystax*: 119, Foretarsus, interior view; 120, Foretarsus, exterior view; 121, Labrum and rostral region; 122, Lacinia, galea, and mandible; 123, Right side of head, dorsal view; 124, Posterolateral margins of mesonotum and metanotum; 125, Metatarsus; 126, Praecosta of tergum VI; 127, Posterior margin of tergum VII; 128, Posterior margin of tergum VIII; 129, Squama genitalis. (20 μm scale applies to Figs. 123–124, 15 μm scale to all others.)

Table 11.—Abdominal chaetotaxy of *Eosentomon xenomystax*, n. sp.

	I	II–III	IV–VII	VIII	IX–X	XI	XII
Dorsal	$\frac{4}{12}$	$\frac{8^1}{16}$	$\frac{8^1}{16}$	$\frac{6}{9}$	8	8	9
Ventral	$\frac{4}{4}$	$\frac{6}{4}$	$\frac{6}{10}$	$\frac{2}{7}$	4	8	12

[1] Seta *a3* absent.

turneri Bonet, *E. vermiforme* Ewing, *E. wheeleri* Silvestri, and *Styletoentomon rostratum* (Ewing). This total of 13 species from the SRS represents a more diverse fauna than hitherto observed in North America, and is a richer assemblage of species for the size of the area than reported either in Europe or Japan, two well-studied regions. Imadate (1974) reported 13 species from all of Japan, and Nakamura (1983a, 1983b) has since decribed two more. Nosek (1973) listed 14 species from all of Europe; since then 26 additional species have been described, mostly by Szeptycki (e.g., 1986); the majority of these are very similar forms separated by small setal and sensilla differences. The greater perceived diversity in the SRS may be due partly to very intensive collecting and the discrimination of isolated specimens of very small species (e.g., *E. crypticum, E. renateae, E. xenomystax*), which relates to the method of extraction. Proturans usually are extracted with Tullgren-type funnels, which favor the collection of larger, more heavily sclerotized species (>1 mm length). All of the new species from the SRS described in this paper have lengths usually much less than one mm, whereas all of the previously described SRS species, except *E. pseudoyosemitense,* are longer than one mm. Small proturan species tend to inhabit soil, rather than leaf litter and fermentation layers. Since there is no reason to assume that small species are rarer than large species, it is likely that the choice of extraction method is critical in the quantitative study of Protura.

The species described in this paper help clarify geographical relationships among various *Eosentomon* species groups, which Tuxen (1964) differentiated on the basis of the squama genitalis. The primarily European "*transitorum*" group is represented in North America by three species: *E. bernardi* (Quebec), *E. vermontense* (Vermont), and *E. richardi* (South Carolina). The east Asian "*kumei*" group is represented in North America by *E. pusillum* (Michigan, Florida) and *E. snideri* (Michigan). Conversely, the "*wheeleri*" group is almost exclusively North American, with two species in western Europe and one in Japan. The "*maya*" group, which includes *E. ewingi* (North Carolina), *E. pseudoyosemitense* (North Carolina, South Carolina, Tennessee), *E. savannahense* (South Carolina), and *E. yosemitense* (California), appears restricted to North America, except for *E. brevicorpusculum* in China.

Acknowledgments

This research was partially supported by the U.S. Department of Energy's National Environmental Research Park Program under contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

Literature Cited

Bernard, E. C. 1975a. A new genus, six new species, and records of Protura from Michigan.—Great Lakes Entomologist 8:157–181.

———. 1975b. New species and additional records of Protura from Michigan.—Great Lakes Entomologist 8:187–195.

———. 1985. Two new species of Protura (Insecta) from North America.—Proceedings of the Biological Society of Washington 98:72–80.

Bonet, F. 1950. Descripcion preliminar de especies nuevas del genero *Eosentomon* (Protura). II. El *E. pallidum* Ewing y sus especies afines.—Anales de la Escuela Nacional de Ciencias Biologicas 6:109–130.

———, & S. L. Tuxen. 1960. Reexamination of species of Protura described by H. E. Ewing.—Proceedings of the United States National Museum 112:265–305.

Copeland, T. P. 1964. New species of Protura from Tennessee.—Journal of the Tennessee Academy of Science 39:17–29.

Ewing, H. E. 1940. The Protura of North America.—Annals of the Entomological Society of America 33:495–551.

Imadate, G. 1974. Fauna Japonica. Protura (Insecta). Tokyo, Keigaku Publishing Company, Ltd., 351 pp.

———. 1989. Proturans from Java.—Azao 1:91–118.

Nakamura, O. 1983a. A new species of the genus *Eosentomon* (Protura, Eosentomidae) from Hokkaido, northern Japan.—Kontyu 51:140–143.

———. 1983b. *Eosentomon nupri* sp. nov. from Hokkaido (Protura, Eosentomidae).—Kontyu 51:596–600.

Nosek, J. 1973. The European Protura. Geneva, Museum L'Histoire Naturelle, 345 pp.

———, & D. K. McE. Kevan. 1984. New species of *Eosentomon* Berlese, 1909 (Protura: Eosentomidae) from Quebec and Vermont.—Canadian Entomologist 116:19–26.

Szeptycki, A. 1984. Three new species of *Eosentomon* Berlese, 1909, from Poland with redescription of *Eosentomon germanicum* Prell, 1912.—Polskie Pismo Entomologiczne 54:195–213.

———. 1985. Polish Protura. II. *Eosentomon delicatum* Gisin, 1945, and related species.—Polskie Pismo Entomologiczne 55:139–186.

———. 1986. Polish Protura. IV. *Eosentomon "transitorium"* group.—Polskie Pismo Entomologiczne 56:481–530.

Tuxen, S. L. 1964. The Protura. Paris, Hermann, 360 pp.

———. 1976. The Protura (Insecta) of Brazil, especially Amazonas.—Amazoniana 5:417–463.

Yin, Wen-ying. 1965. Studies on Chinese Protura I. Ten species of the genus *Eosentomon* from Nanking-Shanghai regions.—Acta Entomologica Sinica 14:71–92 (in Chinese with English summary).

———. 1982. Studies on Chinese Protura: Twelve species of the genus *Eosentomon* from Yunnan Province.—Zoological Research 3:11–30 (in Chinese with English summary).

Department of Entomology and Plant Pathology, University of Tennessee, Knoxville, Tennessee 37901-1071.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 891–906

TAXONOMIC NOTES ON EPHYDRIDAE (DIPTERA)

Wayne N. Mathis and Tadeusz Zatwarnicki

Abstract.—Several zoological and nomenclatural items concerning Nearctic Ephydridae, which will be modified in a forthcoming checklist of North American Diptera, are presented and explained. Usage of the family-group names Gymnomyzinae and Gymnomyzini is discussed; *Athyroglossa* (*Parathyroglossa*) *dinorata,* a new species, is described (= *A. ordinata* of American authors, not Becker); the synonymy of the genus *Gymnomyza* Fallén with *Mosillus* Latreille is explained; the tribe Ochtherini is transferred to the subfamily Gymnomyzinae where character evidence allies it with the tribe Gymnomyzini; the tribe Lipochaetini is recognized and Nearctic genera assigned; *Pelignellus* is synonymized with *Atissa*; *Pelignus salinus* Cresson is transferred to *Schema* Becker; *Hecamedoides glaucellus unispinosus* is given species status (= *H. glaucellus* of American authors, not Stenhammar); *Nesopsilopa* Mathis & Wirth is relegated to subgeneric status under *Guttipsilopa* Wirth; the subfamily Hyadininae Phillips et al. is given precedence over Gastropinae Cresson by our present action as first revisors; three subspecies in the genus *Pelina* (*bispinosa, latiforma,* and *prospinosa*) are given species status; possible relationships of the tribe Parydrini are discussed; *Parydra parasocia* Clausen is synonymized with *Ephydra fossarum* Haliday; *Parydra halteralis joaquinensis* Clausen is given species status; the tribe *Philygriini* is diagnosed for the first time; *Philygris opposita* Loew, 1861 is synonymized with *Notiphila puanctatonervosa* 1813; *Ephydra lata* Walker, 1858 is synonymized with *Ephydra ripara* Fallén, 1813; *Ephydra oscitans* Walker is discussed; and *Ephydra gracilis* Packard, 1871 is given precedence over *Ephydra cinerea* Jones, 1906.

While preparing material for a catalog on the dipterous family Ephydridae, more commonly known as shore flies, we noted several zoological and nomenclatural changes that should be explained in greater detail than the format of a catalog normally permits. The changes that pertain to the Nearctic fauna are explained here, as that fauna will soon be treated in a checklist of Diptera to be published by the United States Department of Agriculture. Some of the problems concern only nomenclature; others entail both zoological and nomenclatural matters.

Methods.—As a framework for this paper and to be explicit about the classification that results from changes made herein, we have arranged each taxon being treated by its subfamily. If taxa being treated within a subfamily belong to different tribes, then tribes are also cited. The general methodology used in this study was explained previously (Mathis 1986). The descriptive terminology, with the exceptions noted (Mathis 1986), follows that published in the recent Manual of Nearctic Diptera, Vol. 1 (McAlpine 1981). One head and two venational ratios are used commonly in the descriptions and are defined here for the convenience of the user (all ratios are averages of three specimens, the largest and smallest available and one other).

Eye-to-cheek ratio: genal height (immediately below eye)/eye height.

Costal vein ratio is the straight line distance between the apices of R_{2+3} and R_{4+5}/distance between the apices of R_1 and R_{2+3}.

M vein ratio: straight line distance along vein M between crossveins r-m and dm-cu/distance apical of crossvein dm-cu.

The illustrations of the male terminalia were first drawn in pencil by the second author (TZ) and then inked by Elaine R. S. Hodges.

Most specimens we examined are in the National Museum of Natural History, Smithsonian Institution (USNM). Numerous others were borrowed from the following collections: Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard (MCZ); National Museum of Ireland (NMI); Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS); Hope Entomological Collection, Oxford University, England.

Subfamily Gymnomyzinae

Gymnomyzides Latreille, 1829:535. Type genus: *Gymnomyza* Fallén, 1810 (= *Mosillus* Latreille, 1804).

Tribe Gymnomyzini

Gymnomyzides Latreille, 1829:535. See subfamilial listing.

Gymnopini Cresson, 1922:326. Type genus: *Gymnopa* Fallén, 1820 (= *Mosillus* Latreille, 1804).

Remarks.—The family-group names Gymnomyzinae and Gymnomyzini are both based on the genus *Gymnomyza* Fallén (see treatment of this genus under *Mosillus*). At the subfamilial and tribal levels, these names are nearly 100 years older and clearly have precedence over Psilopinae (Cresson, 1925) or Gymnopini (Cresson, 1922), the family-group names used at the subfamilial and tribal levels in recent catalogs (Wirth 1965, 1968; Cogan & Wirth 1977; Cogan 1980, 1984; Mathis 1989). We are advocating use of Gymnomyzinae and Gymnomyzini rather than requesting their suppression because priority will promote stability at these categorical levels. For example, two other family-group names, Lipochaetinae Becker (1896) and Discocerinini Cresson (1925), are also older than Psilopinae, and they would also have precedence over the latter. Thus to promote stability, we are using Gymnomyzinae and Gymnomyzini, as both are the oldest family-group names in Ephydridae and are unlikely to be replaced with still older names.

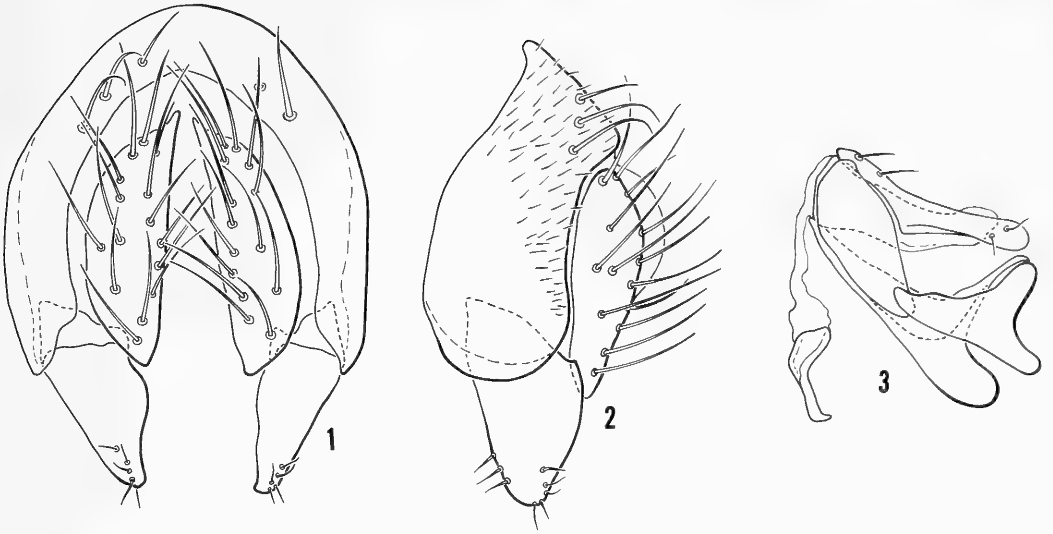
The priority of Gymnomyzidae does pose a problem, however. As a family-group name, Gymnomyzidae is also older than Ephydridae Zetterstedt (1837). Because Ephydridae has and remains the commonly used name for the family, we have requested that the ICZN use its plenary powers to give precedence to Ephydridae over Gymnomyzidae when the two are considered to be synonyms (Mathis & Zatwarnicki, 1990b).

Athyroglossa (*Parathyroglossa*) *dinorata*, new species
Figs. 1–3

Athyroglossa ordinata of various American authors, not Becker, 1896.—Wirth, 1965: 735 [Nearctic catalog].

Diagnosis.—Small to moderately small shore flies, length 1.65 to 2.50 mm.

Head: Two proclinate fronto-orbital setae, anterior seta subequal in size to reclinate seta, posterior seta about ⅓ length of anterior seta; frons mostly uniformly smooth, shiny; pseudopostocellar setae well developed, about ½ length of ocellar setae; ocelli arranged to form an isosceles triangle, distance between posterior pair greater; antenna blackish; arista with 5–8 dorsal rays, length of longer dorsal rays about ⅔ width of 1st flagellomere; antennal groove bare ventrally to invested with distinctly whitish microtomentum dorsally; face pointed, transversely grooved; parafacials bare of microtomentum; eye-to-cheek ratio 0.45.



Figs. 1–3. Male terminalia of *Athyroglossa dinorata*: 1, Epandrium, cerci, and surstyli, posterior view; 2, Epandrium, cercus, and surstylus, lateral view; 3, Internal male genitalia, lateral view.

Thorax: Mesonotum mostly bare, shiny, microtomentum only along posterior margin of scutum and anterior margin of scutellum; acrostichal setae conspicuous in 4 rows. Halter blackish. Wing unicolorous, nearly hyaline; venation unicolorous, brownish black; costal vein ratio 0.33; M vein ratio 0.48. Legs concolorous, each with coxae, femora, tibiae, and apical 2–3 tarsomeres black, basitarsomeres yellowish to whitish; fore femur unarmed.

Abdomen: Dorsum of tergum 1, most of 2, anterior margin of 3, and most of 5 microtomentose, otherwise bare and shiny. Male terminalia (Figs. 1–3) as follows: width of epandrium in posterior view about as wide as high (Fig. 1); surstylus in lateral view roughly conical, ventral apex broadly rounded, bearing a few setulae apicad (Figs. 1, 2); gonite (postgonite) in lateral view clavate (Fig. 3); hypandrium in lateral view broadly Y-shaped (Fig. 3).

Type material.—The holotype male is labeled "[USA] COLORADO.Rio GrandeCo. [,]8000′[,]South Fork[,] 20 June 1972[,], W. W. Wirth[,] Malaise trap." The allotype female and one male paratype bear the same locality label as the holotype. The holotype is double mounted (minute nadel in polyporus block), is in excellent condition, and is deposited in the USNM.

Other specimens examined.—CANADA. ALBERTA. Banff, 20 Aug 1925, O. Bryant (1 ♂; USNM). Okotoks, Sheep River, 27 Jun 1968, W. W. Wirth (4 ♂, 2 ♀; USNM). NOVA SCOTIA. Truro, 16 Aug 1913, R. Matheson (1 ♀; USNM). ONTARIO. Hearst (75 mi W), 5 Jul 1954, A. H. Sturtevant (1 ♀; USNM).

UNITED STATES. ARIZONA. Maricopa Co., Wickenburg, 16–18 May 1950, A. H. Sturtevant (3 ♂; USNM). CALIFORNIA. Monterey Co., Lucia, 28 Jul 1940, A. L. Melander (1 ♂; USNM). "Toumey Park," 19 Jun 1935, A. L. Melander (1 ♂; USNM). COLORADO. Gunnison Co., Crested Butte (8300 ft), 9 Jul–5 Aug, 1957, A. H. Sturtevant (1 ♂, 1 ♀; USNM). Rio Grande Co., South Fork (8000 ft, Malaise trap), 20 Jun 1972, W. W. Wirth (2 ♂, 1 ♀; USNM). CONNECTICUT. Litchfield Co., Woodbury, 8 Jun 1931, A. L. Melander (1 ♀; USNM). IDAHO. Bonner Co., Priest Lake, 1–22 Aug 1916, 1920, A. L. Melander (1 ♂, 1 ♀;

USNM); Priest Lake (4-mile camp), Aug 1920, A. L. Melander (1 ♂; USNM); Priest Lake (Tule Bay), 19 Aug 1919, A. L. Melander (2 ♂; USNM). Latah Co., Moscow, J. M. Aldrich (1 ♀; USNM); Potlatch (1 ♂; USNM); Viola (1 ♂; USNM). INDIANA. Tippecanoe Co., LaFayette, 25 May 1915 (1 ♀; USNM). MICHIGAN. Cheboygan Co., 2 Aug 1935, H. B. Hungerford (1 ♀; USNM). Midland Co., 22 Jun 1953, R. R. Dreisbach (1 ♀; USNM). MONTANA. Glacier Co., St. Mary River, 2 Aug 1935, A. L. Melander (1 ♀; USNM). Lake Co., Swan Lake (2.5 mi S), 9 Aug 1972, W. N. Mathis (1 ♀; USNM). Mineral Co., Upper St. Regis River, 28 Jul 1918, A. L. Melander (2 ♂; USNM). Sheridan Co., Medicine Lake, 9 Jun 1969, W. W. Wirth (2 ♀; USNM). NEW YORK. Genesee Co., Portageville, Genesee River, 13 Jun 1963, W. W. Wirth (1 ♂; USNM). Tompkins Co., Ithaca, 15 Aug 1928, A. L. Melander (1 ♂; USNM). Wyoming Co., Warsaw, Oatka Creek, 11 Jun 1963, W. W. Wirth (1 ♂; USNM). Fish Creek Pond, 13 Aug 1941, A. L. Melander (1 ♀; USNM). OHIO. Ashtabula Co., Pymatuning Lake State Park, 13 Sep 1976, B. A. Steinly (7 ♀; USNM). Erie Co., Huron River, 17 Jul 1976, B. A. Steinly (1 ♀; USNM). Lorain Co., Amherst, Beaver Creek, 24 Aug 1977, B. A. Steinly (2 ♀; USNM); Mill Hollow C. P., Vermillion River, 22 Sep 1976, B. A. Steinly (1 ♂; USNM). Mercer Co., Grand Lake, Montezuma, 26 May 1977, B. A. Steinly (1 ♂, 1 ♀; USNM); St. Marys, Windy Point, Grand Lake, near Montezuma, 11 Oct 1976, B. A. Steinly (1 ♀; USNM). OREGON. Benton Co., Cary's Grove, 2 Sep 1974, W. N. Mathis (1 ♂; USNM); Rock Creek (4 mi SW Philomath), 29 May 1972, W. N. Mathis (1 ♀; USNM). Curry Co., Gold Beach (30 mi E), 2 Sep 1965, K. Goeden (1 ♀; USNM). Linn Co., Waterloo, 24 Jul 1974, W. N. Mathis (1 ♀; USNM). Polk Co., Helmick State Park, 20 Mar 1972, W. N. Mathis (1 ♀; USNM). UTAH. Duchesne Co., Mountain Home (20 mi N), 7 Jul 1968, W. N. Mathis (1 ♂; USNM). VERMONT. Caledonia Co., Lyndon, 13 Jun 1914 (1 ♀; USNM). WASHINGTON. Benton Co., Prosser, 4 May 1911 (1 ♀; USNM). Chelan Co., Lake Chelan, Stehekin, 30 Jul 1919, A. L. Melander (1 ♂; USNM). Clallam Co., Lake Crescent, Fairholm, 26 Jul 1917, A. L. Melander (1 ♀; USNM). Ferry Co., Keller, 4 Jul 1935, A. L. Melander (1 ♀; USNM). Grant Co., O'Sullivan Dam, 13 Jul 1968, W. N. Mathis (1 ♂; USNM). Klickitat Co., Glenwood, Klickitat River, 27 Jun 1917, A. L. Melander (2 ♂, 1 ♀; USNM). Mason Co., Lake Cushman, 22 Jul 1917, A. L. Melander (1 ♂; USNM); Lilliwaup, 23 Jul 1917, A. L. Melander (1 ♂; USNM); Potlatch, Hood Canal, 28 Jul 1917, A. L. Melander (1 ♂; USNM). Spokane Co., Spokane, 24 Jun, J. M. Aldrich (1 ♂; USNM). Walla Walla Co., Walla Walla, Mill Creek, 2–6 Jul 1922, A. L. Melander (1 ♂; USNM). Whitman Co., Wawawai, 7 Apr 1954, M. T. James, J. Quist (1 ♀; USNM). WYOMING. Park Co., Yellowstone National Park, Old Faithful, 14 Jul 1923, A. L. Melander (1 ♀; USNM); Yellowstone Lake, 9 Aug 1916, A. L. Melander (1 ♂; USNM). State unknown: "Pipestone Pass," 3 Jul 1923, A. L. Melander (1 ♂; USNM; this could be a pass associated with Pipestone Canyon, Okenagan Co., Washington).

Distribution.—Nearctic: British Columbia to Nova Scotia, south to Arizona and Maryland.

Remarks.—This species was confused with and usually misidentified as *Athyroglossa ordinata* Becker, a species from the Old World. We are revising the species of *Athyroglossa* from the western Palearctic Region (Mathis & Zatwarnicki, 1990a), and as part of that study, we compared European material of *A. ordinata* with those that were labeled as such from North America. Although very similar, the North American species differs as follows (for comparisons, characters of *A. ordinata* are cited in parenthesis): aristal rays comparatively short, length up to 1.5× width of aristal base (3× basal aristal width); three to four proclinate fronto-orbital setae (one proclinate fronto-orbital seta); face in lateral view prominent (face in lateral view shallowly prominent, nearly flat); and structures of male terminalia (Figs. 1–3): ventral apex of the surstylus rounded in lateral view (somewhat pointed); gonite with narrow process extended from near middle (extended process not as narrow and arising from posterior end).

Genus *Mosillus* Latreille

Mosillus Latreille, 1804:196. Type species: *Mosillus arcuatus* Latreille, 1805 (= *Syrphus subsultans* Fabricius, 1794), subsequent monotypy, Latreille, 1805:390.

Gymnomyza Fallén, 1810:19. Type species: *Syrphus subsultans* Fabricius, 1794), by present designation.

Remarks.—With designation of *Syrphus subsultans* as the type species of *Gymnomyza,* this generic name becomes an objective, junior synonym of *Mosillus. Gymnomyza* is an available name and is the type genus for the oldest family-group name in the family (see "Remarks" section under our treatment of Gymnomyzinae and Gymnomyzini).

Tribe Ochtherini

Ochtherinae Dahl, 1959:105. Type genus: *Ochthera* Latreille, 1802.

Genus *Ochthera* Latreille

Ochthera Latreille, [1802]:462. Type species: *Musca manicata* Fabricius, 1794, subsequent designation, Latreille, 1810: 444.

Remarks.—Members of this genus and monobasic tribe are among the most easily recognized shore flies, largely because of their raptorial forelegs and triangular-shaped head. Although easily recognized, the phylogenetic status of the genus and tribe remains unresolved. Most recent authors (Wirth 1965, 1968; Cogan & Wirth 1977; Cogan 1980, 1984) have preferred placement of *Ochthera* in the tribe Hyadinini of the subfamily Parydrinae (= Hyadininae); others (Dahl 1959, Miyagi 1977, Mathis 1989) as a separate subfamily, Ochtherinae, or as a tribe, Ochtherini, within the subfamily Parydrinae (= Hyadininae). Our studies indicate that *Ochthera* is better placed in the subfamily Gymnomyzinae, close to the tribe Gymnomyzini. For the present, we are also recognizing the tribe Ochtherini. The character evidence we have found to support this relationship is as follows:

1. Oral margin deeply emarginate anteriorly.
2. Clypeus button-shaped and exposed through deeply emarginate oral margin.
3. Arista and branching rays typical of gymnomyzine type (3–4 rays inserted toward base).
4. Mesonotum lacking well developed setae anterior of transverse suture.
5. Surstyli well developed, posteroventral margin extended under anterior margin of epandrium.

Apomorphies that indicate the monophyly of the genus and tribe are:

1. Head triangular-shaped from an anterior view.
2. Face in profile with distinct protuberance near middle.
3. Eyes relatively large, characteristic of predators.
4. Foreleg raptorial, with coxa and femur greatly enlarged and tibial apex projected as a ventroapical spinelike process.
5. Fronto-orbital setae greatly reduced or lacking.
6. Surstyli undulate ventrally, apices recurved medially.
7. Gonal arch fused distally with gonites.

Tribe Lipochaetini

Lipochaetini Becker, 1896:275. Type genus: *Lipochaeta* Coquillett, 1896.

Remarks.—In the most recent catalog of Nearctic Diptera (Wirth 1965), the tribe Lipochaetini was placed in the subfamily Parydrinae (= Hyadininae). We suggest, however, that the character evidence of this tribe indicates a closer relationship to members of the subfamily Gymnomyzinae, especially those of the tribe Atissini, as was indicated by Mathis (1984). We are tentatively leaving Lipochaetini and Atissini as distinct tribes, although other studies now in progress may alter this status. Genera of this tribe that occur in the Nearctic Region are the following: *Glenanthe* Haliday and *Lipochaeta* Coquillett.

Tribe Atissini

Atissini Cresson, 1942:102. Type genus: *Atissa* Haliday, 1837.

Genus *Atissa* Haliday

Atissa Haliday *in* Curtis, 1837:281. (Published in synonymy, first used for a taxon by Haliday, 1839:401.) Type species: *Ephydra pygmaea* Haliday, 1833, monotypy.

Pelignellus Sturtevant & Wheeler, 1954:252. Type species: *Pelignellus subnudus* Sturtevant & Wheeler, 1954, original designation. New synonym.

Remarks.—Sturtevant & Wheeler (1954: 252) noted that *Pelignellus* resembled *Atissa* and *Pelignus* Cresson (= *Schema* Becker), and further, that J. E. Collin, to whom they submitted a paratype for examination, recommended that *P. subnudus* would be "... best considered an aberrant *Atissa.*"

To resolve whether *Pelignellus* should be recognized as separate or a part of *Atissa,* we re-examined characters, external as well as those of the male terminalia. We found that the position of the interfrontal setae (anterior in *Pelignellus,* and posterior to median ocellus in *Atissa*) is of trivial value at the generic level. This observation, moreover, is corroborated by the close similarity in the shape of the male terminalia. Although the exact shape differs slightly (see Figs. 4–5 of *A. subnuda*), the differences are but variations on the theme of *Atissa,* hence our synonymy.

Atissa subnuda (Sturtevant & Wheeler), new combination
Figs. 4–5

Pelignellus subnudus Sturtevant & Wheeler, 1954:252.—Wirth, 1965:737 [Nearctic catalog].

Distribution.—California.

Remarks.—The structures of the male terminalia are as illustrated in Figs. 4–5. Also see our remarks under the generic synonymy.

Genus *Schema* Becker

Schema Becker, 1907:302. Type species: *Schema minutum* Becker, 1907, monotypy.

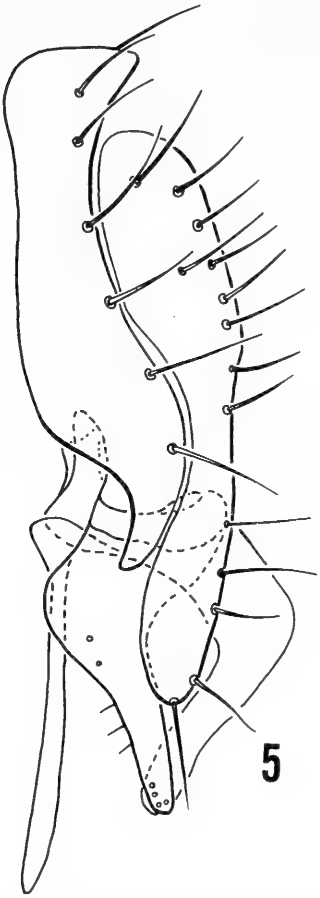
Pelignus Cresson, 1926:254. Type species: *Atissa durrenbergensis* Loew, 1864, original designation.—Cogan, 1984:130 [synonymy].

Discussion.—In the recent catalog of Palearctic Ephydridae, Cogan (1984) listed *Pelignus* as a junior synonym of *Schema.* Until then, *Schema* and its type species, *S. minutum,* had been obscure and for the most part forgotten names. Now that the status of these taxa and their names have been clarified, we are adhering to that precedent (Cogan 1984) and are here transferring *P. salinus* Cresson to the genus *Schema,* which is neuter in gender.

Schema salinum (Cresson), new combination

Pelignus durrenbergensis of Cresson (in part), 1926:254, not Loew.

Pelignus salinus Cresson, 1942:109.—Wirth, 1965:737 [Nearctic catalog].



Figs. 4, 5. Male terminalia of *Atissa subnuda*: 4, Epandrium, cerci, surstyli, and aedeagus, posterior view; 5, Epandrium, cercus, surstylus, aedeagus, and hypandrium, lateral view.

Tribe Discocerinini

Discocerini Cresson, 1925:228. Type genus: *Discocerina* Macquart, 1835.

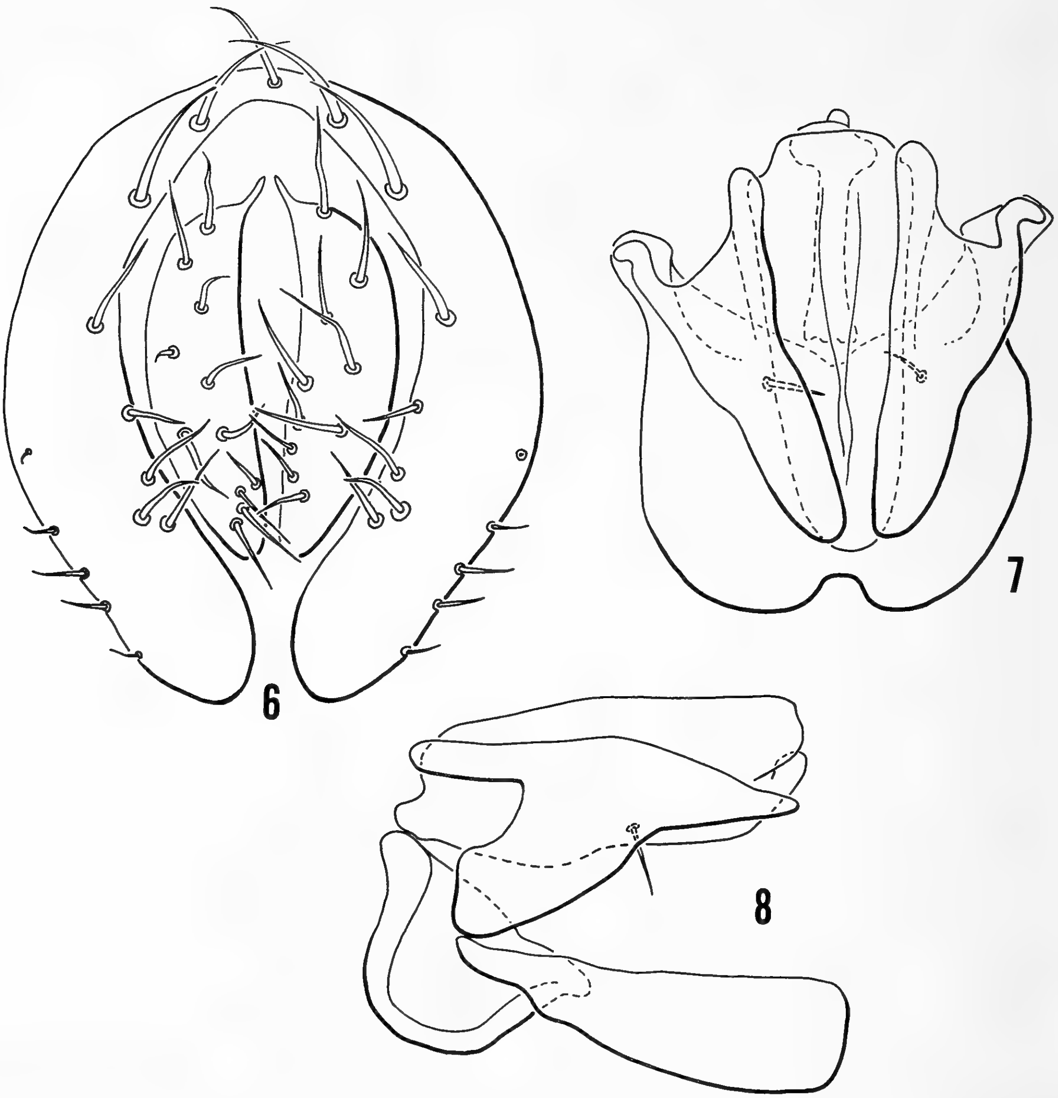
Hecamedoides unispinosus (Collin), new status
Figs. 6–8

Discocerina (*Hecamedoides*) *glaucella* var. *unispinosa* Collin, 1943:148.

Hecamedoides glaucella var. *unispinosa.*—Cogan, 1976:83 [generic combination].

Hecamedoides glaucellus of American authors, not Stenhammar, 1844.

Diagnosis (for comparison, external characters of *H. glaucellus* are cited in parenthesis).—Length 2.05–2.20 mm (2.75–3.0 mm); eye-to-cheek ratio 3.0–3.2 (2.1–2.4); fore femur with 1 posteroventral, spinelike seta (5 setae); general coloration brownish gray (light gray); costal vein ratio 1.8–2.1 (2.4–3.0); aedeagus elongate in dorsal view, slightly narrower anteriorly, rounded apically and with cleft in lateral view, generally conical in shape (divided into 2 elongate parts, these united basally); aedeagal apodeme semicircular in lateral view with dorsal margin straight (spoonlike, rounded ba-



Figs. 6–8. Male terminalia of *Hecamedoides unispinosus*: 6, Epandrium and cerci, posterior view; 7, Internal genitalia (gonites, aedeagus, and hypandrium), dorsal view; 8, Internal genitalia (gonite, aedeagus, aedeagal apodeme, and hypandrium), lateral view.

sally). The following characters of the male terminalia (Figs. 6–8) also distinguish *H. unispinosus*: anterior margin of hypandrium with medial cleft (Fig. 7); gonite with 1 ventromedial seta (Figs. 7–8); gonite wide at base, thereafter tapered and elbowed to moderately pointed apex (Figs. 7–8).

Type material.—Lectotype male, here designated, is labeled "Monnow Valley, 10. 7. 09 [10 Jul 1909]/LECTOTYPE Discocerina (Hecamedoides) glaucella var. unispinosa Collin." There is also a paralectotype female that is labeled "Monnow Valley, 15. 8. 34 [15 Aug 1934]." The lectotype and paralectotype are preserved in the Hope Entomological Collection (Oxford).

Distribution.—Holarctic. Palearctic: Great Britain. Nearctic: Alberta to Ontario, south to California, Colorado, and New York; Mexico (Baja California).

Remarks.—Study of the appropriate type material reveals that *H. glaucellus* and *H. unispinosus* are distinct species and that only the latter occurs in North America. North American specimens were usually misidentified as *H. glaucellus*.

Although Collin published this species as a variety of *H. glaucellus,* it is clear from his paper that his "variety" is of subspecific status, and being published before 1961, his varietal name is available at the species level.

Tribe Psilopini

Psilopini Cresson, 1925:241. Type genus: *Psilopa* Fallén, 1823.

Genus *Guttipsilopa* Wirth

Guttipsilopa Wirth, 1956:9. Type species: *Guttispsilopa haydeni* Wirth, 1956, original designation.

Nesopsilopa Mathis & Wirth, 1977:64. Type species: *Psilopa umbrosa* Loew, 1862, original designation. New synonym.

Discussion.—Although these two taxa represent monophyletic lineages, they are sister groups and are sufficiently similar that recognition of them as separate genera is unwarranted. *Nesopsilopa* will be used at the subgeneric level, however. In accordance with this change, the following species names are transferred from *Nesopsilopa* to *Guttipsilopa* as new combinations: *Guttipsilopa* (*Nesopsilopa*) *bahamaensis* (Mathis & Wirth), *G.* (*N.*) *caeruleiventris* (Loew), *G.* (*N.*) *stonei* (Mathis & Wirth), *G.* (*N.*) *umbrosa* (Loew), and *G.* (*N.*) *wirthi* (Mathis & Freidberg).

Subfamily Hyadininae Phillips et al., revised status

Hyadinini Phillips et al., *in* Cresson, 1949: 251. Type genus: *Hyadina* Haliday, 1837.

See "Discussion" under tribe Hyadinini for comments.

Tribe Hyadinini Phillips et al.

Hyadinini Phillips et al., *in* Cresson, 1949: 251. Type genus: *Hyadina* Haliday, 1837.

Discussion.—Cresson's last publication (1949) was assembled and published posthumously by a "Publication Committee" of the American Entomolgoical Society (1949: 225). The committee was headed by Maurice E. Phillips, who served as editor for the Society's publications. Most of the paper was taken directly from Cresson's notes and a nearly completed manuscript that he was preparing at the time of his death. Where necessary for clarification, the publication committee inserted brief annotations that are clearly indicated by being included within brackets. One such annotation, this one rather lengthy, contains the family-group name Hyadinini and an explanation of the name, including a brief but adequate diagnosis (adequate in the sense of complying with the rules of nomenclature). The name is available, having been published correctly, but is attributable to the members of the "Publication Committee," not Cresson.

The oldest available family-group names for this subfamily, Gastropinae and Hyadininae, were both published in the same paper (Cresson 1949). As first revisors, we elect to use Hyadininae for the subfamilial name because its type genus, *Hyadina,* is a better known taxon that is also more widespread. *Gastrops* Williston, the type genus for Gastropinae, is known only from the New World.

The relationships among the genera and tribes of this subfamily are being studied by Edmiston & Mathis, and it would be premature to cite their results, which are still inconclusive.

Pelina bispinosa Clausen, new status

Pelina truncatula bispinosa Clausen, 1973: 139.

Pelina latiforma Clausen, new status

Pelina truncatula latiforma Clausen, 1973: 141.

Pelina prospinosa Clausen, new status

Pelina truncatula prospinosa Clausen, 1973: 143.

Remarks.—Clausen (1973:137) described these three taxa as subspecies of *P. truncatula* Loew because of an "... apparent tendency toward intergradation." He noted, however, that (p. 137) "All groups show overlaps in distribution" and further, that "... two groups are often found in the same collections but in these collections no intergradation can be found." After publication of Clausen's revision, more field work, especially in western US, was conducted, and in more than one locality, two or more of these taxa were found occurring together, often collected in the same sweep of an aerial net. The available evidence now suggests that these taxa represent independent populations that can be consistently distinguished by characters of the male terminalia and that ought to be recognized as full species.

Tribe Parydrini

Parydrini Wirth & Stone, 1956:464. Type genus: *Parydra* Stenhammar, 1844.

Remarks.—This tribe may be the sister group to the subfamily Ephydrinae. If evidence corroborates this relationship, the concept of Ephydrinae would need to be broadened to include most genera that were previously placed under Parydrini. Ephydrinae would thus include four tribes, viz., Ephydrini, Dagini, Parydrini, and Scatellini. At present, we have not opted to recognize Ephydrinae in this sense (Ephydrinae + Parydrini), preferring to accumulate additional and more convincing evidence. As a preliminary step toward better resolution of these relationships, we have identified the following characters that may be synapomorphies and that would confirm the monophyly of this lineage and the sister-group relationship:

1. Fronto-orbital setae lateroclinate. These setae are well developed in most but not all species of the subfamily, but even when weakly developed, they are lateroclinate. Elsewhere in the family, these setae are proclinate and/or reclinate.
2. Face broadly projected anteriorly, shieldlike. This condition may have evolved more than once within the Ephydridae, where a projected, shieldlike face appears in the Hydrelliinae, i.e., *Paralimna* and related genera, and in the Ephydrinae. In both cases, it is probably a synapomorphy. Other shore flies usually have the face slightly convex or flat.
3. Oral opening large, gaping. See number 2.
4. Clypeus broadly developed, commensurate with the gaping oral opening.
5. Anterior spiracle of larvae protrusile, mostly with 3–7 digitiform papillae (in a few cases with 2–18).

For the Nearctic Region the tribe Parydrini includes: *Callinapaea* Sturtevant & Wheeler, *Eutaenionotum* Oldenberg, *Parydra* Stenhammar, and *Rhinonapaea* Wirth.

Parydra (*Chaetoapnaea*) *fossarum* Haliday

Ephydra fossarum Haliday, 1833:175.

Parydra fossarum.—Loew, 1860:32 [generic combination].

Parydra (*Chaetoapnaea*) *parasocia* Clausen, *in* Clausen & Cook, 1971:83, new synonym.

Type material.—The lectotype female of *Ephydra fossarum,* here designated, is labeled "Ireland [Northern Ireland, Downshire, Holywood; green]/Haliday 20. 2. '82 [NMI's registration number]/fossarum [handwritten, apparently by J. E. Collin]/ Named by J. E. Collin/LECTOTYPE ♀ Ephydra fossarum Haliday by Mathis &

Zatwarnicki [gender symbol, name and author, designators all handwrittten]." The lectotype is in poor condition (pointed to paper triangle), and is deposited in NMI. There are two additional female syntypes (NMI) that bear the same label data as the lectotype except they lack the handwritten, determination label; these two specimens are designated as paralectotypes.

The holotype male of *Parydra parasocia* was collected in Sidney, Fremont County, Iowa, and is deposited in the collection at Iowa State University.

Distribution.—Holarctic. Nearctic: British Columbia and Northern Territories to Nova Scotia, south to California, Arkansas, and Michigan. Palearctic: Austria, Great Britain, Hungary, Italy, Finland, Germany (FRG), Netherlands, Poland, Sweden.

Remarks.—We compared European and North American specimens, especially characters of the male genitalia, and consider the specimens to be conspecific. For figures of the male terminalia of *P. fossarum,* please refer to those (fig. 100) in Clausen & Cook (1971:132).

Parydra (*Chaetoapnaea*) *joaquinensis* Clausen, new status

Parydra halteralis joaquinensis Clausen, *in* Clausen & Cook, 1971:79.

Remarks.—This taxon was described as a subspecies of *P. halteralis* (Cresson). Although the two "subspecies" are similar, especially externally, they can be distinguished by the shape of the aedeagus, and there is no apparent intergradation. The populations of the two taxa are allopatric, and as the only available evidence suggests that they are independent, both are given species status.

Philygriini, new tribe

Philygriini of authors (Nomen nudum, lacking a diagnosis).—Wirth, 1965:745; Wirth, 1968:16.—Cole, 1969:400.—Cogan & Wirth, 1977:335.—Cogan, 1980: 666; Cogan, 1984:149.—Ferrar, 1987: 169.

Diagnosis.—A tribe of Hyadininae that is distinguished from others of this subfamily by the following characters: Head: Ocellar setae weakly developed or lacking; face narrow, slightly to distinctly convex, most prominent at mid facial height and with receding lower facial margin; eye microsetulose; subcranial cavity small to moderately large; clypeus not prominent. Thorax: Posterior notopleural seta inserted distinctly dorsad from level of anterior seta; katepisternal seta lacking or greatly reduced. Costa extended to vein M. Abdomen: Tergum 4 at most twice length of 5. Male terminalia: Cerci connected anterodorsally with epandrium; gonites united with hypandrium and bearing long setae anterodorsally.

Remarks.—Although Philygriini has been widely used in the literature for the last few decades, it is a nomen nudum, lacking a diagnosis. The North American genera that are included in this tribe are *Philygria* Stenhammar and *Nostima* Coquillett. *Lemnaphila* Cresson, which was included in Philygriini (Wirth 1965, and elsewhere, see synonymy listed above), is better placed in the tribe Hydrelliini (subfamily Hydrelliinae) near the genus *Hydrellia* Robineau-Desvoidy based on characters of the male terminalia and larvae (Johannsen 1935, Hennig 1943, Lizarralde de Grosso 1978, and Edmiston & Foote, pers. comm.).

Philygria punctatonervosa (Fallén)
Figs. 9–13

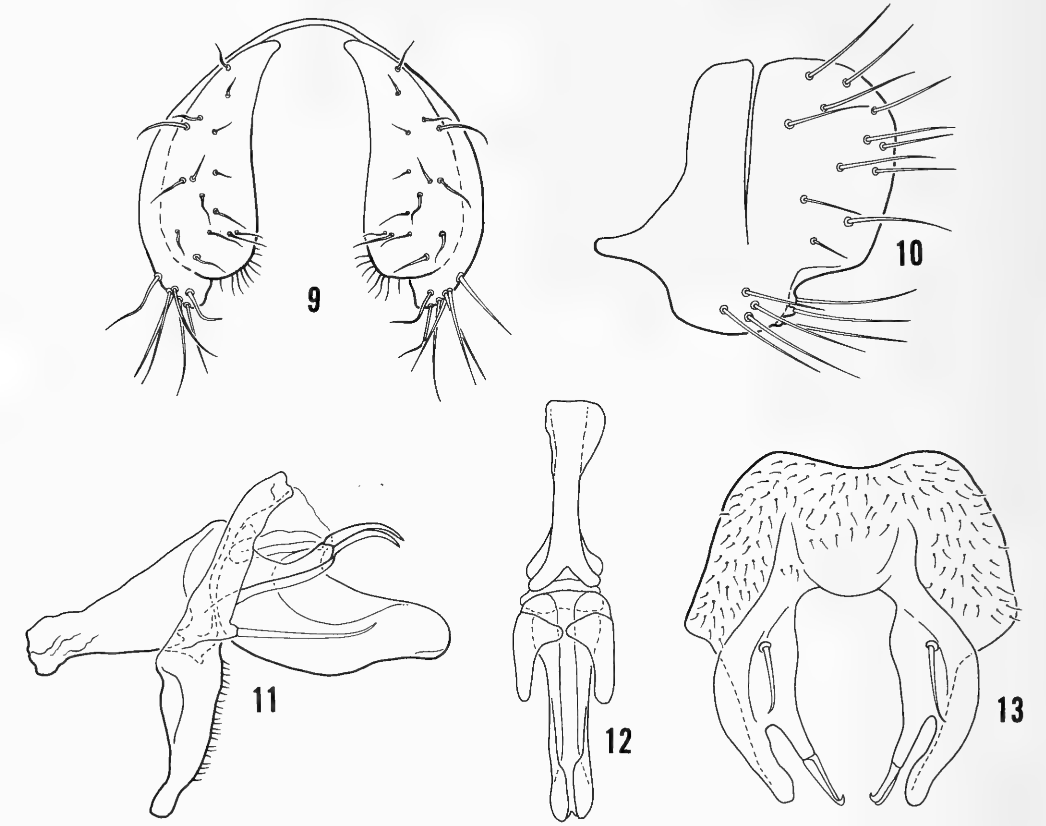
Notiphila punctatonervosa Fallén, 1813:254.

Philygria punctatonervosa.—Loew, 1860:25 [generic combination].

Hydrina punctatonervosa.—Becker, 1926:57 [generic combination].

Philygria opposita Loew, 1861:356, new synonym.

Diagnosis.—Specimens with short stump veins on veins R_{2+3}, R_{4+5}, and M. Male terminalia (Figs. 9–13): Cerci semicircular and broad, fused anteroventrally with narrow epandrium (Figs. 9, 10); anteroventral



Figs. 9–13. Male terminalia of *Philygria punctatonervosa*: 9, Epandrium and cerci, posterior view; 10, Epandrium and cercus, lateral view; 11, Gonite, hypandrium, aedeagal apodeme, and aedeagus, lateral view; 12, Aedeagal apodeme and aedeagus, dorsal view; 13, Hypandrium and gonite, ventral view.

margin of epandrium with 6–7 long setae (Figs. 9, 10); gonite with 1 anterodorsal long seta and 2 short apical spinulae (Fig. 11); aedeagal apodeme triangular in lateral view (Fig. 11); aedeagus curved upwards, C-shaped, basal part with 2 laterodorsal processes (Figs. 11, 12); hypandrium flat, U-shaped, closely associated with gonites (Fig. 13).

Type material.—The lectotype ♂ of *Notiphila punctatonervosa,* here designated, is labeled "N. puncta-to-nervosa ♂ [handwritten, apparently by Fallén; species name underlined]/355 90[pink; "90" handwritten]/Riksmuseum Stockholm [green]/LECTOTYPE ♂ Notiphila punctatonervosa Fallén By Mathis & Zatwarnicki [black subborder; gender, name, author and designators handwritten]." Six other specimens (1♂, 2♀, 3?) from the Fallén collection, all in poor condition (mouldy, missing structures), are designated as paralectotypes. The lectotype is in poor condition (mouldy, left wing stuck to pin), is pinned directly, and is deposited in the NRS.

The lectotype male of *Philygria opposita,* here designated, is labeled "Penn./Loew Coll./opposita/Type 11161 [red]/Philygria opposita Lw det. W. Wirth '61." Two paralectotype males bear labels as follows "Penn./Loew Coll./Type 11161." The lectotype and paralectotypes are deposited in the MCZ.

Distribution.—Holarctic. Palearctic: Belgium, Denmark, Germany (GDR), USSR. Nearctic: British Columbia to Quebec, south to California, Illinois, and Maryland.

Remarks.—Loew (1861) characterized *P. opposita* as being very similar to *P. punctatonervosa,* differing mainly by the darker coloration and fewer number of wing spots. The number of wing spots is unstable in populations occurring in the Holarctic Region, and in specimens from both the Palearctic and Nearctic Regions there is only very slight variation in the shape of the male terminalia, hence our synonymy. The shape of the male terminalia appears to provide good characters for recognition of species in *Philygria.*

Subfamily Ephydrinae

Ephydrinae Zetterstedt, 1837:48. Type genus: *Ephydra* Fallén, 1810.

Ephydra (*Ephydra*) *riparia* Fallén

Ephydra riparia Fallén, 1813:246.
Ephydra lata Walker, 1858:233, new synonym.

Remarks.—The primary type of *E. lata* is apparently lost, but the description is adequate to identify this species as being conspecific with *E. riparia.*

Ephydra oscitans Walker

Ephydra oscitans Walker, 1858:253, preoccupied, Walker, 1849:1106.

Remarks.—Walker's 1858 name is a homonym and, therefore, is unavailable, being preoccupied by *E. oscitans* Walker, 1849:1106. As the primary type of the species described in 1858 is apparently lost and unrecognizable from the description, the species will not be renamed.

Ephydra (*Halephydra*) *gracilis* Packard, revised status

Ephydra gracilis Packard, 1871:105.—Aldrich, 1912:78 [biology, description].
Ephydra cinerea Jones, 1906:159.—Sturtevant & Wheeler, 1954:168 [distribution, notes, synonymy].—Wirth, 1956:19 [distribution in Bahamas]; 1968:22 [Neotropical catalog].
Ephydra (*Halephydra*) *cinerea.*—Wirth, 1971:371 [revision].—Simpson, 1976:264 [description and figures of larva and puparium].

Remarks.—Our usage of *Ephydra gracilis* as the senior synonym for this species reverses the precedent of Sturtevant & Wheeler (1954:168–169) who cited *Ephydra cinerea* Jones as the valid name for this species and listed *Ephydra gracilis* as a questionable synonym. Sturtevant & Wheeler's (1954) argument, in part, is a misleading paraphrase of Aldrich (1912), i.e., that Packard's description of the "larva [sic, Packard described the puparium] does not agree with the present species—a point that we can confirm." We reexamined the characters and have concluded that *Ephydra gracilis* can indeed be recognized. The evidence is as follows. Packard's description of the puparium, although brief, does mention a few salient characters that are unique to this species (1871:78). The respiratory tube is much longer than that of any other species, "being as long as the body," the body is generally smaller and more slender, and the "feet" (prolegs) are more prominent. In addition, as Packard also noted, this species occurs abundantly around the Great Salt Lake. This combination of characters is unique to and clearly identifies *E. gracilis,* which is the most abundant species around Great Salt Lake.

Aldrich (1912:79), contrary to Sturtevant & Wheeler's (1954) incorrect paraphrase, did not say that Packard's description "does not agree with the present species." Instead, Aldrich (1912) noted the brevity of Packard's description, which, according to Aldrich, was "scarcely" recognizable and unsatisfactory by the omission of a striking distinction (the basal filaments of the "anal" tube).

Nevertheless, Aldrich (1912) went on to conclude that "... it is certain that Packard was describing a strikingly small *Ephydra* common in Great Salt Lake, and there is but one species [*E. gracilis*], whether he [Packard] described it well or not."

Acknowledgments

Several individuals contributed to this paper by loaning specimens, answering letters, and providing space, equipment, and general assistance while visiting museums and studying collections. D. Azuma (ANSP), Charles Vogt (MCZ), James P. O'Connor (NMI), Per Inge Persson (NRS), G. McGavin (Hope Entomological Collection, Oxford). This draft was also reviewed by F. C. Thompson, W. W. Wirth, James Edmiston, Philip J. Clausen, and Amnon Freidberg and made substantially better as a result. We wish to acknowledge the special interest and contribution of Curtis W. Sabrosky, who provided much time, knowledge, and many discussions to this paper. Donald Azuma kindly provided information on the "Publication Committee" of Cresson's last paper (1949), and Elaine R. S. Hodges skillfully inked the illustrations of the male terminalia.

Literature Cited

Aldrich, J. M. 1912. The biology of some western species of dipterous genus *Ephydra.*—Journal of the New York Entomological Society 20:77–99.

Becker, T. 1896. Dipterologische Studien IV: Ephydridae.—Berliner Entomologische Zeitschrift 41: 67–195.

———. 1907. Zur Kenntnis der Dipteren von Central-Asien. I. Cyclorrhapha schizophora holometopa und Orthorrhapha brachycera.—Annuaire du Musée Zoologique de L'Academie Impériale des Sciences de St.-Petersbourg 12: 253–317.

———. 1926. Ephydridae und Canaceidae: Families 56a, 56b. *In* E. Lindner, ed., Die Fliegen der Paläarktischen Region. 6(1):1–115, figures 66–134. Stuttgart.

Clausen, P. J. 1973. A revision of the Nearctic species of the genus *Pelina* (Diptera: Ephydridae).—Transactions of the American Entomological Society 99:119–156.

Clausen, P. J., & E. F. Cook. 1971. A revision of the Nearctic species of the tribe Parydrini (Diptera: Ephydridae).—Memoirs of the American Entomological Society 27:1–150.

Cogan, B. H. 1976. 67. Ephydridae. Pp. 83–85 *in* G. S. Kloet and W. D. Hicks, eds., A check list of British insects, 2nd edition. 5:1–139 + ix pp.

———. 1980. Family Ephydridae. Pp. 655–669 *in* R. W. Crosskey, ed., Catalogue of the Diptera of the Afrotropical Region. British Museum (Natural History), London, 1437 pp.

———. 1984. Family Ephydridae. Pp. 126–176 *in* A. Soós and L. Papp, eds., Catalogue of Palaearctic Diptera. Vol. 10. Elsevier Press, Budapest, 402 pp.

Cogan, B. H., & W. W. Wirth. 1977. Family Ephydridae. *In* M. D. Delfinado and D. E. Hardy, eds., A catalog of the Diptera of the Oriental Region. Vol. III. Suborder Cyclorrhapha (excluding Division Aschiza). University Press Hawaii, Honolulu, 854 pp.

Cole, F. R. (with the collaboration of E. I. Schlinger). 1969. The flies of western North America. Univ. Calif. Press, Berkeley and Los Angeles, 673 pp.

Collin, J. E. 1943. The British species of *Psilopa* Fln. and *Discocerina* Mcq. (Dip., Ephydridae).—The Entomologist's Monthly Magazine 79:147–152.

Cresson, E. T., Jr. 1922. Studies in American Ephydridae (Diptera). III. A revision of the species of *Gymnopa* and allied genera constituting the subfamily Gymnopinae.—Transactions of the American Entomological Society 47:325–343.

———. 1925. Studies in the dipterous family Ephydridae, excluding the North and South American faunas.—Transactions of the American Entomological Society 51:227–258.

———. 1926. Descriptions of New Genera and Species of Diptera (Ephydridae and Micropezidae).—Transactions of the American Entomological Society 52:249–274.

———. 1942. Synopses of North American Ephydridae (Diptera) I. The Subfamily Psilopinae, with descriptions of new species.—Transactions of the American Entomological Society 68:101–128.

———. 1949. A systematic annotated arrangement of the genera and species of the North American Ephydridae (Diptera) IV. The subfamily Napaeinae.—Transactions of the American Entomological Society 74:225–260.

Curtis, J. 1837. A guide to an arrangement of British insects; being a catalogue of all the named species hitherto discovered in Great Britain and Ireland. 2nd edition. London, 294 pp.

Dahl, R. G. 1959. Studies on Scandinavian Ephydridae (Diptera Brachycera).—Opuscula Entomologica, Supplementum 15:1–224.

Fallén, C. F. 1810. Specimen Entomologicum novam Diptera disponendi methodum exhibens. Lund, 26 pp.

———. 1813. Beskrifning Öfver några i Sverige funna Vattenflugor (Hydromyzides).—Kongliga Vetenskaps-Academiens Handlingar, series 3 1813: 240–257.

Ferrar, P. 1987. A guide to the breeding habits and immature stages of Diptera Cyclorrhapha.—Entomolograph 8:1–907.

Haliday, A. H. 1833. Catalogue of Diptera occurring about Holywood in Downshire.—The Entomological Magazine (London) 1:147–180.

———. 1839. Remarks on the generic distribution of the British Hydromyzidae (Diptera).—Annals of Natural History 3:217–224, 401–411.

Hennig, W. 1943. Übersicht über die bisher bekannten Metamorphosestadien der Ephydriden, mit Neubeschreibungen nach dem Material der Deutschen Limnologischen Sundaexpedition. (Diptera: Ephydridae).—Arbeiten über morphologische und taxonomische Entomologie 10(2–3):105–136.

Johannsen, O. A. 1935. Aquatic Diptera. Part II. Orthorrhapha-Brachycera and Cyclorrhapha.—Cornell University Agricultural Experiment Station. Memoir 177, 62 pp., 12 plts.

Jones, B. J. 1906. Catalogue of the Ephydridae with bibliography and description of new species.—University of California, Publications in Entomology 1:153–198.

Latreille, P. A. [1802]. Histoire naturelle, générale et particulière, des Crustacés et des Insectes. Tome troisième. *In* C. S. Sonnini, ed., Histoire naturelle par Buffon. Paris, 468 pp.

———. 1804. Tableau methodique des Insectes. *In* Tableaux methodiques d'histoire naturelle, pp. 129–200, 5 plts. Paris, 238 pp.

———. 1805. Histoire naturelle, générale et particulière, des Crustacés et des Insectes. Tome quatorzième. *In* C. S. Sonnini, ed., Histoire naturelle par Buffon. Paris, 432 pp.

———. 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes; avec un tableau méthodique de leurs genres, disposés en familes. Paris, 444 pp.

———. 1829. Suite et fin des Insectes. *In* [Cuvier, G.C.L.F.D.] Le règne animal distribué d'après son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée. Ed. 2, Volume 5. Paris, 556 pp.

Lizarralde de Grosso, M. 1978. Nuevos aportes al conocimiento del genero *Lemnaphila* Cresson (Diptera-Ephydridae).—Neotropica 24(71):13–20.

Loew, H. 1860. Neue Beiträge zur Kenntniss der Dipteren. Siebenter Beitrag.—Programm K. Realschule zu Meseritz 1860:1–46.

———. 1861. Diptera Americae Septentrionalis Indigena. Centuria prima.—Berliner Entomologische Zeitschrift 5:307–359.

Mathis, W. N. 1984. A revision of the genus *Asmeringa* Becker (Diptera: Ephydridae).—Israel Journal of Entomology 17[1983]:67–79.

———. 1986. Studies of Psilopinae (Diptera: Ephydridae), I: A revision of the shore fly genus *Placopsidella* Kertész.—Smithsonian Contributions to Zoology 430, 30 pp.

———. 1989. 66. Family Ephydridae. Pp. 639–649 *in* N. L. Evenhuis, ed., Catalog of the Diptera of the Australasian and Oceanian regions. E. J. Brill and B. P. Bishop Museum special publication 86, 1155 pages.

———, & W. W. Wirth. 1977. A new genus of psilopine flies (Diptera: Ephydridae) with notes on its relationships.—Proceedings of the Entomological Society of Washington 79:63–74.

———, & T. Zatwarnicki. 1990a. A revision of the palearctic species of *Athyroglossa* (Diptera: Ephydridae).—Transactions of the American Entomological Society 116(1):103–133.

———, & ———. 1990b. Ephydridae Zetterstedt, 1837 (Insecta, Diptera): proposed conservation.—Bulletin of Zoological Nomenclature (in press).

McAlpine, J. F. 1981. Morphology and terminology—adults [chapter]. Pp. 9–63 *in* J. F. McAlpine et al., eds., Manual of Nearctic Diptera, Volume 1. Agriculture Canada, Research Branch, Monograph 27, Hull, Quebec, 674 pp.

Miyagi, I. 1977. Ephydridae (Insecta: Diptera). *In* Fauna Japonica. Keigaku Publishing, Tokyo, 113 pp.

Packard, A. S., Jr. 1871. On insects inhabiting salt water. No. 2. American Journal of Science and Arts (3)1[whole series 101]:100–110.

Simpson, K. W. 1976. The mature larvae and puparia of *Ephydra* (*Halephydra*) *cinerea* Jones and *Ephydra* (*Hydropyrus*) *hians* Say (Diptera: Ephydridae).—Proceedings of the Entomological Society of Washington 78:263–269.

Sturtevant, A. H., & M. R. Wheeler. 1954. Synopses of Nearctic Ephydridae (Diptera).—Transactions of the American Entomological Society 79: 151–257.

Walker, F. 1849. List of the specimens of dipterous insects in the collection of the British Museum 4:689–1172.

———. 1858. Characters of undescribed Diptera in the collection of W. W. Saunders.—Transactions of the Entomological Society of London, new series [= series 2] 4:190–235.

Wirth, W. W. 1956. The Ephydridae (Diptera) of the Bahama Islands.—American Museum Novitates 1817, 20 pp.

———. 1965. Family Ephydridae. *In* A. Stone et al., eds., A catalog of the Diptera of America north of Mexico. U.S. Department of Agriculture, Agriculture Handbook, 276, iv + 1696 pp.

———. 1968. 77. Family Ephydridae. *In* N. Papavero, ed., A catalogue of the Diptera of the Americas south of the United States. Departamento de Zoologia, Secretaria de Agricultura, São Paulo, 43 pp.

———. 1971. The brine flies of the genus *Ephydra* in North America (Diptera: Ephydridae).—Annals of the Entomological Society of America 64:357–377.

———, & A. Stone. 1956. Aquatic Diptera. Pp. 372–482 *in* R. L. Usinger, ed., Aquatic insects of California. Univ. Calif. Press, Berkeley, 508 pp.

Zetterstedt, J. W. 1837. Conspectus familiarum, generum et specierum dipterorum, in fauna insectorum Lapponica descriptorum.—Isis (Oken's), 1837:28–67.

(WNM) Department of Entomology, NHB 169, Smithsonian Institution, Washington, D.C. 20560; (TZ) Department of Zoology, Academy of Agriculture, ul. Cybulskiego 20, Wroclaw, 50-205, Poland.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 907–912

A NEW SPECIES OF *PARASPADELLA* (CHAETOGNATHA) FROM THE COASTAL WATERS OF JAPAN

Jean-Paul Casanova

Abstract.—A new species of the benthic chaetognath genus *Paraspadella, P. gotoi,* is described from Amakusa Island, Japan. It differs from the hitherto known species mainly by the shape of adhesive organs and seminal vesicles and the ventral position of the female genital orifices.

During the first workshop on chaetognaths held in the University of Surrey (Great Britain) in September 1988, Dr. Taichiro Goto (Mie University, Japan) gave me several specimens of a *Paraspadella* that looked like *P. schizoptera* Conant, 1895 but which appeared to him to be different from this species. Indeed, it is a new species and thus named *P. gotoi.*

Paraspadella gotoi, new species
Figs. 1–2, Table 1

The holotype and four paratypes are deposited in the National Science Museum Tokyo (NSMT-Ch. 006 and 007–010 respectively). Other paratypes are presented to the Muséum national d'Histoire Naturelle, Paris (UC 96) and to the National Museum of Natural History, Washington, D.C. (USNM 128300). All were collected in April 1987 and 1988.

Description.—Eighteen specimens studied. Body stumpy (Fig. 1), reaching up to 5.9 mm without tail fin. Caudal segment represents 46.5 to 51% of body length.

Head bears 8 to 10 very recurved hooks. Anterior teeth only, 4–6 on each side, thin and long, the second innermost being the longer (Fig. 2d). Eyes large, with a large four or three branched pigmented cell (Fig. 2e). Corona ciliata unique and easier to describe with a drawing and photographs (Figs. 1a, 2f, g, h): outline of the three lengthened parts very irregular, one extending towards the eyes and the two others on both sides of neck. Thick collarette stretching from the neck to the end of caudal segment, covered with numerous sensory tufts. Numerous colored pits (dark grey or brownish yellow) arranged in symmetrical areas on the dorsal and lateral sides from head to tail. Gut sinuous, of a brick reddish color. Well-marked intestinal diverticula at the level of neck, clearly visible since the body is rather transparent. Longitudinal muscles not strongly developed as in other spadellids and lateral fields rather wide. Transverse musculature extends from neck to end of trunk. Ventral ganglion large, occupying about one third of trunk length.

Lateral fins divided into two parts, a small one (length ≃ 0.7 mm) before the female genital orifice and a considerably larger one, extending from this orifice to seminal vesicle. Different directions of rays in the small part and in the beginning of the larger one (Fig. 2i) seem to indicate that there are in fact two pairs of lateral fins as in *Paraspadella schizoptera.* Caudal fin spatulate; all fins completely provided with rays.

Two adhesive organs on each side meet and unite on half their length at level of anterior part of the seminal vesicle; finger-like processes which constitute each adhesive organ themselves united so that adhesive organs look like a cockscomb surrounding ventrally each seminal vesicle (Fig. 1b).

Ovaries reaching the level of neck when

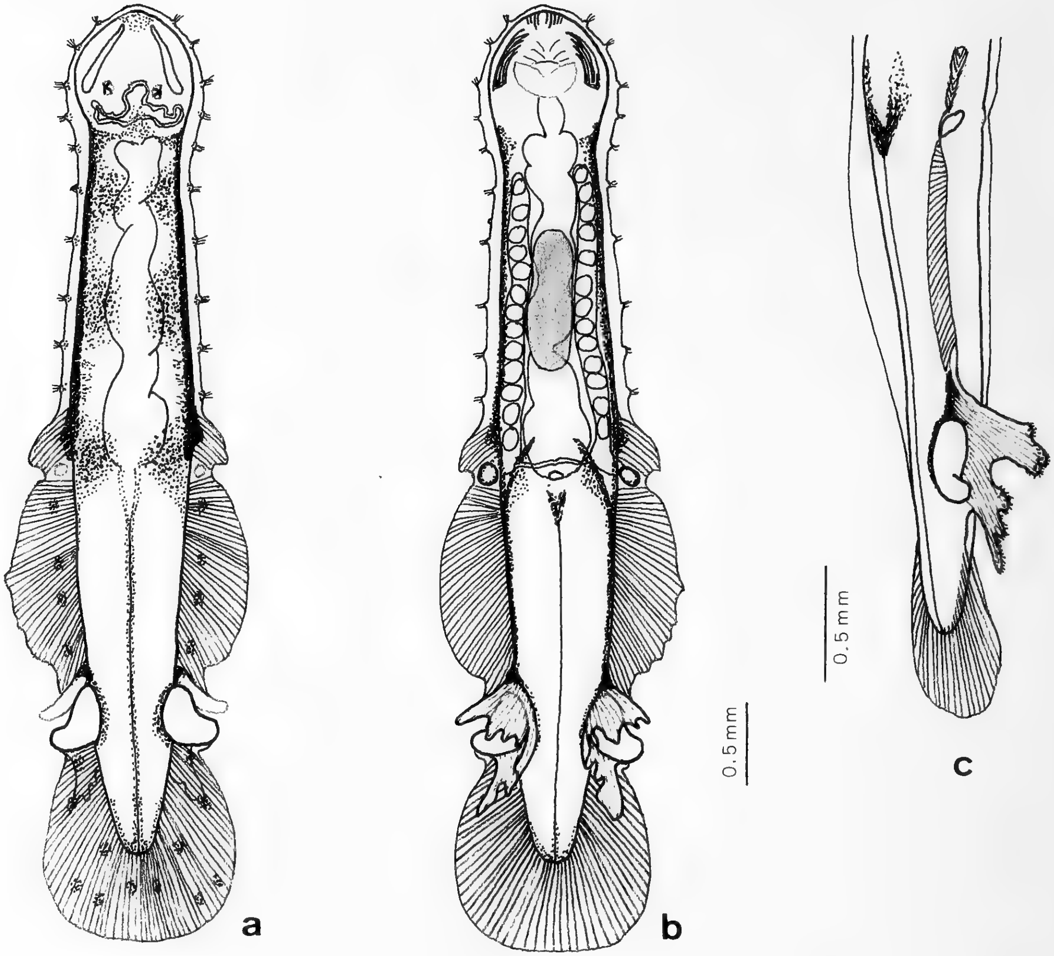


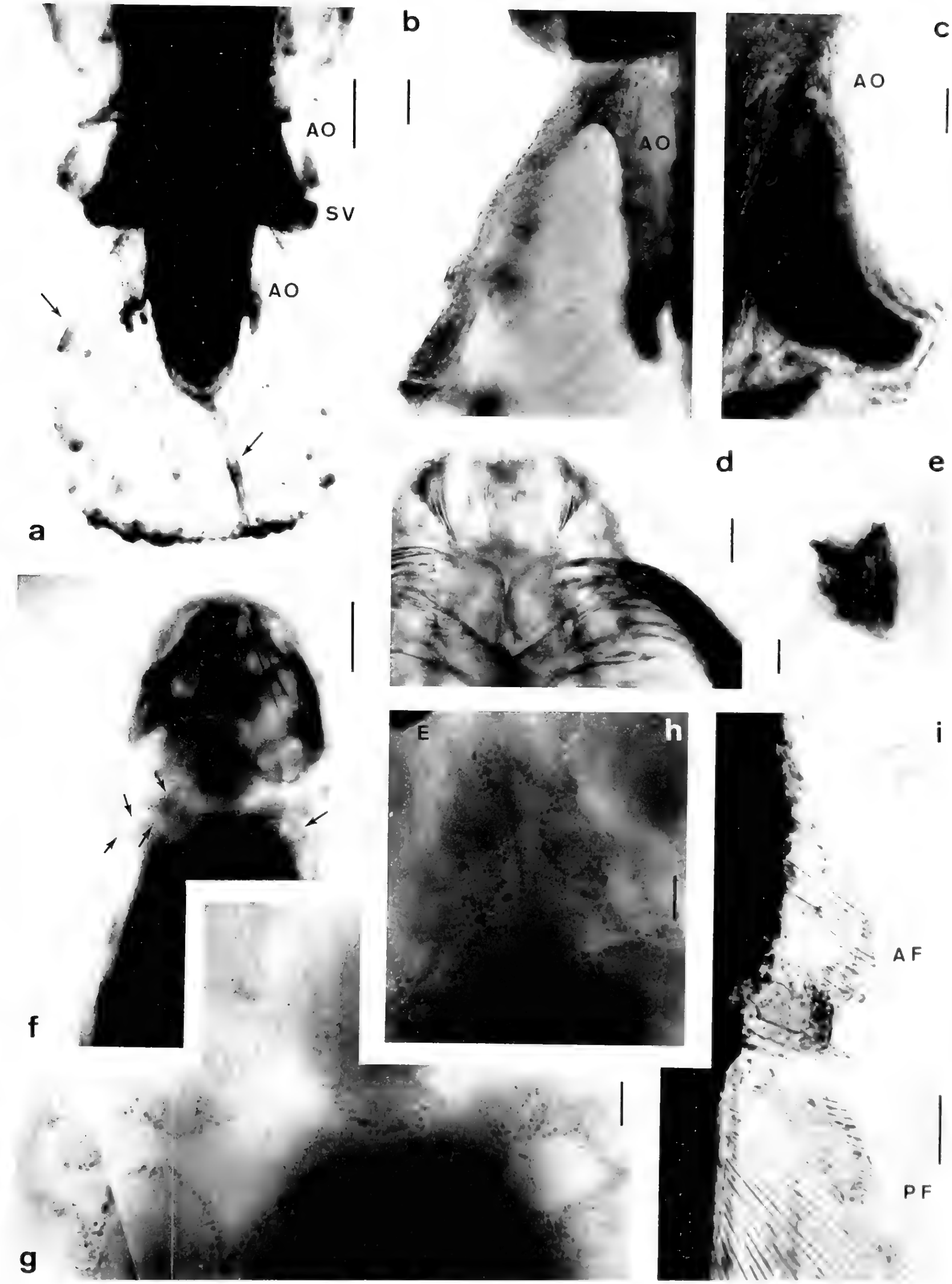
Fig. 1. *Paraspadella gotoi,* n. sp.: a, Dorsal view; b, Ventral view; c, Right lateral view, with pigmented areas. In a, sensory tufts on fins are stained with methylene blue.

fully mature and filled with about twenty large ova of 0.20–0.22 mm in diameter arranged into two rows (only one row when small). Ovaries connected near their base by a duct surrounding ventrally the intestine as already described in three other species of *Paraspadella* (Conant 1895, Mawson 1944) and in *Heterokrohnia* and *Archeterokrohnia* (Casanova 1985, 1986). Female genital orifices ventral with regard to lateral fins (Fig. 1b, c). Seminal vesicles crooked, their orifice at the top of a stout tube perpendicular to the axis of tail (Fig. 2c).

Comparisons with other species.—Species

→

Fig. 2. *Paraspadella gotoi,* n. sp.: a, Ventral view of caudal segment showing adhesive organs and seminal vesicles. Arrows indicate the thickenings on the tail fin analogous to the finger-like processes of the adhesive organs; b, Enlargement of the right part of the tail fin showing that the thickened edge is an extension of the adhesive organ; c, Seminal vesicle (rays of the anterior part of the adhesive organ laying above the vesicle are visible); d, Teeth and tips of hooks; e, Right eye; f, Dorsal view of the anterior part of a mature specimen (black



area in the trunk = ovaries) showing the corona ciliata (arrows); g, Enlargement of the corona ciliata; h, Central part of the corona ciliata of another specimen; i, Anterior and posterior fins with rays in different directions. AF = anterior fins, AO = adhesive organs, E = eyes, PF = posterior fins, SV = seminal vesicles. Scale bars: 0.25 mm (a, f, i), 0.05 mm (b, c, d, g, h) and 0.02 mm (e).

Table 1.—Diagnostic characters of the two species of *Paraspadella* with two pairs of adhesive organs.

Characteristics	*Paraspadella sheardi* Mawson, 1944	*Paraspadella gotoi*, n. sp.
Maximal length	6.5 mm	5.9 mm
Tail segment	44–45%	46.5–51%
Intestinal diverticula	absent	well developed
Anterior teeth	3	4–6
Posterior teeth	0	0
Hooks	11	8–10
Eyes	small	large
Corona ciliata	three cornered shape with regular outline	three lengthened, irregularly shaped processes
Lateral fins	anterior and posterior fins almost rectangular, well separated	anterior fins triangular and posterior ones roundish, in close contact
Position of female genital orifices	lateral, between anterior and posterior fins	ventral, below the junction of anterior and posterior fins
Seminal vesicles	small, crescent shaped	very large, crooked
Adhesive organs	anterior and posterior separated, each with 10–11 free processes	anterior and posterior more or less united, cockscomb shaped

of the genus *Spadella* s. l. have been separated into two groups by Tokioka & Pathansali (1964), and into three other ones by Alvariño (1981a). The latter three were raised to the rank of genus by Salvini-Plawen (1986): *Spadella* s. s. for the species of the *cephaloptera* group, *Gephyrospadella* for those of the *schizoptera* group with one pair of lateral fins, and *Paraspadella* for those of the *schizoptera* group with two pairs of lateral fins. Finally, Bowman & Bieri (1989) combined the last two groups because they did not recognize the existence of two separate pairs of lateral fins, thus minimizing the importance of that characteristic. This proposal agrees with Tokioka and Pathansali's groups, making two genera: *Spadella* and *Paraspadella,* which differ by the absence or presence of adhesive organs.

There are ten known species of *Paraspadella* if, as it is very probable, *P. hummelincki* Alvariño, 1970 is a junior synonym of *P. pulchella* Owre, 1963 (Owre 1973). The following species have only one pair of adhesive organs with finger-like processes: *P. schizoptera* Conant, 1895; *P. johnstoni* Mawson, 1944; *P. pulchella* and *P. nana* Owre, 1963; *P. legazpichessi* Alvariño, 1981b; *P. pimukatharos* Alvariño, 1987; *P. coecafera* Salvini-Plawen, 1986; and *P. anops* Bowman & Bieri, 1989. Only one species, *P. sheardi* Mawson, 1944, has also two pairs of adhesive organs, but they differ from those of *P. gotoi* since they are well separated and consist of numerous finger-like processes.

The principal characteristics of these species of *Paraspadella* with two pairs of adhesive organs are summarized in Table 1.

Remarks.—*P. gotoi* is the most highly colored chaetognath. The numerous colored pits on the body are reminiscent of *Archeterokrohnia rubra* Casanova, 1986 in which they are localized dorsally in the transverse septum region (unpublished data). The color of its gut also is similar to the bathyal *A. rubra* that is rather unusual in a superficial form, but it must be noted also that orange-brown spots of pigment have been described on the body of *Spadella angulata* (Tokioka & Bieri, 1966) and clusters of reddish cells in the walls of the intestine of *Spadella* (= *Paraspadella*) *pulchella* (Owre 1963), which are both neritic species.

A detailed observation of the adhesive organs of *P. gotoi* shows that they probably have the same origin as fins, the former being modified parts of the latter. Indeed, in

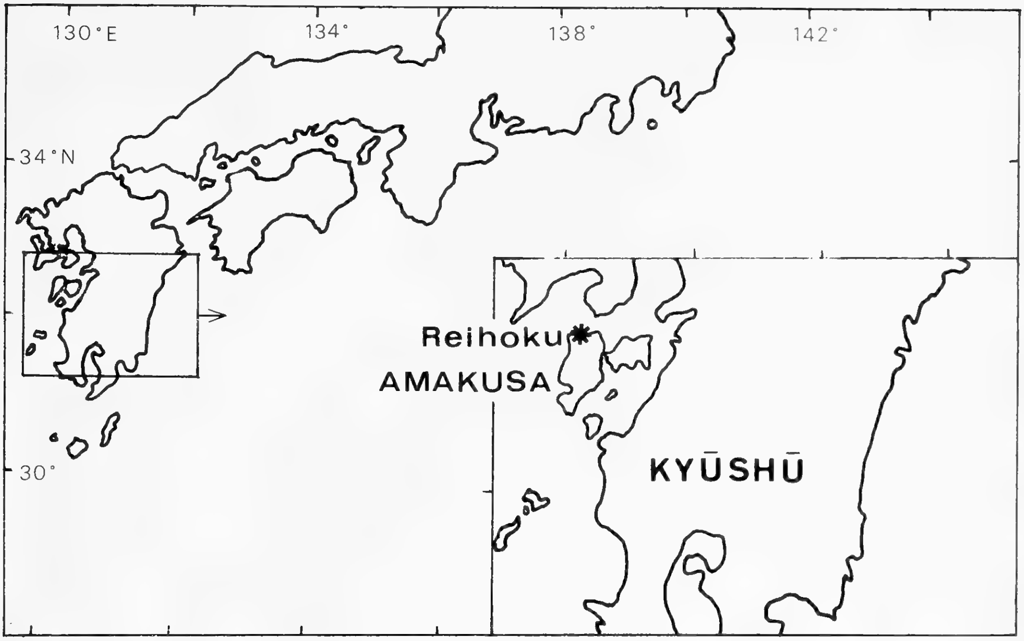


Fig. 3. *Paraspadella gotoi,* n. sp.: Sampling station in Japan (type locality).

one specimen, one finger-like process of the right posterior adhesive organ is fused with the tail fin (Fig. 2a, b). In many others, the posterior edges of both lateral and caudal fins bear tiny papillae as those observed on the extremity of adhesive organs. Lastly, when the collarette tissue is stripped off, these organs appear to be rayed as fins. This is contrary to Mawson's (1944:330) opinion when she wrote: "They [finger-like processes] are therefore not to be regarded as part of the fin," but agrees with previous opinions (Conant 1895, Yosii & Tokioka 1939).

Some morphological features of *P. gotoi* are unique and can be explained by the mating behavior described by Goto & Yoshida (1985). There is cross-fertilization and, when mating, the two partners stand face-to-face. Then, the one that acts as a male jumps and deposits a sperm cluster on the genital orifice of the other, which acts as a female. Thus this orifice is ventral and cannot be dorsal as in all the other chaetognaths but one, *P. sheardi,* where it is exactly lateral, and the particular shape of the seminal vesicles can help to precisely deposit the sperm. Likewise, the two adhesive organs on each side (one directed forward and the second backwards) allow perhaps the complete erection of the body when mating. In *P. sheardi,* the other species of the genus with two pairs of adhesive organs, the outspread adhesive processes, according to Mawson (1944), serve as "props" to support the body in an almost vertical position. This fact, as with also the lateral opening of oviducts, seems to indicate that the mating behavior is the same as in *P. gotoi.*

Distribution.—Two species of *Paraspadella* are known from the coasts of Japan: *Paraspadella coecafera* was described as *Spadella schizoptera* by Yosii & Tokioka (1939) from a single specimen caught near Misaki, not far from Tokyo, but differs from Conant's description of *Spadella* (= *Paraspadella*) *schizoptera* by the absence of anterior fins and the presence of intestinal diverticula. These reasons recently led Salvini-Plawen (1986) to recognize its specific status. *Paraspadella gotoi,* known as *S. schizoptera* in papers dealing with ultrastructural studies, has been collected in tide pools (type locality) near the Amakusa Marine Biological Laboratory, Amakusa Island, Reihoku, in Kyūshū, southwestern Japan (Fig. 3).

Acknowledgments

I wish to express my sincere thanks to Dr. Taichiro Goto of the Mie University in Japan who gave me the specimens to describe this new species.

Literature Cited

Alvariño, A. 1970. A new species of *Spadella* (benthic Chaetognatha).—Studies on the Fauna of Curaçao and Other Caribbean Islands 34:73–89.

———. 1981a. Los quetognatos benticos, estudios y distribucion.—Mem VIIIe Latino-American Congress of Zoology, Merida (Venezuela, Nov. 1980) 2:1109–1128.

———. 1981b. *Spadella legazpichessi,* a new benthic chaetognath from Enewetak, Marshall Islands.—Proceedings of the Biological Society of Washington 94:107–121.

———. 1987. *Spadella pimukatharos,* a new benthic chaetognath from Santa Catalina Island, California.—Proceedings of the Biological Society of Washington 100:125–133.

Bowman, T. E., & R. Bieri. 1989. *Paraspadella anops,* new species, from Sagittarius cave, Grand Bahama Island, the second troglobitic chaetognath.—Proceedings of the Biological Society of Washington 102:586–589.

Casanova, J.-P. 1985. Description de l'appareil génital primitif du genre *Heterokrohnia* et nouvelle classification des chaetognathes.—Compte-rendus hebdomadaires des Séances de l'Académie des Sciences, Paris t.301, III(8):397–402.

———. 1986. *Archeterokrohnia rubra* n. gen., n. sp., nouveau chaetognathe abyssal de l'Atlantique nord-africain: description et position systématique, hypothèse phylogénétique.—Bulletin du Muséum national d'Histoire naturelle, Paris 4è série, 8, section A, (1):185–194.

Conant, F. S. 1895. Description of two new chaetognaths (*Spadella schizoptera* and *Sagitta hispida*).—Annals and Magazine of Natural History, Series 6, 16:288–292.

Goto, T., & M. Yoshida. 1985. The mating sequence of the benthic arrow-worm *Spadella schizoptera.*—Biological Bulletin 169:328–333.

Mawson, P. M. 1944. Some species of the chaetognath genus *Spadella* from New South Wales.—Transactions of the Royal Society of South Australia 68:327–333.

Owre, H. B. 1963. The genus *Spadella* (Chaetognatha) in the western North Atlantic Ocean, with descriptions of two new species.—Bulletin of Marine Science of the Gulf and Caribbean 13: 378–390.

———. 1973. A new chaetognath genus and species, with remarks on the taxonomy and distribution of others.—Bulletin of Marine Science 23(4):948–963.

Salvini-Plawen, L. Von. 1986. Systematic notes on *Spadella* and on the Chaetognatha in general.—Zeitschrift für Zoologische Systematik und Evolutionsforschung 24(2):122–128.

Tokioka, T., & D. Pathansali. 1964. *Spadella cephaloptera* forma *angulata* raised to the rank of species.—Publication of the Seto Marine Biological Laboratory 12:145–148.

———, & R. Bieri. 1966. The colour pattern of *Spadella angulata* Tokioka.—Publication of the Seto Marine Biological Laboratory 14:323–326.

Yosii, N., & T. Tokioka. 1939. Notes on Japanese *Spadella* (Chaetognatha).—Annotationes Zoologicae Japonenses 18:267–273.

Laboratoire de Biologie animale (Plancton), Université de Provence, 13331 Marseille Cedex 3, France.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 913–921

A NEW COMBINATION AND SYNONYMY FOR TWO SUBSPECIES OF *CUCUMARIA FISHERI* WELLS (ECHINODERMATA: HOLOTHUROIDEA)

Philip Lambert

Abstract.—Cucumaria fisheri fisheri Wells is a junior subjective synonym of *Cucumaria piperata* (Stimpson). *Cucumaria fisheri astigmata* Wells is referred to the genus *Pseudocnus* Panning. The new combination *Pseudocnus astigmatus* (Wells) is redescribed here.

The taxonomy of Cucumariidae from the west coast of North America needs revision. This paper addresses one taxonomic problem as part of a larger study into the systematics of a group of brooding holothuroids, to be reported on later. Wells (1924) described *Cucumaria fisheri* (later in the same paper he referred to it as *C. f.* forma *fisheri*) as yellow with brown spots, and with podia in double rows. *C. f. astigmata* was described as orange yellow, without spots, and having scattered podia. The obvious differences in podia arrangement led me to question whether the two forms were conspecific. In this paper I shall assume "forma" to be equivalent to subspecies (Int. Trust Zool. Nomen., 1985, Section 45(g)).

My examination of the holotypes (Figs. 1, 2) confirmed that the external characters are as Wells originally described. He stated that the ossicles of *C. f. astigmata* were ". . . identical with those of *Cucumaria fisheri,* forma *fisheri*" (Wells, 1924:118). I sampled skin ossicles from the holotypes and found them to be substantially different. Skin ossicles from the holotype of *C. f. astigmata* (USNM E01196) are thick, knobbed, perforated buttons or plates (Fig. 3). A few are pine-cone shaped with a spiny handle-like extension at one end. They appear to match the ossicles illustrated by Wells (1924, fig. 1). Ossicles from the holotype of *C. f. fisheri* Wells (USNM E01198) are, on the other hand, relatively thin, perforated plates with serrated edges. Most are oval with a handle-like extension and pointed bumps on both surfaces (Fig. 4). The ossicles from these two forms are undoubtedly from distinct species rather than from two conspecifics as suggested by Wells.

The holotype of *C. fisheri fisheri* should be referred to *Cucumaria piperata* (Stimpson, 1864). *Cucumaria piperata* was described from specimens collected in Puget Sound. Unfortunately, the type specimen has been lost. There is little doubt, however, that Stimpson was describing the white, speckled sea cucumber commonly found in the sheltered waters of Washington and British Columbia (Fig. 5). Deichmann (1937: 169) confused the identification of this species by referring a specimen from off San Jose Point, west of Lower California, to *C. piperata* (Stimpson); however, that specimen had ". . . knobbed perforated plates with dentate handle and small four-holed swollen or knobbed buttons." *C. piperata* does not have the latter "four-holed . . . buttons." Deichmann probably had either *C. californica* Semper or *C. f. astigmata.* Panning (1962) illustrated the ossicles of *C. piperata* for the first time, and also stated that the four-holed plates, mentioned by Deichmann, were absent.

As a result of this confusion in the literature, the identification of white, spotted sea cucumbers on the west coast of North America has been unclear. I have collected

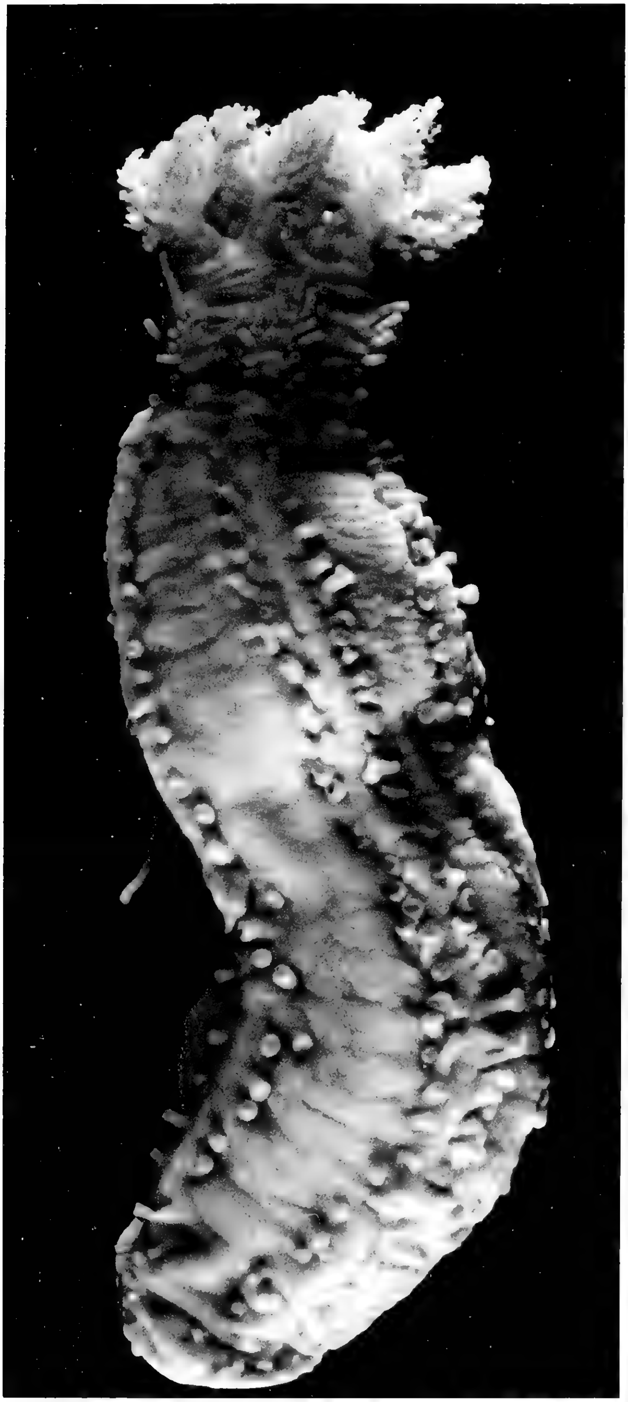


Fig. 1. Holotype of *Cucumaria fisheri fisheri* Wells (USNM E01198); length 41 mm.

plain white and spotted individuals with ossicles that match those described for *C. f. astigmata* (Fig. 6). It appears that Wells combined the external features of *C. piperata* and the ossicles of the spotted form of *C. f. astigmata* in describing *C. f. fisheri.*

Based on my re-examination of the two holotypes, I consider *C. f. fisheri* Wells, 1924 to be a junior subjective synonym of *C. piperata* (Stimpson). The subspecies *astigmata* should be raised to species status as *Cucumaria astigmata* Wells.

In his revision of the Family Cucumariidae, Panning (1949) placed *fisheri* Wells and *fisheri* forma *astigmata* Wells in the genus *Stereoderma.* He also placed *piperata* (Stimpson) into *Pseudocnus.* In two later papers (Panning 1962, 1964) he reversed his decision, returned *piperata* to *Cucumaria,* and then removed *fisheri* from *Stereoderma.* Panning (1962:58) also redefined the ossicles of *Pseudocnus.* His description translates from German as "plates in the shape of pine cones, tightly layered. Below those, more deeply within the skin, round plates can be found." *C. astigmata* has pinecone ossicles in variable numbers usually clustered around the bases of the podia, and numerous thick buttons; thus, I believe *astigmata* should be placed in the genus *Pseudocnus.*

Genus *Pseudocnus* Panning, 1949

Pseudocnus astigmatus (Wells, 1924)

(Figs. 2, 3, 6)

Cucumaria fisheri forma *astigmata* Wells, 1924:117, fig. 2.

Stereoderma fisheri forma *astigmata* Panning, 1949:422.

Stereoderma fisheri Cherbonnier, 1951:42, plates 11 and 12.

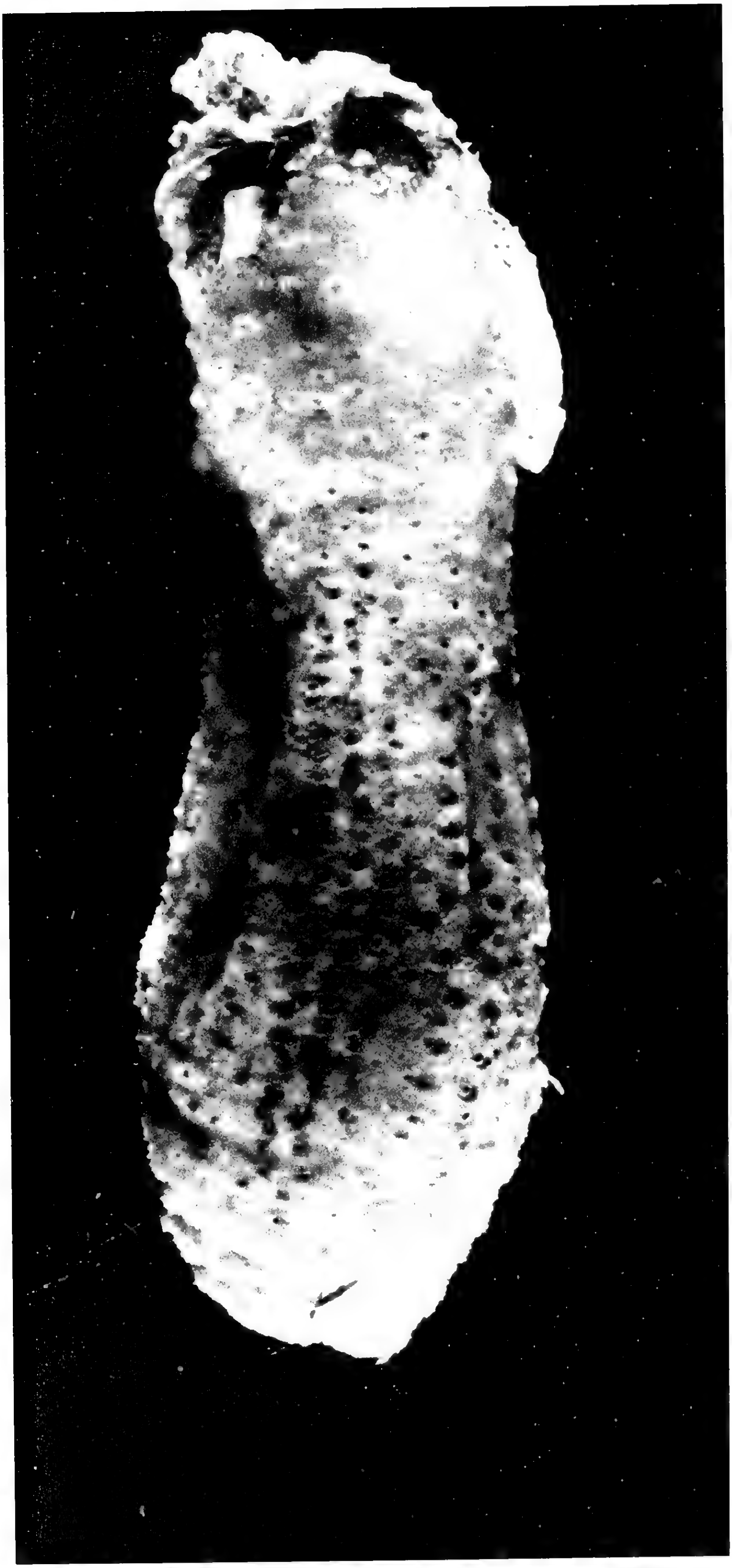
Material examined.—Collections by P. Lambert unless otherwise indicated. Ossicles were examined from 1 to 5 specimens in each lot.

California: Holotype USNM E01196, length 33 mm, H. Wells, 1923, off Monterey and Cabrillo Point, Pacific Grove, depth 22 m; CASIZ 021555, 2 specimens, length 20, 25 mm, 10 May 1904, Albatross Station 4441, Point Pinos, Monterey Bay, depth 51–64 m; CASIZ 15222, 5 specimens, length 20, 14, 22, 20, 8 mm, M. H. Spaulding, Pacific Grove, Monterey Bay, no depth; CASIZ 021554, 3 specimens, length 45, 40, 20 mm, summer 1908, China Point to Del Monte, depth 31 m; CASIZ 1200, 1 specimen, length 8 mm, 8 Apr 1973, Ano Nuevo Cove, San Mateo Co., intertidal.

British Columbia: RBCM 982-237-2, 4 specimens, 30 Sep 1982, Ogden Point, Victoria, Juan de Fuca Strait, 15 m; RBCM 988-751, 32 specimens, 2 Jun 1988, Whiffin Spit, Sooke, Juan de Fuca Strait, low intertidal; RBCM 973-154-5, 5 specimens, 28 Jun 1973, Dicebox I., Barkley Sound, depth 21 m; RBCM 973-183-30, 100 specimens, 25 Jul 1973, Cree Island, Barkley Sound, depth 26 m; RBCM 973-152-32, 2 specimens, 27 Jun 1973, Gilbert Island, Barkley Sound, depth 12 m; RBCM 974-595-2, 2 specimens, D. B. Quayle, 20 Jul 1959, Louie Creek, Esperanza Inlet, intertidal; RBCM 980-343, 1 specimen, 6 Jul 1980, Rugged Point, Kyuquot Sound, depth < 21 m; RBCM 985-384-7, 6 specimens, 1 Jun 1985, Sobry Island, Kyuquot Sound, intertidal; NMC 2221, 2 specimens, R. O'Clair, 29 Jun

→

Fig. 2. Holotype of *Cucumaria fisheri astigmata* Wells (USNM E01196) herein called *Pseudocnus astigmatus* (Wells); length 33 mm.



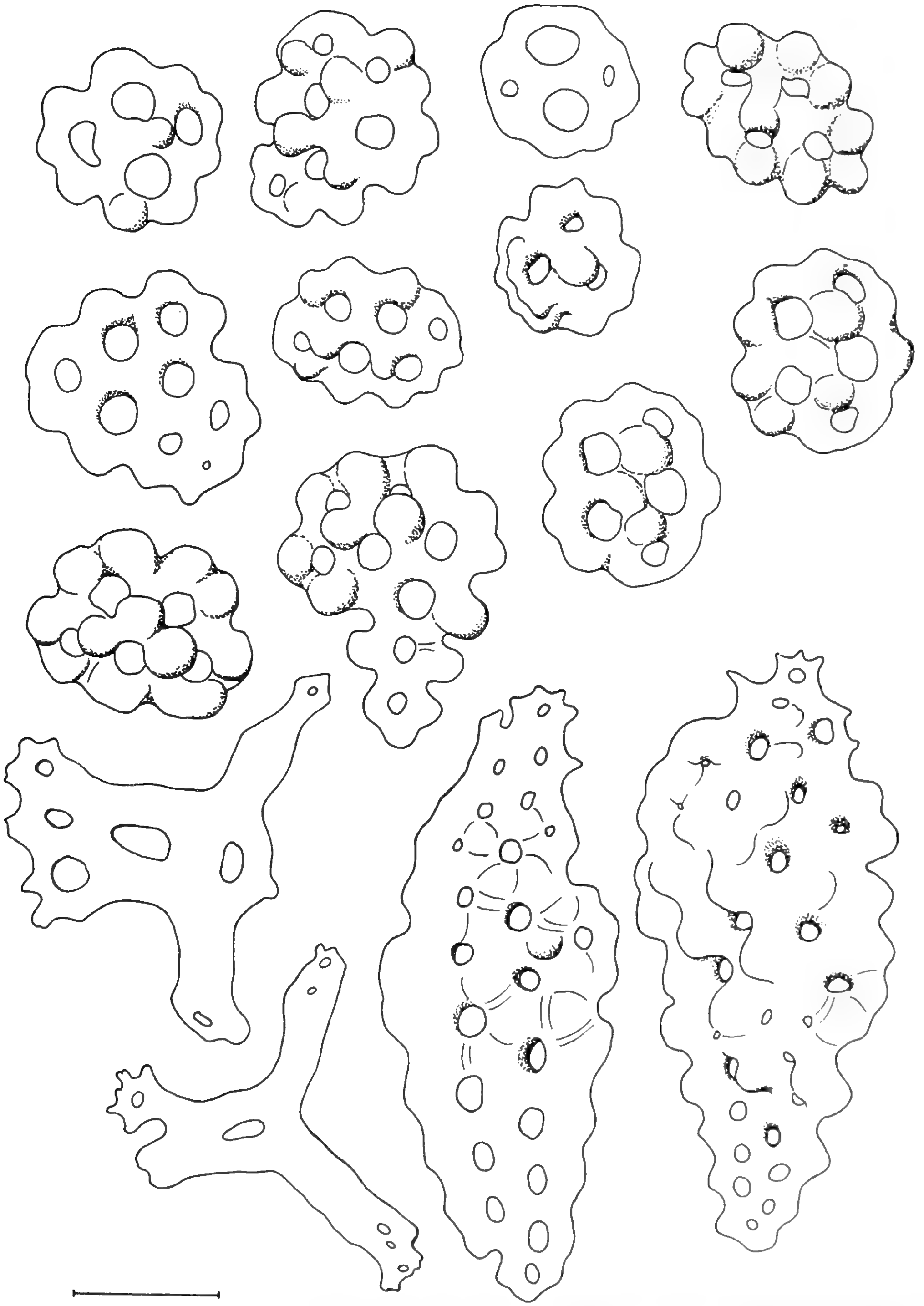


Fig. 3. Ossicles from the mid-dorsal skin of the holotype of *C. f. astigmata* Wells (= *Pseudocnus astigmatus* (Wells)); scale bar = 100 μm.

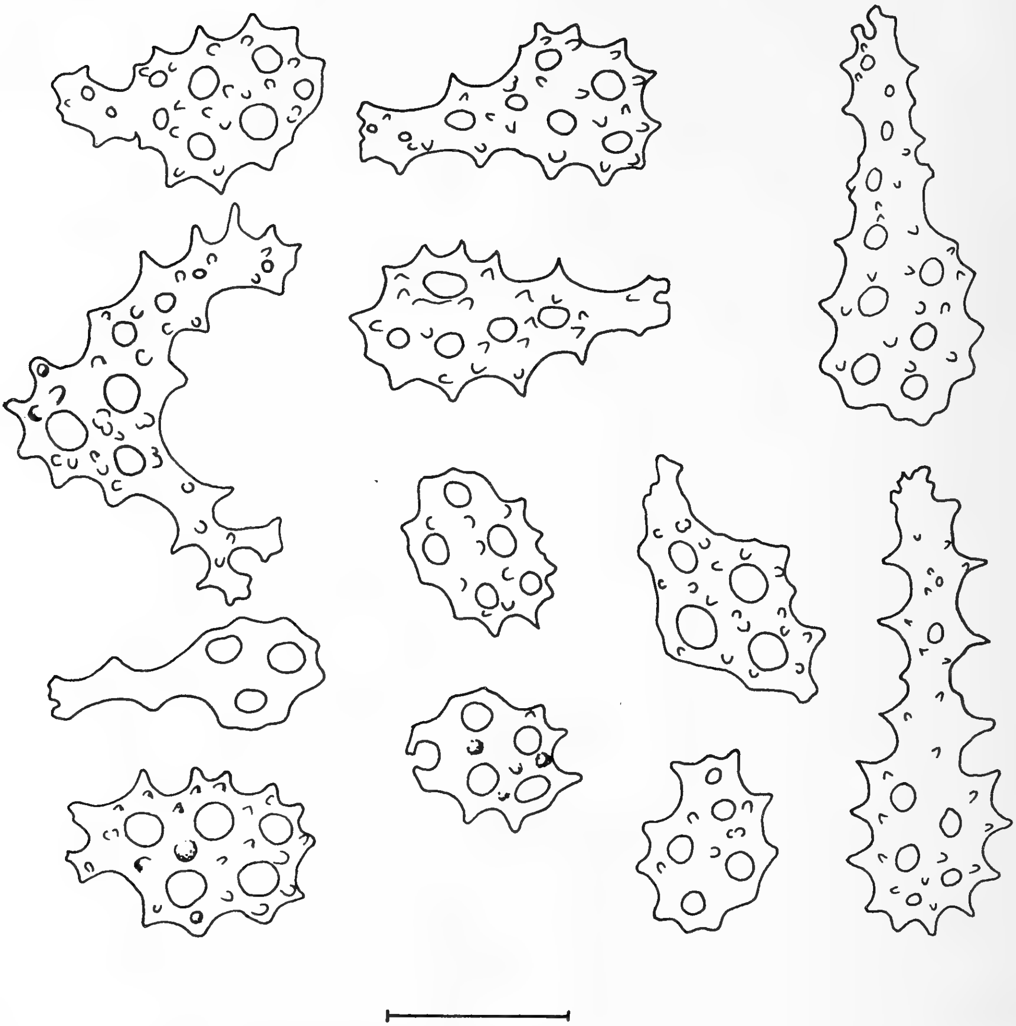


Fig. 4. Ossicles from mid-dorsal skin of the holotype of *C. f. fisheri* Wells (= *Cucumaria piperata* Stimpson); scale bar = 100 μm.

1976, San Josef Bay, Vancouver Island, intertidal; RBCM 980-338, 2 specimens, 1 Jul 1980, Cliffe Point, Quatsino Sound, depth 18 m; RBCM 980-329-7, 3 specimens, 28 Jun 1980, Hunt Islets, Queen Charlotte Strait, depth < 21 m; RBCM 977-444-5, 3 specimens, 12 Jan 1963, D. B. Quayle, FRB 63-2, Cormorant Channel, Queen Charlotte Strait, depth 26 m; RBCM 976-1037-7, 1 specimen, 27 Mar 1976, Juan Perez Sound, Queen Charlotte Islands, depth < 18 m; RBCM 102-19, 1 specimen, 3 Jun 1969, G. C. Carl, Frederick Island, Queen Charlotte Islands, intertidal; RBCM 108-18, 7 specimens, 4 Jun 1969, G. C. Carl, Louis Point, Graham Island, Queen Charlotte Islands, intertidal; RBCM 984-219-1, 1 specimen, 29 Apr 1961, D. B. Quayle, FRB S-4 H-9.7, Langara Island, Dixon Entrance, depth 82 m.

Diagnosis.—Small form with robust ventral podia in rows as well as between the ambulacra. Dorsal podia visible as scattered dimples. Ten tentacles of equal size. Cal-

careous ring without posterior prolongations. Majority of ossicles are knobbed buttons with from 4 to 10 perforations, some with a spiny, handle-like extension and more than 20 perforations; three-armed supporting rods in podia. Color varies from yellowish-white to white with fine brown spots primarily on the dorsum and ends of animal.

Holotype.—USNM E01196.

Type locality.—Monterey, California, 22 m.

Range.—British Columbia to California; intertidal to 82 m.

Remarks.—*Pseudocnus astigmatus* (Wells) appears to be closely related to *Cucumaria curata* Cowles and *Cucumaria lubrica* Clark. Like these latter two species, *P. astigmatus,* collected at Whiffin Spit, Juan de Fuca Strait, brood large yolky eggs and juveniles between the ventral surface and the substrate. *P. astigmatus* also has similar tentacles, podia, body shape and has certain ossicle shapes in common with *C. curata* and *C. lubrica.* Further studies are planned to investigate the systematics of these closely related forms.

Acknowledgments

I wish to thank Dave Pawson, National Museum of Natural History (USNM); Ailsa Clark, British Museum (BM); Peter Frank, Canadian Museum of Nature (CMN) (formally National Museums of Canada (NMC); and Elizabeth Kools, California Academy of Sciences (CASIZ), for loan of specimens. Translations of relevant German papers were kindly provided by Dave Pawson, Mary Bergen and Maria Abbott. I especially thank my colleagues Alex Peden and Rob Cannings for their constructive suggestions to improve the manuscript and to Rich Mooi

←

Fig. 5. *Cucumaria piperata* (Stimpson) collected from Nasparti Inlet, west coast Vancouver Island; depth 12 m; length 71 mm (RBCM 985-409-3).

and an anonymous reviewer for their useful comments. Thank you also to Barbara Kuluah for typing it. Funding was provided by the Royal British Columbia Museum (RBCM) and the Friends of the Royal B.C. Museum.

Literature Cited

Cherbonnier, G. 1951. Holothuries de L'Institut Royal des Sciences Naturelles de Belgique.—Memoires de L'Institut Royal des Sciences Naturelles de Belgique, 2 serie, fasc 41.

Deichmann, E. 1937. 10. The Templeton Crocker Expedition. IX. Holothurians from the Gulf of California, the West Coast of Lower California and Clarion Island.—Zoologica 22:161–176.

International Trust for Zoological Nomenclature. 1985. International Code of Nomenclature. Third edition. British Museum (Natural History), 338 pp.

Panning, A. 1949. Versuch einer Neuordnung der Familie Cucumariidae (Holothurioidea, Dendrochirota).—Zoologische Jahrbücher Abteilung für Systematik, Okologie und Geographie der Tiere 78:404–470.

———. 1962. Bemerkungen über die Holothurien-Familie Cucumariidae (Ordnung Dendrochirota). 3. Tiel. Die Gattung *Pseudocnus* Panning, 1949.—Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 60:57–80.

———. 1964. Bemerkungen über die Holothurien–Familie Cucumariidae (Ordnung Dendrochirota). 3 Teil. Die Gattungen *Stereoderma, Staurothyone* und *Trachythyone.*—Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut. Kosswig-Festschrift 61:159–174.

Stimpson, W. 1864. Descriptions of new species of marine invertebrata from Puget Sound, collected by the naturalists of the Northwest Boundary Commission.—Proceedings of the Academy of Natural Sciences of Philadelphia 16:153–161.

Wells, H. 1924. *IV.* New species of *Cucumaria* from Monterey Bay, California.—Annals and Magazine of Natural History Series 9, 14:113–121.

Invertebrate Unit, Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, Canada, V8V 1X4.

←

Fig. 6. Plain and spotted forms of *Pseudocnus astigmatus* (Wells) (= *C. f. astigmata* Wells) collected at Whiffin Spit, Sooke, British Columbia; low intertidal amongst holdfasts of *Hedophyllum*; length of spotted specimen, 42 mm; plain specimen, 37 mm (RBCM 988-751).

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 922–930

A NEW GENUS AND SPECIES OF ANTHIINE FISH (PISCES: SERRANIDAE) FROM THE EASTERN SOUTH PACIFIC WITH COMMENTS ON ANTHIINE RELATIONSHIPS

William D. Anderson, Jr., N. V. Parin, and John E. Randall

Abstract.—*Anatolanthias apiomycter,* a new genus and species of anthiine fish, is described from two specimens collected in the eastern South Pacific, about 1500 km west of Chile at almost 26°S, near the southwest end of the Nazca Ridge. It is distinguished from all other serranids in having the following combination of characters: maxilla abruptly expanded distally, anterior naris somewhat remote from posterior naris, vomer edentate, vertebrae 26 (10 precaudal + 16 caudal), dorsal fin continuous—not incised between spinous and soft portions, opercle with three well-developed spinous processes, pleural ribs on vertebrae 3 through 11, epipleural ribs associated with first 11 vertebrae, epihaemal ribs on vertebrae 12 through 19, predorsal bones 2, principal caudal-fin rays 15, scales ctenoid with only marginal cteni, maxilla with scales, dorsal and anal fins naked (but each with low scaly sheath as its base), supramaxilla absent, and preopercle without antrorse spines. Characters that may be useful in clarifying relationships within the Anthiinae are discussed.

During a recent cruise in the eastern South Pacific, personnel aboard the Soviet research vessel *Prof. Shtokman* collected two specimens of a new species of anthiine serranid fish. These specimens are so distinctive that they also warrant description as a new genus. The main purpose of this paper is to describe the new genus and species. In addition, because of the inadequately understood relationships of the serranid subfamilies and the chaotic generic classification within the Anthiinae, we discuss characters that appear to be useful in elucidating serranid intrarelationships—particularly those within the Anthiinae.

The Anthiinae include a plethora of brightly colored species of small to medium size that inhabit tropical to temperate seas worldwide at shallow to moderate depths, usually on rocky bottoms or coral reefs which provide shelter. Most species feed on zooplankton a short distance above the bottom to which individuals rapidly retreat when predators approach. These fishes often occur in aggregations, and, as far as known, are protogynous hermaphrodites. The sexes are often colored differently and may exhibit morphological differences, particularly in fin structure; typically males attend large harems.

There are about 165 valid described species of Anthiinae, variously classified in more than 20 genera. A remarkable 73 species of the subfamily were first described between 1975 and 1987—46 of them in the years 1979–1982. At least 14 undescribed species (in addition to the one described herein) are in museum collections, and still more must remain to be discovered. This explosive increase in the number of anthiine species known is due to more intensive collecting. Of particular importance has been the relatively recent advent of SCUBA, which has allowed collecting at previously inaccessible depths.

Because only one genus of anthiines has

been revised since 1975 (*Plectranthias*, Randall 1980), it is not surprising that the generic classification is inadequate. We hope that our comments on relationships will contribute to a better understanding of generic limits and relationships within the Anthiinae.

Materials and Methods

The holotype is deposited in the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); the paratype, in the Zoological Institute, Academy of Sciences USSR, Leningrad (ZIL).

Counts and measurements follow Anderson & Heemstra (1980), except as indicated below. The first vertebra with a haemal spine was considered the first caudal vertebra; the urostylar vertebra, the last. Mabee (1988) interpreted the predorsal bones of teleosts as the phylogenetic homologues of supraneurals, and because supraneural is the more widely used senior synonym, she recommended its use for those bones in teleosts. We prefer to use the term "predorsal bone" because it is firmly entrenched in the literature of percoid fishes. Gillrakers and pseudobranchial filaments were counted on the right side. Internarial distance was the distance between the posterior border of the anterior naris and anterior border of the posterior naris. Body depth was measured at the dorsal-fin origin and at greatest depth; body width, just posterior to gill opening; and prepelvic length, from premaxillary symphysis to origin of pelvic fin. Caudal concavity was the horizontal distance between verticals at distal tips of longest and shortest caudal-fin rays. The symbol > preceding the measurement of a fin ray indicates that the element measured was slightly damaged. Most measurements are presented as percentages of the standard length (SL), but some are given as quotients of SL, head length, snout length, or orbital diameter. These quotients are rounded to the nearest 0.05.

Anatolanthias, new genus

Diagnosis.—A genus of Anthiinae distinguishable from all other genera of Serranidae by the following combination of characters. Maxilla abruptly expanded distally, particularly on labial border, where a shelf or rostrally directed hook is present at point of expansion. Anterior naris located rather far anteriorly on snout, somewhat remote from posterior naris. Vomer edentate. Vertebrae 26 (10 precaudal + 16 caudal). Dorsal fin single, not incised between spinous and soft portions. Posterior margin of bony opercle with three well-developed spinous processes, middle one largest. Pleural ribs on vertebrae 3 through 11. Epipleural ribs associated with first 11 vertebrae. Epihaemal ribs (bones in the same series as the epipleural ribs which appear to be modified intermuscular bones; see Stiassny & Jensen 1987:300) on vertebrae 12 through 19. Formula for configuration of predorsal bones, anterior neural spines, and anterior dorsal pterygiophores 0/0/2/1+1/1/ (using symbolization of Ahlstrom et al. 1976). Caudal fin forked; principal rays 15 (8 + 7); branched rays 13 (7 + 6). Scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni; see Hughes 1981); no secondary squamation. Scales present on maxilla and in interorbital region. Well-developed axillary process of modified scales at pelvic-fin base. Dorsal and anal fins without scales, but each with low scaly sheath at its base. No supramaxilla. Preopercle without antrorse spines.

Description.—Characters included in the generic diagnosis form part of the generic description and are not repeated. Mouth terminal; upper and lower jaws about equal. Premaxillae protrusile. Posterodorsal border of maxilla not covered by elements of circumorbital series when mouth closed. Palatine with teeth. Pterygoids and tongue edentate. Fleshy papillae on posterior half of orbital border. Posterior margin of preopercle serrate; ventral margin of preopercle essentially smooth. Branchiostegals 7. Pseudobranch present. Gill arches 4, with slit behind fourth. Longest gillrakers longer than longest gill filaments. Lateral line complete, extending to base of caudal fin (running parallel to dorsal body contour below dorsal fin, curving gently to near mid-lateral axis of body on caudal peduncle). Squamation well developed on bases of pectoral, pelvic, and caudal fins and continuing onto fins. Pelvic-fin rays I, 5; pelvic fin inserted slightly posterior to vertical through pectoral-fin base. Procurrent spur (Johnson 1975) absent; penultimate ventral procurrent caudal-fin ray not shortened basally. Parhypural with well-developed hypurapophysis. Autogenous hypurals 5. Epurals 3. Uroneurals 1 pair (posterior pair absent). No trisegmental pterygiophores associated with dorsal and anal fins. Other characters are those of the single species.

Etymology.—*Anatolanthias* (anatole, east; anthias, a seafish) is from the Greek, referring to the occurrence of the genus in the eastern Pacific. The gender is masculine.

Type species.—*Anatolanthias apiomycter,* new species.

Anatolanthias apiomycter,
new species
Figs. 1, 2

Holotype: USNM 309202, 93.9 mm SL; 25°41.7′S, 85°23.7′W; 160–168 m; R/V *Prof. Shtokman* cruise 18, station 1922; 26 April 1987; bottom otter trawl.

Paratype: ZIL 49471, 89.0 mm SL; same data as for holotype.

Description.—Characters presented in the generic diagnosis and description form part of the species description and are not repeated unless necessary for clarification. Most of the scales have been lost from the paratype; as a consequence it is impossible to enumerate or accurately estimate most of its scale counts. Data for the holotype are followed, in parentheses, by those for the paratype, when different. Dorsal-fin rays X,16. Anal-fin rays III, 7. Pectoral-fin rays 21, both sides (22 both sides); dorsalmost pectoral-fin ray unbranched on both sides (right ventralmost unbranched), other rays branched. Procurrent caudal-fin rays 14, both dorsally and ventrally. Gillrakers on first arch 10 + 27 (11 + 26), no rudimentary rakers. Pseudobranchial filaments 18 (16). Fleshy papillae on posterior half of orbital border 22 left, ca. 20 right (20 left, 21 right). Tubed lateral-line scales 63 left, ca. 62 right (estimated ca. 62 left). Rows of cheek scales ca. 8 left, ca. 9 right. Scale rows between lateral line and mid-base of spinous dorsal fin 3. Scales from dorsal-fin origin to lateral line 5. Scales from anal-fin origin to lateral line ca. 17. Serrae on posterior margin of preopercle ca. 19 left, ca. 20 right (16 left, ca. 14 right); serrae enlarged into bifurcate spinous process at angle on right side (blunt process at angle), not enlarged on left side; ventral margin of preopercle essentially smooth.

Body depth (at dorsal-fin origin) 3.95 (4.15), head length 3.75 (3.60) in SL. Bony orbital diameter 3.05 (3.40) in head length. Bony interorbital width 3.75 (4.50) in head length, 1.20 (1.35) in bony orbital diameter. Snout length 1.60 (1.50) in bony orbital diameter. Internarial distance 3.05 (2.80) in snout length. The following morphometric data are in percentages of SL. Head length 26.7 (27.9). Snout length 5.5 (5.4). Bony orbital diameter 8.7 (8.2). Postorbital head length 12.9 (13.7). Upper jaw length 12.5. Maxilla width 4.2 (4.3). Internarial distance 1.8 (1.9). Least bony interorbital width 7.1 (6.2). Body depth at dorsal-fin origin 25.3 (24.0). Greatest body depth 26.9 (24.0). Body width 16.4 (14.4). Predorsal length 28.8 (28.5). Prepelvic length 35.0 (32.0). Preanal length 64.9 (63.9). Caudal-peduncle length 21.7. Least caudal-peduncle depth 11.1 (10.6). Pectoral-fin length 29.8 (28.4). Pelvic-fin length 23.6 (21.9). Pelvic spine 13.0 (13.1). Dorsal-fin base 56.7 (58.2). First dorsal spine >3.7 (4.4). Second dorsal spine 8.1 (8.4). Third dorsal spine 10.1 (>9.1). Fourth dorsal spine 10.8 (11.3). Longest dorsal spine 11.8, fifth (11.6, sixth). Tenth dorsal spine >7.8 (9.3). Longest dorsal soft ray ca. 14.0, tenth (broken). Anal-fin base 17.5 (17.8). Depressed anal-fin length 28.6 (27.9). First anal spine 4.3 (5.1). Second anal spine >9.2 (10.2). Third anal spine >8.3 (9.2). Longest anal soft ray ca. 14.1, second (ca. 15.2, fourth). Upper caudal-fin lobe ca. 33.8 (broken). Lower caudal-fin lobe ca. 31.9 (broken). Caudal concavity ca. 20.7 (fin damaged).

Premaxilla with lateral row of conical teeth and medial series of much smaller conical teeth; one or two small canines at anterior end of lateral row; medial series with one to a few small posteriorly directed canines adjacent to symphysis; no teeth at symphysis. Dentary with row of conical teeth, teeth smaller near symphysis; one to a few teeth enlarged into small canines about 30 to 35 percent of distance from anterior end of jaw to posterior end of row of teeth; exserted canine at anterior end of jaw; no teeth at symphysis. Vomer edentate, but with several fleshy papillae. Palatine with band of small conical teeth.

Maxilla reaching just posterior to vertical through middle of eye. Posterior border of anterior naris produced into flap which falls well short of posterior naris when reflected. Free margins of interopercle and subopercle somewhat irregular, but not serrate. Maxilla, interorbital region, lachrymal, cheek, preopercle, interopercle, opercle, and subopercle densely covered with scales; scales on dorsum of snout not reaching anterior end of snout—leaving considerable area scaleless (anteriormost scales on dorsum of snout very small); most of lateral aspect of snout naked; no scales on lower jaw, gular region, branchiostegals, and branchiostegal membranes. Modified scales (interpelvic process) overlapping pelvic fin bases along mid-ventral line. Tubes in lateral-line scales simple.

Distal margin of anal fin rounded. Second anal spine more robust than first or third, about twice as long as first, slightly longer

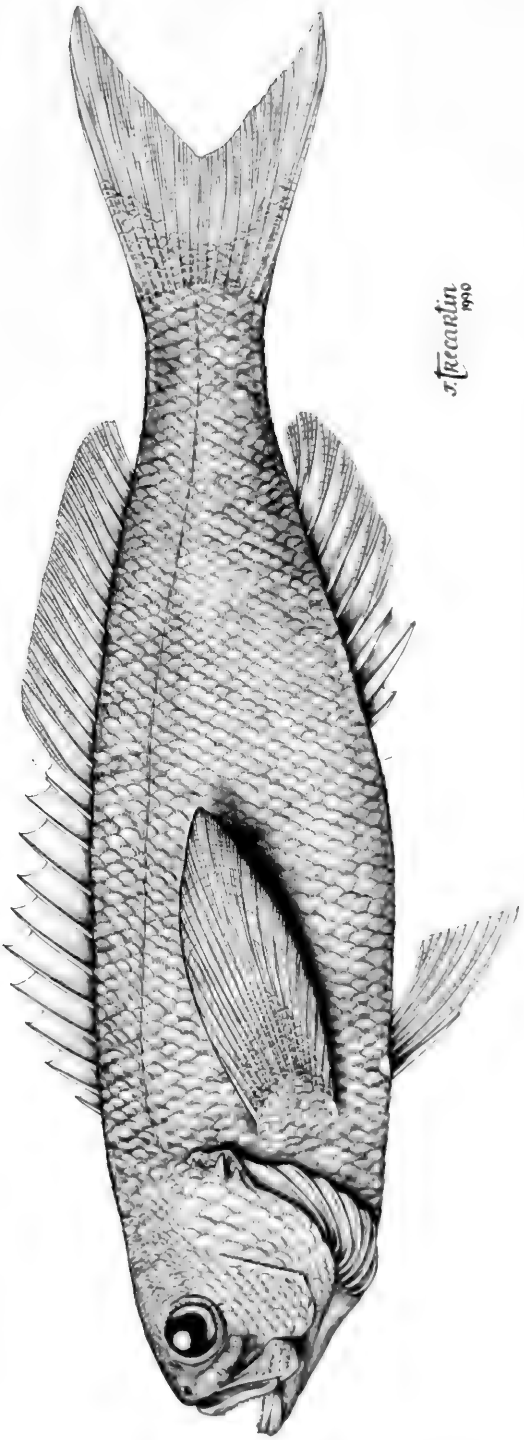


Fig. 1. Holotype of *Anatolanthias apiomycter*, USNM 309202, 93.9 mm SL; eastern South Pacific.

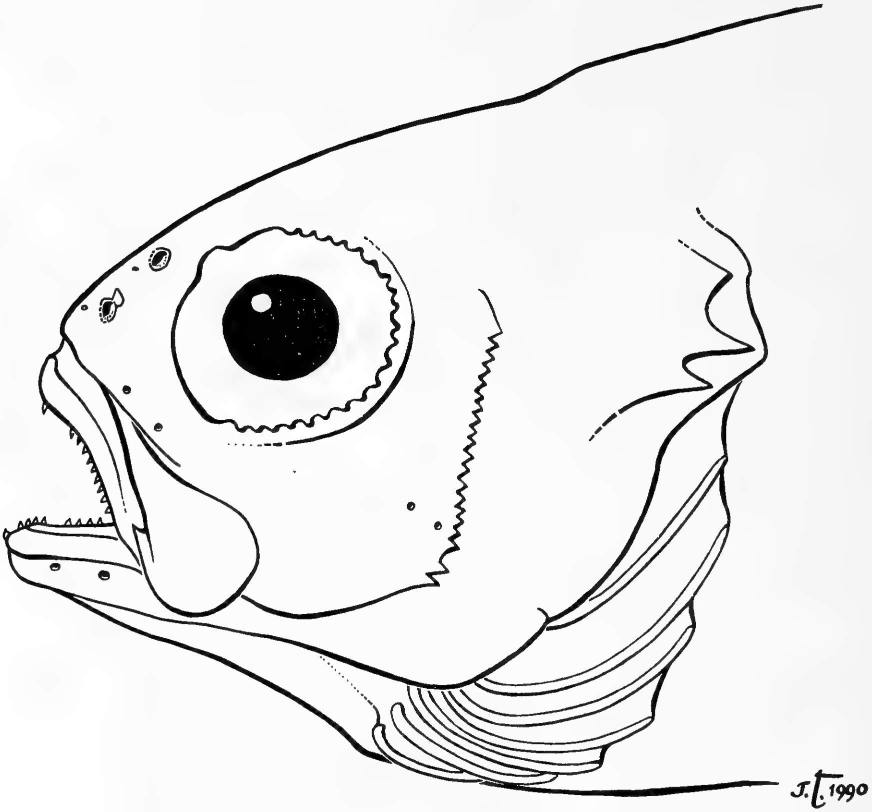


Fig. 2. Head of holotype of *Anatolanthias apiomycter,* USNM 309202, 93.9 mm SL; eastern South Pacific.

than third. Pectoral fin symmetrical, middle rays longest. Pectoral fin reaching vertical between bases of first and second dorsal soft rays (vertical through base of first dorsal soft ray), falling short of vertical through vent. Pelvic fin reaching vertical through base of ninth dorsal spine (vertical between bases of eighth and ninth dorsal spines), falling short of vent.

Coloration.—In alcohol the types are straw-colored with no distinctive pigmentation. A color transparency of the holotype, taken shortly after capture, shows: body uniformly red, iris red, dorsal and caudal fins red, anal fin paler, paired fins not clearly visible.

Distribution.—*Anatolanthias apiomycter* is known only from the type-locality in the eastern South Pacific, about 1500 km off the coast of Chile, near the southwest end of the Nazca Ridge.

Etymology.—The name *apiomycter* (apios, far away; mykter, nostril) is from the Greek and is an allusion to the unusual position of the anterior nostril. The new name is a masculine noun in apposition to *Anatolanthias.*

Relationships

Johnson (1983) defined the Serranidae with respect to the Percichthyidae (sensu Gosline 1966) on the basis of three reductive specializations (absence of the posterior uroneural, procurrent spur, and third preural radial cartilages), and showed that members of the Serranidae share at least one innovative specialization (the presence of three spines on the opercle)—thus supporting the hypothesis of monophyly for the family. Following Gosline (1966), Johnson (1983, 1988) recognized three subfamilies in the Serranidae: the Serraninae, Epinephelinae, and Anthiinae, but identified an autapomorphy for only the Epinephelinae. Anderson & Heemstra (1989) mentioned two characters (one reductive, the other innovative) that may prove useful in defining the Anthiinae. The reductive character, absence of a tooth plate on the second epibranchial, was discussed by Baldwin (1990) and interpreted as an autapomorphy of the Anthiinae.

As noted by Johnson (1983), it is difficult to evaluate the significance of vertebral number in determining relationships among the Percoidei; nevertheless, this character may be of value in delimiting the boundaries of the Anthiinae. Species of Serraninae and Epinephelinae almost always have 24 vertebrae, but species of Anthiinae have 25 to 28, usually 26. (*Acanthistius,* a serranine, has 26 vertebrae, and *Niphon,* a primitive epinepheline, has 30 [Johnson 1983]. *Pseudogramma* has 26 vertebrae; *Suttonia* has 26 or 27; and *Aporops* has 27 or 28 [Leis & Rennis 1983; Carole C. Baldwin, pers. comm.]. These last three genera are highly derived grammistin epinephelines, whose progenitors presumably acquired additional vertebrae subsequent to the divergence of the grammistins from the main line of epinepheline evolution.) Anderson & Heemstra (1989) presented an analysis of vertebral number as a character in the Serranidae; they considered 24 or 25 as the most primitive state in the Serranidae and 26, 27, and 28 as progressively more derived states.

Realizing that additional study is needed before the Anthiinae can be definitively defined, we accept, at present, the absence of the second epibranchial tooth plate and high vertebral number (26 to 28, usually 26) as autapomorphies delimiting this subfamily. Recognition of the Anthiinae as a distinct taxon is of considerable practical value because the concept anthiine unites a large number of look-alike species that share uniquely derived characters at some level within the Serranidae.

According to Johnson (1984), the primitive and most common number of principal caudal-fin rays (branched rays + 2) in percoids is 17 (9 + 8), and the most common and presumably primitive number of predorsal bones is three. Johnson (1984) noted that most percoids (59 groups) have ctenoid scales in which the cteni are discrete bony plates that are added continually to the posterior field as the scale grows, and that in most of these the posterior field is filled with the remains of old cteni (ctenial bases of Hughes 1981). The retention of ctenial bases in the posterior field is presumably more primitive in the Percoidei than the condition in which only primary and secondary rows of marginal cteni are present (i.e., no ctenial bases remaining in the posterior field) because, according to Johnson (1984), only a few groups (including the Anthiinae) have species lacking ctenial bases in the posterior field. If, in the Serranidae, 15 principal caudal-fin rays, one or two predorsal bones, and absence of ctenial bases in the posterior field are derived states, as they appear to be, they may be helpful in clarifying the generic classification of the Anthiinae.[1]

Baldwin (1990) found that all of the species of Anthiinae that she examined that have 17 principal caudal-fin rays also have three predorsal bones, whereas those with 15 principal rays have either two or three predorsal bones (all Atlantic and eastern Pacific species with 15 principal rays have only two predorsal bones). Our data corroborate

---

[1] We realize that the argument common equals plesiomorphous is logically flawed, but, because the sister group of the Serranidae has not been identified and because there are no other pertinent data, it is the only argument available.

Baldwin's with the exceptions of *Giganthias immaculatus* (if it is an anthiine) from Japanese waters and *Plectranthias vexillarius* from the Gulf of Oman, which have 17 principal rays and two predorsal bones, and *Plectranthias japonicus* from the western Pacific, which has 16 or 17 principal rays and two predorsal bones (also see Randall & Heemstra 1978, Randall 1980). Randall (1980) reported five other species of *Plectranthias* that have variable or unusual numbers of principal caudal-fin rays (one species with 15 to 17, two with 16, one with 15 or 16, and one with 14 to 16), but he did not give counts of predorsal bones. Randall & Lubbock (1981) reported that four species of *Pseudanthias,* of the Indo-Pacific subgenus *Mirolabrichthys,* have 15 principal rays but only one predorsal bone and that one other *Mirolabrichthys* has 15 principal rays and either one or two predorsal bones.

Among anthiines there is a strong correlation in number of principal caudal-fin rays, number of predorsal bones, and type of ctenoid scale. Species with 17 principal rays and three predorsal bones usually have scales in which ctenial bases have been retained in the posterior field, but among those with 15 principle rays apparently all lack ctenial bases in the posterior field (Anderson, unpublished data). Although all three of the presumed derived states (15 principal caudal-fin rays, one or two predorsal bones, and absence of ctenial bases in the posterior field) are reductive, the shared possession of all three may be indicative of propinquity of descent. (Based on our incomplete data we speculate that the sequence of appearance of these derived characters in the main line of anthiine evolution was: loss of ctenial bases in the posterior field, reduction in number of principal caudal-fin rays, and reduction in number of predorsal bones.) *Anatolanthias* belongs to a large group of anthiines (which includes, e.g., species of *Anthias, Hemanthias, Holanthias, Luzonichthys, Pronotogrammus,* and *Rabaulichthys*) that displays all three derived traits.

Anatolanthias shares the following apparently derived traits with species of the Indo-Pacific genera *Luzonichthys* (six nominal species) and *Rabaulichthys* (two species): anterior naris rather remote from posterior naris (nares usually close together in anthiines; in the above genera internarial distance 2.45–4.35 times in snout length, other anthiines for which data are available—with the exception of *Anthias tenuis*—5.10–14.00 [usually 6.00–11.00], *A. tenuis* 4.30–4.95), vomerine dentition absent or extremely reduced (vomerine dentition usually well developed in anthiines, *Pseudanthias fucinus* being the only other anthiine known to lack vomerine teeth; see Randall 1981, Allen 1984, Randall & Ralston 1984, Randall & Pyle 1989), and the sum of numbers of pairs of epipleural and epihaemal ribs 16 to 19 (specimens of about 60 species of anthiines representing 14 other genera with 8–15 [usually 9–13], *Nemanthias carberryi* with 16 and one species of *Pseudanthias* with 17). In addition, another character state that may be a synapomorphy for *Anatolanthias, Luzonichthys,* and *Rabaulichthys* is the number of pleural ribs; these genera have nine pairs, but anthiines usually have eight (about three-fourths of the species for which data are available with eight). Based on these characters we hypothesize that the genera *Luzonichthys, Rabaulichthys,* and *Anatolanthias* constitute a monophyletic assemblage. We recognize three genera for this assemblage because all three possess characteristics that can be interpreted as autapomorphies and no two of the genera bear identified synapomorphies.

Luzonichthys is quite distinctive (Randall 1981); species of this genus have two dorsal fins (other anthiines have a single dorsal fin) and have the third or ventralmost opercular spine greatly reduced—apparently absent in some specimens (other anthiines have three well developed opercular spines). Also *Luzonichthys* has 11 precaudal and 15 caudal vertebrae; among anthiines with 26 vertebrae the vast majority (including *Anatolan-*

thias and *Rabaulichthys*) have 10 and 16, respectively. *Rabaulichthys* (Allen 1984, Randall & Pyle 1989) is characterized by the possession of a high sail-like spinous dorsal fin in males (no other anthiines have a dorsal fin with this shape) and the absence of palatine dentition (other anthiines have teeth on the palatine). In *Anatolanthias* the maxilla is abruptly expanded distally, particularly so on the labial border where a shelf or a rostrally directed hook is present at the point of expansion (the shelf or hook is absent in *Luzonichthys* and *Rabaulichthys* and the distal expansion of the maxilla is not particularly abrupt). This configuration of the maxilla has, to our knowledge, not been reported in the literature for any anthiine, although Phillip C. Heemstra informed us (pers. comm.) that he has observed it in several species, including *Anthias nicholsi, A. salmopunctatus, A. tenuis, Hemanthias vivanus,* and *Sacura parva*; we have observed it in a number of other species, e.g., *Anthias anthias, A. asperilinguis, Hemanthias peruanus,* and *Holanthias martinicensis.* The abrupt expansion of (or shelf or hook on) the maxilla is easily overlooked because it is usually hidden by the lip. Despite the fact that other anthiine species (apparently not closely related to *Anatolanthias*) have the abruptly expanded maxilla, this trait may have been independently derived in *Anatolanthias* and thus be an autapomorphy for this genus.

Acknowledgments

P. C. Heemstra called the senior author's attention to the hook on the maxilla of the holotype of *Anatolanthias apiomycter*; W. F. Hoffman and P. P. Maier made the radiographs used in this study; J.-E. Trecartin prepared the illustrations; M. Jones typed the manuscript; and C. C. Baldwin, P. C. Heemstra, V. G. Springer, and C. C. Swift reviewed the manuscript. This research was supported by a grant from the Faculty Research and Development Committee of the College of Charleston to the senior author. To all who contributed to the completion of this research we express our appreciation. This is contribution number 87 of the Grice Marine Biological Laboratory, College of Charleston.

Literature Cited

Ahlstrom, E. H., J. L. Butler, & B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic.—Bulletin of Marine Science 26:285–402.

Allen, G. R. 1984. A new genus and species of anthiid fish from Papua New Guinea.—Revue française d'Aquariologie 11:47–50.

Anderson, W. D., Jr., & P. C. Heemstra. 1980. Two new species of western Atlantic *Anthias* (Pisces: Serranidae), redescription of *A. asperilinguis* and review of *Holanthias martinicensis.*—Copeia 1980:72–87.

———, & ———. 1989. *Ellerkeldia,* a junior synonym of *Hypoplectrodes,* with redescriptions of the type species of the genera (Pisces: Serranidae: Anthiinae).—Proceedings of the Biological Society of Washington 102:1001–1017.

Baldwin, C. C. 1990. Morphology of the larvae of American Anthiinae (Pisces: Serranidae) with comments on relationships within the subfamily.—Copeia (in press).

Gosline, W. A. 1966. The limits of the fish family Serranidae, with notes on other lower percoids.—Proceedings of the California Academy of Sciences, 4th Ser., 33:91–111.

Hughes, D. R. 1981. Development and organization of the posterior field of ctenoid scales in the Platycephalidae.—Copeia 1981:596–606.

Johnson, G. D. 1975. The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications.—Occasional Papers of the California Academy of Sciences 121:1–23.

———. 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae.—Copeia 1983:777–787.

———. 1984. Percoidei: development and relationships. Pp. 464–498 *in* H. G. Moser et al., eds., Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists, Special Publication No. 1.

———. 1988. *Niphon spinosus,* a primitive epinepheline serranid: corroborative evidence from the larvae.—Japanese Journal of Ichthyology 35:7–18.

Leis, J. M., & D. S. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales University Press, Sydney, Australia, 269 pp.

Mabee, P. M. 1988. Supraneural and predorsal bones in fishes: development and homologies.—Copeia 1988:827–838.

Randall, J. E. 1980. Revision of the fish genus *Plectranthias* (Serranidae: Anthiinae) with descriptions of 13 new species.—Micronesica 16:101–187.

———. 1981. *Luzonichthys earlei* a new species of anthiine fish from the Hawaiian Islands.—Freshwater and Marine Aquarium 4(9):13–18.

———, & P. C. Heemstra. 1978. Reclassification of the Japanese cirrhitid fishes *Serranocirrhitus latus* and *Isobuna japonica* to the Anthiinae.—Japanese Journal of Ichthyology 25:165–172.

———, & R. Lubbock. 1981. A revision of the serranid fishes of the subgenus *Mirolabrichthys* (Anthiinae: *Anthias*), with descriptions of five new species.—Contributions in Science, Natural History Museum of Los Angeles County, No. 333:1–27.

———, & R. M. Pyle. 1989. A new species of anthiine fish of the genus *Rabaulichthys* (Perciformes: Serranidae) from the Maldive Islands.—Special Publication, J. L. B. Smith Institute of Ichthyology, No. 47:1–7.

———, & S. Ralston. 1984. A new species of serranid fish of the genus *Anthias* from the Hawaiian Islands and Johnston Island.—Pacific Science 38:220–227.

Stiassny, M. L. J., & J. S. Jensen. 1987. Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity.—Bulletin of the Museum of Comparative Zoology 151:269–319.

(WDA) Grice Marine Biological Laboratory, College of Charleston, 205 Fort Johnson, Charleston, South Carolina 29412; (NVP) P. P. Shirshov Institute of Oceanology, Academy of Sciences USSR, Krasikova 23, Moscow 117218, USSR; (JER) Bernice Pauahi Bishop Museum, Box 19000-A, Honolulu, Hawaii 96817.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 931–954

THREE NEW SPECIES OF SYMPHURINE TONGUEFISHES FROM TROPICAL AND WARM TEMPERATE WATERS OF THE EASTERN PACIFIC (*SYMPHURUS*: CYNOGLOSSIDAE: PLEURONECTIFORMES)

Madhu N. Mahadeva and Thomas A. Munroe

Abstract.—Three new species of *Symphurus* are described based on specimens collected from the Gulf of California southward along Central America and northern South America to northern Peru. *Symphurus oligomerus,* n. sp., occurs from the southern Gulf of California to northern Peru and is a relatively deep-water (84–481 m) species characterized by: a 1-3-2 pattern of interdigitation of dorsal pterygiophores and neural spines (ID pattern), 85–97 dorsal-fin rays, 71–83 anal-fin rays, 12 caudal-fin rays, 48–52 total vertebrae, 5 hypurals, black peritoneum, an alternating series of dark rectilinear pigment blotches and unpigmented areas on the posterior portion of the dorsal fin and throughout the anal fin, a dark pigment blotch on the proximal portion of the caudal fin, with distal portions distinctly unpigmented, and the absence of a pupillary operculum. *Symphurus chabanaudi,* n. sp., occurs from the northern Gulf of California to northern Peru and is among the largest species in the genus, reaching lengths of at least 233 mm SL. This shallow-water species (2–59 m) is characterized by: a 1-5-3 ID pattern, 12 caudal-fin rays, 4 hypurals, small scales on blind-side dorsal- and anal-fin rays, a prominent black spot on the ocular-side opercle, and absence of a pupillary operculum. *Symphurus diabolicus,* n. sp., known only from a single specimen collected at 501 m off Chatham Island in the Galapagos Archipelago, is readily distinguished by the combination of: a 1-3-2 ID pattern, 12 caudal-fin rays, 5 hypurals, 109 dorsal-fin rays, 94 anal-fin rays, 58 total vertebrae, small scales (ca. 135 in longitudinal series), spotted peritoneum, and large eyes (18.6% of head length).

Symphurus is the only genus of tonguefishes (Cynoglossidae) occurring in the New World, with over 40 nominal species recorded from marine waters on both sides of the Americas (Ginsburg 1951, Mahadeva 1956, Menezes & Benvegnú 1976, Munroe 1987). In the eastern Pacific, at least 14 species inhabit coastal and deep-waters (Jordan & Evermann 1898, Mahadeva 1956, Munroe & Mahadeva 1989, Munroe & Nizinski 1990) from southern Oregon (Eschmeyer et al. 1983) to northern Peru (Hildebrand 1946, Mahadeva 1956, Chirichigno 1974). The majority of species occur in tropical waters.

Recent collecting in inshore and deeper areas off the coasts of Mexico, Central, and South America have resulted in the capture of many tonguefishes, including specimens of the new species described herein. This paper provides formal descriptions of three of these new species.

Methods.—Specimens examined are listed by collection acronym following Leviton et al. (1985). Counts and measurements follow Mahadeva (1956), Munroe & Mahadeva (1989), and Munroe (1990a). Standard length (SL) is used throughout. Where possible, measurements to 150 mm were taken to the nearest 0.1 mm with dial calipers or ocular micrometer; measurements larger than 150 mm were made to the nearest mm with a steel ruler. Measurements are expressed either as thousandths of standard length or thousandths of head length. Abbreviations in text and tables are: head length (HL), head width (HW), eye diameter (ED), snout length (SNL). Unless stated otherwise, observations and descriptions of pigment patterns are based on fishes preserved in formalin and stored in ethyl or isopropyl alcohol.

Interdigitation pattern (ID pattern).—Patterns of interdigitation of proximal dorsal pterygiophores and neural spines were counted and recorded for the first three, or in unusual cases, the first four interneural spaces. The number of dorsal pterygiophores inserted into interneural spaces 1–3 was found to be diagnostic for species or groups of species of *Symphurus* (Munroe 1987). ID patterns are indicated by a pterygiophore formula such as 1-3-2. The 1-3-2 ID pattern indicates one pterygiophore inserts in interneural space one, three in interneural space two, and two in interneural space three. The first neural spine abuts directly against the cranium so there is no obvious space between it and the cranium. Therefore, the first interneural space reflected in the formula is that between the first and second neural spines.

Variation in dorsal- and anal-fin rays and total vertebrae were examined using SYSTAT programs (Wilkinson 1988) for one-way *ANOVA* and Tukey HSD multiple comparison test on log-transformed variables of specimens divided into groups based on capture location.

Symphurus oligomerus, new species

Figs. 1a, b, 2, Tables 1–3

Symphurus atramentatus (not of Jordan & Bollman).—Garman 1899:229 (counts; measurements; color description; Panama and Colombia).

Symphurus sp.—Lavenberg & Fitch 1966: 108 (Gulf of California; photograph).

Holotype.—SIO 84-70, (female, 85.8 mm), Mexico, Gulf of California, Bahia La Paz, 24°26.7′–24°24.8′N, 110°36.0′–110°37.5′W (Toadhop I, Station 4), 240 m, collected with 25′ otter trawl by R. Rosenblatt and party aboard RV *E. B. Scripps,* 14 Jul 1984.

Paratypes.—(171 specimens, 38.0–145 mm SL):

Gulf of California: SIO 68-94, (15 of 40, 38–121), 29°19.9′–29°20.4′N, 113°10.4′–113°12.0′W, 273 m, 20 Jan 1968. LACM 21719, (1, 64.2), ca. 23°N, 109°W, 6.5 mi from Punta Gorda, outer Gorda Bank, ca. 130 m, 12 Mar 1949. LACM 20407, (19, 49–76), outer Gorda Bank, 12 Mar 1949. UCLA W56-79, (10, 54–71), outer Gorda Bank, 12 Mar 1949. LACM 20261, (3, 44–55.5), 29°33′45″N, 113°30′35″W, Puerto Refugio, Isla Angel de la Guarda, 94 m, 29 Jan 1940.

Nicaragua: SIO 73-280, (25 of 174, 66.7–119.4), 11°07.4–07.8′N, 86°35.0–35.5′W, 159 m, 18 Apr 1973.

Costa Rica: UF 33932, (3, 97.4–109.6), Gulf of Nicoya. LACM 33827-10, (6, 87.4–120.6), Gulf of Nicoya, central Puntarenas Province, 29 Jun 1973. SIO 73-281, (24, 86.2–110), 10°50.2–53.2′N, 86°20–24.3′W, 196 m, 18 Apr 1973. UCR 425-18, (1, 113.9), Puntarenas Province, between Cabo Blanco and Punta Herradura, 310 m. UCR 494-6, (1, 91.6), Puntarenas Province, off Parrita, 259 m.

Panama: MCZ 28540, (14, 74.2–105.1), 7°40.0′N, 79°17.9′W, 235 m, 8 Mar 1891. USNM 57882, (2, 110.5–113.8), 7°33′40″N, 79°43′20″W, 283 m, 9 Mar 1891. UMML 26051, (12, 91.7–113.1), Bay of Panama, 7°30.5′–7°31.0′N, 79°41.5′–79°43.3′W, 210 m, 4 May 1967. MCZ 28537, (1, 145), 7°12.3′N, 80°55′W, 337 m, 23 Feb 1891. UMML 31935, (20, 80.1–111.5), 6°31.2–32.1′N, 77°32.2–34.4′W, 205 m, 16 Jan 1972. UMML 31947, (7, 70.7–116.2), 6°28.8–29.3′N, 77°29.2–30′W, 216 m, 16 Jan 1972.

Ecuador: CAS 57858, (1, 126.3), 2°14′S, 81°11′30″W, 481 m, 31 Aug 1968.

Peru: CAS 24201, (6, 93.1–111.9), 5°02′S, 81°24′W, 254 m, 3 Jun 1966.

Diagnosis.—A *Symphurus* with a 1-3-2 ID pattern; 12 caudal-fin rays; a black peritoneum usually showing through abdominal wall on both sides of body; 8–13 black, irregularly rectilinear, blotches alternating with unpigmented areas on posterior two-thirds of dorsal fin and entire length of anal fin; similar black blotch across base of caudal fin with distal three-fourths of caudal fin distinctly unpigmented; 85–97 dorsal-fin rays; 71–83 anal-fin rays; 48–52 (usually 49–51) total vertebrae; 5 hypurals; 86–96 scales in a longitudinal series; 39–46 scales in transverse row; no pupillary operculum; relatively large eyes (ED/SNL 1.3 to 1.5); upper jaw not extending beyond vertical line through posterior margin of pupil of lower eye; well-developed dentition on ocular-side jaws; dorsal-fin origin at vertical line through middle of pupil of upper eye; and body color yellowish tan to dark brown with 3–7, mostly incomplete, crossbands.

Description.—Frequency distributions of meristic data are provided in Table 1. ID pattern typically 1-3-2 (182/205), infrequently 1-3-3 (8/205), 1-2-3 (5/205), or 1-4-2 (4/205), rarely otherwise. Caudal-fin rays 12 (215 of 228 specimens), less frequently 11 (9 individuals) or 13 (two specimens), rarely 10 or 14 (one each). Dorsal-fin rays 85–97, usually 88–94, $\bar{X}$ = 91.3. Anal-fin rays 71–83, usually 74–80, $\bar{X}$ = 77.2. Pelvic-fin rays 4. Total vertebrae 48–52, usually 49–51, rarely 48 or 52, $\bar{X}$ = 50.3; abdominal vertebrae 9 (3+6). Hypurals 5 (180/202), less frequently 4 (22/202). Longitudinal scale rows 86–96, $\bar{X}$ = 90.5. Scale rows on head posterior to lower orbit 20–23. Transverse scales 39–46, $\bar{X}$ = 43.3.

Proportional measurements are provided in Table 2. Medium-sized *Symphurus* with relatively deep body, 259–307 SL, $\bar{X}$ = 281; greatest depth in anterior third of body; gradual posterior taper to body beginning approximately at anterior third of standard length. Trunk length 709–750 SL, $\bar{X}$ = 729. Head relatively long (250–291 SL, $\bar{X}$ = 271), usually slightly shorter than body depth. Snout length 40–69 SL, $\bar{X}$ = 58; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout. Mouth moderately sized, upper jaw length 58–94 SL, $\bar{X}$ = 78. Posterior margin of jaws reaching verticals between mid-eye and posterior margin of pupil of lower eye. Lower eye moderately sized, 32–38 SL, $\bar{X}$ = 34; eyes usually slightly subequal in position with upper in advance of lower eye. Anterior and medial surfaces of eyes with 2 or 3 rows of 3 or 4 scales lying posterior to posterior nostril, and in narrow interorbital region; no scales posteriorly between eyes or on posterior surface of eyes. Pupillary operculum absent. Dorsal-fin origin at vertical line through mid-point of upper eye; predorsal length 61–115 SL, $\bar{X}$ = 100. Longest dorsalfin ray 85–115 SL ($\bar{X}$ = 100). Dorsal- and anal-fin rays without scales on blind side. Pelvic fin relatively long, 64–99 SL, $\bar{X}$ = 86. Anal-fin origin at vertical line approximately through bases of dorsal-fin rays 12–13. Caudal fin with three or four rows of scales on base; scales diminishing in size posteriorly.

Teeth well developed on blind- and ocular-side jaws. Blind-side dentary with 3–4 rows of teeth in middle of crescentic tooth band. Crescent tapers smoothly laterally with number of tooth rows decreasing distally, ending in single tooth. Tooth band on blind-side premaxilla with 3–4 rows of teeth posteriorly, tapering anteriorly to single tooth. Ocular-side premaxilla with one irregular row of prominent conical teeth extending from anterior tip to below anterior margin of lower eye; one irregular row of prominent conical teeth on lower jaw extending to vertical through anterior margin of pupil of lower eye.

Pigmentation.—Ground color tan to dark brown, with variable number (usually 3–7) of darker brown, mostly incomplete crossbands (6–9 scales wide) extending from behind nape to base of caudal fin; 8–11 well-defined, rectilinear, black blotches alternating with unpigmented areas on median fins.

Fig. 1. *Symphurus oligomerus.* a. SIO 84-70, holotype; female, 85.8 mm SL; Gulf of California, Bahia La Paz, 24°25.45′N, 110°36.75′W. b. SIO 73-280, paratype; male, 87.2 mm SL; Nicaragua, 11°07.4–07.8′N, 86°35.0–35.5′W.

Specimens from southern Mexico, Costa Rica, Nicaragua, and Panama generally darker than those from other locations. Blind side usually unpigmented, suggesting creamy whiteness in life. Some specimens with longitudinal series of small melanophores along body midline on blind side. Peritoneum black, showing through abdominal wall on both sides of body.

Head usually uniformly pigmented; occasionally with diffuse, faint crossband, 4–5 scales wide, extending from dorsal margin to ventral border at posterior margin of operculum. Ocular-side outer opercle occasionally with diffuse, irregularly-shaped spot on ventralmost surface. Inner linings of both ocular- and blind-side opercles speckled with melanophores. Isthmus unpigmented on both sides of body. Ocular-side lips with dark band of pigment.

Posterior two-thirds of dorsal fin and entire anal fin with clearly defined, rectilinear blotches, not extending to tips of fin rays. Blotches (8–13 in dorsal fin and 8–12 in anal fin) covering proximal three-fourths of fin rays, often continuous at fin-ray bases with body crossbands. Dark blotches on dorsal fin increase in intensity and size posteriorly; blotches to about middle of body lighter and smaller (covering only 2–4 rays) compared with those on posterior half of fin (black and better defined, covering 5–10 rays). Blotches in anal fin roughly parallel those in dorsal fin in position and intensity of pigmenta-

Table 1.—Frequency distributions of meristic features for *Symphurus oligomerus*. (Asterisks indicate counts for holotype.)

	Dorsal-fin rays													
	85	86	87	88*	89	90	91	92	93	94	95	96	97	$\bar{X}$
Frequency	1	1	1	13	28	37	41	50	44	21	2	1	1	91.3

	Anal-fin rays													
	71	72	73	74*	75	76	77	78	79	80	81	82	83	$\bar{X}$
Frequency	1	2	4	13	22	39	38	59	39	17	2	1	1	77.2

	Caudal-fin rays				
	10	11	12*	13	14
Frequency	1	9	215	2	1

	Hypurals	
	4	5*
Frequency	22	180

	Total vertebrae					
	48	49*	50	51	52	$\bar{X}$
Frequency	3	35	75	84	5	50.3

	Longitudinal scale rows											
	86	87	88	89	90	91	92*	93	94	95	96	$\bar{X}$
Frequency	2	—	7	1	19	2	11	—	1	1	2	90.5

	Transverse scale count								
	39	40	41	42	43	44	45	46*	$\bar{X}$
Frequency	2	2	2	7	4	23	2	4	43.3

	Pattern	Frequency	%
Interdigitation Pattern	1-3-2-2*	182	88.8
	1-3-3-2	8	3.9
	1-2-3-2	5	2.4
	1-4-2-2	4	2.0
	1-2-2-2	3	1.5
	1-3-3-1	2	1.0
	2-3-2-2	1	0.5

tion. Posteriormost blotch in dorsal and anal fins often coalescing with blotch at base of caudal-fin rays.

Distal three-fourths of caudal-fin rays hyaline, contrasting sharply with strongly pigmented posterior dorsal and anal fins, and base of caudal fin. Specimens occasionally with heavy pigmentation on proximal fourth of caudal fin on blind side of body.

Etymology.—"Oligomerus" from the Greek "oligos" meaning few and "meros" meaning part of segment, in reference to the relatively low number of vertebrae and dorsal- and anal-fin rays of this species compared with most other eastern Pacific *Symphurus*.

Distribution.—Offshore habitats on the continental shelf (Fig. 2) from the Gulf of California at Puerto Refugio, off Isla Angel de la Guarda (29°33′45″N, 113°30′35″W), including Gorda Banks at the entrance to the Gulf, and continuing southwards to the

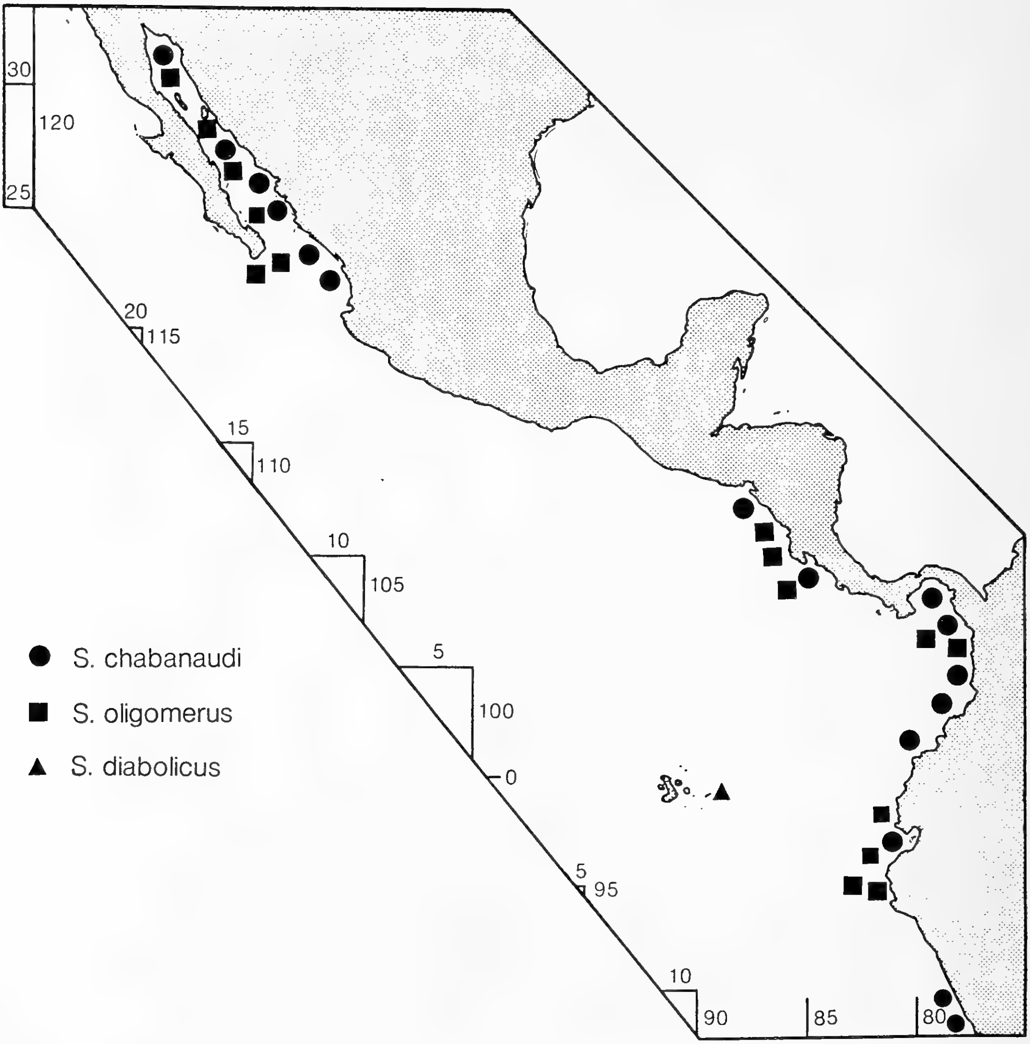


Fig. 2. Geographical distribution of *Symphurus oligomerus, S. chabanaudi,* and *S. diabolicus.* Symbols may represent more than one locality and/or more than a single lot from each locality.

continental shelf off Peru (6°21′S, 80°59′W). There were no specimens collected between ca. 20°N and 10°N available for our study. At this time, the occurrence or abundance of this species between these latitudes is unknown, however, there is no a priori reason to assume that *S. oligomerus* does not occur in this region. The disjunct distribution indicated in Fig. 2 is presumed to be an artifact of collecting intensity.

Symphurus oligomerus has been collected at depths ranging from approximately 80 to 481 m. Ninety-three percent of 356 specimens for which reliable depth information is available were collected between 111 and 300 m. Only five specimens have been collected shallower (one each at 80 and 84 m; three at 94 m) while approximately 6% were taken deeper than 300 m (17 specimens between 301–350 m, 3 specimens at 389 m, and one specimen at 481 m).

Available information for ca. 10% of the

Table 2.—Summary of morphometrics for the holotype (SIO 84-70) and 33 paratypes of *Symphurus oligomerus*. Proportional measurements, except standard length in mm, in thousandths of standard length.

	Holotype	Paratypes	
		Range	Mean
Standard length	85.8	44.4–76.2	—
Body depth	295	259–307	281
Predorsal length	61	85–115	100
Pelvic-fin length	64	75–99	86
Head length	256	250–291	271
Snout length	40	49–69	58
Upper jaw length	68	58–94	78
Eye diameter	35	32–38	34

Table 3.—One-way *ANOVA* for selected meristic features of *Symphurus oligomerus* collected from different portions of the species range. (Asterisk indicates difference at $P < 0.001$.)

	n	Range	Mean	*SD*
Dorsal-fin rays ($f = 43.84$; $P < 0.001$)				
*Gulf of California	46	85–93	90.1	1.35
Central America	146	89–97	92.3	1.37
South America	11	90–94	91.8	1.47
Anal-fin rays ($f = 36.60$; $P < 0.001$)				
*Gulf of California	46	71–79	76.1	1.42
Central America	146	74–83	78.1	1.39
South America	11	76–80	77.8	1.47
Total vertebrae ($f = 66.78$; $P < 0.001$)				
*Gulf of California	46	48–50	49.3	0.59
Central America	145	49–52	50.6	0.67
South America	11	50–51	50.4	0.50

specimens indicates this species is frequently collected on substrates containing a large sand component, including muddy sand (1 collection, 7 specimens), sand (4 collections, 5 specimens), sand and gravel (1 collection, 3 individuals), rock (1 collection, 1 specimen), and a sand, shell, and rock mixture (1 collection, 30 individuals).

Geographical variation.—Comparisons of selected meristics (Table 3) revealed that specimens collected from the Gulf of California and Mexico had significantly fewer dorsal- ($f = 43.84$; $P < 0.001$) and anal-fin rays ($f = 36.60$; $P < 0.001$), and total vertebrae ($f = 66.78$; $P < 0.001$) than those fishes collected from Central America (El Salvador, Costa Rica, and Panama) and northern South America (Colombia to northern Peru). Fin-ray and vertebral counts of *S. oligomerus* taken between El Salvador and Panama, although slightly greater, were not significantly different from those of specimens collected off northern South America.

Comparisons.—*Symphurus oligomerus* is the third species described (of four known species) from eastern Pacific waters characterized by a 1-3-2 ID pattern, 12 caudal-fin rays, and black peritoneum. Other eastern Pacific species with these characteristics are *S. microlepis* Garman, *S. gorgonae* Chabanaud and *S. diabolicus* (described below). These other species are quite different from *S. oligomerus* and easily distinguished either by their lack of alternating rectilinear pigmented blotches and unpigmented areas on the dorsal and anal fins characteristic of *S. oligomerus* (fin pigmentation uniformly pigmented in *S. diabolicus* and *S. gorgonae*) or by differences in meristic values. *Symphurus oligomerus* has lower vertebral and fin-ray counts than *S. microlepis* and *S. diabolicus* (total vertebrae 48–52 versus 57 in *S. microlepis* and 58 in *S. diabolicus*; dorsal-fin rays 85–97 versus 106 in *S. microlepis* and 109 in *S. diabolicus*; anal-fin rays 71–83 versus 94 in *S. microlepis* and 92 in *S. diabolicus*). Furthermore, the body of *S. oligomerus* is deepest in the anterior third of the standard length with a relatively rapid posterior taper compared with that of *S. diabolicus* in which the body is relatively elongate with almost uniform depth occurring throughout much of the mid-body region and with only a gradual posterior taper. *Symphurus oligomerus* is readily distinguished from *S. gorgonae* in that the blind side is uniformly creamy-white compared with that of *S. gorgonae* in which the blind side has a pepper-dot pattern of melanophores, especially well developed along the basal pterygiophore regions of the dorsal and anal fins. These two species differ further in that there is little overlap for several meristic features (total vertebrae 48–52 in *S. oligomerus* versus 46–49 in *S. gorgonae*; dorsal-fin rays 85–97 versus 80–89; anal-fin rays 71–83 versus 63–74; hypural numbers 5 versus 4).

Other eastern Pacific *Symphurus* possessing pigmented spots or blotches on the dorsal and anal fins that may be confused with *S. oligomerus* are *S. callopterus* Munroe & Mahadeva (sometimes collected with *S. oligomerus*) and *S. atramentatus* Jordan & Bollman. However, both *S. callopterus* and *S. atramentatus* have an unpigmented peritoneum (versus black in *S. oligomerus*) and a well-developed pupillary operculum (absent in *S. oligomerus*). Additionally, *S. oligomerus* has 5 hypurals (4 in *S. callopterus* and *S. atramentatus*) and a 1-3-2 ID pattern (usually 1-3-4 in *S. callopterus*; 1-3-3 in *S. atramentatus*). *Symphurus atramentatus* also has well-defined oval black spots on the fins (versus rectilinear black blotches in *S. oligomerus*). *Symphurus oligomerus* differs further from *S. callopterus* in several counts (total vertebrae 48–52 versus 57–61 in *S. callopterus*; dorsal-fin rays 85–97 versus 105–114; anal-fin rays 71–83 versus 91–98; longitudinal scale rows 86–96 versus 97–114), and the distal half of the caudal fin is unpigmented in *S. oligomerus,* whereas in *S. callopterus,* the distal half of the caudal fin either has an ill-defined blotch or the entire fin is uniformly darkly pigmented.

Some meristic features of seven other eastern Pacific species, *S. varius* Garman, *S. williamsi* Jordan & Culver, *S. fasciolaris* Gilbert, *S. leei* Jordan & Bollman, *S. atricaudus* (Jordan & Gilbert), *S. melanurus* Clark, and *Symphurus* sp. (the species described by Munroe & Nizinski (1990) with the lower meristic values; hereafter referred to as *Symphurus* sp.) overlap those of *S. oligomerus. Symphurus oligomerus,* however, differs from all of these species in having alternating blotches in the dorsal and anal fins (versus uniformly pigmented fins without alternating blotches, or dorsal and anal fins with posterior intensification of pigment, or with dorsal and anal fins speckled). *Symphurus oligomerus* also differs from these species in ID pattern (1-3-2 versus 1-3-3 in *S. varius*; 1-4-3 in *S. fasciolaris* and *S. leei*; 1-5-3 in *S. atricaudus, S. melanurus,* and *Symphurus* sp.; and 1-5-3 or 1-4-3 in *S. williamsi*) and in the number of hypurals (5 in *S. oligomerus* versus 4 in all others, except *S. varius*). *Symphurus oligomerus* has larger scales (86–96 in a longitudinal series) than does *S. varius* (120–124). Certain meristic values of *S. oligomerus* completely overlap those of *S. williamsi,* but the two species are easily distinguished. *Symphurus oligomerus* has a black peritoneum (unpigmented in *S. williamsi*), lacks a pupillary operculum (present in *S. williamsi*), and lacks scales on the blind side dorsal- and anal-fin rays (present in *S. williamsi*). *Symphurus fasciolaris* and *Symphurus* sp. differ further from *S. oligomerus* in caudal-fin ray counts (12 in *S. oligomerus* versus 10 in *S. fasciolaris* and 11 in *Symphurus* sp.).

Among *Symphurus* species occurring outside the eastern Pacific region, some counts for *S. oligomerus* overlap those of *S. piger* (Goode & Bean), *S. pusillus* (Goode & Bean), *S. plagiusa* (Linnaeus), *S. plagusia* (Schneider, in Bloch & Schneider), *S. diomedeanus* (Goode & Bean), and *S. civitatium* Ginsburg from the western Atlantic, and *S. trifasciatus* (Alcock) from the Indian Ocean. All of these species, except *S. diomedeanus,* lack the highly pigmented fins found in *S. oligomerus.* Although *S. diomedeanus* has counts and pigmented dorsal and anal fins reminiscent of those of *S. oligomerus,* these two species are distinct in caudal-fin ray counts (12 versus 10 in *S. diomedeanus*), hypural numbers (5 versus 4), and ID patterns (1-3-2 versus 1-4-3). *Symphurus diomedeanus* also has a pupillary operculum (absent in *S. oligomerus).*

Additional Material Examined

Counts were taken from the following 150 non-type specimens (28.5–117.5 mm):

Gulf of California: LACM 8818-10, (15, 67–109), 28°55′N, 112°50.5′W, midway between southern tip of Isla Tiburon and Isla Angel de la Guarda. SIO 60-97, (7, 54.1–81.1), 28°13.8–15.0′N, 111°46.7–48.0′W, off Estero de Tastiuta, Costa de Hermosillo, Sonora. SIO 60-110, (1, 82.2), 28°12.9′N, 112°3.2′W, off Costa de Hermosillo, Sonora. SIO 60-98, (25, 79.4–110.1), 28°02′–28°06′N, 111°47.2′–111°53.2′W, 162 m, 21 Mar 1960. LACM 20259, (2, 42.0–52.5), 27°58′40″N, 111°24′10″W, Isla San Pedro Nolasco, 111 m, 12 Mar 1936. LACM 20262, (1, 86.5), 27°58′35″N, 110°22′40″W, Isla San Pedro Nolasco, 6 Feb 1940. LACM 8842-5, (1, 65.5), 26°57′N, 111°49.8′W, 3–5 mi north of Punta Concepcion. SIO 65-293, (7, 28.5–58.9), 25°40.6–44.3′N, 111°05.3–5.6′W, northwest of Isla Monserrate, Baja California Sur. SIO 84-70, (1, 86.5), Bahia La Paz, 24°25.45′N, 110°36.75′W, 240 m, 14 Jul 1984. SIO 84-80, (3, 91.6–100.7), Baja California Sur, 23°31.5–32.5′N, 110°28–30′W, 143 m, 17 Jul 1984. SIO 84-81, (7, 76.1–117.0), northwest of Lobos Point, 23°29.95′N, 110°27.1′W, 17 Jul 1984. LACM 20260, (1, 54.9), 23°02′N, 109°0′15″W, Inner Gorda Bank, Baja California Sur, 20 Jan 1940.

Costa Rica: CAS 43872, (1, 97.9), Cabo Blanco, 268 m, 9 Mar 1974. CAS 44104, (1, 100.4), Cabo Blanco, 268 m, 9 Mar 1974.

Panama: UMML 27031, (73 of 101, 54.1–137.7), Bay of Panama, 7°39.5′–7°40.9′N, 79°40.7′–79°42.7′W, 117 m, 4 May 1967. USNM 57883, (1, 99.7), 7°16′45″N, 79°56′30″W, 389 m, 9 Mar 1891.

Peru: CAS 24200, (1, 118.5), 4°53′S, 81°20–23′W, 84 m, 2 Jun 1966. IMARPE 4, (1, 94.0), 5°0.5′S, 83°24.5′W. CAS 24979, (1, 100.1), 6°21′S, 80°59′W, 142 m, 4 Jun 1966.

Additional material examined but not counted or measured (277 specimens):

Gulf of California: SIO 68-94, (25 of 40, 38–121), 29°19.9′–29°20.4′N, 113°10.4′–113°12.0′W, 273 m, 20 Jan 1968. SIO 60-98, (37, 79.4–110.1), 28°2–6′N, 111°47.2–53.2′W, off San Juan Bautista Flats, Sonora, 162 m, 21 Mar 1960. SIO 68-103, (15, 73.2–101.3), 28°19.3′–28°20.1′N, 112°8.0′–112°10.5′W, 303 m, 21 Jan 1968.

Nicaragua: SIO 73-280, (149, 64–120), 11°07.4–07.8′N, 86°35.0–35.5′W, 159 m, 18 Apr 1973.

Costa Rica: SIO 73-281, (12 of 24, 86.2–110), 10°50.2–53.2′N, 86°20–24.3′W, 196 m, 18 Apr 1973. LACM 33827-56, (1, 106.9), Gulf of Nicoya, central Puntarenas Province, 29 Jun 1973. UCR 682-6, (1, 79.7), Puntarenas Province, Isla del Cano, 80 m. UCR 2190-1, (2, 70.8–81.9), off Cabo Matapalo, tip of Osa Peninsula, 23 Jun 1973.

Panama: UMML 27031, (28 of 101, 54.1–137.7), Bay of Panama, 7°39.5′–7°40.9′N, 79°40.7′–79°42.7′W, 117 m, 4 May 1967. MCZ 28539, (5, 107.0–121.2), 7°33.7′N, 79°43.3′W, 283 m, 9 Mar 1891. MCZ 70978, (2, 89.4–100.8), 7°16.8′N, 79°56.5′W, 389 m, 9 Mar 1891.

Symphurus chabanaudi, new species

Figs. 2, 3a, b, Tables 4–7

Aphoristia elongata (not of Günther).—Jordan & Gilbert, 1883:24 (in part) (listed, Panama).

Symphurus elongatus (not of Günther).—Jordan & Goss, 1889:323 (in part) (after Jordan & Gilbert; Panama).—Jordan & Evermann, 1898:2707 (in part) (after Jordan & Gilbert; Panama).—Gilbert & Starks, 1904:203 (in part) (fish market, Panama City).—Meek and Hildebrand, 1928:1006 (counts; measurements; color description; in key; Panama).—Breder, 1936:5 (in part) (Gulf of California).—Seale, 1940:14 (listed, Tenacatita Bay, Mexico and Colombia).—?Fowler, 1944: 495 (listed, Panama).—Phillips, 1981:54 (in part) (Jiquilisco Bay, El Salvador).

Symphurus atricaudus (not of Jordan & Gilbert).—Breder, 1936:6 (in part) (Gulf of California).—Phillips, 1981:54 (in part) (Jiquilisco Bay, El Salvador).

Symphurus sechurae Hildebrand, 1946:476 (in part) (Gulf of California).

Holotype.—USNM 305717, (male, 130.8 mm), El Salvador, El Potrero, Jiquilisco Bay, Station Number 6, 13°16′N, 88°38′W, on mud bottom canal in mangroves, 5 m trynet, collected 14 Jul 1976, P. Phillips and party.

Paratypes.—(115 specimens, 47.5–233 mm):

Gulf of California: Near San Felipe, 31°18–22′N, 114°47–50′W, ca. 5 m, 6–9 Apr 1947, 50 specimens distributed to the following collections: USNM 164493, (1, 139), USNM 164494, (10, 47.5–152), BMNH 1956.3.1:6–14, (9, 90.5–159), CAS 20696, (10, 59.5–156), UCLA W53-196, (19, 93–153), SIO 47-53, (1, 109). YPM 630, (10, 124–157), north of San Felipe, 26 m, 20 May 1926. UCLA W52-46, (4, 72–127), 10 mi off Santa Clara, Sonora. USNM 119742, (1, 184), south of Guaymas, 1940.

El Salvador: USNM 236606, (2, 185–188), Saite, 26 m, 28 Oct 1975. USNM 291339, (1, 188), La Libertad, 26 m, 29 Oct 1975. USNM 220701, (5, 110.1–131.0), El Potrero, Jiquilisco Bay, 14 Jul 1976.

Costa Rica: LACM 30716-11, (4, 182–211), Puntarenas Province, Gulf of Nicoya, Isla Negritos, 13 Feb 1968. LACM 30714-15, (3, 178–185), Puntarenas Province, Isla Chira, 1968. UCR 1122-3, (2, 147.8–149.5), Puntarenas and Guanacaste Provinces, Golfo de Nicoya and Playa Hermosa, 18–28 m.

Panama: UCLA W53-275, (11, 137–217), Panama Bay. SIO 80-23, (5, 128–184), Panama Bay, Isla Verde, 4 m, 9 Apr 1980.

Colombia: USNM 305718, (5, 138–200), 4°20–18′N, 77°28–29′W, off Río Togorama. USNM 305719, (7, 164–178), 2°57′N, 77°48′W, Punta Coco, south of Buenaventura.

Ecuador: CAS 24199, (5, 161–233), Gulf of Guayaquil, 3°16′S, 80°25′W.

Diagnosis.—A *Symphurus* with 1-5-3 ID pattern; 12 caudal-fin rays; 98–109 dorsal-fin rays; 82–92 anal-fin rays; 52–57 total vertebrae; 91–104 scales in longitudinal series; 32–42 transverse scales; no pupillary operculum; relatively small eye (ED/SNL 2.4 to 2.7); 2–5 small, ctenoid scales on blind-side dorsal- and anal-fin rays; distinct, large black blotch on ocular-side outer opercle (not to be confused with black branchial cavity lining showing through operculum in many species of *Symphurus*); upper jaw usually reaching to or just posterior to vertical line through middle of pupil of lower eye (rarely extending posteriorly to vertical through rear margin of lower eye); dorsal-fin origin usually equal with or just posterior to vertical line through middle of pupil of upper eye (rarely originating at vertical line through anterior margin of upper eye); posterior dorsal and anal fins and caudal fin dusky to dark black; body tan to dark brown usually with 6–8, sharply contrasting crossbands 6–10 scales wide; and unpigmented peritoneum.

Description.—Frequency distributions of meristic data are provided in Table 4. ID pattern usually 1-5-3 (47 of 95 individuals), less frequently 1-4-3 (28/95) or 1-4-4 (13/95), rarely 1-4-3-3, 1-5-2, or 1-5-3-3. Caudal-fin rays 12 (103/108), rarely 11 (5/108). Dorsal-fin rays 98–109, usually 100–107, $\bar{X} = 103.4$. Anal-fin rays 82–92, usually 84–89, $\bar{X} = 86.6$. Pelvic-fin rays 4. Total vertebrae 52–57, usually 53–56, rarely 57 (1 of 125), $\bar{X} = 54.1$; abdominal vertebrae 9 (3 + 6). Hypurals 4 (90/90). Longitudinal scale rows 91–104, $\bar{X} = 97.9$. Scale rows on head posterior to lower orbit 21–23. Transverse scales 32–42, $\bar{X} = 39.0$.

Proportional measurements appear in Table 5. Large-sized (to at least 233 mm SL) species with relatively deep body (239–293 SL, $\bar{X} = 265$); greatest depth in anterior third of body with gradual posterior taper starting near middle of body. Trunk length

Table 4.—Frequency distribution of meristic features for *Symphurus chabanaudi*. (Asterisks indicate counts for holotype.)

	Dorsal-fin rays												
	98	99	100	101	102	103	104	105*	106	107	108	109	$\bar{X}$
Frequency	1	1	10	14	14	20	6	17	14	8	—	2	103.4

	Anal-fin rays											
	82	83	84	85	86*	87	88	89	90	91	92	$\bar{X}$
Frequency	1	3	10	20	23	17	15	13	3	2	1	86.6

	Caudal-fin rays	
	11	12*
Frequency	5	103

	Hypurals
	4*
Frequency	90

	Total vertebrae						
	52	53	54	55	56*	57	$\bar{X}$
Frequency	8	22	27	22	12	1	54.1

	Longitudinal scale rows														
	91	92	93*	94	95	96	97	98	99	100	101	102	103	104	$\bar{X}$
Frequency	1	2	1	4	3	10	5	16	9	5	1	4	4	1	97.9

	Transverse scale count											
	32	33	34	35	36	37	38	39*	40	41	42	$\bar{X}$
Frequency	2	1	—	2	3	3	10	14	17	8	6	39.0

	Pattern	Frequency	%
Interdigitation Pattern	1-5-3-2*	47	49.5
	1-4-3-2	28	29.5
	1-4-4-2	13	13.7
	1-5-3-3	1	1.0
	1-5-2-2	2	2.1
	1-4-3-3	2	2.1
	1-5-4-2	1	1.0
	1-4-2-2	1	1.0

770–816 SL, $\bar{X} = 799$. Head relatively short, 185–213 SL, $\bar{X} = 201$; somewhat shorter than body depth. Snout length 42–57 SL, $\bar{X} = 47$; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout, chin, and head region just ventral to anterior portion of dorsal fin. Mouth moderately sized, upper jaw length 49–69 SL, $\bar{X} = 64$; usually reaching to or just posterior to vertical line through middle of pupil of lower eye (rarely extending posteriorly to vertical through rear margin of lower eye). Lower eye relatively small, 15–21 SL, $\bar{X} = 19$; eyes usually slightly subequal in position with upper in advance of lower eye. Surface of head from region posterior to posterior nostril and including narrow interorbital region to posterior margin of eyes with 13–14 rows of scales, each row with 6–8 scales (difficult to discern in juveniles). Pupillary operculum absent. Dorsal-fin origin at or just posterior to a vertical line through mid-

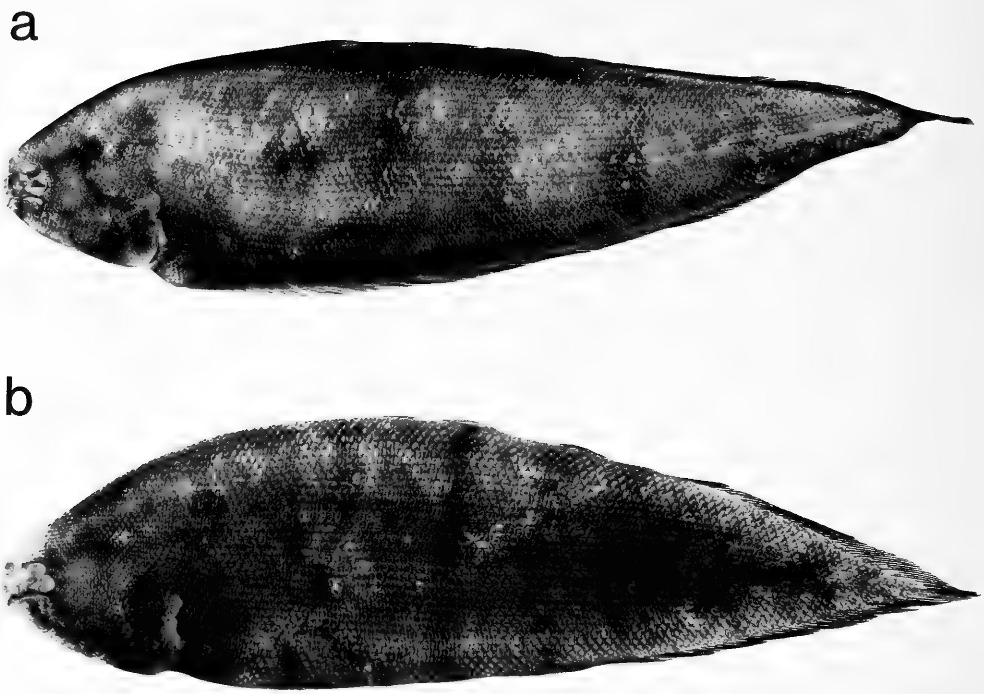


Fig. 3. *Symphurus chabanaudi.* a. USNM 305717, holotype; male, 130.8 mm SL; El Salvador, Jiquilisco Bay, El Potrero. b. USNM 291339, paratype; male, 188 mm SL; El Salvador, La Libertad.

dle of upper eye, occasionally at a vertical line through anterior margin of upper eye; predorsal length, 50–88 SL ($\bar{X} = 80$); longest dorsal-fin ray, 62–86 SL ($\bar{X} = 71$). Blind sides of dorsal- and anal-fin rays with 3–5 very thin, ctenoid scales (difficult to discern in juveniles). Anal-fin origin approximately at vertical line through base of dorsal-fin rays 14–16. Pelvic fin relatively long, 60–83 ($\bar{X} = 73$); reaches first or occasionally second anal-fin ray when depressed posteriorly. Caudal fin with approximately 9–10 relatively large scales on basal half of fin; distal half of caudal fin with numerous minute scales diminishing in size distally.

Teeth well developed on blind-side jaws. Lower jaw on blind side with crescentic tooth band about 5–8 rows wide. Arms of crescent tapering smoothly to a single tooth at extremities. Upper jaw on blind side with 5–8 rows of teeth posteriorly; band tapering to single tooth anteriorly. Juveniles with only 4–5 visible rows of teeth in bands on blind-side jaws. Teeth on ocular-side jaws in irregular rows. Ocular-side premaxilla with one irregular row of feeble teeth extending from anterior tip to point equal with vertical line through anterior base of anterior nostril; ocular-side dentary with irregular row of very feeble teeth extending posteriorly to vertical line through anterior base of anterior nostril.

Pigmentation.—Ground color of live specimens tannish brown with pinkish hue. Median fins pale lavender. Blind side pinkish to creamy white.

Ground color in preserved specimens tannish to dark brown, usually with variable number (6–10) of sharply contrasting blackish-brown crossbands 6–10 scale rows wide extending from behind nape to base of caudal fin. Color of specimens from the Gulf of California typically lighter than those collected on muddy bottoms along coastal El Salvador, Costa Rica, and Panama. Blind side uniformly creamy white. Occasionally, individuals of both sexes have dark pigment patches on caudal region and scattered along bases of dorsal and anal fins on blind side. Crossbands on body varying in intensity, usually somewhat darker than ground color. Peritoneum unpigmented.

Head with one, or occasionally two, faint crossbands. Anterior band diffuse, about 3–4 scales wide, located immediately posterior to eyes and barely reaching ventral margin of head. Posterior band crossing opercular region and extending ventrally slightly onto blind side of head; often incomplete in dorsal area of head, usually fading, disappearing completely, or occasionally forming faintly pigmented crossband, about 6 scales wide, at dorsal margin of operculum; ventralmost portion of band always expanded into distinct black blotch about 6–10 scale rows wide composed of large epidermal melanophores; clearly visible even in very young specimens; covering more than half the outer surface of ocular-side operculum. Inner linings of opercles on both sides of body heavily pigmented; inner lining on ocular-side opercle more heavily pigmented than that on blind side, often visible externally on outer opercular surface as poorly-defined, dusky blotch. Isthmus heavily spotted on both sides of body.

Basal portions of dorsal and anal fins to about a fifth or sixth the height of fin paler than remainder of fin. Dorsal fin anterior to a vertical line through anal-fin origin usually unpigmented; remainder of dorsal fin and entire anal fin light to dark brown or black without discrete spots or blotches; progressively darker posteriorly, with the posteriormost fourth or fifth of fins almost black in mature fish (fins usually darker in mature males). Posterior portions of dorsal, anal, and caudal fins on blind side often with small patches of melanophores. Caudal fin dark, similar to posterior portions of dorsal and anal fins. Median fins of juveniles usually only lightly pigmented or appearing almost unpigmented to naked eye, but with melanophores discernible under magnification.

Table 5.—Summary of morphometrics for holotype (USNM 305717) and 35 paratypes of *Symphurus chabanaudi*. Measurements, except standard length in mm, in thousandths of standard length.

		Paratypes	
	Holotype	Range	Mean
Standard length	130.8	70.8–226	—
Body depth	263	239–293	265
Predorsal length	50	70–88	80
Pelvic-fin length	60	63–83	73
Head length	193	185–213	201
Snout length	42	43–57	47
Upper jaw length	49	58–69	64
Eye diameter	17	15–21	19

Etymology.—Named in honor of Paul Chabanaud who contributed greatly to our knowledge of flatfishes, especially of the genus *Symphurus*.

Distribution.—A widespread and commonly collected species (Fig. 2) in shallow warmer waters ranging throughout the Gulf of California and extending coastally southward to approximately Callao, Peru (12°06′S, 76°55′W). There were no specimens collected between ca. 20°N and 10°N available for our study. At this time, the occurrence or abundance of this species between these latitudes is unknown, however, there is no a priori reason to believe that *S. chabanaudi* does not occur in this region. The disjunct distribution indicated in Fig. 2 is presumed to be an artifact of collecting intensity.

Symphurus chabanaudi has been collected at depths ranging from approximately 2 to 59 m; however, the majority of specimens (97%) were taken at depths shallower than 28 m. The deepest captures of 277 specimens for which depth information is available are for seven fish taken between

Table 6.—One-way *ANOVA* for selected meristic features of *Symphurus chabanaudi* collected from different portions of the species range. (Asterisk indicates difference at $P < 0.001$.)

	n	Range	Mean	*SD*
Dorsal-fin rays ($f = 30.68$; $P < 0.001$)				
*Gulf of California	33	99–103	101.2	1.14
*Central America	46	98–109	103.8	2.00
*South America	5	103–109	105.7	1.49
Anal-fin rays ($f = 39.77$; $P < 0.001$)				
*Gulf of California	33	82–87	84.8	1.18
*Central America	51	84–91	86.8	1.56
*South America	5	86–92	88.4	1.50
Total vertebrae ($f = 50.44$; $P < 0.001$)				
*Gulf of California	33	52–54	53.0	0.71
*Central America	53	53–57	54.6	0.92
*South America	5	55–56	55.8	0.45

30 and 37 m and for solitary specimens taken at 39 m and 59 m.

Symphurus chabanaudi has most often been collected on muddy or sand-mud substrates. Available substrate data list mud for 13 collections (123 specimens), mud and sand (11 collections, 76 specimens), mud and shell (2 collections, 9 specimens), mud and rocks (1 collection, 2 specimens), sand (5 collections, 13 specimens), clay and bits of shell (1 collection, 50 specimens), and rock (1 collection, 1 specimen).

Geographical variation.—Numbers of dorsal- ($f = 30.68$; $P < 0.001$) and anal-fin rays ($f = 39.77$; $P < 0.001$), and total vertebrae ($f = 50.44$; $P < 0.001$) differed significantly (Table 6) in specimens collected in each of three different portions (Mexico, Central America, and northern South America) of the species range. Specimens collected in the Gulf of California and coastal waters off northern Mexico had the lowest numbers of meristic elements, whereas specimens taken off Colombia and Peru had the highest numbers of finrays and vertebrae for any group examined.

Remarks.—Earlier investigators frequently misidentified *Symphurus chabanaudi* as *S. elongatus,* undoubtedly due to similarities in meristic features of these species. *Symphurus elongatus* occurs sympatrically with *S. chabanaudi,* especially in southern Central America and in coastal waters of northern South America, and the two species are collected syntopically. However, these species are quite distinct (see comparisons below).

Jordan & Gilbert (1883) and later, Jordan & Goss (1889) and Jordan & Evermann (1898) included specimens of *S. chabanaudi* in their accounts of *S. elongatus.* These accounts were based on three specimens of *S. chabanaudi* (CAS-SU 6900), misidentified as *S. elongatus* by Jordan and co-workers, collected from *Albatross* station 2804 off Colombia, together with numerous specimens of *S. leei* and 10 specimens of *S. elongatus.*

At least one specimen (USNM 50333) identified as *S. elongatus* by Gilbert & Starks (1904) is *S. chabanaudi,* but their account probably included other specimens. Morphometric proportions reported (table on p. 204) more closely match those of *S. chabanaudi* than *S. elongatus,* especially body depth measurements. These authors reported body depths equalling 24.5–28.0% SL, which are larger values than those (20.4–25.5% SL) noted for specimens of *S. elongatus* examined by Mahadeva (1956). Also, the large sizes (up to 255 mm) reported for specimens referred to as *S. elongatus* by Gilbert & Starks more nearly reflect sizes attained by *S. chabanaudi*; *S. elongatus* is a much smaller species usually not exceeding 150 mm SL.

It is apparent that Meek & Hildebrand (1928) included specimens of *S. chabanaudi* in their account of *S. elongatus* from Panama, given the pigment characters listed in their key, especially references to dark crossbars, a dark blotch on the opercle, and posterior darkening of dorsal and anal fins (pigment characters not found in *S. elongatus*). Two lots (USNM 81032 and 81674) examined in the present study, cited as *S.*

elongatus by Meek & Hildebrand, are *S. chabanaudi.* It is possible that Meek & Hildebrand did not examine any *S. elongatus* in their study, as they noted that the maxilla in their specimens reached a point only equal with the middle of the lower eye, whereas, in *S. elongatus,* the maxilla usually extends to a point well beyond the vertical line through the posterior margin of the lower eye.

Specimens (YPM 630–633a) collected in the Gulf of California and reported as *S. elongatus* and *S. atricaudus* by Breder (1936) are *S. chabanaudi.* Hildebrand (1946) tentatively identified specimens of *S. chabanaudi* (USNM 126741 and USNM 50333) collected in the Gulf of California and Panama Bay as *S. sechurae,* a nominal species now placed in the synonymy of *S. melanurus* Clark (Munroe 1990b). Hildebrand (1946) also incorrectly identified as *S. elongatus* several lots (USNM 144788–144791) collected in the Miraflores Locks, Panama Canal, in which were actually represented four different species, including juvenile *S. chabanaudi, S. elongatus, S. melanurus* and *S. williamsi.*

Comparisons.—Eastern Pacific *Symphurus* with counts comparable to those of *S. chabanaudi* include *S. elongatus* (Günther), *S. atricaudus, S. fasciolaris, S. leei, S. melanurus, S. diabolicus,* and *S. microlepis.* The pigmentation of *S. chabanaudi* (well-defined crossbands and a black blotch on the ocular-side opercle) differs from that of *S. elongatus, S. melanurus, S. microlepis,* and *S. diabolicus,* which usually lack crossbands and an opercular spot. *Symphurus leei* and *S. atricaudus* both have crossbands in a pattern different from *S. chabanaudi. Symphurus leei* has four or fewer wide bands (when bands are present) and lacks an opercular spot. The crossbands of *S. atricaudus,* in turn, are disrupted and incomplete. *Symphurus leei* and *S. atricaudus* also lack an opercular spot. In *S. fasciolaris,* the ocular-side of the body often has a number of spherical spots accompanying crossbands (when present), an ocellated spot in the caudal fin (absent in *S. chabanaudi*), and this species lacks the opercular spot characteristic of *S. chabanaudi. Symphurus chabanaudi* and *S. fasciolaris* also differ in caudal-fin ray counts (12 versus 10 in *S. fasciolaris*).

Symphurus chabanaudi and *S. elongatus* are further distinguished in the length of the upper jaw, which in *S. chabanaudi* does not extend beyond a vertical line through the posterior margin of the pupil of the lower eye, whereas in *S. elongatus* it extends to a vertical line through or beyond the posterior margin of the lower eye. *Symphurus chabanaudi* also has small ctenoid scales on the blind-side dorsal- and anal-fin rays (absent in *S. elongatus*) and the posterior taper of the body starts anterior to the body midpoint rather than near the middle of the standard length as in *S. elongatus.* Additionally, *S. chabanaudi* has a much larger eye ranging from 1.5–2.1% ($\bar{X}$ = 1.9) SL versus only 0.9–1.5% ($\bar{X}$ = 1.2) SL in *S. elongatus.*

Symphurus chabanaudi can be further distinguished from *S. atricaudus* in lacking both a pupillary operculum and small ctenoid scales on the ocular-side dorsal- and anal-fin rays that are present in *S. atricaudus.*

Symphurus chabanaudi differs most notably from *S. leei* in having the head length (185–213 SL, $\bar{X}$ = 201) considerably less than the body depth (239–293 SL, $\bar{X}$ = 265), in contrast to *S. leei,* in which the head length (235–256 SL, $\bar{X}$ = 245) nearly equals body depth (237–269 SL, $\bar{X}$ = 253).

Symphurus chabanaudi is easily distinguished from *S. melanurus* in the possession of small ctenoid scales extending onto distal portions of the blind-side dorsal- and anal-fin rays and in lacking a pronounced fleshy ridge on the posterior extent of the ocular-side lower jaw. In contrast, in *S. melanurus,* scales are either absent or there are 1–2 scales limited to the bases of the fin rays and the posterior extent of the ocular-side lower jaw has a distinct fleshy ridge. The dorsal-fin origin is always posterior to a vertical line through the anterior margin of the upper eye in *S. chabanaudi,* whereas in *S. melanurus,* the dorsal-fin originates more anteriorly with the first dorsal-fin ray located anterior to a vertical line through the anterior margin of the upper eye. In *S. chabanaudi,* the posterior margin of the jaw does not extend posterior to a vertical line through the posterior margin of the lower eye, whereas in *S. melanurus,* the jaw always reaches a vertical line through, or posterior to, the posterior margin of the lower eye.

Symphurus chabanaudi is readily distinguished from *S. microlepis* and *S. diabolicus* in: having an unpigmented peritoneum (versus black in *S. microlepis* and spotted in *S. diabolicus*); in ID pattern (1-5-3 or 1-4-3 versus 1-3-2); hypural number (4 versus 5); and by the number of scales in a longitudinal series (91–104 versus 126 and 135, respectively, in *S. microlepis* and *S. diabolicus*).

Species of *Symphurus* possessing 1-5-3 or 1-4-3 ID patterns (patterns occurring in *S. chabanaudi*) are found only in the New World (Munroe 1987). Western Atlantic *Symphurus* with similar ID patterns, fin-ray counts, or pigment patterns to those observed in *S. chabanaudi* include *S. tessellatus* (Quoy & Gaimard), an undescribed species (species D of Munroe 1987), and *S. plagusia* (Schneider, in Bloch & Schneider). *Symphurus chabanaudi* is easily distinguished from *S. plagusia* by the large black opercular spot and scales on blind-side dorsal- and anal-fin rays (both absent in *S. plagusia*); the absence of a fleshy ridge on the ocular-side lower jaw (present in *S. plagusia*); the dorsal-fin origin placed at a vertical line through the middle or anterior margin of the upper eye (versus dorsal-fin origin at a vertical line anterior to anterior margin of upper eye); and meristic values (dorsal-fin rays 98–109 versus 89–98 in *S. plagusia*; anal-fin rays 82–92 versus 73–81; total vertebrae 52–57 versus 47–51; and scales in a longitudinal series 91–104 versus 79–89).

Of all species in the genus, *S. chabanaudi* is most similar in form, size, and pigmentation pattern to *S. tessellatus. Symphurus chabanaudi,* however, differs from *S. tessellatus* in its modally higher counts of dorsal- and anal-fin rays and total vertebrae (Table 7). The most useful character to distinguish *S. chabanaudi* from *S. tessellatus* is the number of dorsal-fin rays, which range from 98–109 in *S. chabanaudi* compared with only 91–102 in *S. tessellatus.* Comparison of frequency distributions for dorsal-fin ray counts in these species (Table 7) reveals that about 12% of the specimens overlap with respect to dorsal-fin ray number. However, *S. chabanaudi* usually has 101 or more dorsal-fin rays (95 of 107 specimens) while *S. tessellatus* usually has 100 or fewer dorsal-fin rays (224 of 233 with 100 or fewer dorsal-fin rays). Corresponding modal differences, although not as great as those noted for dorsal-fin rays, also occur in number of anal-fin rays (82–92 versus 74–86 in *S. tessellatus*) and total vertebrae (52–57, usually 53–56 in *S. chabanaudi* versus 48–54, but usually 50–53 in *S. tessellatus*). There are also differences in the relative frequencies of occurrence of particular ID patterns in the two species. In *S. chabanaudi,* 50% (47/95) of the individuals had a 1-5-3 ID pattern and only 30% (28 specimens) featured a 1-4-3 pattern. In contrast, 173 of 233 (74%) *S. tessellatus* possessed a 1-4-3 ID pattern, while only 6% (13 specimens) had a 1-5-3 pattern.

Many meristic features of *S. chabanaudi* completely overlap those of undescribed species D from the Caribbean Sea. *Symphurus chabanaudi* differs from undescribed species D, however, in having 4–8 small, but well-developed scales on the blind-side dorsal- and anal-fin rays (especially prominent in specimens larger than 60 mm); a somewhat larger eye (1.5–2.1, $\bar{X}$ = 1.9 SL versus 1.2–1.9, $\bar{X}$ = 1.5 SL); and *S. chabanaudi* lacks a fleshy ridge on the ocular-side lower jaw (usually present and well developed in undescribed species D). The

Table 7.—Comparison of selected meristic features for the eastern Pacific *Symphurus chabanaudi* and the western Atlantic *S. tessellatus.*

	Dorsal-fin rays																		
	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109
S. chabanaudi								1	1	10	14	14	20	6	17	14	8	—	2
S. tessellatus	2	1	5	16	37	30	51	35	28	19	8	1							

	Anal-fin rays																		
	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
S. chabanaudi									1	3	10	20	23	17	15	13	3	2	1
S. tessellatus	1	—	—	5	21	33	43	45	37	26	18	3	1						

	Total vertebrae									
	48	49	50	51	52	53	54	55	56	57
S. chabanaudi					8	22	27	22	12	1
S. tessellatus	1	2	45	81	71	32	2			

posterior extension of the jaws is slightly more anterior in *S. chabanaudi,* reaching only to a vertical line through the rear margin of the pupil or rear margin of the lower eye. In undescribed species D, the jaws extend further backwards reaching a vertical line through the posterior margin of the eye and in many specimens, the jaws actually extend slightly beyond the eyes. *Symphurus chabanaudi* also differs from undescribed species D in the relative frequencies of specimens possessing 1-5-3 and 1-4-3 ID patterns. *Symphurus chabanaudi* has a much higher frequency of occurrence of the 1-5-3 ID pattern (50% of individuals examined) compared with only 30% with a 1-4-3 pattern. In contrast, 40 of 45 (89%) of the undescribed species D examined had a 1-4-3 pattern and only one specimen possessed a 1-5-3 pattern.

Symphurus chabanaudi also differs from undescribed species D in subtle features of its pigmentation. *Symphurus chabanaudi* generally has about nine wide, dark-brown crossbands; undescribed species D has 10–14 (usually 10–12) narrower bands. Additionally, the posterior third of the dorsal and anal fins, and the caudal fin in *S. chabanaudi* are usually uniformly dark brown or black without alternating blotches and unpigmented areas. In undescribed species D, the posterior two-thirds of the dorsal and anal fins usually have an alternating series of blotches and unpigmented areas.

Additional material examined.—The following non-type specimens were also examined (393 specimens, 19–226 mm):

Gulf of California western shore: UCLA W54-367, (52, 106–145), about 5 mi north of San Felipe. CAS 24062, (5, 120–133), between Punta Majoro and Punta Ensenada Blanca, about 3 mi north of San Felipe. UCLA W49-427, (2, 152–161), off Ensenada Blanca, 31°03′30″N, 114°50–51′W. CAS-SU 47384, (1, 101). UCLA W55-26, (1, 160). CAS 24060, (1, 162) and CAS 24071, (11, 119–164), near San Felipe. UCLA W55-2, (13, 99–168), about 9 mi east of San Felipe. YPM 632 (1, 111), San Felipe Bay, 6 m, 19 May 1926. YPM 631 and 633a, (2, 75–122), San Felipe Bay, 6 m, 14 May 1926. CAS 24065, (2, 138–149), 2–3 mi north of Punta Estrella (Diggs), about 7 mi south of San Felipe. CAS 24066, (2, 144–161), about 9 mi south of San Felipe. CAS 24064, (1, 138), about 10 mi south of San Felipe. UCLA W62-61, (22, 66–154), off Punta Estrella (Diggs). UCLA W52-45, (6, 90–182), about 2–3 mi off Punta San Fermin. CAS 24063, (3, 100–150), about 15 mi south of San Felipe. UCLA W59-17, (1, 191), off Punta Willard, Bahia San Luis Gonzaga. USNM 126741, (2, 122–132) and CAS-SU 5571, (2, 126–128), 30°50′45″N, 114°29′45″W, off Isla San Luis.

Gulf of California eastern shore: UCLA W49-55, (20, 114–178), 20 mi southwest of El Golfo, Sonora. UCLA W56-28, (10, 156–166), north of Punta Lobos, Sonora. UCLA W58-233, (1, 149), north of Punta Lobos, Sonora. UCLA W50-27, (1, 166), near mouth of Río Muerto, in tidal waters west of Mapoli, Sonora. CAS 24059, (2, 70–101), Bahia Guaymas, Sonora. CAS 24061, (2, 96–97), just south of channel and east of Punta Baja, Guaymas Harbor, Sonora. UCLA W52-40, (7, 71–105), Guaymas Harbor, Sonora. UCLA W50-42, (10, 111–180), south of Boca del Río Mayo, Sonora. CAS 24068, (1, 122) and UCLA W50-43, (2, 19–22) (larvae with eyes recently migrated), 26°40′N, 109°47′W, in vicinity of Boca del Río Mayo, Sonora. UCLA W56-113, (2, 150–168), south of mouth of Bahia Topolobampo, Sinaloa. SIO 60-95, (1, 218), 24°32.6–33.4′N, 108°03–04.5′W, off Altata, Sinaloa. UCLA W51-36, (2, 98–103), near Astillero at Mazatlan, Sinaloa.

Pacific coast of southern Mexico: CAS 4670, (1, 168), near Isla Isabela. SIO 60-87, (2, 173–200), 21°46.4–50.5′N, 105°25.2–44.9′W, near mouth of Río San Pedro, Nayarit. UCLA W58-18, (12, 43–97), Boca del Asodero, Nayarit. UCLA W58-3, (3, 161–197), 1–3 mi north of Ensenada Chacala, Nayarit.

El Salvador: CAS-SU 46259, (2, 144–159), 13°20′03″N, 87°48′57″W, off La Union, Gulf of Fonseca. USNM 220804, (7, 122.0–133.7, five specimens cleared and stained), Río Chaguantique, Jiquilisco Bay, 14 Sep 1976. USNM 291340, (19, 66.7–123.3), Jiquilisco Bay, Sept 1975–Mar 1976.

Nicaragua: CAS-SU 46258, (1, 160), 13°02′30″N, 87°29′30″W, off Punta Monypenny, Gulf of Fonseca.

Costa Rica: SIO 64-465, (1, 179), vicinity of Cabo Blanco. LACM 9754-1, (1, 198), between Isla San Lucas and Isla Negritas, Gulf of Nicoya. UCLA W54-35, (4, 67–101), Erdman Cove, Isla Caballo, Gulf of Nicoya. CAS 24067, (2, 64–106), off Isla Chira, Gulf of Nicoya. UCR 297-16 and 297-17, (7, 150–193), Puntarenas Province, Gulf of Nicoya. UCLA W54-434, (23, 116–165), exact locality unknown. UMMZ 194670, (2, 199–206), Gulf of Nicoya, off Puntarenas, Puntarenas Province, 1 Jul 1973.

Panama: YPM 4369, (8, 149–201), Canal Zone. ANSP 123572, (2, 174–181), Canal Zone, Oct 1953. CAS 24965, (3, 123–136), 8°58′15″N, 79°25′15″W. CAS 24962, (7, 146–191), 8°43′15″N, 79°41′W. CAS 24967, (8, 174–204), 8°43′10″N, 79°15′W. SIO 52-193, (1, 126), 8°40′N, 79°45′W, off Punta Chame. CAS 24963, (14, 152–214), 8°38′N, 78°40′W. CAS 24961, (1, 116), 8°27′15″N, 78°49′50″W, Isla del Ray. UMML 34330, (2, 167–186), 8°19′N, 78°36′W, 29 m, 7 May 1967. CAS 24964, (1, 162), 8°15′N, 78°26′W. CAS 24968, (2, 156–183), 8°08′15″N, 80°20′W. CAS 24966, (4, 133–176), San Miguel, Bay of Garachine. UCLA W54-325, (1, 136). UCLA W54-345, (1, 107.5). UCLA W58-278, (1, 208). UCLA W58-304, (20, 82.5–158). UCLA W58-305, (17, 84–170). CAS 24070, (1, 202). LACM 6509-26, (2, 189–193), Bahia de Panama. CAS-SU 6900, (3, 172–226), 8°16′30″N, 79°37′45″W. USNM 50333, (1, 220). USNM 81674, (1, 43.5) and USNM 81032, (1, 189), from Panama City Market. CAS 24069, (2, 208–212), off Chiman, Gulf of Panama. ANSP 123579, (1, 194), off Chiman Province, Gulf of Panama, 9 m, 10 Sep 1953. USNM 291357, (1, 161), Canal dredge effluent, Fort Amador, 16 Mar 1967.

Colombia: USNM 305725, (3, 160–180), 3°37–39′N, 77°20.5–21′W, Tortugas grounds south of Buenaventura, 18 m, 22 Oct 1970. USNM 305722, (1, 172), 3°39′N, 77°18′W, Tortugas grounds south of Buenaventura, 9 m, 19 Sep 1969. USNM 305724, (1, 178), 3°31–33′N, 77°22–22.5′W, Tortugas grounds south of Buenaventura, 9 m, 22 Oct 1970. USNM 305720, (1, 202), 3°18–16′N, 77°33.5–34′W, 9 m, 23 Oct 1970. USNM 305723, (1, 197), 2°43′N, 77°51′W, Timbiqui, 7 m, 25 Jan 1969. USNM 305721, (1, 205), 1°42′N, 79°00′W, Punta Manglares, 11 m, 28 Jan 1969.

Peru: IMARPE 2, (1, 204), 5°11′S, 81°12′W, Paita. IMARPE 13, (1, 142), 12°06′S, 76°55′W, Lima.

Symphurus diabolicus, new species

Figs. 2, 4a, Table 8

Holotype.—USNM 135653 (male, 112.6 mm), collected by the U. S. Fish Commission Steamer *Albatross,* Sta. 2817, 15 Apr 1888, west of Isla San Cristobal (Chatham Island), Galapagos Islands (0°46′S, 89°42′W), Ecuador, 501 m.

Diagnosis.—A *Symphurus* with a 1-3-2 ID pattern, 109 dorsal-fin rays; 94 anal-fin rays; 12 caudal-fin rays; 58 total vertebrae; 5 hypurals; extremely small scales, 135 in longitudinal series and 58 in transverse row; no pupillary operculum; large, prominent eyes (ED/SNL 0.96), with narrow interorbital space; upper jaw reaching vertical line just posterior to anterior margin of lower eye; well-developed dentition on ocular-side jaws; origin of dorsal fin at vertical between anterior margin and mid-point of pupil of upper eye; head length slightly larger (1.04 times) than body depth, spotted peritoneum (possibly black in life); and uniform body color without crossbands.

Description.—ID pattern 1-3-2. Caudal-fin rays 12 (caudal fin broken and nearly completely severed from body). Dorsal-fin rays 109. Anal-fin rays 94. Pelvic-fin rays 4. Total vertebrae 58; abdominal vertebrae 9 (3 + 6). Hypurals 5. Longitudinal scale rows approximately 135. Scales on head posterior to lower orbit missing. Transverse scales approximately 58.

Body medium-sized, relatively elongate, depth at anus 203 SL; greatest body depth 212 SL, beginning about at base of anal-fin ray 5 and continuing almost uniformly over large area in middle of body (to approximately anal-fin rays 60–70); body taper anterior and posterior of that region smooth and gradual. Anterior curvature of body not pronounced. Preanal length 248 SL; somewhat longer than body depth. Head relatively long, 220 SL, greater than body depth. Head length greater than head width (194 SL). Postorbital length 131 SL. Lower head lobe (97 SL) slightly smaller than upper head lobe (103 SL). Snout length 194 HL, with small number of small ctenoid scales. Dermal papillae scarcely evident on blind-side snout. Anterior nostril relatively long, but not reaching lower eye when depressed pos-

Table 8.—Comparison of meristic and morphometric features for holotypes and only known specimens of *Symphurus diabolicus* (USNM 135653, male, 112.6 mm) and *S. microlepis* (MCZ 28535, male, 99.5 mm).

	S. diabolicus	*S. microlepis*
ID pattern	1-3-2	1-3-2
Caudal-fin rays	12	12
Dorsal-fin rays	109	106
Anal-fin rays	94	92
Total vertebrae	58	57
Hypurals	5	5
Longitudinal scales	135	126
Postorbital scale rows	—	30
Transverse scale count	ca. 58	55
Morphometrics (thousandths of SL)		
Body depth at anus	203	279
Greatest body depth	212	279
Preanal length	248	271
Dorsal-fin base	938	967
Anal-fin base	756	746
Head length	220	248
Head width	194	275
Postorbital length	131	176
Upper head lobe	103	110
Lower head lobe	97	170
Predorsal length	62	33
Morphometrics (thousandths of HL, except HW/HL)		
HW/HL	0.88	1.11
Postorbital length	597	708
Snout length	194	154
Upper jaw length	230	231
Eye diameter	186	130
Chin depth	157	109

Fig. 4. a. *Symphurus diabolicus,* USNM 135653, holotype; male, 112.6 mm SL; Ecuador, Galapagos Islands (00°46′S, 89°42′W). b. *Symphurus microlepis,* MCZ 28535, holotype; male, 99.5 mm SL; off Panama (7°32.6′N, 79°16′W).

teriorly. Evidently 6–8 rows of 2–4 tiny and flimsy scales behind posterior nostril and in narrow interorbital region to posterior margin of eyes (most scales lost; counts made from scale pockets). Mouth relatively large, upper jaw 230 HL, reaching to a vertical line through anterior margin of lower eye. Chin depth 157 HL, shorter than snout length. Lower eye large, 186 HL; eyes slightly subequal with upper in advance of lower; eyeballs almost touching. Pupillary operculum absent. Length of dorsal-fin base 938 SL. Dorsal-fin origin reaching vertical line through point between anterior margin and mid-point of pupil of upper eye; predorsal length relatively long, 62 SL. Length of anal-fin base 756 SL; blind sides of dorsal and anal fins apparently without scales. Anal-fin origin approximately at vertical line between bases of fourteenth and fifteenth dorsal-fin rays. Pelvic fin with 4 rays; distal half of fin rays broken. Caudal fin damaged posteriorly; with four or five rows of tiny scales to point where rays broken.

Teeth well developed on both jaws. Blind-side dentary with 5–6 rows of strong teeth across middle of crescentic tooth band. Arms of crescent tapering to fewer rows, ending in single tooth. Premaxilla on blind side with tooth band as broad posteriorly as middle of lower jaw crescent, but narrowing anteriorly to fewer rows, terminating in single tooth. Ocular-side premaxilla with single row of prominent teeth extending from tip to about mid-point of bone (at point equal with vertical midway between anterior margin of lower eye and posterior margin of anterior nostril). Ocular-side dentary with row of teeth extending to point below anterior margin of lower eye.

Scales small (smallest among eastern Pacific tonguefishes), numerous, ctenoid on both sides of body. Scales on blind side with fewer cteni than those on ocular side (a feature not observed in other eastern Pacific *Symphurus*).

Pigmentation.—Specimen uniformly yellowish throughout without visible signs of any other form of pigmentation. Whether yellowish color is natural pigmentation of the species or results from bleaching of natural pigment during fixation and long-term storage is unknown.

Etymology.—From the Latin "diabolus" meaning devil, in reference to the large, grotesque eyes; an apparent adaptation to the deep-water habitat occupied by this species.

Distribution.—Known only from the holotype collected at 501 m on white sand substrate west of Isla San Cristobal (Chatham Island) in the Galapagos Islands (Fig. 2).

Comparisons.—*Symphurus diabolicus* is only the fourth known eastern Pacific *Symphurus* with the following combination of characters: a 1-3-2 ID pattern, 12 caudal-fin rays, and a black peritoneum (although the peritoneum in the holotype is spotted and not now solid black, it is thought to have had a black peritoneum and that most natural pigment has been bleached from this specimen during fixation and storage. Fourteen nominal species in addition to *S. diabolicus* are characterized by a 1-3-2 ID pattern and 12 caudal-fin rays (Munroe 1987). Of these, ten species, all occurring in deep water (>50 m), have a black peritoneum. Only four species inhabiting relatively shallow-waters (<45m) have an unpigmented peritoneum.) Other eastern Pacific species characterized by this combination of characters include *S. microlepis, S. gorgonae,* and *S. oligomerus. Symphurus diabolicus* differs strikingly from these other *Symphurus* with the exception of *S. microlepis* (see below). *Symphurus diabolicus* differs from *S. gorgonae* and *S. oligomerus* in vertebral counts (total vertebrae 58 versus 46–49 in *S. gorgonae* and 48–52 in *S. oligomerus*); numbers of dorsal-fin rays (109 versus 80–89 in *S. gorgonae* and 85–97 in *S. oligomerus*); numbers of anal-fin rays (94 versus 63-74 in *S. gorgonae* and 71–83 in *S. oligomerus*); and body shape (relatively elongate with gradual posterior taper in *S. diabolicus* versus much deeper body with greatest body depth in anterior third of body and rapid posterior taper in *S. gorgonae* and *S. oligomerus*). *Symphurus diabolicus* differs further from *S. gorgonae* in having 5 hypurals (versus 4) and in its much larger size (112.6 mm versus adults smaller than 70 mm).

Among all other congeners, *S. diabolicus* is most similar in morphology and meristic features to *S. microlepis,* a second eastern Pacific species known only from the holotype collected in deep-water off the coast of Panama. Although only the types are available for comparison, the differences between these specimens are, nevertheless, substantial and beyond the range of intraspecific variation normally encountered in other species of *Symphurus.* These differences are particularly noteworthy in light of the fact that both specimens are males and of nearly the same size (112.6 versus 99.5 mm SL), which reduces or eliminates confounding factors attributable to size or sexually related variations in morphology. The two species have similar meristic features, especially ID pattern (1-3-2), total vertebrae (58 versus 57 in *S. microlepis*), numerous small scales in a longitudinal series (ca. 135 and 126), and caudal-fin rays (12); however, they are easily distinguished by a number of characters (compare Figs. 4a and 4b and see Table 8 for detailed comparison of morphological characteristics of both species). Notable differences between these species are body shape and relative size and shape of the head. *Symphurus diabolicus* has a more elongate body featuring a smooth, gradual taper with the greatest depth (21.2%

SL) occurring slightly posterior to the anus and diminishing posteriorly only slightly throughout the middle of the body. In contrast, *S. microlepis* has a much deeper body (27.9% SL) with the greatest depth occurring at the anus and the body tapers posteriorly much more rapidly. In *S. diabolicus,* the head is shorter (HL = 22.0% SL versus 24.8% SL in *S. microlepis*) and longer than wide (HW/HL = 0.88 versus 1.11) compared with that of *S. microlepis.* Differences in head shape between these species are particularly evident in the relative size of the lower head lobe, which is only 0.94 the width of upper head lobe in *S. diabolicus,* in contrast to being 1.6 times larger in *S. microlepis.* Although both species have relatively large eyes, that of *S. diabolicus* is larger, more elliptically-shaped, and equal in length to about one-fifth of the head length while that of *S. microlepis* is only about one-eighth of head length and almost spherical.

None of the Atlantic *Symphurus* possessing 1-3-2 ID pattern, 12 caudal-fin rays, and black peritoneum have vertebrae or fin-ray counts approaching those of *S. diabolicus.*

Other species in the genus with meristic features similar to *S. diabolicus* include two rarely collected, Indian Ocean, deep-water species, *S. macrophthalmus* Norman and *S. fuscus* Brauer. *Symphurus macrophthalmus* is a large-eyed, deep-water species known only from the holotype and a single paratype collected in the Gulf of Oman near the Persian Gulf (Norman 1939). Large eye size, black peritoneum, and generally slender body are the only similarities this otherwise distinctive species shares with *S. diabolicus. Symphurus diabolicus* has a different ID pattern than that observed in *S. macrophthalmus* (1-3-2-2-2 versus 1-2-2-1-2); fewer caudal-fin rays (12 versus 14); and some higher counts (total vertebrae 58 versus 48; 109 versus 87 dorsal-fin rays and 94 versus 75 anal-fin rays).

Certain similarities exist in meristic features of *S. diabolicus* and those observed for *S. fuscus* known only from the holotype collected off the east coast of equatorial Africa (Brauer 1906). Both species have 58 total vertebrae and similar numbers of dorsal- (109 in *S. diabolicus* versus 105 in *S. fuscus*) and anal-fin rays (94 versus 93). However, *S. diabolicus* differs from *S. fuscus* primarily in ID pattern (1-3-2-2-2 versus 1-2-2-1-2) and caudal-fin ray counts (12 versus 14).

Discussion

Interestingly, southward increases in several meristic features occurred in *S. oligomerus* and *S. chabanaudi* (Tables 3, 6). Similar increases in meristic features occur in other eastern Pacific tonguefishes that range from the Gulf of California to northern Peru, including *S. atramentatus, S. fasciolaris, S. leei, S. melanurus,* and *S. gorgonae* (Mahadeva 1956). Increased meristic elements in tonguefishes occurring in the southernmost extent of the species range in the Northern Hemisphere contradicts the well-known Jordan Rule (Jordan 1891), in which specimens of Northern Hemisphere species inhabiting the northernmost portions of the species range usually have the highest number of meristic elements. Hubbs (1924, 1926, 1934), in reviewing probable causes of latitudinal variation in meristic elements, noted strong correlations between the number of elements formed during development and ambient water temperatures, but he recognized that other factors such as salinity could also influence the complement of meristic elements formed during ontogeny. One or more of those factors may account for the cline we find in these *Symphurus* species; however, because virtually nothing is known concerning the seasonality and location of spawning and rates of larval development of these tonguefishes, it is premature to speculate which factors contribute to this trend in these species.

Acknowledgments

The following curators and support staff generously provided space and arranged for loan of specimens: W. Smith-Vaniz and W. Saul (ANSP); A. Wheeler, M. Halloway, and J. Chambers BM(NH); W. Eschmeyer, M. E. Anderson, W. Follett, L. Dempster, and D. Catania (CAS); N. Chirichigno (IMARPE); R. Lavenberg, J. Seigel, and R. Feeney (LACM); K. Hartel (MCZ); C. Hubbs, R. Rosenblatt, D. Gibbons, and H. J. Walker (SIO); L. Knapp (SOSC); B. Walker and D. Buth (UCLA); W. Bussing (UCR); C. R. Robins (UMML); R. R. Miller, D. W. Nelson, and A. S. Creighton (UMMZ); V. G. Springer, R. P. Vari, and S. L. Jewett (USNM); L. P. Schultz (formerly USNM); and K. Thompson (YPM). We thank R. Gibbons and R. Wisner for assistance with photography and radiography. M. Nizinski provided assistance reading radiographs and prepared Fig. 2. The manuscript was improved through critical reviews by B. Collette, R. Vari, and R. Lavenberg. Portions of this study comprised a partial requirement for the Ph.D. degree from UCLA to the first author. Portions of this study were independently initiated while the second author was a postdoctoral fellow in the Division of Fishes, USNM. Travel funds enabling Munroe to work at UMML in 1982 were provided by the Department of Fisheries, VIMS.

Literature Cited

Brauer, A. 1906. Wissentschaftliche ergebnisse der deutchen tiefsee expedition auf dem Dampfer "Valdivia", 1898–1899.—Jena (G. Fischer) 15: 1–432.

Breder, C. M., Jr. 1936. Heterosomata to Pediculati from Panama to Lower California. Scientific results of the Second Oceanographic Expedition of the "Pawnee", 1926.—Bulletin of the Bingham Oceanographic Collection 2(3):1–56.

Chirichigno, F. N. 1974. Clave para identificar los peces marinos del Perú.—Informes Instituto del Mar del Perú 44:1–387.

Eschmeyer, W. N., E. S. Herald, & H. Hammann. 1983. A field guide to Pacific coast fishes from the Gulf of Alaska to Baja California. Boston, Houghton Mifflin Company, 336 pp.

Fowler, H. W. 1944. Results of the fifth George Vanderbilt Expedition (1941) (Bahamas, Caribbean Sea, Panama, Galapagos Archipelago and Mexican Pacific Islands).—Monograph of the Academy of Natural Sciences of Philadelphia 6:57–583.

Garman, S. 1899. The fishes. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross", during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding.—Memoir of the Museum of Comparative Zoology, Harvard 24:1–431.

Gilbert, C. H., & E. C. Starks. 1904. Fishes of Panama Bay.—Memoir of the California Academy of Sciences 4:3–304.

Ginsburg, I. 1951. Western Atlantic tonguefishes with descriptions of six new species.—Zoologica, N.Y. 36:185–201.

Hildebrand, S. F. 1946. A descriptive catalog of the shore fishes of Peru.—Bulletin of the United States National Museum 189:1–530.

Hubbs, C. L. 1924. Seasonal variations in the number of vertebrae.—Occasional Papers of the Michigan Academy of Sciences and Arts 11:207–214.

———. 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution.—American Naturalist 60:57–81.

———. 1934. Racial and individual variation in animals, especially fishes.—American Naturalist 68:115–128.

Jordan, D. S. 1891. Relations of temperature to vertebrae among fishes.—Proceedings of the United States National Museum 14:107–120.

———, & B. W. Evermann. 1898. The fishes of North and Middle America.—Bulletin of the United States National Museum 47(3):2183–3136.

———, & C. H. Gilbert. 1883. List of fishes collected at Panama by Charles Henry Gilbert.—Bulletin of the United States Fish Commission 2:109–111.

———, & D. K. Goss. 1889. A review of the flounders and soles (Pleuronectidae) of America and Europe.—Report of the United States Fish Commission for 1886 14:225–342.

Lavenberg, R. J., & J. E. Fitch. 1966. Annotated list of fishes collected by mid-water trawl in the Gulf of California, March–April 1964.—California Fish and Game 52:92–110.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Mahadeva, M. N. 1956. A review of the tonguefishes of the eastern Pacific, with descriptions of six new species. Unpublished Ph.D. dissertation, University of California at Los Angeles, 272 pp.

Meek, S. E., & S. F. Hildebrand. 1928. The marine fishes of Panama.—Field Museum of Natural History Publication 249, Zoological Series 15(Part 3):709–1045.

Menezes, N. A., & G. De Q. Benvegnú. 1976. On the species of the genus *Symphurus* from the Brazilian coast, with descriptions of two new species (Osteichthyes, Pleuronectiformes, Cynoglossidae).—Papeis Avulsos de Zoologia, São Paulo 30:137–170.

Munroe, T. A. 1987. A systematic revision of Atlantic tonguefishes (*Symphurus*: Cynoglossidae: Pleuronectiformes), with a preliminary hypothesis of species group relationships. Unpublished Ph.D. dissertation, College of William and Mary, Williamsburg, Virginia, 598 pp.

———. 1990a. Eastern Atlantic tonguefishes (*Symphurus*: Cynoglossidae; Pleuronectiformes), with descriptions of two new species.—Bulletin of Marine Science 47(3) (in press).

———. 1990b. *Symphurus melanurus* Clark, 1936, a senior synonym for the eastern Pacific tonguefishes, *S. seychellensis* Chabanaud, 1955 and *S. sechurae* Hildebrand, 1946.—Copeia 1990:229–232.

———, & M. N. Mahadeva. 1989. *Symphurus callopterus* (Cynoglossidae, Pleuronectiformes), a new deepwater tonguefish from the eastern Pacific.—Proceedings of the Biological Society of Washington 102:458–467.

———, & M. S. Nizinski. 1990. *Symphurus* ——— and *S.* ——— (Cynoglossidae, Pleuronectiformes), two new eastern Pacific tonguefishes with 11 caudal-fin rays.—Copeia 1990(4) (in press).

Norman, J. R. 1939. Fishes. John Murray Expedition, 1933–34.—Scientific Report of the British Museum (Natural History) 7:1–116.

Phillips, P. C. 1981. Annotated checklist of fishes at Jiquilisco Bay, El Salvador.—Revista de Biologia Tropical 29:45–58.

Seale, A. 1940. Report on fishes from Alan Hancock Expeditions in the California Academy of Sciences.—Alan Hancock Pacific Expeditions 9(1): 1–46.

Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Illinois, 822 pp.

(MNM) Department of Biology, University of Wisconsin–Oshkosh, Oshkosh, Wisconsin 54901; (TAM) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560. (All correspondence should be addressed to the second author.)

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 955–961

CROCODYLUS RANINUS S. MÜLLER AND SCHLEGEL, A VALID SPECIES OF CROCODILE (REPTILIA: CROCODYLIDAE) FROM BORNEO

Charles A. Ross

Abstract.—*Crocodylus raninus* S. Müller & Schlegel 1844, described on the basis of two syntypes from Borneo, is resurrected and diagnosed. Squamation and cranial morphology of *C. raninus* are compared with other sympatric and neighboring Indopacific species.

The systematics and distribution of Indopacific *Crocodylus* are inadequately known. Many museum specimens identified as the widely distributed *Crocodylus porosus* Schneider, 1801, actually represent unrelated and poorly known insular species. This is particularly true in the Indonesian Archipelago, where specimens of undescribed *Crocodylus* have been examined from Banka Island and Sulawesi (Ross 1986).

Unfortunately, diagnoses of many of these populations are precluded by insufficient material and complicated by a long history of misidentifications in the literature. One exception is the palustrine crocodile of Borneo which, although equally confused in the older literature and known from very few specimens, can be diagnosed on the basis of limited museum material and as an unequivocal name is available, its resurrection is uncomplicated.

Methods

Scale counts used in this study were made on 481 individual crocodiles from the Indopacific region. Specimens were examined from museums, private collections, and from the wild. Some specimens critical to this study in European museums were not examined autoptically but photographs of them were examined and scale counts made from the photographs.

Scale counts follow Ross & Roberts (1979), King & Brazaitis (1971), and Brazaitis (1973, 1974). Dorsal and neck armor terminology of F. Ross & Mayer (1983) is given in parentheses where pertinent.

Museum abreviations follow Leviton et al. (1985).

Historical Discussion

S. Müller & Schlegel (1844) described *Crocodylus raninus* (as a race of *C. biporcatus* Cuvier = *C. porosus*) on the basis of an adult skull and a whole juvenile from Borneo. They differentiated *C. raninus* from *C. porosus* on the basis of snout shape and neck squamation but the name was not formally proposed and specific locality data and disposition of the syntypes were not included. Many crocodile specimens collected by M. S. Müller from Borneo in 1836 were in the Muséum d'Histoire Naturelle des Pays-Bas and listed by Lidth de Jeude (1898) in the "Catalogue Ostéologique." These specimens are individually identified by letter of the alphabet and are now in the Rijksmuseum van Natuurlijke Historie, Leiden. The syntypes of *C. raninus* were not specifically noted by Lidth de Jeude (1898) and have not been located. They were, however, clearly figured (S. Müller & Schlegel 1844, pl. 3, figs. 7, 8), and show an adult skull (fig. 7) and the neck and head of a juvenile (fig. 8). There is no indication that any subsequent worker examined the syntypes as all later comments refer directly to S. Müller & Schlegel's (1844) figures.

Gray was clearly confused by the status of S. Müller & Schlegel's *C. b. raninus.* In 1844 he synonymized it (in part, the juvenile syntype) with *C. porosus* Schneider (1844:58) which he correctly characterized as having reduced nuchal (= postoccipital) squamation. He (1844:62) referred the adult skull to *Crocodylus palustris* Lesson. Later (1862), he synonymized the adult skull with both *C. porosus* and *C. trigonops* Gray (= *C. palustris*) but failed to mention the juvenile. He later concluded that the adult skull was *C. porosus,* and suggested that the juvenile syntype may be a species similar to *C. siamensis* (1869, 1872).

Strauch (1866) identified the juvenile syntype with *C. palustris* and the adult skull with *C. porosus.* Bartlett (1895), without referring to earlier authors, presumed that the second species of crocodile occurring in Borneo (that is, other than *C. porosus*) must be *C. palustris* but did not examine any specimens of it.

More recently several authors, often without access to specimens or data, have speculated on the identity of the palustrine, or "freshwater," crocodile of Borneo. Schmidt (1935) suggested that the name *C. raninus* may be referable to it. But later authors (Peters 1967; Neill 1971, 1973; Hooijer 1972; Steel 1973; Fuchs 1974; Wermuth & Mertens 1977; Groombridge 1982, 1987; Whitaker & Whitaker 1989) either refer to the Bornean palustrine crocodile as *C. siamensis* or *C. palustris* (which is restricted to the Indian subcontinent) or ignore it completely. The name *Crocodylus raninus* has remained in the synonomy of *C. porosus* (Boulenger 1889; Mertens & Wermuth 1955; Wermuth 1953; Wermuth & Mertens 1961, 1977; Werner 1933).

Results

While examining a large number of Indopacific crocodiles I reidentified three specimens as a "palustrine" species possibly referable to *C. raninus,* following Schmidt (1935). These were a 36 cm long skull lacking mandibles ostensibly from Borneo (AMNH 24294) and two preserved juveniles from Borneo but without further locality data (MCZ 6727 and RMNH 3219) that had previously been identified as *C. porosus.*

The skull (AMNH 24294, Fig. 1) has a transverse palatine-pterygoid suture. In *C. porosus* this suture is directed posterolaterally and deeply indents the anterior margin of each pterygoid (Schmidt 1928, 1932, fig. 28 & pl. 7). The lacrymal ridges are less developed and angled from the orbit directly to the posterolateral margin of the frontals (60–65°), instead of running from the orbit parallel to the frontals as in *C. porosus.* The skull is robust with heavy surface pitting. The maxillaries at the level of the 5th maxillary tooth are distinctly flared outward, accentuating the constriction of the snout at the level of the crocodylid notch at the lateral edges of the maxillary-premaxillary suture. *Crocodylus porosus* skulls of similar size are more attenuate, lack the obvious lateral sculpturing and have less surface pitting.

The two juveniles have four well-developed postoccipital scales (PC 24–26) (absent or poorly developed in *C. porosus*; 0–2 scales, $n = 60$, $\bar{X} = 0.5$, ± 0.83 *SD,* Fig. 2) and 25 transverse ventral scale rows (*porosus* has 29–35 scale rows $n = 67$, $\bar{X} = 31.6$, ± 1.29 *SD,* Fig. 3).

The skull (AMNH 24294) differs from another southeast Asian palustrine crocodile, *C. siamensis,* which has a broad and rounded snout with weak 5th maxillary tooth bulges, flat or raised nasals forming a promenade (in AMNH 24294 they are sunken), lacrymal ridges that are poorly developed or absent (in AMNH 24294 they are well developed) and more similar in orientation to those of *C. porosus* in being gently angled inward from the orbits along the frontals (60°). This skull (AMNH 24294)

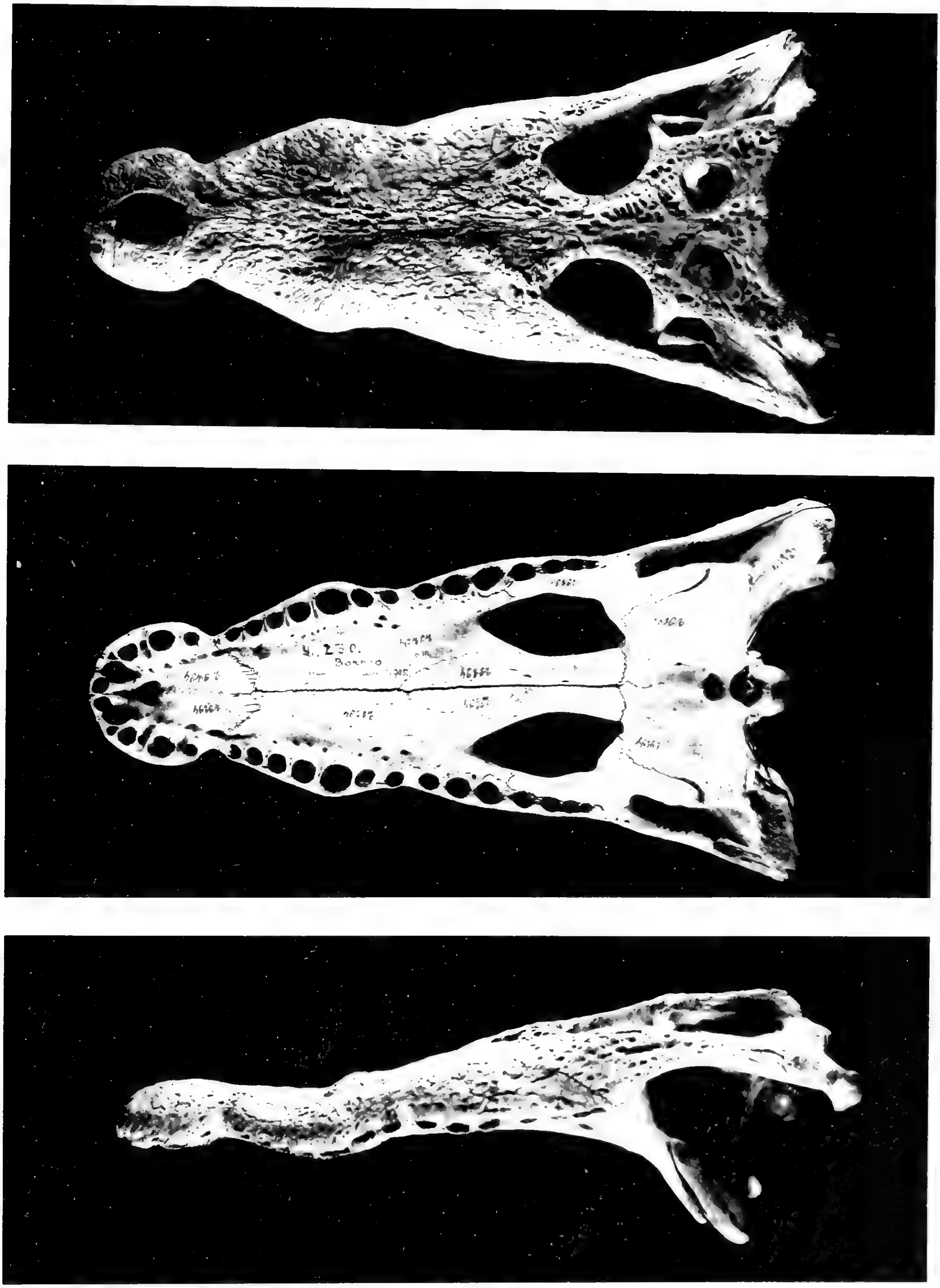


Fig. 1. Skull of *Crocodylus raninus*, AMNH 24294 (from top to bottom), dorsal, ventral, and lateral views.

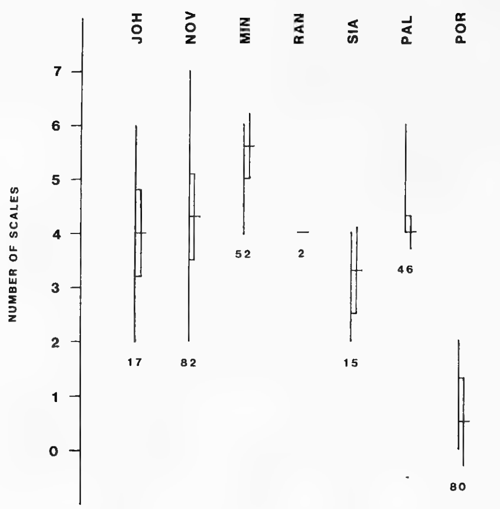


Fig. 2. Mean number of postoccipital scales (PC 25–26) of Indopacific crocodiles. Numbers at the base of each vertical line indicate number of specimens examined. The vertical line represents the range, the rectangle is one standard deviation, and the horizontal line represents the mean. Species are identified by the first three letters of their specific names.

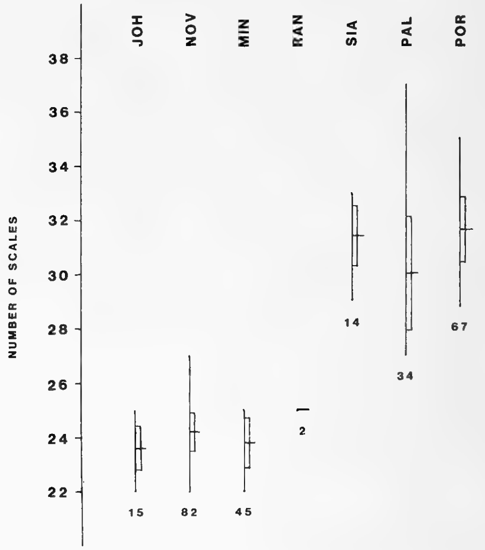


Fig. 3. Mean number of transverse ventral scale rows of Indopacific crocodiles. Numbers at the base of each vertical line indicate number of specimens examined. The vertical line represents the range, the rectangle is one standard deviation, and the horizontal line represents the mean. Species are identified by the first three letters of their specific names.

completely lacks the distinctive interorbital ridge characteristic of *C. siamensis* ($n = 4$), and the cranial table is distinctly trapezoidal in shape, being much narrower anteriorly. In *C. siamensis* the cranial table has parallel sides.

The two juveniles differ from *C. siamensis* by having fewer transverse ventral scale rows, 25 (versus 29–33, $n = 14$, $\bar{X} = 31.3$, ± 1.14 *SD,* Fig. 3). The anterior throat scales are flat and relatively large and not small and almost granular in appearance as in *C. siamensis* (Fig. 4). There are 38–39 transverse throat scale rows (49–53 in *C. siamensis,* $n = 15$, $\bar{X} = 50.3$, ± 1.49 *SD,* Fig. 5).

Both juveniles are in poor condition and it is not possible to detect whether the anterior ventral caudal scale irregularity of *C. siamensis* (Brazaitis 1973) is present.

On the basis of external morphology, the three Borneo specimens are most similar to *Crocodylus novaeguineae* Schmidt of New Guinea (Ross 1986), *Crocodylus mindorensis* Schmidt of the Philippine Islands (Ross & Alcala 1983), and *Crocodylus johnsoni* Krefft, of northern Australia. They agree with these taxa in having, among other characters, similarly well-developed postoccipital squamation (Fig. 2), a reduced number of transverse ventral scale rows (Fig. 3), relatively symmetrical dorsal armor with weak keels, poorly developed lacrymal ridges, and a transverse palatine-pterygoid suture. In combination these characters separate these crocodiles from all other *Crocodylus.*

The skull (AMNH 24294) can easily be distinguished from *C. johnsoni* by its robust snout with the dorsal median suture of the premaxillaries nearly separated by the nasals and barely in contact. In *C. johnsoni* the snout is attenuate and the dorsal median suture of the premaxillaries is in contact and not separated by the anterior edge of the nasals.

Crocodylus mindorensis and AMNH 24294 both have relatively robust snouts

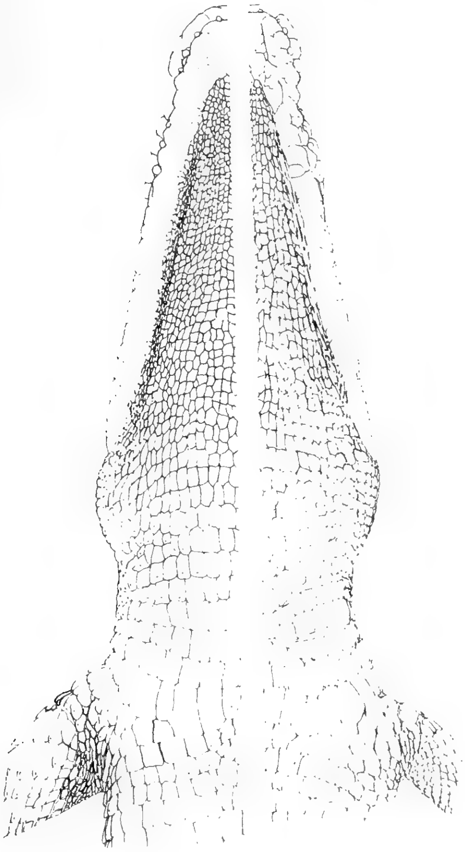


Fig. 4. Throat squamation of *Crocodylus siamensis* USNM 76089 (left), and *C. porosus* BMNH 71.9.1.46 (right), showing the small granular anterior throat scales of *C. siamensis* and typical Indopacific crocodile throat squamation.

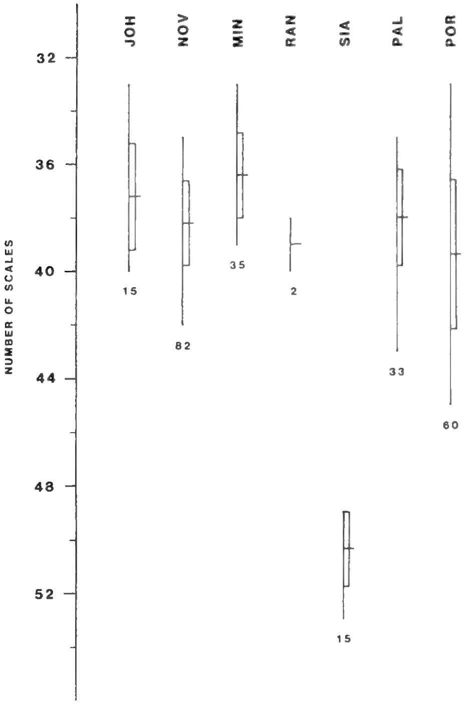


Fig. 5. Mean number of throat scales of Indopacific crocodiles. Numbers at the base of each vertical line indicate number of specimens examined. The vertical line represents the range, the rectangle represents one standard deviation, and the horizontal line represents the mean. Species are identified by the first three letters of their specific names.

with well-developed 5th maxillary tooth bulges and similar lacrymal ridge development and shape. In both species the squamosals are slightly elevated and the cranial table is slightly concave. They differ in the shape of the cranial table, which is nearly parallel sided in *C. mindorensis* but anteriorly narrowed in AMNH 24294; the relative width of the dorsal bridge between the supratemporal fenestrae, which is narrow in *C. mindorensis*; the interorbital bridge, which is concave in *C. mindorensis* but flat in the other; and the flat nasals of *C. mindorensis* at the level of the 8th maxillary tooth, which are concave in AMNH 24294.

The skull is most similar to *C. novaeguineae* from the north coast of New Guinea but differs in palatal suture lengths and in the shape of the infraorbital fenestrae, which are more attenuate in *C. novaeguineae* reflecting its generally longer and narrower skull shape. The squamosal elevations of similarly-sized *C. novaeguineae* are better developed than those of AMNH 24294.

Conclusions

S. Müller & Schlegel's (1844) pl. 3, fig. 8, clearly shows a crocodile with four well-developed postoccipital scales, a condition I have not observed in *C. porosus* but agreeing with the material from Borneo that I examined. The figured skull (S. Müller & Schlegel 1844, pl. 3, fig. 7) likewise agrees in general with the single skull, ostensibly from Borneo, currently available to me. Consequently I conclude the "palustrine" crocodile of Borneo is distinct at the species level and that the name *Crocodylus raninus* S. Müller & Schlegel, 1844, should be resurrected for this poorly-known population of Indopacific crocodile. There is no evidence that more than two species of recent *Crocodylus, C. porosus* and *C. raninus,* occur on Borneo, and, as both of the figured syntypes of *C. raninus* are conspecific and distinguishable from *C. porosus,* there appears no need to designate a lectotype or neotype for *C. raninus.*

Acknowledgments

I would like to thank Marinus S. Hoogmoed (RMNH); Konrad Klemmer (SNM); Roger Bour (MNHN); Jose Rosado and Franklin D. Ross (MCZ); Richard G. Zweifel and George Foley (AMNH); George R. Zug and W. Ronald Heyer (USNM); William E. Duellman (KU); and, Andrew F. Stimson (BMNH), for permitting the examination of *C. siamensis* and/or *C. raninus* material used in this study. Franklin D. Ross also provided literature critical to this study. Chip Clark provided photographs used in Fig. 1 and Edward Phillips illustrated comparative throat squamation (Fig. 4). Innumerable individuals facilitated and assisted with field examination of wild and live crocodiles. In particular I would like to thank Angel C. Alcala, the late Howard W. Campbell, Pedro C. Gonzales, F. Wayne King, and John Lever. I wish to thank Ronald I. Crombie and Leslie K. Overstreet for providing photographs of, and scale counts on, critical material in European collections which were not available on loan. Ronald I. Crombie, Storrs L. Olson, George R. Zug, and Gregory C. Mayer read drafts of this manuscript. Peter Brazaitis and James M. Clark reviewed this article for the editor and I wish to thank them for their valuable comments.

Literature Cited

Bartlett, Edward. 1895. The crocodiles and lizards of Borneo in the Sarawak Museum with descriptions of supposed new species, and the variation of colours in the several species during life.—Journal of the Royal Asiatic Society, Straits Branch 28:73–96.

Boulenger, G. A. 1889. Catalogue of the Chelonians, Rhynchocephaliens, and Crocodiles in the British Museum (Natural History). Taylor and Francis, London, x + 311 pp.

Brazaitis, Peter. 1973. The identification of *Crocodylus siamensis* Schneider.—Zoologica 58:43–45.

———. 1974. The identification of living crocodilians.—Zoologica 58:(3–4):59–101.

Fuchs, Karlheinz. 1974. Die Krokodilhaut. Eduard Roether, Darmstadt, 183 pp.

Gray, John Edward. 1844. Catalogue of the Tortoises, Crocodiles, and Amphisbaenians, in the collection of the British Museum. Edward Newman, London, viii + 80 pp.

———. 1862. A synopsis of the species of crocodiles.—Annals and Magazine of Natural History Ser. 3, 10(58):265–274.

———. 1869. Synopsis of the species of recent Crocodilians or Emydosaurians, chiefly founded on the specimens in the British Museum and the Royal College of Surgeons.—Transactions of the Zoological Society of London 6(4):125–169, pls. 31–34.

———. 1872. Catalogue of the shield reptiles in the collection of the British Museum. Part 2. Emydosaurians, Rhynchocephalia, and Amphisbaenians. Taylor and Francis, London, vi + 41 pp.

Groombridge, B. 1982. The IUCN Amphibia—Reptilia Red Data Book. Pt. 1, Testudines, Crocodylia, Rhynchocephalia. Unwin Brothers Limited, Old Woking. xliii + 426 pp.

———. 1987. The distribution and status of world crocodilians. Pp. 9–21 *in* G. J. W. Webb et al., eds., Wildlife management: crocodiles and alligators. Surrey Beatty and Sons Pty Limited, Chipping Norton, xiv + 552 pp.

Hooijer, D. A. 1972. Pleistocene vertebrates from Celebes. XIV. Additions to the *Archidiskodon—Celebochoerus* fauna.—Zoologische Mededelingen 46(1):1–16, pls. 3–4.

King, F. Wayne, & Peter Brazaitis. 1971. Species identification of commercial crocodilian skins.—Zoologica 56(2):15–70.

Leviton, Alan E., Robert H. Gibbs, Jr., Elizabeth Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985(3):802–832.

Lidth de Jeude, T. W. van. 1898. Catalogue ostéologique des poissons, reptiles et amphibies.—Muséum d'Histoire Naturelle des Pays-Bas 10(2): 1–16.

Mertens, Robert, & Heinz Wermuth. 1955. Die rezenten Schildkröten, Krokodile und Brückenechsen.—Zoologische Jahrbucher (Systematik) 83(5):323–440.

Müller, S., & H. Schlegel. 1844. Over de Krokodillen van den Indischen Archipel. 28 pp., pls. 1–3 *in* C. J. Temminck 1839–1844. Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen, door de leden der Natuurkundige Commissie in Indië en andere Schrijvers. Leiden, 259 pp., pls. 1–70.

Neill, W. T. 1971. The last of the ruling reptiles, alligators, crocodiles, and their kin. Columbia University Press, New York and London, xvii + 486 pp.

———. 1973. Twentieth-century Indonesia. Columbia University Press, New York and London, 391 pp.

Peters, Gunther. 1967. Klasse Reptilia–Kriechtiere. Urania Tierreich. Band: Fische, Lurche, Kriechtiere: Klasse Reptilia–Kriechtiere, pp. 355–507.

Ross, Charles A. 1986. Comments on Indopacific crocodile distributions. Pp. 349–354 *in* Crocodiles. Proceedings of the 7th working meeting of the Crocodile Specialists Group convened at Caracas, Venezuela, 21–28 October 1984. IUCN Publ. NS.

———, & Angel C. Alcala. 1983. Distribution and status of the Philippine Crocodile (*Crocodylus mindorensis*).—Kalikasan (Philippine Journal of Biology) 12(1–2):169–173.

———, & Charles D. Roberts. 1979. Scalation of the American Alligator.—Fish and Wildlife Service, Special Scientific Report—Wildlife 225:1–8.

Ross, Franklin D., & Gregory C. Mayer. 1983. On the dorsal armor of the Crocodilia. Pp. 305–331 *in* Anders G. J. Rhodin and Kenneth Miyata, eds., Advances in herpetology and evolutionary biology. Museum of Comparative Zoology, Cambridge.

Schmidt, Karl P. 1928. A new crocodile from New Guinea.—Field Museum of Natural History, Publication 247, Zoological Series 12(14):177–181.

———. 1935. A new crocodile from the Philippine Islands.—Zoological Series of the Field Museum of Natural History 20(8):67–70.

Steel, R. 1973. Crocodylia.—Encyclopedia of Paleoherpetologie 16:vii–116.

Strauch, Alexander. 1866. Synopsis der gegenwärtig lebenden Crocodiliden.—Mémoires de L'Académie Impériale des Sciences de St.-Pétersbourg (Series 7) 10(13):1–120.

Wermuth, Heinz. 1953. Systematik der rezenten krokodile. Mitteilungen aus dem Zoologischen Museum, Berlin 29:375–514.

———, & R. Mertens. 1961. Schildkröten, Krokodile Brückenechsen. Gustav Fischer, Jena, xxvi + 422 pp.

———, & ———. 1977. Das Tierreich. Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia. Walter de Gruyter, Berlin, xxvii + 174 pp.

Werner, Franz. 1933. Das Tierreich. Loricata. Walter de Gruyter, Berlin and Leipzig, xiv + 40 pp.

Whitaker, Rom, & Zai Whitaker. 1989. Status and conservation of the Asian crocodilians. Pp. 297–308 *in* Crocodiles. Their ecology, management, and conservation. IUCN Special Publication, NS.

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 962–965

A NEW SUBSPECIES OF *DIGLOSSA GLORIOSISSIMA* (AVES: THRAUPINAE) FROM THE WESTERN ANDES OF COLOMBIA

Gary R. Graves

Abstract.—A new subspecies of flower-piercer, *Diglossa gloriosissima boylei,* is described from two localities at the northern end of the Western Cordillera of the Colombian Andes in the Department of Antioquia. The nominate race is apparently restricted to the highest part of the Western Cordillera west of Popayán, Department of Cauca.

The Chestnut-bellied Flower-Piercer, *Diglossa gloriosissima* (Chapman 1912), an allospecies of the *Diglossa lafresnayii* superspecies (Vuilleumier 1969), is known from only three isolated páramos in the Western Cordillera of the Colombian Andes (Hilty & Brown 1986) (Fig. 1). Specimens are scarce in collections and those reported in the literature were collected on two expeditions sponsored by the American Museum of Natural History (AMNH) in the early part of this century. Leo E. Miller and W. B. Richardson collected the type series of ten specimens (six adults) in July 1911 on the crest of the coast range west of Popayán (Chapman 1912), and Miller and Howarth Boyle collected a series some 500 km north of that locale on Cerro Paramillo in January 1915 (Chapman 1917, Zimmer 1929). The species was discovered at a third locality in August 1951 by Melbourne A. Carriker, Jr., who collected a series of six adults on Páramo Frontino for the National Museum of Natural History (USNM), Smithsonian Institution.

In a systematic review of the *D. lafresnayii* superspecies, Zimmer (1929:30) noted that, "specimens of *gloriosissima* from the western Andes near Popayan show considerable black along the flanks, and in this respect approach closer to *lafresnayii* than do birds from Paramillo. . . ." Contrary to his penchant for attaching subspecific names to the most subtly marked populations, Zimmer declined to designate the specimens from Cerro Paramillo as a new subspecies.

With the exception of the type, the adult specimens from Popayán were dispersed to other museums soon after Chapman's description of the species. I was able to examine three of these, most of the adults from Páramo Paramillo, and all of Carriker's specimens from Páramo Frontino. My analyses confirm Zimmer's observations and indicate that the northern populations from Páramo Frontino and Cerro Paramillo represent an undescribed subspecies.

Materials and methods.—Measurements of wing chord, tail from point of insertion of central rectrices to tip of longest rectrix, tarsus, and bill from anterior edge of nostril, were taken with digital calipers (Table 1). Wing and tail measurements were rounded to the nearest millimeter, those of tarsus and bill to the nearest 0.1 mm. T-tests were performed on untransformed data with SYSTAT software.

Diglossa gloriosissima boylei, new subspecies

Holotype.—National Museum of Natural History, Smithsonian Institution (USNM) No. 436792; male in adult plumage from Páramo Frontino, 11,850 ft (ca. 3613 m), Department of Antioquia, Colombia, collected 25 Aug 1951 by Melbourne A. Carriker, Jr. (original number 21013).

Diagnosis.—*Diglossa gloriosissima boylei* differs from *D. g. gloriosissima* in having uniformly chestnut flanks, sides, and undertail coverts, these regions in *D. g. gloriosissima* being sooty black or chestnut with black markings and spots.

Measurements of Holotype (mm).—Wing (chord) 68; tail 60; tarsus 22.9; bill 10.5.

Geographic range.—As far as known, restricted to elfin forest at timberline and patches of shrubbery in páramo on Páramo Frontino and Cerro Paramillo, Department of Antioquia, Colombia.

Specimens examined.—*Diglossa g. gloriosissima*: Coast range west of Popayán, Department of Cauca (AMNH Holotype, ♂; USNM ♂; FMNH ♂; MCZ ♂). *D. g. boylei*: Páramo Frontino, Department of Antioquia (USNM including Holotype, 6 ♂♂); Cerro Paramillo (AMNH 4 ♂♂, 2 ♀♀; USNM 1 ♂; MCZ ♂). Specimens of *D. gloriosissima* were compared directly with series of all named taxa of the *D. lafresnayii* (Vuilleumier 1969) and *D. carbonaria* superspecies (Graves 1982).

Etymology.—I am pleased to name this flower-piercer for Howarth S. Boyle, who with Leo Miller, made the first collections of *D. glorisissima boylei.*

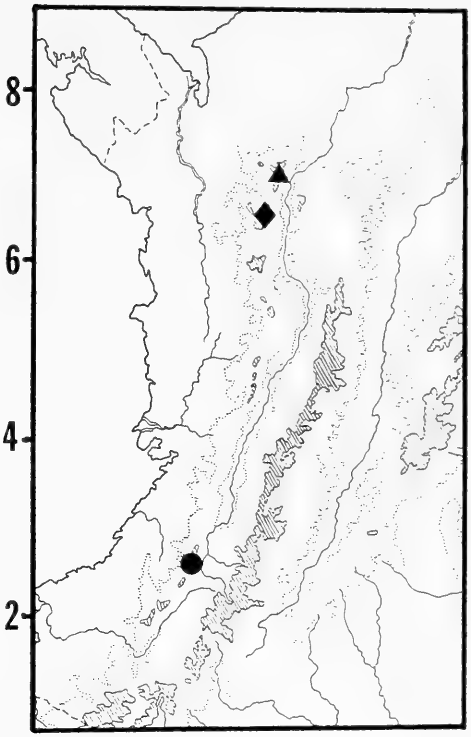


Fig. 1. Distribution of specimens of *D. gloriosissima* examined in this study from the Western Cordillera of the Colombian Andes. *D. g. gloriosissima*: W. Popayán (circle). *D. g. boylei*: Páramo Frontino (diamond); Cerro Paramillo (triangle). Degrees of north latitude are labeled along the y-axis. Dotted lines outline the 1000 m contour interval. Hatching indicates areas above 3000 m elevation.

Table 1.—Ranges and means of measurements (mm) of *Diglossa gloriosissima.*

Subspecies	Sex	*n*	Wing chord	Tail	Tarsus	Bill
D. g. gloriosissima						
W Popayán	♂♂	4	74–77 $\bar{X} = 75.3$	64–67 $\bar{X} = 65.3$	24.0–24.9 $\bar{X} = 24.5$	9.2–9.8 $\bar{X} = 9.4$
D. g. boylei						
Páramo Frontino	♂♂	6	68–71 $\bar{X} = 69.7$	59–63 $\bar{X} = 60.2$	22.9–24.3 $\bar{X} = 23.7$	9.5–10.5 $\bar{X} = 9.8$
Cerro Paramillo	♂♂	6	71–75 $\bar{X} = 72.7$	64–65 $\bar{X} = 64.6$	23.5–24.6 $\bar{X} = 24.2$	9.9–10.7 $\bar{X} = 10.1$
	♀♀	2	69–70	63	22.5–23.9	10.3–10.4

Table 2.—One-tailed *t*-tests of character means of male population samples of *Diglossa gloriosissima* (see Table 1). Significant *t* values, adjusted for the number of simultaneous tests ($P = 0.05/12 = 0.004$), are indicated by *.

Population contrasts			Wing chord	Tail	Tarsus	Bill
Popayán	versus	Páramo Frontino	5.00*	4.84*	2.52	1.70
Popayán	versus	Cerro Paramillo	2.35	1.06	1.10	3.58
Páramo Frontino	versus	Cerro Paramillo	3.80*	6.04*	1.83	1.45

Results

There appear to be significant size differences among populations of *D. gloriosissima,* with specimens from Páramo Frontino, geographically interposed between Popayán and Cerro Paramillo, having shorter wings and tails than those from the other localities (Table 2). Because intraspecific size variation in birds may reflect environmental induction as well as genetic differentiation (James 1983), it is deemed unwise to recognize these differences nomenclaturally. Moreover, significant geographic size variation occurs within several subspecies of *Diglossa carbonaria* that exhibit little or no variation in plumage color and pattern. In these cases, I consider size as a taxonomically unreliable character. On the other hand, qualitative plumage differences, such as those expressed among populations of *D. gloriosissima,* are thought to be genetically determined.

The avifauna of the Western Cordillera is poorly known relative to other parts of the Colombian Andes. As an example, Hilty & Brown (1983) documented 63 major range extensions of species in the Western Cordillera based on previously unreported material collected by Carriker in the 1940's and 1950's. Although populations of *D. gloriosissima* and other taxa now restricted to Cerro Paramillo and Páramo Frontino (e.g., *Coeligena orina, Metallura williami recisa*) may occur on several of the ornithologically unexplored peaks between Popayán and Páramo Frontino, the insular nature of habitat above 3000 m elevation suggests that gene flow among populations of *D. gloriosissima* has been drastically reduced since the Wisconsinan glacial (Graves 1980).

Acknowledgments

I thank Richard Banks, Scott Lanyon, and Storrs Olson for comments on the manuscript and the curators of the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), and Museum of Comparative Zoology, Harvard University (MCZ) for permission to examine specimens. Museum work was partially funded by the Frank M. Chapman Memorial Fund of the American Museum.

Literature Cited

Chapman, F. M. 1912. Diagnoses of apparently new Colombian birds.—Bulletin of the American Museum of American History 31:139–166.

———. 1917. The distribution of bird-life in Colombia: a contribution to a biological survey of South America.—Bulletin of the American Museum of Natural History 36:1–729.

Graves, G. R. 1980. A new subspecies of *Diglossa* (*carbonaria*) *brunneiventris.*—Bulletin of the British Ornithologist's Club 100:230–232.

———. 1982. Speciation in the Carbonated Flower-piercer (*Diglossa carbonaria*) complex of the Andes.—Condor 84:1–14.

Hilty, S. L., & W. L. Brown. 1983. Range extensions of Colombian birds as indicated by the M. A. Carriker Jr. collection at the National Museum of Natural History, Smithsonian Institution.—Bulletin of the British Ornithologist's Club 103: 5–17.

———, & ———. 1986. A guide to the birds of Colombia. Princeton, New Jersey, Princeton University Press, 717 pp.

James, F. C. 1983. Environmental component of morphological variation in birds.—Science 221: 184–186.

Vuilleumier, F. 1969. Systematics and evolution in *Diglossa* (Aves, Coerebidae).—American Museum Novitates 2381:1–44.

Zimmer, J. T. 1929. Variation and distribution in two species of *Diglossa*.—Auk 46:21–37.

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
103(4), 1990, pp. 966–972

THE HOLOTYPE OF *NATALUS STRAMINEUS* GRAY (MAMMALIA: CHIROPTERA: NATALIDAE)

Charles O. Handley, Jr. and Alfred L. Gardner

Abstract.—The description of *Natalus stramineus* Gray was based on an unspecified number of specimens of unknown provenance. We review the critical specimens and their history in the mammal collections of the British Museum (Natural History). We identify the holotype of *N. stramineus,* and we believe that Goodwin (1959) was correct in claiming that it originated in the West Indies rather than in South America.

In the original description of *Natalus stramineus,* Gray (1838) did not specify the number of specimens examined and indicated that he did not know the origin of his material. Later Gray (1843) said that he had a fluid-preserved specimen from South America and another (presumedly dry) from St. Blas, North America; this information was repeated by Tomes (1856). Dobson (1878) listed a male in alcohol from Brazil, an unsexed skin from South America, and a male in alcohol from Dueñas, Guatemala. Authors subsequent to Dobson gave Brazil as the type locality of *N. stramineus.* Goodwin (1959), however, suggested with good reason that the type came from the West Indies, not Brazil as previously supposed. When he shifted the type locality from Brazil to the West Indies, Goodwin synonymized Shamel's (1928) West Indian *Natalus dominicensis* with *N. stramineus,* and renamed the Brazilian population *N. stramineus natalensis.* Goodwin (1959) argued correctly that the specimen in the British Museum (Natural History) he believed to be the holotype of *N. stramineus* was the same as that listed by Gray (1843) and Tomes (1856) from South America and by Dobson (1878) from Brazil. Following Goodwin (1959), the nomenclature of *N. stramineus* appeared stable, but some authors (Carter & Dolan 1978, Honacki et al. 1982) have continued to list Brazil as the type locality. We intend to set the record straight in this report.

The Evidence

In 1971, Handley examined the putative holotype of *N. stramineus* in the British Museum, reviewed its history in collections of the Mammal Section, and attempted to determine its provenance. However, there are alternative possible types or syntypes of *N. stramineus* in the British Museum that represent other populations, and the situation is complicated by apparent multiple relabeling of specimens. Because the clues leading to recognition of the holotype and a second specimen reported by Gray in 1843 come from a number of sources, we list the evidence in considerable detail.

Gray 1838.—Gray (1838:496) described *Natalus* as a new genus and *N. stramineus* as a new species. He gave no morphological measurements, but indicated that he actually had a specimen by his statement, "inhabits _____? British Museum." By implication he had at least one specimen of unknown origin.

Gray's mss. catalogue.—Soon Gray had another specimen, as his undated handwritten catalog of Primates and Chiroptera in the British Museum (referred to in literature as "Gray's Mss. Catalogue") shows the following entry: "69./ Vespertilio longicaudatus, *Gray Mss/* Natalus stramineus Gray Mag Zool & Bot. 1837 [sic]/ a. S. America/ b. St. Blass/ Purchased of Mr. Gould/ 42.8.17.10."

Museum register 1842.—The museum register has the following information for number 42.8.17.10 (in the registry system of the Mammal Section this was the tenth specimen registered on 17 August 1842): "Vespertilio/ St. Blas/ Purchased of Mr. Gould,/ Cheirop. 69b."

Gray 1843.—The data from Gray's *mss.* catalogue and the museum register were repeated in Gray's published "Catalogue" (1843:28) with important additions:

> "The Natale. Natalus stramineus, *Gray, Mag. Zool. and Bot.* II. 14. Vespertilio longicaudatus, *Gray, Brit. Mus.*
> *a.* In spirits. South America.
> *b.* N. America, St. Blas."

In the British Museum copy of his 1843 "Catalogue," Gray inked the figure "69" in the margin beside specimen "*a,*" referring back to his "Mss. Catalogue" number. Recognition of handwriting in books, papers, and specimen labels in the Mammal Section of the British Museum is a relatively simple task because the Section has preserved samples of handwriting of all who have worked there.

Evidently, by August 1842, there were only two specimens of *N. stramineus* in the British Museum. The facts that specimen "69"*a* was from an indefinite locality and that it was preserved in spirits are two important bits of information. Clearly the holotype of *N. stramineus* must be "69"*a,* because *b* was from a definite locality, and Gray's original reference (1838) specified "inhabits ______? British Museum."

Tomes 1856.—Tomes (1856:176–178, pl. 43) redescribed the genus *Natalus* and the species *N. stramineus* in great detail. He concluded with the statement, "The whole of the above [description] has been taken, by the kind permission of Dr. Gray, from the two examples mentioned in his Catalogue [1843], and the following are their dimensions. The first column [No. 1.] refers to the specimen in spirits from South America, and the second [No. 2.] to the one from St. Blas, North America." A table of measurements of the two specimens followed. Plate 43 is colored, shows great detail, has accurate proportions, and seems to have been drawn life size. Although its source was not specified, measurements taken from the figure on Plate 43 coincide closely with those listed by Tomes for his specimen No. 2, the one from "St. Blas." Thus, at the time of Tomes' writing there continued to be only two specimens of *N. stramineus* in the British Museum. The specimen labeled "South America" and preserved in spirits must be the holotype Gray described in 1838. It is the larger of the two. The other, evidently dry, labeled "St. Blas," and figured by Tomes (1856:pl. 43), is smaller.

Dobson 1878.—Dobson (1878:343) listed three specimens of *N. stramineus* in his catalogue of Chiroptera in the British Museum and gave the distribution of the species as "Brazil; Central America." The first two specimens were listed as:

a. ♂ ad., al.	Brazil.
b. ad. sk.	South America.

The third was listed on the same page under Var *a.* as:

a. ♂ ad., al.	Dueñas, Guatemala. O. Salvin, Esq. [C.].

Dobson (1878:344) gave a table of external measurements of two of the specimens. The first column is headed "*N. stra-/mineus*" and the second, "Var *a.*" The measurements under *N. stramineus* must have been of either Dobson's specimen "*a*" or "*b.*" Some time later, Thomas wrote "type" in the margin beside specimen "a. ♂ ad., al. Brazil" in the Mammal Section's copy of Dobson's catalogue.

Cabrera 1958.—Cabrera (1958:73) restricted the type locality of *N. stramineus* to Lagoa Santa, Minas Gerais, Brazil, on the basis of Winge's (1892) report of the first definite locality for the species from the country where Dobson (1878) said the type had originated.

Goodwin 1959.—Goodwin (1959:4–5, 16), on the basis of measurements and cranial morphology, stated that the holotype of *N. stramineus* matched representatives of populations inhabiting the Lesser Antilles. As is evident from material in the mammal collections of the National Museum of Natural History, Washington, D.C., the Brazilian population differs sufficiently from that of the Lesser Antilles to make confusion of specimens between the two populations unlikely. On the same basis, Goodwin (1959) ruled out Venezuela, Trinidad and Tobago, Central America, and México as possible origins. He said that Gray's type could not have come from Brazil or anywhere else in South America and proposed restricting the type locality to the island of Antigua, British West Indies.

Carter & Dolan 1978 and subsequent reports.—Carter & Dolan (1978) said that of the two specimens of *Natalus stramineus* reported by Gray (1843:23), the one in fluid labeled Brazil was the only identifiable one remaining. They said it was an unnumbered adult male in alcohol (with skull removed), and gave the type locality as Lagoa Santa, Minas Gerais, as restricted by Cabrera (1958: 95). Because they reported this specimen as unnumbered, their information must have come from Carter's visit to the British Museum in 1966. In 1970 this specimen was registered as No. 70.2324. Presumably, it was during 1966 and not when they revisited the British Museum in 1976 that Carter & Dolan (1978:11) were unable to find the second specimen listed by Gray (1843) from "N. America, St. Blas." Apparently misled by Gray's (1843) mention of two specimens, Carter & Dolan (1978) presumed them to be syntypes. They also commented that Goodwin (1959), in disagreement with Cabrera (1958), designated the type locality as Antigua, Lesser Antilles. They probably followed Cabrera's restriction of the type locality to Lagoa Santa, Minas Gerais, because of Dobson's jar label, which said Brazil. Hall (1981) followed Goodwin's designation of Antigua; but Honacki et al. (1982) followed Cabrera's (1958) restriction.

The specimens.—All three specimens listed by Dobson were still in the British Museum in February 1971 when Handley examined them, and in October 1987 when Gardner examined them. Numerous other specimens of *Natalus stramineus* now in the British Museum bear dates later than 1878, have definite locality data, and are not relevant in this discussion. Presuming that it still exists, the holotype of *N. stramineus* must be one of the three specimens listed by Dobson (1878:343). The oldest label attached to each of these three specimens was written by Dobson himself. Presumably, he was responsible for changes where the label data differed from those published by Gray (1838, 1843) and Tomes (1856).

The male in alcohol with skull removed and cleaned is labeled "Natalus stramineus Gray/ (G. E. Dobson)." This specimen was finally registered in 1970, and at that time the jar label was emended to read: "Type/ ♂/ Natalus stramineus, Gray/ 70.2324/ Brazil." Unfortunately and unaccountably, 15 of the 20 finger bones and both tibiae of this specimen have been broken. Otherwise its condition was reasonably good in 1971.

The second specimen is an unsexed, dry skin with skull inside that lacked a registry number in 1971. It is labeled "Natalus stramineus, Gray/ (G. E. Dobson) ? (type) South America," all in Dobson's handwriting.

The third specimen, number 75.2.27.72, a male in alcohol with skull removed and cleaned, was labeled "Natalus stramineus/ (G. E. Dobson)/ Dueñas, Guatemala/ O. Salvin, Esq." It agrees morphologically with other specimens of *Natalus* from Guatemala, and because there is no reason to doubt the accuracy of its label information, it can be eliminated from the search for the holotype of *N. stramineus.*

Discussion

The specimens.—The situation thus posed is of a single specimen of *N. stramineus* described by Gray in 1838 without data, two specimens in the period 1842–1856 with data (Gray 1843, Tomes 1856), and two specimens in 1878 (Dobson) with different data. Correlation of the measurements (Table 1) from Tomes' (1856) table and plate, Dobson's (1878) table, and the two specimens in the British Museum in 1971 with the information published by Gray (1838, 1843), Tomes (1856), and Dobson (1878), and with the present label data of the specimens leads to the conclusion that only two specimens have been involved throughout, that the label data for the holotype changed at least twice, and that neither specimen was properly labeled in 1971 (Table 2).

The coincidence of measurements is too great (see Table 1) to suggest other than that the "*b*" of Gray (1843), specimen BM 42.8.17.10 from St. Blas, "No. 2" and plate 43 of Tomes (1856), "*b*" of Dobson (1878), and the unregistered specimen labeled "South America" in 1971 are all the same. This specimen, which agrees morphologically with *Natalus* from western México, is the other implied "syntype" Carter & Dolan (1978) were unable to recognize because it was labeled "South America" when Carter examined it in 1966. Evidently Dobson, or someone else between 1856 and 1878, confused the data and transferred "South America" from the holotype (which originally had been without locality data) to the San Blas specimen. As of 1971, no bat in the British Museum was labeled "St. Blas" or "42.6.17.10."

The possibility exists that specimen "*a*" of Dobson (1878) from "Brazil" (presently no. 70.2324) was a new specimen obtained sometime between 1856 and 1878, and had nothing to do with Gray's type of *N. stramineus.* However, again based on the coincidence of measurements given by Tomes (1856) and Dobson (1878), and those of specimen BM 70.2324 (Table 1), as well as the mode of preservation, the evidence is compelling that BM 70.2324 is the specimen Gray had at hand in 1838 when he described *N. stramineus.*

Table 1.—Measurements (in millimeters) of the holotype (BM 70.2324) and contemporaneous specimen (BM 42.8.17.10) of *Natalus stramineus* from a table in Tomes (1856:178), plate XLIII in Tomes (1856; measured by Handley), a table in Dobson (1878:344), and the specimens in the British Museum (Nat. Hist.) measured by Handley in 1971. Measurements in brackets indicate approximations.

Measurement Specimen	Tomes (1856)		Dobson (1878)	Specimens 1971 (left/right)
	Table	Plate	Table	
Forearm				
70.2324	37.5		37.9	38.3/38.1
42.8.17.10	35.4	36.5		[35.9]/
Tibia				
70.2324	20.1		19.1	[19.0]/
42.8.17.10	16.9	17.2		18.0/
Third finger				
70.2324	76.2			71.7/72.4
42.8.17.10	69.9	66.0		67.3/
Fourth finger				
70.2324	55.0			54.0/53.5
42.8.17.10	48.9	50.5		51.6/

The labels.—Having established that Gray (1838) had only one specimen before him when he described *N. stramineus,* and having identified that specimen from among others now in the British Museum, we attempt to account for the several changes in localities assigned to it (see Table 2). We start with Gray's original statement (1838) that the provenance of the holotype was unknown. One can see how Gray later could have come to label it "South America." Receipt of the second specimen from a definite locality, "St. Blas" (= San Blas, Nayarit,

Table 2.—An outline and chronology of the information available on specimens of *Natalus stramineus* reported by Gray in 1838 and 1843.

Reference	Specimen	Specimen
Gray (1838)	"Inhabits ____?" (holotype of *N. stramineus*)	
Gray (ca. 1842, mss. catalogue)	S. America "Natalus stramineus Gray Mag. Zool. & Bot. 1837 [sic]" 69.a	St. Blass "purchased of Mr. Gould" 42.8.17.10 69.b
Gray (1843)	South America In spirits *a.*	North America St. Blas [Dry?] *b.*
Tomes (1856)	South America In spirits No. 1 in table of measurements	North America St. Blas [Dry?] No. 2 in table of measurements
Dobson (1878)	Brazil In alcohol *N. stramineus* in table of measurements *a.*	South America [Dry?] *b.*
Specimen labels (1971)	Brazil In alcohol BM 70.2324	South America Dry Unregistered
Goodwin (1959)	Antigua, Lesser Antilles	
Conclusions herein	Origin unknown [Lesser Antilles] BM 70.2324	San Blas, Nayarit, México 42.8.17.10

México), must have prompted him to assume that the unlabeled holotype also came from somewhere in Latin America and led him to label it, in the broad sense, as from "South America" (a common euphemism for Latin America). If these events are properly reconstructed, this was the first of other erroneous relabelings of this specimen. Emending labels or relabeling, practices at the British Museum that began with Gray and were continued by Tomes, Dobson, and Thomas, have produced some label data that are unreliable or suspect. Another potential problem with Mammal Section spirit specimens is that, in the 19th Century, usually the jars rather than the specimens themselves were labeled, leading to possible confusion between jars or within jars when they contained more than one specimen (e.g., Smith 1971:80–81).

Although we can understand how the holotype of *N. stramineus* could have been erroneously labeled "South America," it is a mystery how Dobson (1878) came up with the label "Brazil" for it. Possibly, when relabeling specimens, Dobson's selection of "Brazil" as the origin of the holotype was influenced by the similarity between the name *Natalus* and Natal, the capital of the Brazilian State of Rio Grande do Norte (eventually to be the type locality of *N. stramineus natalensis* Goodwin, 1959). It seems unlikely that he could have mistaken the handwritten "St. Blas" in Gray's "Mss. Catalogue" for Brazil. Equally unlikely is the possibility that he got new information directly from Gray. Dobson and Gray overlapped only briefly at the British Museum. Dobson, an army surgeon who came to London in 1873, took up the project of listing the Chiroptera in the British Museum while he continued medical work at Nethley Hospital. Gray suffered a stroke in 1869 and, although paralyzed on the right side, he returned to the Museum after a few months and continued to work there until the latter part of 1874. He died in 1875 (Günther 1912). Besides, if Gray had had new information, surely it would have been used by Tomes. There is nothing to suggest that Dobson's "Brazil" and "South America" localities for two of the three specimens he reported were based on actual information on their origins.

We are not aware of any South American populations clearly assignable to *N. stramineus* except for the widespread Brazilian population Goodwin (1959) named *N. stramineus natalensis.* Cuervo D. et al. (1986) listed *N. stramineus* for Colombia, but indicated neither specimens nor localities. According to Goodwin (1959) the two specimens Sanborn (1941) listed as *N. stramineus* from Trinidad proved to be *N. tumidirostris.* Goodwin (1959) also pointed out that the Guyanan (British Guiana) specimen identified as *N. stramineus* by Jentink (1893:79), Young (1896:44), and Beebe (1919:219), is a *Furipterus horrens.*

Conclusions

Gray (1838) had only a single specimen before him when he described *Natalus stramineus* as a new genus and species. It was an adult male in spirits. Its origin was not known, but we believe as did Goodwin (1959) that it came from the Lesser Antilles (restricted type locality, Antigua). It is BM 70.2324, erroneously labeled "Brazil," and preserved in fluid with skull removed.

The second specimen is a dry skin with skull inside from San Blas, Nayarit, México (= St. Blas, North America), first mentioned in Gray's mss. catalogue, probably in 1842. It is BM 42.8.17.10; but is erroneously labeled "South America" without registry number. It is an example of *N. stramineus saturatus* Dalquest & Hall, 1949.

Acknowledgments

We express our appreciation to the staff of the Mammal Section of the British Museum, and particularly to Mr. J. E. Hill, for the many courtesies and assistance graciously accorded us during our work in the mammal collections. Darelyn Handley was indispensable in the search for information in London in 1971 and in assembly of early drafts of this manuscript.

Literature Cited

Beebe, W. 1919. High vertebrates of British Guiana.—Zoologica 2:205–227.

Cabrera, A. 1958. Catálogo de los mamíferos de América del Sur.—Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoológicas 4(1):iv + 308 pp.

Carter, D. C., & P. G. Dolan. 1978. Catalogue of type specimens of Neotropical bats in selected European museums.—Special Publications the Museum, Texas Tech University 15:1–136.

Cuervo D., A., J. Hernández C., & A. Cadena G. 1986. Lista actualizada de los mamíferos de Colombia anotaciones sobre su distribución.—Caldasia 15: 471–502.

Dalquest, W. W., & E. R. Hall. 1949. A new subspecies of funnel-eared bat (Natalus mexicanus) from eastern Mexico.—Proceedings of the Biological Society of Washington 62:153–154.

Dobson, G. E. 1878. Catalogue of the Chiroptera in the collection of the British Museum. British Museum (Natural History), London, xlii + 567 pp., 30 pls.

Goodwin, G. G. 1959. Bats of the subgenus *Natalus.*—American Museum Novitates 1977:1–22.

Gray, J. E. 1838. A revision of the genera of bats (Vespertilionidae), and the description of some new genera and species.—Magazine of Zoology and Botany 2:482–505.

———. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum (Natural History), London, xxviii + 216 pp.

Günther, A. 1912. General history of the Department of Zoology from 1856–1895. Pp. i–ix + 1–109 *in* The history of the collections contained in the natural history departments of the British Museum. British Museum (Natural History), London, Vol. 2, Appendix.

Hall, E. R. 1981. The mammals of North America. Second edition. J. Wiley & Sons, New York, 1: xv + 1–600 + 90.

Honacki, J. H., K. E. Kinman, & J. W. Koeppl. 1982. Mammal species of the world. Allen Press, Incorporated, and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Jentink, F. A. 1893. On a collection of bats from West-Indies.—Notes Leyden Museum 15:278–283.

Sanborn, C. C. 1941. Descriptions and records of Neotropical bats.—Field Museum of Natural History, Zoological Series 27:371–387.

Shamel, H. H. 1928. A new bat from Dominica.—Proceedings of the Biological Society of Washington 41:67–68.

Smith, J. D. 1971. Review of the Mormoopidae.—Miscellaneous Publication Museum of Natural History, University of Kansas 56:1--132.

Tomes, R. E. 1856. On three genera of Vespertilionidae, Furipterus, Natalus and Hyonycteris, with descriptions of two new species.—Proceedings of the Zoological Society of London 1856:172–181, pls. 42 and 43.

Winge, H. 1892. Jordfundne og nulevende Flagermus (*Chiroptera*) fra Lagoa Santa, Minas Geraes, Brasilien.—E Museo Lundii, Kjøbenhavn 2(part 1):1–65, 2 pls.

Young, C. G. 1896. Notes on Berbice bats.—Timehri, New Series 10:44–46.

(COH) Division of Mammals, National Museum of Natural History, Washington, D.C. 20560; (ALG) Biological Survey Field Station, National Ecology Research Center, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 29 June 1990 in Vol. 47, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.	
2630	*Helix* (*Helicigona*) *barbata* Férussac, 1832 (currently *Lindholmiola barbata*; Mollusca, Gastropoda): proposed confirmation of lectotype designation.
2699	RISSOOIDEA (or RISSOACEA) Gray, 1847 (Mollusca, Gastropoda): proposed precedence over TRUNCATELLOIDEA (or TRUNCATELLACEA) Gray, 1840.
1643	*Mytilus anatinus* Linnaeus, 1758 (currently *Anodonta anatina*; Mollusca, Bivalvia): proposed designation of a neotype.
2762	*Griffithides* Portlock, 1843 (Trilobita): proposed confirmation of *Griffithides longiceps* Portlock, 1843 as the type species, so conserving *Bollandia* Reed, 1943.
2687	*Longitarsus symphyti* Heikertinger, 1912 (Insecta, Coleoptera): proposed conservation of the specific name.
2738	*Acanthophthalmus* van Hasselt in Temminck, 1824 (Osteichthyes, Cypriniformes): proposed conservation, and proposed designation of *Cobitis kuhlii* Valenciennes in Cuvier & Valenciennes, 1846 as the type species.
2693	*Trionyx sinensis* Wiegmann, 1834 (Reptilia, Testudines): proposed conservation of the specific name.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 29 June 1990 in Vol. 47, Part 2 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1587 *Orbitolina* d'Orbigny, 1850 (Foraminiferida): *Orbulites concava* Lamarck, 1816 confirmed as the type species.

1588 *Hapalorhynchus beadlei* Goodman, 1987 (Trematoda, Digenea): holotype replaced by a lectotype.

1589 *Phyllodoce* (*Carobia*) *rubiginosa* Saint-Joseph, 1888 (currently also *Nereiphylla rubiginosa*; Annelida, Polychaeta): specific name conserved.

1590 *Pleuromma princeps* Scott, 1894 (currently *Gaussia princeps*; Crustacea, Copepoda): specific name conserved.

1591 *Fizesereneia* Takeda & Tamura, 1980 (Crustacea, Decapoda): *Troglocarcinus heimi* Fize & Serène, 1956 confirmed as the type species.

1592 *Bodotria* Goodsir, 1843 (Crustacea, Cumacea): conserved.

1593 *Iphinoe* Bate, 1856 (Crustacea, Cumacea): conserved.

1594 *Leucon* Krøyer, 1846 (Crustacea, Cumacea): conserved.

1595 *Aleuropteryx* Löw, 1885 (Insecta, Neuroptera): *Aleuropteryx loewii* Klapálak, 1894 designated as the type species.

1596 *Semblis* Fabricius, 1775 (Insecta, Trichoptera): *Phryganea phalaenoides* Linnaeus, 1758 conserved as the type species, thus conserving *Sialis* Latreille, 1802 (Insecta, Megaloptera).

1597 *Coryphium angusticolle* Stephens, 1834 (Insecta, Coleoptera): generic and specific names conserved.

1598 *Ophonus* Dejean, 1821 and *Tachys* Dejean, 1821 (Insecta, Coleoptera): *Carabus sabulicola* Panzer, 1796 and *Tachys scutellaris* Stephens, 1828 designated as the respective type species.

1599 *Papilio carthami* Hübner, [1813] and *Syrichthus serratulae major* Staudinger, 1879 (currently both in *Pyrgus*; Insecta, Lepidoptera): the specific names *carthami* and *major* conserved.

1600 *Tachina orbata* Wiedemann, 1830 (currently *Peribaea orbata*; Insecta, Diptera): neotype designation confirmed.

1601 *Rapport sur les Myodaires du Docteur Robineau Desvoidy* (1826): suppressed for nomenclatural purposes.

1602 *Tenthredo zonula* Klug, 1817 (Insecta, Hymenoptera): specific name conserved.

1603 *Saccopharynx* Mitchill, 1824 (Osteichthyes, Saccopharyngiformes): conserved.

1604 ICHTHYOPHIIDAE Taylor, 1968 (Amphibia, Gymnophiona): conserved.

1605 *Thorius pennatulus* Cope, 1869 (Amphibia, Caudata): specific name conserved.

1606 *Semioptera wallacii* Gray, 1859 (Aves, PARADISAEIDAE): conserved as the correct spelling of the generic and specific names.

1607 *Mus musculus domesticus* Schwarz & Schwarz, 1943 (Mammalia, Rodentia): specific name conserved.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

GUIDELINES FOR MANUSCRIPTS
For Publications of the
BIOLOGICAL SOCIETY OF WASHINGTON

Supplement to Volume 103, No. 1
March 1990
Proceedings of the Biological Society of Washington

VOLUME 103 NUMBER 1
MARCH 1990

Send Proof To;

Dr. C. Brian Robbins
Division of Mammals
National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20560

GUIDELINES FOR MANUSCRIPTS FOR PUBLICATIONS OF THE BIOLOGICAL SOCIETY OF WASHINGTON

C. Brian Robbins and David B. Lellinger

Abstract.--The abstract should be ≤3% of the length of the text of the article. It should be a concise statement of findings, rather than a listing of subjects covered, and should be written as a single paragraph and double spaced. Except under unusual circumstances, references should not be cited in the abstract. All newly described taxa must be given by name in the abstract.

This paper provides authors with guidelines and examples to aid in preparing manuscripts for the Biological Society of Washington. The required format for manuscripts for the Proceedings and Bulletin is presented and followed herein as a model of format and style. However, except for the title, author(s), abstract, and figure and table captions, the final printed papers appear in double-column format rather than occupying a complete page as does this manuscript. It is neither possible nor desirable to provide detailed examples of every format or style item, but we have attempted to address most of the potential questions facing an author preparing a manuscript.

As a general guide, we recommend the fifth edition of the CBE Style Manual (CBE Style Manual Committee 1983), available from the Council for Biology Editors, 9650 Rockville Pike, Bethesda, Maryland 20814; cost is $24.00, including postage. The latest edition is a more comprehensive guide for scientific writers than were previous editions. A shorter but useful guide is Day's (1988) How to Write & Publish a Scientific Paper, Third Edition; softcover copies of this guide are available from Oryx Press, 2214 North Central at Encanto, Phoenix, Arizona 85004; $14.95 for copies mailed to North America, $17.95 mailed elsewhere.

Methods

Manuscript preparation.--Type manuscripts on letter size (215- by 280-mm, 8 1/2- by 11-in.) or A4 (210- by 297-mm, 8 1/4- by 12 1/8-in.) paper. All parts of the manuscript should be double-spaced, including text, literature cited, tables, table headings, and figure legends, so that reviewers, editors, printers, and proofreaders can make essential notations. Do not justify the right margin. Allow ≥3-cm (1 1/2 in) margins on all sides.

Do not use a title page. Type name, address, and telephone number of the author to whom all correspondence and proof is to be sent at the upper left of the first page. (Note to foreign authors: this is the place to indicate the name and address of the person in the U.S.A. who will read proof.) Place page numbers at upper right of all pages except the first.

Titles should be brief and include key words that will be useful for indexing and information retrieval. Include phylum, class, order, and family names (separated by a colons and a space [e.g., Crustacea: Copepoda: Caligidae]) for species likely to be unfamiliar to many readers. In subsequent use of scientific names, abbreviate generic names where possible (e.g., Studies on Botrychium meridionale and B. virginianum); do not abbreviate scientific names in titles or subheadings if they have not been previously spelled out in the same title or subheading. Center the title and type it in uppercase letters, including underlined scientific names.

Three spaces below the title, type the name(s) of the author(s) centered on the page. Triple-space after the author(s) name(s) and begin the abstract, using a normal paragraph indentation as shown on page 1 (secondary heading - see below) and write the entire abstract as a single paragraph. Also, indent five spaces at the beginning of each paragraph throughout the text. Double-space after the abstract and insert a 5-cm horizontal line. Double space after the line (as on page 1) and begin the introductory material. Do not use "Introduction" as a heading.

In general, use no more than three levels of organization: primary headings (centered); secondary headings (indented from left-hand margin, underlined, followed by a period and two dashes); and tertiary headings (indented from left-hand margin, ending with a colon). New taxon names and associated citation of their taxonomic placement (phylum, class, order, family, etc.), and figure and table references are primary headings, for example: (Note: unless the higher taxonomic categories are the primary topic, author and date citations are not necessary.)

Systematic Paleontology
Class Mammalia Linnaeus, 1758
Order Chiroptera Blumenbach, 1779
Family Desmodontidae Gill, 1884
Genus Desmodus Maximilian, 1824
Desmodus archaeodaptes, new species
Fig. 1

Long lists or complex material that is related only indirectly to the primary subject should be placed in an appendix at the end of the manuscript. Items that are appropriate for appendices include: lists of specimens examined; lists of morphometric characters, or ecologic characters; derivations of complex mathematical or statistical formulas; and algorithms for computer programs. Appendices may be arranged as paragraphs, in tables, or in other formats as appropriate. Short lists, single formulas, and material related more directly to the subject should be placed in the text. Material not essential to the article should be omitted.

Never break words at the right-hand margin anywhere in the manuscript for any reason. This includes hyphenated words as well as words divided between syllables.

Spell out the entire scientific name the first time a plant or animal is mentioned; thereafter, abbreviate generic names (first letter and period), except at the beginning of a paragraph or sentence. Include author(s) and date where such is essential to identification of a taxon (such as in a synonymy). If subgeneric names are used, they should be placed between the generic and specific names, and be enclosed in parentheses; abbreviate them after their initial use, using the first letter of their name. Use subspecies or infraspecific names only when they are essential to the understanding of the article. New descriptions in zoology should be spelled out, as: "new genus," "new species," "new subspecies", and "new combination," or for botanical papers use: "gen. nov.", "sp. nov.", "subsp. nov.", or "comb. nov." Each of these should be preceded by a comma. Descriptions must be in English, except for Latin descriptions or diagnoses in botanical papers (fossils excepted).

Provide the scientific name (generic and specific names) of all organisms at first mention of the vernacular name both in abstract and text (even if the name appears in the title); use the scientific name of the appropriate taxon if a vernacular name is inclusive (e.g., crickets [Gryllidae]).

<u>Tables and Figures</u>.--Because of the cost of publication, tables should be used only when large quantities of data must be summarized or trends in data illustrated to support inferences. Pertinent data in most small tables (two-row or two column tables) usually can be presented in the text in less space and without loss of intelligibility. Consider carefully the presentation of non-tabular data in the two-

column format of the Proceedings. In many instances, a table would be easier to read and type-set.

Figures and tables should be numbered in the sequence in which they are referred to in text. Reference in text should be in the style: (Fig. 1) and (Table 1). Reference to several tables or figures in text should be in the style: (Tables 1, 2) and (Figs. 1, 2). Parts of composite figures should be labeled with uppercase or lowercase letters, or numbers, and should be used to refer to parts of figures both in legends and in text (e.g., Fig. 1a, b, d; Figs. 1-3, 5; or Figs. 1B-D, 2D-F). Then note the desired location for each figure and table in pencil in the left margin of the manuscript.

Because many readers prefer to scan data before reading text, each table or figure with its title or legend should be understandable without reference to the text. Be sure to include species, localities, and dates of study, if appropriate, in addition to a description of the content. Abbreviate words in column heads or data identifiers (stub columns) only when necessary. Spell out names of months except where space does not permit. When abbreviated, and in the Materials section, use three-letter abbreviations without periods (e.g., Jan, Jun, Oct). Reference in the text to tabular and graphic presentations of data should be in support of inferences, not simply to direct the reader to specific tables or graphs. For example, use sentences such as "Litter size did not seem related to month of onset or duration of the reproductive season (Table 1)," but avoid sentences such as "Data on litter size, and month of onset and duration of the reproductive season in some Spermophilus are presented in Table 1." Do not describe the content of tables and figures in text; the need for such description indicates that the tables and figures are not understandable by themselves. Data should be presented either in graphic (figures) or tabular form, whichever is more understandable or economical of space. Figures should be constructed to be fully legible and not wasteful of space when reduced to column width or page width. Orient multiple graphics having two or three illustrations one above the other if reduction to a single column is desired. Illustrations that are intended for a full-page presentation, should be mounted accordingly.

TABLE 1
near here

Type each table on a separate sheet(s), give it a complete, intelligible title, and refer to it by number in text. In titles of tables, italicized and Roman type is presented as in the text. Capitalize only the first word of column heads and items in the secondary or data identifier column heads; do not use all uppercase letters in headings. Do not use a dash or minus sign in a table to indicate lack of observations or tests if the table contains plus and minus signs; otherwise its use is clear (= missing data). Footnotes to tables should be kept to a minimum. Lowercase letters should be used to denote footnotes except those limited to probability; one, two, or three asterisks (*) should be used for $\underline{P} < 0.05$, 0.01, and 0.001, respectively.

Provide a legend for each figure and refer to the figures in the text. Type all figure legends, double-spaced, on a separate sheet at the end of the manuscript; the typescript format for figure legends is illustrated in Appendix I. In legends, underline only those words or terms (i.e., genus and species names) that will be set in italics (as listed elsewhere in this guide).

Place any necessary identifications (e.g., symbols, cover types, scale bars, regression formulas) directly on the figure rather than in the figure legend. Do not submit figures larger than 360 by 620 mm (15 by 24 in.); figures that are 215 by 280 mm (8 1/2 by 11 in.) are preferred. Figures exceeding this size are difficult to mail, handle, and store. Photographically reduce figures larger than 15 in. wide to page width (5.5 in.) or larger than 24 in. long to page length (8 in.). Prepare line drawings with lines of sufficient width and letters of sufficient size to remain legible when the figures are reduced to final page or column width (CBE Style Manual Committee 1983). Graphics produced by coarse dot-matrix printers are not satisfactory for reproduction. Legibly mark all photographs and figures on the back with the author(s) name(s), figure number, and indicate "TOP." Use soft pencils (blue preferred) on the backs of photographs and drawings, because markings and pencil or pen indentations may show through. Leave a margin at the top of each figure (including photographs) of at least 5 cm (1/2 in.). Provide photocopies of figures to be sent with the manuscript to reviewers. Use press-on letters very carefully, and only if the illustration is mounted on a board. Pressed-on letters on a large oversized illustration often flake and break. The use of a clear spray fixative and a cover sheet is suggested. The best solution, when pressed-on letters are used, is to keep the original illustration approximately the size of the desired final reproduction. This will reduce handling problems and damage. Submission of photographs (either those produced by standard processes or by diffusion-transfer imaging [PMT]) of graphics is recommended. Submitted photographs must not be produced by making a photograph through a halftone screen (pre-screened). Mount original graphics or photographs on cardstock or other heavy material; use the same material when several small graphics are submitted for a composite figure. In the case of composite graphics, they must be mounted as the author desires. If more than one photo is mounted on a plate, it is best to cut square edges and mount photos neatly together so that no white space appears between the photos. Also, try to place the identifying letters or numbers inside each individual photograph. The editors will not mount photographs. For clarity of presentation, the Biological Society of Washington prefers to print photographs in their original submitted size, or a size reduction to fit a journal page; consideration of size should be made before preparing a composite figure.

Results and Discussion

Style and Usage

Punctuation.--Use quotation marks sparingly for emphasis or special use of a word or term, thus preserving them mainly for actual quotations. Use the slant line or solidus (/) only to indicate "divided by" or in dental, vertebral, or chaetotaxy formulas.

Underline generic and specific names in the text (underlined words will become italic in print). Do not use _italic_ or **bold** type in manuscripts even if your typewriter or word processor has that capability. Underlined words (italics) are discouraged for use other than scientific names and headings. However, all terms and symbols in mathematical equations and those used to denote statistical tests should be underlined.

Hyphenate compounds used as adjectives (e.g., 3-year-old male, 77-day gestation period, 10- by 10-trap grid, home-range area, life-history strategy, 0.5-m plot). The same holds for adverbs (e.g., well-developed dentition) except those ending in "ly." However, to emphasize the true subject, use prepositions to avoid strings of modifiers (e.g., estimates of home-range size, _not_ home-range-size estimates). Hyphenation in formation of compounds is complex (e.g., "semi-independent" but "semiarboreal" and "mid-July" but "midday"); use of _Webster's Third New International Dictionary, Unabridged_ is advised.

Always use serial commas, including that preceding the conjunction (mice, voles, and shrews). Use no punctuation between state and zip code in addresses (address line of these guidelines is an example). Do not use "back-to-back" parentheses () (), as for citing a reference and referring to a table in text; use (Smith 1984, Table 1) _not_ (Smith 1984)

(Table 1). To separate a parenthetical statement from a reference in the text, use a 1-em dash (two dashes on typewriter) if the authority is cited in support of statement as in (. . . as commonly seen in *Peromyscus*--Smith 1984); otherwise, separate with a semicolon as in (. . . as commonly seen in deer mice [*Peromyscus leucopus*; Wolff 1988]).

Abbreviations, spelling, and miscellaneous items.--Paragraphs and sentences should not begin with an abbreviation (such as - *P. maniculatus* was taken . . .). Do not use contrived acronyms or mnemonics for names of localities, study areas, morphological characteristics, governmental agencies, physiological parameters, statistical tests, or most other items. Acronyms for museums, standard abbreviations for protein and enzyme loci, and symbols used in mathematical equations are acceptable if referenced or defined at first use (words should be used for the latter when not used in a mathematical sense; e.g., "The area is πr^2, but the radius is shorter than the diameter").

Spelling and use of words should be in accordance with *Webster's Third New International Dictionary, Unabridged*. Use of words not included therein should be avoided, but newly coined words and foreign words may be used sparingly if precisely defined at first use in manuscripts. Scientific terms should follow recent specialized dictionaries and glossaries. Refrain from using words in other than their standard meanings.

Use only "male" and "female" to distinguish the two sexes. Avoid terms such as rams, ewes, bucks, or other similar names.

Numbers and mathematics.--Use decimals rather than fractions except in equations. Decimals not preceded by a whole number always should be preceded by a zero (0.75) in text, tables, and figures.

In the text (introduction, discussion, conclusions, etc.) and in titles, use numerals for numbers greater than nine except when starting a sentence (associated units should then not be abbreviated: "Eleven minutes," but "About 11 min"; "Fifteen percent," but "More than 15%"). For numbers one through nine, use words except when used with units of measure (6 mm), time (3 days, 3 summers, 4 years), but not enumeration (five dugongs, two crabs, seven observations). Also, use numerals for all items in a series that includes at least one number greater than nine (1 dik-dik, 7 numbats, and 19 slow lorises). Treat ordinal numbers in the same manner as cardinal numbers (first panda, 14th deer mouse, 1st month, 6th min, fourth trial).

In the specimens examined and description or diagnosis sections, use numerals throughout.

Avoid the use of numbered sentences or phrases in text. Reference to specific items by number in text is acceptable but names of items should be lowercase (e.g., day 1, experiment 4, setiger 5, grid 6, site 1, coxa 3, segment 7). Do not refer to individual animals either by name or field-catalog number; reference to individual animals tends to indicate that the material being presented is anecdotal.

Use commas in numbers of five digits or more (e.g., 10,000 and 100,000). The exceptions are field and catalog numbers of museum specimens, and pagination in references.

Use a colon (not a solidus [/]) to express ratios (e.g., 1:3.2, males:females). Do not present the numbers of males and females in a total sample (e.g., 15:48) as sex ratios but calculate the true ratio and give the sample size. For example, ". . . 1:3.2 ($\underline{n}$ = 63) in favor of females." Use < and > for "less than" and "greater than" with numerals (< 5 g, not "less than 5 g"; > 20 captures, not" more than 20 captures"). Use ≤ for "equal to or less than" or "not more than" and ≥ for "equal to or greater than" or "at least" with numerals.

When giving ranges, use "from 10.1 to 31.0 mm," but "the range is 10.1-31.4 mm." In other words, do not use "to" unless it is preceded by "from."

When presenting equations and formulas, use the solidus (/) for simple fractions and give the meanings of all symbols and variables in the text. When presenting values with respect to another factor such as time or space, use the solidus (/) if only two measurements are involved (g/ha); if three or more measurements are involved use the exponent -1 as in "...43 mg g^{-1} h^{-1}." Do not present equations published elsewhere unless they have been modified; a simple reference will do.

In reporting measures of central tendency (means, modes, etc.) or dispersion (standard deviations, standard errors), units of measure should not be more precise than the original measurements. For example, if mammals are weighed to the nearest 0.1 g, then means such as 54.56 should be reduced to 54.6 and X ± SE should be 54.6 ± 0.1, not 54.6 ± 0.09, both in tables and in text.

Dental formulas should be presented as i 1/1, c 0/0, p 1/0, m 3/3, total 18. Vertebral formulas should be presented as 7 C, 13 T, 6 L, 2-3 S, and 26-31 Ca, total 55-60. Upper teeth should be referred to by capital letters and lower teeth by lowercase letters (e.g., P4 is the fourth upper premolar and m1 is the first lower molar); do not use superscript and subscript numerals to designate upper and lower teeth.

Time and dates.--Write dates as 24 April 1989, with no internal punctuation; an exception is in the specimen examined section where the three-letter month code should be used. Indicate time of day on the 24-h system with four digits. Midnight is written as 0000 h, 8:30 a.m. as 0830 h, and 11:15 p.m. as 2315 h. Also, indicate time similarly as "4-h intervals," and "3 h/day." To express the age of a stratigraphic unit or the time of a particular geologic event, and where a specific dating technique has been used, employ "Ma" for mega-annum (time greater than one million years), or "B.P." (years before present) for radiocarbon dated material, which goes up to 40,000 yrs. To express other time relations, use "m.y." (million years) or m.y.a. (million years ago). For example, from 50 to 25 Ma, 25 m.y. elapsed and it is possible that these organisms lived at least 40 m.y.a. The ratio of light (L) hours to dark (D) hours under laboratory conditions is to be shown in this form: 14L:10D.

Units of measure.--Use of the metric system and the international system of units (Système International d'Unités) is advocated. Exceptions to the use of the metric system and the international system of units are English units in localities from specimen labels and in quotations from other publications. Also, the following variables may be reported in other units:

Temperature in degrees Celsius (^{o}C) instead of degrees Kelvin (^{o}K).

Time in minutes (min) and hours (h) instead of seconds (sec).

Sound intensity (relative terms) in decibels (dB) instead of watts/meter square (W/m^2).

Volume in liters (l) instead of cubic decimeters (dm^3).

Area in hectares (ha) instead of 10^4 m^2.

Accepted abbreviations that can be used in text, tables, and figures of manuscripts, without explanation or punctuation, and some words that should be spelled out follow:

Units of measure (use abbreviations only with numerical values, otherwise spell out; e.g.,". . . FN = 72-76, but populations with low fundamental numbers . . ."):

^{o}C	degrees Celsius
day	

2N (not 2*n*)	diploid number (N = chromosome number)
FN	fundamental number
g	gravity
sec	second
min	minute
h or hr	hour
d	day
wk	week
mo	month
yr	year
m.y.	million years
g	gram (not gm)
mg	milligram
kg	kilogram
Hz	hertz
kHz	kilohertz
MHz	megahertz
km	kilometer(s)
m	meter(s)
mm	millimeter(s)
cm	centimeter(s)
fm	fathom(s)
mi	mile(s)
ft	foot (feet)
in.	inch (note period)
diam	diameter
ha	hectare
M	molar
ppm	parts per million
W	watt (or west)
X	magnification
μg	microgram
μm	micrometer (micron)
gal	gallon

ml	milliliter and cubic centimeter
liter*	should be spelled out when confusion can exist; mainly when it is used alone. When in print, "10 1" looks like a poorly spaced 101. Confusion does not exist in a list of ingredients [(i.e., 14 kg sawdust, 500 g potassium nitrate, 1.5 l water)] or when in combination (ml).

Miscellaneous: Standard abbreviations used in text, their proper punctuation, and some terms that should be spelled out.

AC DC	alternating current and direct current
B.A. B.S. M.A. M.S. M.Sc. Ph.D.	college degrees
Co.	county
counties	spell out (no abbreviation)
elev.	elevation (note period)
Fig. or fig.	figure
maximum	no abbreviation
minimum	no abbreviation
pers. comm.	personal (oral) communication
P.O.	post office
R/V <u>Searcher</u>	name of research vessel is underlined
SEM	scanning electron microscope
States	spell out to avoid confusion
Table	write out completely
TEM	transmission electron microscope
UK	United Kingdom (no spaces)
U.S.A.	United States of America
USNM	National Museum of Natural History
U.S.S.R.	Union of Soviet Socialist Republics
weight	no abbreviation

Directions and coordinates:

N E S W ENE SE SSW	(no periods)
T14N, R10W, SW¼ Sec. 2	legal description for localities
10°06'N, 25°07'W	latitude and longitude

Latin and other foreign language terms (the following are accepted as written, without underlining; definitions follow terms).

aff.	affinis, having affinity with but not identical with
a posteriori	known from experience
a priori	intuitively, independent of experience
ad lib.	ad libitum, freely available
auct.	auctoris, of the author
auctt.	auctorum, or authors
ca.	circa, about
cf.	conferre, compare
e.g.,	(note comma) exempli gratia, for example
emend.	emended, emendation
en masse	in a body, as a whole
et al.	et alia, and others
etc.	et cetera, and so on
i.e.,	(note comma) such as
in litt.	in a letter (Note: data or information in recent unpublished manuscripts should not be cited in any form; however, quotations or use of data extracted from old manuscripts, as exist in archives, libraries, and occasionally herbaria, may be used)
in situ	in place
in utero	in the uterus

in vitro	outside the living organism
in vivo	in the living organism
leg.	collector or collected by
nec	not
nom. dub.	nomen dubium, name of doubtful application
nom. nud.	nomen nudum (plural, nomina nuda), name without validation
part.	partim, part
per se	by itself, as such
p.p.	pro parte, in part
sensu	as defined by
sic	thus (to signal exact transcription)
s.l.	sensu lato, in the broad sense
s.s.	sensu stricto, in the strict sense
via	by way of, by means of
vis-à-vis	in relation to, as compared with
viz.	videlicet, namely
vs. or versus	against, in contrast to

Statistical terms:

ANOVA	analysis of variance
CV	coefficient of variation
df	degrees of freedom
n	sample size or number in sample
P	probability
r or *R*	correlation coefficient
SD	standard deviation
SE	standard error
SEM	standard error of the mean
t *f* *U* *Z* X^2	statistical tests
$\bar{X}$	mean

Symbols.--Male (♂) and female (♀) symbols should not be used in the text, but may be used in figures and lists of specimens examined (8 ♂ or 14 ♀♀ - note space between number and symbol). Write percent as one word in the text, but use the percent sign after numerals (1%, 99%) and in bodies of tables.

Because of possible confusion with similar symbols, do not use X as a symbol for the word "by." Write, for example, "Traps used were 7.6 by 7.6 by 22.8 cm . . . ." If a multiplication sign is used in mathematical formulae or for indications of magnification, identify it as such in the margin of the manuscript.

Documentation and Literature Citation

The function of literature citation is to assist readers in locating material referenced by the author, a process that permits an orderly growth of knowledge through continued testing and reassessment. Documents written primarily to fill administrative requirements are not catalogued in most libraries and do not enter the body of knowledge that supports research. Therefore, such documents are not to be included in the Literature Cited section; the quarterly reports of U.S. Fish and Wildlife Service Cooperative Wildlife Research Units and job completion reports for Pittman-Robertson Federal Aid in Wildlife Restoration projects are examples of this kind of material. Certain other state, provincial, and federal reports also are excluded from lists of citations. Abstracts of oral presentations delivered at professional meetings and printed separately are excluded, but references to abstracts in *Dissertation Abstracts* and *Masters Abstracts* and abstracts published in journals (e.g., *American Zoologist*, *American Journal of Botany*) are permitted.

Style of documentation.--When citing informational references in text, use the form "Jones (1983)" if the author's name is part of the sentence and "(Jones 1983)" if it is not. Two articles by one author cited at one time should be written "(Jones 1975, 1982)"; two articles published by the same author in the same year, "(Jones 1981a, 1981b)." Other examples follow:

(Cameron 1977:507) or Smith (1957:23, table 3) [Note: only cite pagination in text references for direct quotations, in a synonymy, or in reference to a specific table or figure in another publication.] In text, citations of figures or tables other than those in the present manuscript should be in lowercase letters. Citations of figures or tables in the text should begin with a capitol letter, as: Fig. 1 or Table 2.

"In press" citations in text should be avoided. Use the year of expected publication (current or subsequent year) and end the citation listing in the Literature Cited section with "(in press)" - see Appendix II. This allows for less costly corrections when the citation is updated at the page proof stage.

Citations with more than two authors are cited in the text as: Lidicker et al. (1976). Do not underline the "et al.". Multiple citations in the text should be ordered chronologically and then alphabetically if in the same year, for example (Jones 1961, 1963; Hennings & Hoffmann 1977; Phillips 1978; Jones & Smith 1981; Jones & Baker 1983; Mares et al. 1983). Use an ampersand (&) between surnames of authors rather than "and". For in text multiple citations of three or more authors, in the same year and same first author, cite all authors, for example (Jones, Smith, & Williams 1988; Jones, Williams, & Smith 1988; Jones, Williams, Smith, & Baker 1988).

In the text, unpublished material can be referenced as follows: (pers. comm.) denotes information obtained orally; (in litt.) denotes information obtained in a letter. Names of persons providing unpublished information should include initials when referenced in text (e.g., R. H. Tamarin, pers. comm.; D. P. Christian, in litt.). In the Literature Cited section, do not cite or use information from unpublished recent manuscripts (except theses and dissertations) or papers in preparation. Unpublished data may not be referenced in any context.

Citations in the text that indicate the author(s) of zoological scientific names should be as follows: Family Caryophyllidae Dana, 1846; *Didelphys microtarsus* Wagner, 1842:359; and, *Themiste dyscrita* (Fisher, 1952). Note the use of a comma after the author(s) name(s). In botanical scientific names, dates may be used in the case of homonyms.

The proper form for new zoological descriptions, plus their associated synonymy, is as follows:

Chaceon bicolor, new species

Figs. 1-3

Geryon affinis.--Griffin & Brown, 1976:256, figs. 7-9.--Sakai, 1978:9, figs. 18-19, pl. 2, fig. D (color). [Not *Geryon affinis* A. Milne Edwards & Bouvier, 1894]

The proper form for new botanical descriptions, plus their associated synonymy, is as follows:

Pityrogramma mortonii Jackson, nom. nov.

Pityrogramma mutabilis Gleas., Proc. Biol. Soc. Wash. 46:278. 1933, non L., 1753. Type: U.S.A.: Arizona: Cochise Co.: 7 mi NW of Wigwam, 4800 ft elev, *Brooks 482* (US; isotype UC).

All citations or author and date, whether informational, taxon describers, or essential references in the synonymy, except for botanical synonymies, must be listed in Literature Cited. Literature in botanical synonymies should be abbreviated according to the *Botanico-Periodicum-Huntianum* or *Taxonomic Literature, ed. 2*.

The list of references at the end of the manuscript should have the primary heading "Literature Cited." Sample literature citations are listed in Appendix II. Like all other parts of the manuscript, this section must be double-spaced. Only papers referred to in the text may be listed. The list must be alphabetical by authors' last names. Therefore, within this structure, papers with one author would be listed first, then those with two authors (alphabetical by second author), then three authors, and so on. Use first author et al. (e.g., Patton, J. L., et al.) for papers having seven or more authors. Where the author line is identical, the listing should be chronological by publication date. If two or more papers by the same author or sequence of authors are listed, the name(s) are not repeated but are replaced by a 3-em dash (six dashes in typescript) and a period. Use a 3-em dash in subsequent entries for all repeated authors. For example:

Cockrum, E. L. 1974.
------. 1975.
------, & J. K. Jones, Jr. 1978.
------, ------, & J. D. Smith. 1980.

(Note: Throughout the text and in the Literature Cited, insert a space between the initials of a persons name, as above.)

The volume number of a journal or other serial publication should be cited. However, do not include the issue number in journals having continuous pagination throughout the year or volume. When citing publications that have only a number and no volume, treat the number as a volume (Occasional Papers of the Museum of Natural History, University of Kansas 25:1-39). Underline scientific names or other words only if italicized in the original title. In citing books, omit Roman pagination (e.g., "J. Wiley and Sons, New York, 432 pp." <u>not</u> "xxii + 432 pp.") except in instances that those pages contain the first reference to a taxon under consideration. Also, provide only the first city listed for publishers (e.g., John Wiley and Sons, New York" <u>not</u> John Wiley and Sons, New York, Chichester, Brisbane, and Toronto"). Plates (or figures), if not included in paginated materials, should be referenced after pagination (e.g., 286 pp. + pls. 1-24 [or figs. 1-24]). If plates, figures, or tables are paginated, do not cite them again in the reference. Journal names and book titles are set in Roman type, so do not underline.

Abbreviations used in Literature Cited.-- Abbreviations must not be used in the Literature Cited, except for those used in the title of the cited paper. Include and spell out all words that comprise the reference, including articles, conjunctions, and prepositions. Manuscripts will be returned to the author(s) if journal names are not completely spelled out.

Conclusions

A summary in French, German, Russian, or Spanish is acceptable. This summary, which may be a translation of the abstract, should be placed immediately after the English abstract. Do not include a additional summary or summary paragraphs in English at the end.

Before submitting your manuscript, carefully cross-check all citations in the text, including figure and table captions, against listings under Literature Cited, and check each entry in the Literature Cited section against its original source to verify title, year of publication, names, quotations, and page numbers. Include all citations, when appropriate, in synonymy listings. The editors scan the Literature Cited and make spot checks for accuracy, but cannot assume responsibility for verifying all citations.

The sequence of material in each copy should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s) Address(es), Appendix, Figure Legends, Figure copies (each numbered and identified), Tables (each table numbered with an Arabic numeral and with heading provided). Number every page sent with the manuscript, including Literature Cited, figure legends, and tables. Any appendices should appear after Literature Cited. Figure legends and then copies of the figures follow. Next, the tables, each on a separate sheet. Glossy prints of each figure (or original artwork if high-contrast photographs of graphics cannot be obtained), should complete the parcel of manuscript materials. Three copies of all materials, including figures (legible photocopies acceptable), should be submitted with a cover letter stating the title, and full name(s) of author(s), and availability of publication funds. Do not submit manuscripts under consideration for publication elsewhere.

Acknowledgments

Parts of this manuscript were extracted intact and other parts paraphrased from a similar manuscript prepared by D. E. Wilson, A. L. Gardner, and B. J. Verts for *The Journal of Mammalogy*, and from "Standard style for technical publications" prepared for customers of Allen Press, Inc., by G. Dresser. Helpful suggestions for this publication were provided by T. E. Bowman, S. D. Cairns, F. D. Ferrari, G. D. Johnson, R. B. Manning, W. N. Mathis, and D. E. Wilson. The acknowledgments section should contain a few brief statements in a single paragraph to recognize the contribution of others and support from patrons or agencies. Use only initials for names of persons acknowledged, but spell out names of agencies (e.g., National Science Foundation *not* NSF).

Literature Cited

CBE Style Manual Committee. 1983. CBE style manual. Fifth edition. Council of Biology editors, Bethesda, Maryland, 324 pp.

Costain, D. C. 1978. Dynamics of a population of Belding's ground squirrels in Oregon. Unpublished M.S. Thesis, Oregon State University, Corvalis, 66 pp.

Couch, L. K. 1932. Breeding notes on a few Washington mammals.--The Murrelet 13:25.

Day, R. A. 1988. How to write & publish a scientific paper. Third edition. Oryx Press, Phoenix, Arizona, 211 pp.

Junge, R., & D. F. Hoffmeister. 1980. Age determination in raccoons from cranial suture obliteration.--The Journal of Wildlife Management 44:725-729.

Linsdale, J. M. 1946. The California ground squirrel: a record of observations made on the Hastings Natural History Reservation. The University of California Press, Berkeley, 475 pp.

McKeever, S. 1966. Reproduction in *Citellus beldingi* and *Citellus lateralis* in northeastern California. Pp. 365-385 *in* I. W. Rolands, ed., Symposia of the Zoological Society of London, Academic Press, London 15:1-559.

Scheffer, T. H. 1941. Ground squirrel studies in the Four-Rivers country, Washington.--Journal of Mammalogy 22:270-279.

Tomich, P. Q. 1962. The annual cycle of the California ground squirrel.--University of California Publications in Zoology 65:213-281.

Wilson, D. E., A. L. Gardner, & B. J. Verts. 1989. Guidelines for manuscripts for publications of the American society of mammalogists.--Journal of Mammalogy (supplement) 70(4):1-17 + 21 unnumbered.

(CBR) Department of Vertebrate Zoology (Mammals), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (DBL) Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Appendix I

Examples of typescript for page having Figure legends

Fig. 1. Localities at which *Sorex trowbridgii* (open circles) and *S. bendirii* (closed circles) were collected in Benton Co., Oregon, 1975-1986.

Fig. 2. Relationship between body mass and body length for (a) 12 *Sorex trowbridgii*, and (b) five *S. bendirii* collected in Benton Co., Oregon, 1975-1986.

Fig. 3. *Syringonomus dactylatus*. A. Photomicrograph of the cervical region of the holotype, USNM 77172; unlabeled arrows point to amphidial gland; scale equals 100 μm. B. Photomicrograph of the posterior body region and tail of the paratype USNM 77175; scale equals 100 μm. Abbreviations.--AV, anal vent; CG, caudal gland; NR, nerve ring.

Appendix II

Examples of Literature Citations

Journals.--

Bader, R. S. 1965. A partition of variance in dental traits of the house mouse.--Journal of Mammalogy 46:384-388.

Blair-West, J. R., et al. 1968. Physiological, morphological and behavioural adaptation to a deficient environment by wild native Australian and introduced species of animals.--Nature 217:922-928. [use of "et al." for papers with seven or more authors]

Carleton, M. D., & C. B. Robbins. 1985. On the status and affinities of Hybomys planifrons (Miller, 1900) (Rodentia: Muridae).--Proceedings of the Biological Society of Washington 98:956-1003. [Underlined scientific names will be set in italics; note use of an ampersand (&) instead of "and" between author's names]

Fauvel, P. 1936. Sur quelques annélides polychètes de l'Île de Pâques.--Bulletin du Muséum National d'Histoire Naturelle, Série 2, 8:257-259. [Include all diacritical marks]

Ortiz, D. L., P. Costa, & B. J. LeBoeuf. 1990. Water and energy flux in elephant seal pups fasting under natural conditions.--Physiological Zoology (in press). [Note use of probable year of publication after authors names and the use of "in press," in parentheses, after the journal name]

Whitaker, J. O., Jr., & R. E. Wrigly. 1972. Napaeozapus insignis.--Mammalian Species 14:1-6. [underline scientific names only if italicized in original title]

Wicksten, M. K. 1984. Alpheopsis harperi (Decapoda: Alpheidae): A new species of snapping shrimp from Texas.--Northeast Gulf Science 7(1):97-100.

Proceedings and transactions.--

Chitty, D. 1952. Mortality among voles (Microtus agrestis) at Lake Vyrnwy, Montgomeryshire in 1936-9.--

Philosophical Transactions of the Royal Society of London, Series B, 236:505-552.

Kirsch, L. M., & A. D. Druse. 1973. Prairie fires and wildlife.--Proceedings of the Annual Tall Timbers Fire Ecology Conference 12:289-304.

Peek, J. M., M. C. Scott, L. J. Nelson, D. J. Pierce, & L. L. Irwin. 1982. Role of cover in habitat management for big game in northwestern United States.--Transactions of the North American Wildlife and Natural Resources Conference 47:363-373.

Books.--

Baird, S. F. 1857 [1858]. Mammals. *in* Reports of explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. Beverly Tucker, Printer, Washington, D. C., 8(part 1):1-757 + pls. 17-28, 30-60. [give correct publication date in brackets]

Barbour, R. W., & W. H. Davis. 1969. Bats of America. The University of Kentucky, Lexington, 286 pp. [City is not followed by state when name of state is part of the name of the press]

Eisenberg, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. The University of Chicago Press, Chicago, 610 pp. [Names of large, universally recognized cities are not followed by state]

Honacki, J. H., K. E. Kinman, & J. W. Koeppl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Hsu, T. C., & K. Benirschke. 1969. *Microtus oregoni* (creeping vole) 2n = 17 , 18 . An atlas of mammalian chromosomes. Vol. 3, Folio 121, Springer-Verlag, New York, unpaged. [Pages are not numbered]

Linnaeus, C. 1758. Systema nature per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentii, synonymis, locis. Tenth edition. Laurentius Salvius, Stockholm 1:1-824. [give complete title, do not use ellipsis]

Nowak, R. M., & J. L. Paradiso. 1983. Walker's mammals of the world. Fourth edition. Johns Hopkins University Press, Baltimore, 1 and 2:1-1362.

Part of book.--

Bourliere, F. 1955. Ordre des Fissipedes. Systématique. Pp. 215-291 *in* P. -P. Grasse, ed., Traité de Zoologie. Masson et Cie., Paris 17(1):1-1170. [period after title of volume]

Calder, W. A., III. 1974. Consequences of body size for avian energetics. Pp. 86-151 *in* R. A. Paynter, Jr., ed., Avian energetics. Publication of the Nutall Ornithological Club, Cambridge, Massachusetts 15:1-334.

Carleton, M. D., & G. G. Musser. 1984. Muroid rodents. Pp. 289-379 *in* S. Anderson & J. K. Jones, Jr., eds., Orders and families of Recent mammals of the world. John Wiley and Sons, New York, 686 pp. [give pagination for entire volume]

Leach, W. E. 1821. Galatéadées. Pp. 49-56 *in* F. G. Levrault, ed., Dictionnaire des Sciences Naturelles, 18(1820), Strasbourg.

Spezharsky. T. N. 1939. Order Ostracoda. Pp. 193-196, pl. 46 *in* B. Likharev, ed., Atlas rokovodyashchikh form iskopaemykh faun SSSR. Volume 6, Permskaya Systema. Tsentral'nyi Nauchno-Issledova-tel'skiy Geologo-Razvedochnyi Institut (TsNIGRI). (The atlas of the leading forms of the fossil fauna USSR. Volume 6, Permian System. Central Geological and Prospecting Institute) (in Russian).

Theses and dissertations.--

Lackey, J. A. 1973. Reproduction, growth, and development in high-latitude and low-altitude populations of *Peromyscus leucopus* (Rodentia). Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor, 128 pp.

Wrazen, J. 1976. Feeding ecology of a population of eastern chipmunks (Tamias striatus) in southeast Ohio. Unpublished M.S. thesis, Ohio University, Athens, 26 pp.

Table 1.--Some reproductive patterns in four species of Spermophilus in western United States.

Species and	Liter size[a]			Reproductive	
state	n	X	Range	season[b]	Authority
S. washingtoni					
Washington	26	8.0	5-11	February-March	Scheffer 1941
S. beldingi					
Oregon	110	5.2	5-8	April-June	Costain 1978
California	37	7.1	3-10	April-July	McKeever 1966
S. columbianus					
Washington	21	5.8	2-7	March-May	Couch 1932
S. beecheyi					
California	40	7.5	5-12	February-April	Linsdale 1946
California	34	6.1	1-9	March-June	Tomich 1962

[a] Based on counts of embryos.

[b] From first evidence of reproduction behavior to first appearance of young.

Table 2.--Means (±SE) and ranges for mass and length of 514 bacula from raccoons (*Procyon lotor*) among five age classes, northwestern Oregon, 1982-1983 and 1983-1984 furbearer seasons.

Age class[a]		Baculum mass (g)		Baculum length (mm)	
	n	X ± SE	Range	X ± SE	Range
1	205	0.63 ± 0.01	0.30-1.22	71.8 ± 0.5	54.5- 88.9
2	145	2.99 ± 0.04	2.03-4.16	105.9 ± 0.4	92.7-117.5
3	48	3.69 ± 0.08	2.63-4.76	107.9 ± 0.5	102.6-117.7
4	43	4.01 ± 0.07	2.76-4.86	109.3 ± 0.6	102.1-119.5
5[b]	73	4.40 ± 0.07	3.05-5.67	109.2 ± 0.5	99.0-118.8

[a] Age classification based on cranial-suture technique (Junge & Hoffmeister 1980)

[b] Includes all individuals ≥4.5 years old